Appendix M-1

Center for Biological Diversity References (Comment Letter O-9)

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INVITED REVIEW

Genetic consequences of habitat fragmentation in plant populations: susceptible signals in plant traits and methodological approaches

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Abstract

Conservation of genetic diversity, one of the three main forms of biodiversity, is a fundamental concern in conservation biology as it provides the raw material for evolutionary change and thus the potential to adapt to changing environments. By means of meta-analyses, we tested the generality of the hypotheses that habitat fragmentation affects genetic diversity of plant populations and that certain life history and ecological traits of plants can determine differential susceptibility to genetic erosion in fragmented habitats. Additionally, we assessed whether certain methodological approaches used by authors influence the ability to detect fragmentation effects on plant genetic diversity. We found overall large and negative effects of fragmentation on genetic diversity and outcrossing rates but no effects on inbreeding coefficients. Significant increases in inbreeding coefficient in fragmented habitats were only observed in studies analyzing progenies. The mating system and the rarity status of plants explained the highest proportion of variation in the effect sizes among species. The age of the fragment was also decisive in explaining variability among effect sizes: the larger the number of generations elapsed in fragmentation conditions, the larger the negative magnitude of effect sizes on heterozygosity. Our results also suggest that fragmentation is shifting mating patterns towards increased selfing. We conclude that current conservation efforts in fragmented habitats should be focused on common or recently rare species and mainly outcrossing species and outline important issues that need to be addressed in future research on this area.

Keywords: conservation genetics, habitat fragmentation, mating systems, meta-analysis, plant genetic diversity, rarity status

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Introduction

The development of human civilization throughout the last two centuries has resulted in the transformation of vast natural areas into anthropogenic landscapes, resulting in a process of habitat fragmentation that alters the structure, distribution, and functioning of natural ecosystems (Saunders *et al*. 1991). Immediate consequences of this process include habitat loss, the formation of remnant habitat patches of varied forms and sizes, a reduction of population sizes, and an increase in the degree of isolation of the remaining populations immersed in an anthropogenic matrix (McGarigal & Cushman 2002; Fahrig 2003). These persistent phenomena are well recognized as the main current driving forces of biodiversity loss in terrestrial ecosystems across the planet (Sala *et al*. 2000).

Studies of fragmentation effects in plants have largely concentrated on population demographic processes,

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especially evaluating plant reproductive dynamics in fragmented habitats (Hobbs & Yates 2003; Ghazoul 2005; Honnay *et al*. 2005; Aguilar *et al*. 2006). However, within the last decade there has been an increased interest in assessing the genetic consequences of habitat fragmentation in plants as stated by initial and recent reviews on this subject (Young *et al*. 1996; Lowe *et al*. 2005; Ouborg *et al*. 2006; Honnay & Jacquemyn 2007). The expected genetic consequences of fragmentation, which creates small, discrete, and isolated populations, are based on traditional island biogeography and metapopulation theories (MacArthur & Wilson 1967; Levins 1969). Thus, habitat fragmentation is expected to erode genetic variability and to increase inter-population genetic divergence of plant populations due to increased random genetic drift and inbreeding, and reductions in gene flow (e.g. Young *et al*. 1996; Sork *et al*. 1999; Lowe *et al*. 2005).

The most immediate effects of fragmentation on the genetic composition of plant populations depend on two factors: the effective population size within fragments and the patterns of genetic variability of the original populations previous to fragmentation (Nason *et al*. 1997; Hamrick 2004). Once a continuous forest is cleared and subdivided into small patches, from a metapopulation viewpoint, the distribution of genetic variability within and between the remaining populations in the landscape will depend on the spatial scale of fragmentation relative to the spatial scale of the pre-existent breeding neighbourhood (Nason *et al*. 1997; Hamrick 2004). Some hypotheses have been proposed to address the effects of habitat fragmentation on plant population genetics. As an immediate result, the genetic variation of populations is reduced due to genetic bottlenecks; specifically, a lower proportion of polymorphic loci and a reduction in the number of alleles per locus are expected within the fragments (Nei *et al*. 1975; Ellstrand & Elam 1993; Young *et al*. 1996). If fragmentation conditions persist over successive generations, decreased heterozygosity due to random drift and increased inbreeding are expected resulting in the accumulation of deleterious recessive alleles, lowering the fecundity of individuals, increasing seed/seedling mortality, and reducing the growth rate of individuals, eventually driving populations to extinction (e.g. Lande 1988; Young *et al*. 1996). The loss of genetic variation may reduce a population's ability to respond to future environmental change, such that the probability of extinction is increased or, at best, opportunities for evolution are limited (Caro & Laurenson 1994; Young *et al*. 1996; Nason *et al*. 1997; Booy *et al*. 2000).

The hypotheses concerning the negative impact of fragmentation on genetic diversity are the basis for the conservation genetic paradigm (Ouborg *et al*. 2006). The field of conservation genetics is relatively recent, and one of its main concerns is to develop basic and applied knowledge to create tools and strategies for conserving the genetic resources and the evolutionary potential of species (Amos & Balmford 2001; Ouborg *et al*. 2006; Pertoldi *et al*. 2007). In order to develop such tools for effective conservation efforts, it is crucial to arrive to generalizations of plant genetic response patterns of plant species to habitat fragmentation.

Nevertheless, the empirical evidence from the literature provides inconsistent results to support these hypotheses, implying that not all fragmentation episodes necessarily result in genetic erosion of plant populations (e.g. Young *et al*. 1996; Collevatti *et al*. 2001; Lowe *et al*. 2005; Kettle *et al*. 2007). In this regard, quantitative statistical approaches are especially useful tools to integrate and synthesize the body of evidence from published literature (Arnqvist & Wooster 1995). Quantitative reviews such as meta-analysis allow us to reach general conclusions about a domain of research despite the apparent contradictory response patterns of individual studies (Gurevitch & Hedges 2001). This is accomplished by treating individual published results as if they were subjected to sampling uncertainty; thus, we are able to obtain not only the magnitude and direction of each effect (regardless of their P values), but also the variability of effects among individual studies (Hedges & Olkin 1985; Arnqvist & Wooster 1995; Gurevitch & Hedges 2001). Consequently, we can estimate the average magnitude of the effect across all studies, test whether the effect is significantly different from zero, and examine potentially causative differences in the effects among studies (Gurevitch & Hedges 2001).

Particular life-history traits of plants may confer different vulnerability to fragmentation effects. Because genetic erosion in fragmented habitats should be more pronounced after several generations, it is expected to find stronger negative effects on the adult generation of short-lived species compared to long-lived species (Young *et al*. 1996); or more precisely, in any plant population subjected to fragmentation conditions for several generations. Similarly, the ability of plants to reproduce clonally, via vegetative spread, may also buffer the genetic effects of fragmentation as a result of delaying the time between generations (Honnay & Bossuyt 2005). Also, the ploidy level of plants may influence the effects on genetic diversity due to fragmentation; as theory predicts, autotetraploids are less subject to the loss of genetic diversity by genetic drift than diploids (Bever & Felber 1992; Moody *et al*. 1993). Finally, the mating system of plants determines the spatial distribution of genetic variation within and among populations (Loveless & Hamrick 1984). Outcrossing plants typically show higher genetic variation within populations, whereas in selfing plants most of the genetic variation is found among populations (Loveless & Hamrick 1984; Hamrick & Godt 1989). Sudden decreases in effective population sizes due to habitat fragmentation would then have stronger negative effects on within-population genetic diversity of outcrossing species. The fewer individuals remaining after fragmentation, the more severe the genetic bottleneck, which will have particularly large effects on the maintenance of rare alleles (Nei *et al*. 1975).

Likewise, some ecological processes, especially pollination and seed dispersal of plants, can shape the level of demographic and genetic connectivity among populations in fragmented habitats (Nason *et al*. 1997; Nathan & Muller-Landau 2000; Tewksbury *et al*. 2002; Hamrick 2004). The ability of vectors to move pollen and seeds through the fragmented landscape will determine the potential of plant species to offset the effects of genetic drift. In animal-pollinated or animal seed-dispersed plants, the level of genetic connectivity among fragments will depend on vector distribution, abundance, composition, and behaviour (Nason *et al*. 1997), attributes of pollinators and seed dispersers that are usually affected by habitat fragmentation (Didham *et al*. 1996; Graham 2001; Aizen & Feinsinger 2003; Griscom *et al*. 2007). Therefore, animal-pollinated and animal seed-dispersed plant species are expected to show decreased genetic connectivity due to habitat fragmentation compared to abiotically pollinated and abiotically seed-dispersed plants (Nathan & Muller-Landau 2000; García *et al*. 2007). The rarity of species can also determine susceptibility to genetic erosion. Naturally rare species, defined by their narrow geographical range, restricted habitat specificity or small local population sizes (*sensu* Rabinowitz 1981) are usually genetically less diverse than more widespread or common species (Karron 1987; Hamrick & Godt 1989; Ellstrand & Elam 1993). Then, common species may be more susceptible to lose genetic variation due to habitat fragmentation compared to rare species. Including rarity in models is problematic because authors do not uniformly assess rarity; species categorized as rare are not always *naturally* rare, but rather *recently* rare as a consequence of anthropogenic disturbance and habitat fragmentation (Gitzendanner & Soltis 2000). Thus, this categorization usually overlaps with the conservation status of the species (i.e. recently rare species are typically threatened or endangered). Once common and now rare species are expected to show stronger effects on genetic diversity than naturally rare species, as the former have suffered recent (i.e. in non-*evolutionary time*) decreases in regional or local abundance of populations (Huenneke 1991; Gitzendanner & Soltis 2000).

Certain characteristics of published studies may also influence the sensibility to find fragmentation effects. The ability to find fragmentation effects on genetic parameters may be different when using allozymes vs. DNA-based genetic markers. Specifically, because DNA-based genetic markers such as microsatellites have higher mutation rates (and consequently higher levels of variation), they may have higher resolution to detect changes in inter- and intra-population genetic variation compared to allozymes. Also, fragmentation effects on genetic erosion may not be detected on adult individuals of long-lived woody species, but may be detected in their progeny. Thus, in species of long generational time, the type of tissue used by authors to measure genetic diversity (either from adult or progeny) may determine the magnitude of fragmentation effects. Finally, the time elapsed since fragmentation occurred should be an important factor to assess genetic erosion in plants. Effects are expected to be stronger in plant populations subjected to fragmentation conditions for larger periods of time, where a few or several generations have passed.

In this paper, we conduct a quantitative review to assess the overall effects of habitat fragmentation on plant population genetic parameters and test the predictions of the conservation genetic paradigm. Specifically, we determined (i) the overall magnitude and direction of fragmentation effects on the genetic variability of plant populations; (ii) whether longevity, ploidy level, mating system, clonal growth, type of pollen and seed dispersal vector, and rarity status of plants determine differential susceptibility to genetic erosion in fragmented habitats; (iii) whether different methodological approaches used by the authors determine the ability to find fragmentation effects; and (iv) whether there is a relationship between time elapsed in fragmentation conditions and the magnitude of fragmentation effects in genetic parameters.

Methods

Literature search

We surveyed the literature through different databases using a combination of 'fragment*' AND 'genet*' AND 'plant' as keywords. Searches were conducted in the Science Citation Index and Biological Abstracts databases and also in the main editorials (Blackwell Science, Springer-Verlag, and Elsevier) and scientific societies that group the most relevant indexed journals of ecological genetics and conservation biology. We obtained a large number of papers that were examined for suitability in the meta-analyses. Considering that habitat fragmentation produces three main outcomes in the landscape (namely habitat loss, decreased population sizes, and increased isolation among populations), we included studies using any of these measures of fragmentation, which were statistically compared to assess whether any one of them had particularly stronger effects on genetic parameters. Thus, we included studies conducted in real habitat fragments, in natural plant populations of different sizes and/or degrees of isolation. We also considered a few studies evaluating the effects of fragmentation due to selective logging on genetic parameters. This type of disturbance introduces changes in population density of adult trees, a measure of population size (Kunin 1997; Lowe *et al*. 2005), without necessarily creating habitat fragments. We excluded articles that exclusively analysed correlations among population size and genetic variability without any explicit mention to the effects of habitat fragmentation (see Leimu *et al*. 2006). We included only studies that correlated genetic variability with population size as an indirect assessment of habitat fragmentation effects.

As measures of genetic variability, we considered expected heterozygosity (H_E), percent polymorphic loci (P), number of alleles (A), and inbreeding coefficient (F_{IS}). In cases where heterozygosity was not given (typically in studies using random amplified polymorphic DNA or amplified fragment length polymorhphism), we used molecular variance or gene diversity and analysed these parameters together with expected heterozygosity. These four genetic parameters were not necessarily evaluated all together in each study, thus sample sizes for each meta-analysis differed. In several studies, we were able to calculate inbreeding coefficients from observed and expected heterozygosity values ($F_{IS} = H_E – H_O / H_E$). Whenever available, we also included measures of outcrossing rate (OR) in fragmented habitats.

For each plant species studied, we gathered information on several life-history traits and ecological aspects as well as on the methodology used by the authors of each study as potential predictors of the genetic responses to habitat fragmentation. We determined: (i) the longevity associated to the different life forms (woody long lived, herbaceous perennial or herbaceous short lived); (ii) whether vegetative reproduction occurred; (iii) the ploidy level (polyploid or diploid); (iv) the mating system, whether a species was mainly outcrossing (which included strictly self-incompatible species, as well as self-compatible species with a predominant outcrossing mating system) or selfing (including species with predominant selfing mating system and some self-compatible species with mixed mating system with clear capability of selfing) as explicitly declared by the authors; (v) pollen dispersal vector (biotic or wind); (vi) seed dispersal vector (biotic or abiotic); (vii) rarity (common, naturally rare or recently rare). We also evaluated the type of genetic marker (allozyme or DNA based) and the plant tissue used for each study (either from adult individuals or progenies). We further searched in each paper for information regarding the time elapsed in fragmentation conditions; this included rough estimates given by authors (expressed as a *few decades or centuries*, *more than* or *between* certain amount of time) and also more precise dates or time periods elapsed. With this information, we created three categories (less than 50 years, between 50 and 100 years, and more than 100 years) to compare the magnitude of effect sizes. Furthermore, within the group of publications where authors gave a more precise date of when fragmentation started, we searched for the approximate lifespan of each species. We found information on lifespans in the same or different publications for 35 out of 47 species. For some species, we used genus-level lifespan information. For the remaining 12 species, we conservatively assigned a tabulated lifespan for woody and non-woody perennials following Ehrlén & Lehtilä (2002). For these species, we calculated the number of generations under fragmentation conditions by dividing the time period of fragmentation by the lifespan of the species, and ran correlation analyses between the number of generations and the effect sizes for H_E and F_{IS}. Based on theoretical grounds, these two genetic parameters are expected to be correlated with the number of generations under fragmentation conditions, showing stronger negative effects as more generations pass by. All the species' information was obtained from the same article, from other publications on the same species, or by contacting the authors. However, not every species' characteristic was available, thus predictor variables within a meta-analysis do not necessarily share the same sample size.

Seven articles evaluated the effects of fragmentation on genetic parameters in two species simultaneously and we included each of these species in the same analysis. Because the magnitude and sometimes direction of the responses of each species to habitat fragmentation within the same study were quite different, it is reasonable to assume that the effects are independent for each species (Gurevitch & Hedges 2001).

Data analysis

We used a categorical meta-analytical approach due to the large majority of studies evaluating population genetic parameters of plants in contrasting conditions (i.e. fragmented vs. non-fragmented). We obtained the mean value ($\bar{X}$) and standard deviations (SD) of each genetic parameter (H_E, A, P, OR, and F_{IS}) from plant populations (n) in each of the two conditions (fragmented and continuous habitats) in each published study. These data were taken either from text, tables or graphs (data from graphs were scanned using Datathief II software available online).[1] For each study, the magnitude of the effect of fragmentation on each of the genetic parameters (d_i) was estimated as the unbiased standardized mean difference (Hedge's d) between the mean value of the genetic parameter in fragmented and continuous habitats:

$$d_i = \frac{\bar{x}^F - \bar{x}^C}{SD^{FC}} J$$

where $\bar{X}^F$ is the mean value of a given genetic parameter in fragmented habitats, $\bar{X}^C$ is the mean value of the same genetic parameter in continuous habitats, SD^{FC} is the pooled standard deviation, of both groups and J is a term

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[1] http://www.nikhef.nl/~keeshu/datathief/

that corrects for bias due to small sample size (see Gurevitch & Hedges 2001). The effect size *d* can be interpreted as the difference between the genetic diversity of plants in fragmented habitats and continuous conditions, measured in units of standard deviations. Thus, large differences and low variability generate the largest effect sizes (Gurevitch & Hedges 2001). For each genetic parameter, the overall weighted mean effect size estimate (d^*_{++}) was calculated as:

$$d^*_{++} = \frac{\sum_{i=1}^{n} w_i d_i}{\sum_{i=1}^{n} w_i}$$

where d_i is the effect size of the i^{th} study and w_i is the weight (reciprocal of the sampling variance) of the i^{th} study.

Positive values of the effect size (*d*) for H_E, *A*, *P*, and *OR*, imply positive effects of habitat fragmentation on these parameters whereas negative *d* values imply negative effects of fragmentation on these parameters. The interpretation of effect sizes for inbreeding coefficients is exactly the opposite: positive values of *d* imply negative effects of habitat fragmentation (i.e. higher inbreeding) whereas negative *d* values imply positive effects of fragmentation (i.e. lower inbreeding). For studies using correlational approaches to evaluate fragmentation effects (typically using population size as the independent variable), we calculated the mean value, standard deviation and sample size by pooling the data points for the lower-half (used as fragmented condition values) and higher-half values (used as non-fragmented condition values) of the continuous independent variable.

We used MetaWin 2.0 (Rosenberg *et al.* 2000) to run the analyses and bootstrap re-sampling procedures as described in Adams *et al.* (1997) to calculate confidence intervals of effect sizes. An effect of habitat fragmentation was considered significant if the 95% biased-corrected bootstrap confidence intervals (CI) of the effect size (*d*) did not overlap zero (Rosenberg *et al.* 2000). Confidence intervals based on bootstrapping methods are generally wider than standard CI, which implies that re-sampling estimates of CI are more conservative (Adams *et al.* 1997). Data were analysed using random-effect models (Raudenbush 1994). This model assumes that differences among studies are due to both sampling error and random variation, which is usually the rule in ecological data (Gurevitch & Hedges 2001). The heterogeneity among effect sizes was assessed with *Q* statistics. Specifically, we examined the *P* values associated with Q_{between} statistics, which describe the variation in effect sizes that can be ascribed to differences between the categories of each predictor variable (i.e. species' life history and ecological traits, and studies' methodologies). We also used these statistics to compare the effect sizes between studies that used different factors of analyses (e.g. fragment size, logging, population size) to evaluate habitat fragmentation. Within the species used for the meta-analyses, we found few congeneric species (Table S1, Supporting information). We re-ran analyses using data pooled by congeneric species and found no difference in magnitude or direction of effects compared to the analyses performed using all the species as independent data points. We also tested for potential interactions among predictor variables by measuring their pairwise level of dependence with chi-squared tests.

Quantitative reviews of published studies have the intrinsic problem of potential publication bias. That is, studies showing significant results may have a greater probability of publication than those showing non-significant results. We explored this possibility graphically (weighted histograms and funnel plots), and by calculating weighted fail-safe numbers. If the fail-safe number is larger than $5n + 10$, where *n* is the number of studies, then publication bias may be safely ignored (i.e. results are robust regardless of publication bias; Rosenberg 2005).

Results

Sample of studies

From the literature search, we obtained 101 publications from 28 international indexed journals throughout the period of 1989–2008 that evaluated the effects of habitat fragmentation on plant population genetic parameters (Appendix S1, Supporting information). These studies measured at least one parameter of genetic variability on 102 unique plant species to conduct the meta-analyses, which yielded 101 data points for expected heterozygosity (H_E), 77 data points for number of alleles (*A*), 57 data points for percent polymorphic loci (*P*), 18 data points for outcrossing rate (*OR*), and 62 data points for inbreeding coefficients (F_{IS}). Although the species included in this review comprise a wide sample of plants with different biological and ecological attributes, there is some bias in these characteristics and also in the approaches used by authors to study genetic consequences of habitat fragmentation. Herbaceous perennial and woody long lived (shrubs and trees) represent 53% and 40% of the studied species, respectively, while herbaceous short-lived species comprised only 7% of the studied species. There are larger proportions of insect pollinated species (72%) and abiotically seed-dispersed species (77%). Diploid species are also a majority (84%). Although self-compatible (54%) and self-incompatible (46%) plants are approximately equally represented in the sample, within self-compatible plants there is a high number of mainly outcrossing plants as declared by the authors. Hence, there is a higher proportion of mainly outcrossing species (75%) compared with selfing plants (25%). Species without the capability of vegetative reproduction are slightly more represented (61%). Common species represent 48%, whereas naturally and recently rare species represent 25% and 27% of the sample, respectively. We found no significant pairwise associations among any of these predictor variables (not shown), which indicate they can be considered statistically independent. Most of the studies evaluate the effects of habitat fragmentation on the genetic variability of adult individuals (72%), using mainly allozymes (60%) as genetic markers.

A comparison of the different factors of analysis used by the authors as measures of habitat fragmentation showed no significant differences in the effect sizes for H_E ($Q_{between} = 1.35$; $P = 0.493$), A ($Q_{between} = 1.68$; $P = 0.441$), P ($Q_{between} = 2.05$; $P = 0.162$), and F_{IS} ($Q_{between} = 0.76$; $P = 0.652$). That is, fragmentation effects on each of these genetic parameters are comparable whether considering fragment size, degree of isolation, habitat loss, population size, or density of conspecifics (i.e. logging) as factors of analysis.

Weighted histograms showed unimodal distributions with the highest frequency around zero (not shown) and funnel plots of effect sizes vs. sample sizes showed no skewness (not shown), which indicates no bias in reporting results (cf. Aguilar *et al*. 2006 for details of interpretation). Similarly, the calculated weighted fail-safe numbers for each meta-analysis were larger than $5n + 10$ [H_E: $2249.4 > (5 * 101) + 10 = 515$; A: $2805.4 > (5 * 78) + 10 = 400$; P: $1444.2 > (5 * 57) + 10 = 295$; OR: $168.3 > (5 * 18) + 10 = 100$; F_{IS}: $1306.6 > (5 * 62) + 10 = 320$], reinforcing the robustness of these results.

Habitat fragmentation and genetic variability

Overall weighted-mean effect sizes of habitat fragmentation on H_E, A, and P were negative and significantly different from zero (Fig. 1). The OR, which was only consistently assessed in 18 studies, also showed an overall negative weighted-mean effect size (Fig. 1). Habitat fragmentation showed non-significant overall effects on F_{IS} (Fig. 1), despite the small positive value implying a slight trend of increasing inbreeding due to habitat fragmentation.

From the evaluation of all predictor variables associated with the species' life history and ecological attributes for each of the genetic parameters, we present only the results that showed significant P (< 0.05) values of $Q_{between}$ statistics in text and figures. We found that fragmentation effects were significantly different for H_E between common, naturally rare and recently rare species ($Q_{between} = 23.18$; $P < 0.001$). On average, common and recently rare species showed strong, negative and significant effects of fragmentation on H_E, whereas naturally rare species showed non-significant effects on H_E (Fig. 2a). The same trend was found for A and P, although the heterogeneity among effect sizes was only marginally significant (for A: $Q_{between}$

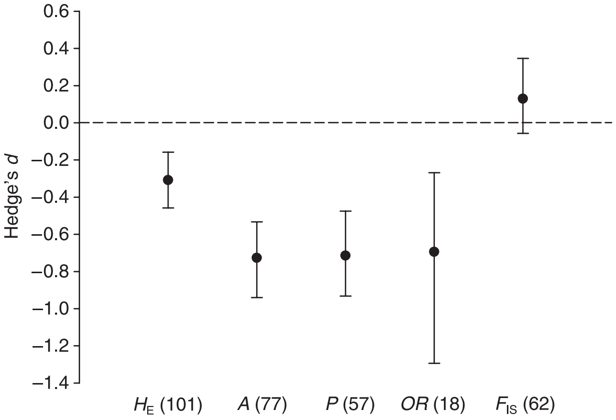

Fig. 1 Overall weighted-mean effect sizes and 95% bias-corrected confidence intervals of habitat fragmentation on expected heterozygosity (H_E), number of alleles (A), percent polymorphic loci (P), outcrossing rate (OR), and inbreeding coefficient (F_{IS}). Sample sizes for each meta-analysis are shown in parenthesis; dotted line indicates Hedge's $d = 0$.

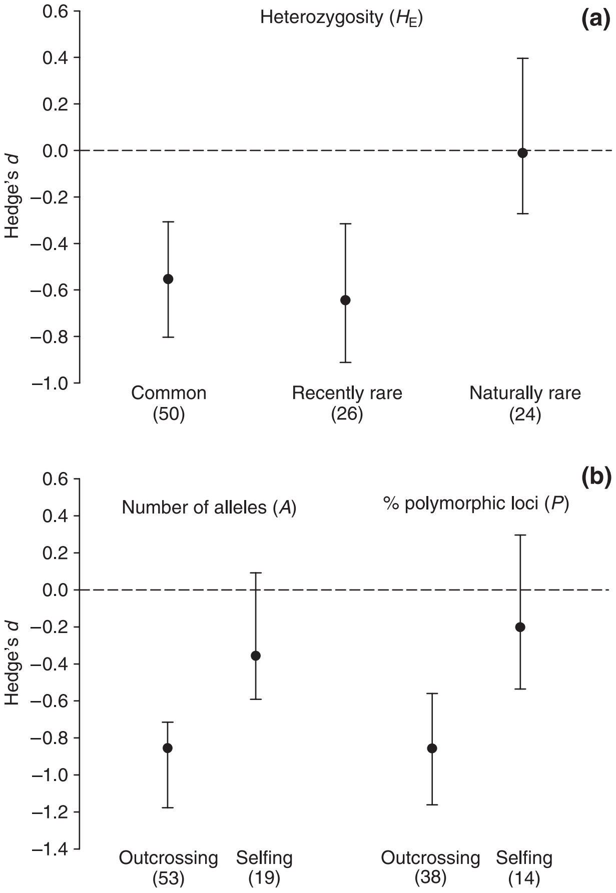

Fig. 2 Weighted-mean effect sizes and 95% bias-corrected confidence intervals of habitat fragmentation on (a) H_E of plant species with different categories of rarity (common, recently rare, and naturally rare) and on (b) A and P of plants with different mating systems (outcrossing and non-outcrossing) showing statistically significant heterogeneity ($Q_{between}$). Sample sizes of each category are given in parentheses. Dotted line shows Hedge's $d = 0$.

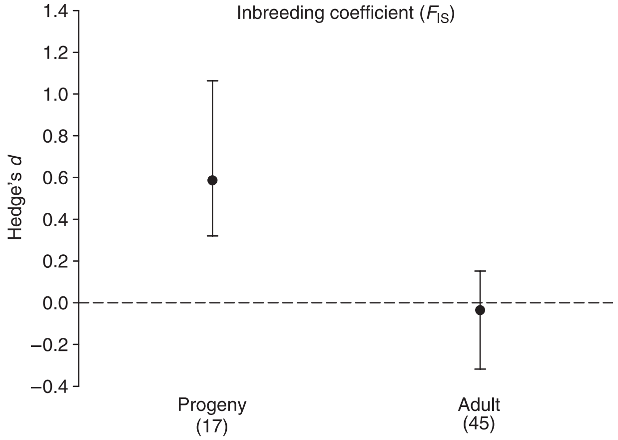

Fig. 3 Weighted-mean effect sizes and 95% bias-corrected confidence intervals of habitat fragmentation on inbreeding coefficient (F_{IS}) of studies evaluating adult and progeny tissues. Sample sizes of each category are given in parentheses. Dotted line shows Hedge's $d = 0$.

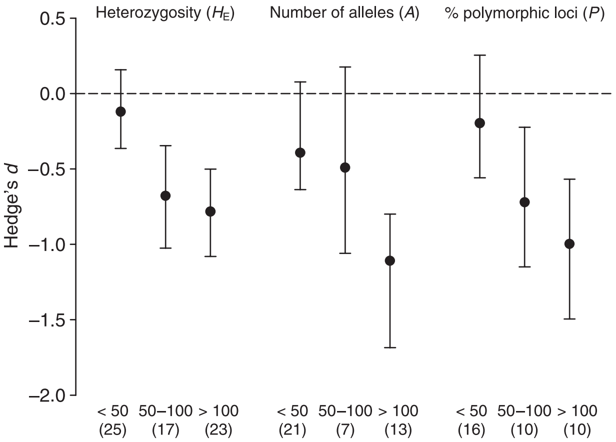

Fig. 4 Weighted-mean effect sizes and 95% bias-corrected confidence intervals of habitat fragmentation on H_E, A, and P of plant populations subjected to different time periods in fragmentation conditions: less than 50 years (< 50), between 50–100 years (50–100), and more than 100 years (> 100). Sample sizes of each category are given in parentheses. Dotted line shows Hedge's $d = 0$.

$= 4.72$; $P = 0.094$; for P: $Q_{\text{between}} = 5.01$; $P = 0.081$). Furthermore, for A and P, there were significant differences in mean effect sizes between outcrossing and selfing species ($Q_{\text{between}} = 14.96$; $P = 0.028$ and $Q_{\text{between}} = 9.17$; $P = 0.05$ for A and P, respectively). Outcrossing species showed stronger negative effects of fragmentation on A and P compared to selfing species (Fig. 2b). A similar but marginally significant trend was observed for H_E, [$d_{\text{outcrossing }(n=69)} = -0.57$, $d_{\text{selfing }(n=24)} = -0.22$; $Q_{\text{between}} = 3.24$; $P = 0.071$]. In the case of inbreeding coefficients, none of these predictor variables showed significant heterogeneity, implying that fragmentation not only does not have an overall effect on inbreeding, but also no particular life-history trait is showing susceptibility to fragmentation (not shown). Surprisingly, fragmentation effects on inbreeding were only studied in one short-lived species, which precluded the formal comparison between short- and long-lived species. None of the other life history (life form, vegetative growth capability, and ploidy level) and ecological traits (pollination and seed dispersal vector types) evaluated as predictor variables showed significant heterogeneity in effect sizes of fragmentation on these genetic parameters (not shown).

The use of different genetic markers (allozymes vs. DNA based) did not significantly alter the magnitude of effect sizes for each of the genetic parameters evaluated in fragmented habitats (not shown). Furthermore, effect sizes of fragmentation on H_E, A, and P were also homogeneous among studies sampling adult or progeny tissues (not shown). For inbreeding coefficients, on the contrary, there was a significant difference in mean effect sizes between studies evaluating adult and progeny tissues ($Q_{\text{between}} = 16.80$; $P = 0.012$; Fig. 3): progenies showed a significant positive overall mean effect size value while adults showed a non-significant mean effect size (Fig. 3). This result implies that progenies generated in fragmented habitats (which comprised mostly non-established seeds) presented higher inbreeding coefficients than progenies produced in continuous habitats; whereas for adult individuals no difference in mean F_{IS} values were observed between fragmented and continuous habitats. Depending on the parameter evaluated, between 53% and 64% of the studies gave at least rough information on the time elapsed in fragmentation condition. Overall, species subjected for more than 100 years in fragmentation conditions had significantly stronger effects on H_E ($Q_{\text{between}} = 17.72$; $P = 0.009$), A ($Q_{\text{between}} = 6.68$; $P = 0.05$), and P ($Q_{\text{between}} = 15.57$; $P = 0.018$; Fig. 4) compared to species evaluated in fragmented systems of less than 50 years, which showed non-significant mean effect sizes on these three genetic parameters (i.e. CI's overlapping zero value; Fig. 4).

Finally, we were able to estimate the number of generations elapsed in fragmentation conditions for 47 and 35 case studies evaluating H_E and F_{IS}, respectively. We log-transformed the number of generations and ran correlations with the effect sizes of fragmentation on these two parameters. We found a significant negative correlation between the number of generations elapsed and the species' effect sizes for H_E ($r = -0.36$, $P = 0.012$, Fig. 5). That is, the more generations elapsed in fragmentation conditions for any given plant population, the stronger negative magnitude of effect sizes on H_E. In the case of fragmentation effects on inbreeding coefficient, we found a non-significant positive correlation with the number of generations ($r = 0.29$, $P = 0.102$, $n = 35$), suggesting a trend of higher inbreeding as more generations pass by in fragmentation conditions.

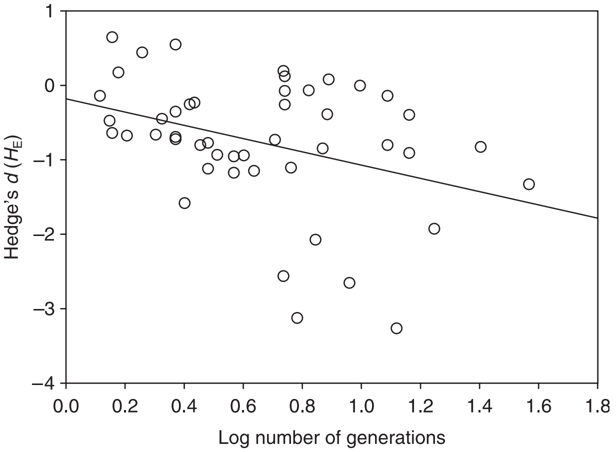

Fig. 5 Correlation between the log-transformed number of generations of plant populations in fragmented habitats and the effect sizes of fragmentation on H_E for 47 plant species. Correlation coefficient $r = -0.36$, $P = 0.012$.

Discussion

Anthropogenic habitat fragmentation is a recent phenomenon in evolutionary time but a pervasive feature of modern landscapes (Fahrig 2003). Plant populations that remain in habitat fragments are confronted with modified environments of reduced area, increased isolation, and new ecological boundaries, potentially affecting their biotic and abiotic interactions (e.g. Fahrig 2003; Ewers & Didham 2006). The genetic consequences of fragmentation on plant populations have been studied for over two decades and no clear response patterns have emerged from the literature. Recently, two reviews have focused on the relationship between genetic diversity and population size (Leimu *et al*. 2006; Honnay & Jacquemyn 2007), one of the immediate possible demographic consequences of habitat fragmentation. Nevertheless, fragmentation is a complex process that involves several different factors simultaneously (McGarigal & Cushman 2002; Fahrig 2003; Ezard & Travis 2006; Leblois *et al*. 2006; Ouborg *et al*. 2006); thus analyzing solely reductions of population size may not fully reflect what is happening in real fragmented scenarios. Population size per se may not be very important for animal pollinators and seed dispersers, whereas the degree of population isolation or the matrix characteristics surrounding the fragments may have more influence on their foraging behaviour (Kunin 1997; Ricketts 2001), affecting their ability to maintain gene flow among fragmented populations. These different factors, which often interact in diverse ways, are difficult to separate in observational or non-experimental designs, the rule in fragmentation studies. Authors tend to focus on one factor and do not usually control for the others (Leblois *et al*. 2006; Ouborg *et al*. 2006; but see e.g. Prober & Brown 1994; Honnay *et al*. 2007). Thus, the cause of reduced genetic diversity in fragmented habitats should not be adjudicated to one single factor, but rather to the interacting effects of, at least, population size, degree of isolation and matrix characteristics (Ezard & Travis 2006).

In this review, we explicitly focused on fragmentation studies and arrived at a conclusive generalization: habitat fragmentation decreases the genetic diversity of plant populations. The vast majority of studies were conducted on adult populations of long-lived species in relatively recently fragmented systems, which indicates the effects observed on genetic diversity, especially on A and P, are probably mainly the result of genetic bottlenecks, the most immediate consequence of fragmentation (e.g. Young *et al*. 1996; Nason *et al*. 1997; Oostermeijer *et al*. 2003; Lowe *et al*. 2005). These species and studies' characteristics may also be the reason for the absence of overall significant effects on inbreeding coefficients (i.e. most sampled adults have probably established before fragmentation took place) and the comparatively smaller mean effect size observed on H_E, which may be mostly due to the overall reduction in number and frequency of alleles (Barret & Kohn 1991; Nason *et al*. 1997). In a closer examination of the subset of studies that provided dates of fragmentation events, it was clearly observed that time and, more precisely, the number of generations elapsed under fragmentation conditions, are crucial in determining stronger genetic diversity reductions in plant populations, especially in heterozygosity, which may take a number of generations to become apparent (Young *et al*. 1996; Lowe *et al*. 2004, 2005). Studies conducted in more than 100-year-old fragmented systems presented significantly stronger negative effects on genetic diversity (Fig. 4). This notion was more specifically supported by the significant correlation between the estimated number of generations for a subset of species and the magnitude of negative fragmentation effects on H_E (Fig. 5), primarily as a result of random genetic drift (e.g. Young *et al*. 1996; Young & Clarke 2000; Lowe *et al*. 2004).

Gene flow and mating patterns in fragmented habitats

The amount of gene flow among remnant populations is a key element that will ultimately determine the genetic consequences of habitat fragmentation (Sork *et al*. 1999; Frankham *et al*. 2002; Hamrick 2004; Sork & Smouse 2006). Moderate or even relatively low levels of gene flow via pollen or seeds between fragmented populations can significantly alleviate the loss of genetic diversity by preventing the effects of genetic drift (e.g. Sork *et al*. 1999; Couvet 2002). In this regard, we found no evidence of any particular pollinator or seed dispersal vector type (either biotic or abiotic) to confer differential susceptibility to the loss of genetic diversity. Although this result does not give us information about the patterns of gene flow per se in fragmented habitats, it does indicate there is no obvious type of vector able to conduct consistently extensive gene flow between fragments within the studies analysed.

In the present review, we were not able to evaluate contemporary gene flow due to the current paucity of this kind of study and the difficulty of generating effect size measures from gene flow parameters. However, the results observed for outcrossing rates and inbreeding coefficients may indirectly support the possibility of disrupted gene flow and/or changes in mating patterns of fragmented plant populations. Outcrossing rates in fragmented populations showed a significant overall decrease compared to populations in continuous habitats (Fig. 1), suggesting that fragmented plant populations are suffering changes in mating patterns towards increased selfing. Moreover, inbreeding coefficients will increase immediately in the first generation of progenies if mating patterns are biased towards higher selfing or mating among related individuals (e.g. Young *et al*. 1996; Lowe *et al*. 2005; Kettle *et al*. 2007). Precisely, we found that progenies in fragmented habitats presented significant mean higher inbreeding coefficients than progenies in non-fragmented habitats (Fig. 3), indicating adult individuals in fragmented populations are mating more frequently among related individuals and/or through autogamous pollination.

In addition to reduced heterozygosity due to random genetic drift in populations that remain fragmented for several generations, heterozygosity erosion is more severe when inbreeding accompanies fragmentation (e.g. Young *et al*. 1996; Nason *et al*. 1997; Young & Clarke 2000). The few species subjected to fragmentation conditions for many generations presented quite strong negative effect sizes on H_E (Fig. 5), probably as a result of both drift and increased inbreeding. In the hypothetical scenario of anthropogenic fragmentation ceasing and landscapes remaining as they are today, the effects on genetic diversity of plants will still be much stronger in the future than we have estimated here if mating patterns continue shifting towards selfing.

Mating systems

Self-incompatible (SI) and mainly outcrossing self-compatible species, which contain most of their genetic variability within populations, suffered greater losses of alleles and polymorphic loci than non-outcrossing self-compatible and selfing species. For self-incompatible species in particular, this may result in the loss of low-frequency self-incompatibility alleles (S) (Wright 1965; Nei *et al*. 1975). In genetically controlled self-incompatibility systems, sharing of even a single S allele can prevent mating between individuals (De Nettancourt 2001). Thus, SI plants surviving in small, isolated populations may experience mate limitation due to reduced S allele diversity so that the effective population size is further reduced (Byers & Meagher 1992; Glémin *et al*. 2008). Such synergism between genetic and demographic processes has great potential to influence population viability of these species (Young & Clarke 2000; Glémin *et al*. 2008). In fact, animal-pollinated SI species are also strongly negatively affected in terms of effective pollination service and seed production by habitat fragmentation (Aguilar *et al*. 2006), thus these species are exceptionally vulnerable to fragmentation as a consequence of both, ecological and genetic mechanisms. These results represent a clear example of how genetic erosion can have short-term impacts on individual fitness and population viability (e.g. Cascante *et al*. 2002; Fuchs *et al*. 2003).

Rarity status

Our results support the initial hypothesis regarding the rarity status of plants: because common species have comparatively higher levels of genetic variability than naturally rare species, they are expected to lose more diversity due to recent fragmentation processes. Whether rarity is a cause or a consequence of evolutionary and ecological processes is still an open question (Rabinowitz 1981; Gitzendanner & Soltis 2000). In this regard, naturally and recently rare species may represent different timescales and origins of disturbance, which affect the genetic characteristics they possess in the present (Karron 1987; Ellstrand & Elam 1993; Gitzendanner & Soltis 2000; Oostermeijer *et al*. 2003). If this is true, it would be important to distinguish in the system under study whether habitat fragmentation is a consequence of natural phenomena, and thus occurred through evolutionary time, or whether is the result of anthropogenic activity, occurring in recent ecological times. While evolutionary fragmentation may be a more gradual and slower process that may also 'have an end', ongoing ecological fragmentation is a much faster increasing, non-random process (Saunders *et al*. 1991; McGarigal & Cushman 2002; Fahrig 2003). Given the ubiquitous nature of anthropogenic habitat fragmentation in today's landscapes, the results presented here are important and of interest to conservation biology as they situate common species in potential risk of genetic erosion, which is counterintuitive to current conservation principles that almost exclusively emphasize efforts on rare or threatened species (Honnay & Jacquemyn 2007; Gaston & Fuller 2008).

Conservation implications and future directions

Conservation of genetic diversity within populations has direct implications not only for ecosystem functioning but also for providing resilience in the face of environmental change (Luck *et al*. 2003; Reusch & Hughes 2006). The controversy about whether ecological and demographic factors are more important than genetic factors in driving species to extinction (Lande 1988; Frankham *et al*. 2002) has been recently quantitatively assessed: most taxa are not driven to extinction before genetic factors affect them adversely (Spielman *et al*. 2004), an assertion also supported by further research on plants in fragmented habitats (e.g. Endels *et al*. 2007). Thus, revealing which plant traits are more susceptible to suffer genetic erosion in fragmented habitats is crucial to detect lowered evolutionary potential, compromised reproductive fitness, and elevated extinction risks of wild populations, which should help generate criteria to prioritize conservation efforts (Young *et al*. 1996; Young & Clarke 2000; Amos & Balmford 2001; Lowe *et al*. 2005). Our results indicate that such efforts should be directed to common or recently rare species and mainly outcrossing species. Strictly self-incompatible, animal-pollinated species are at even greater risk due to their additional reproductive impairment in fragmented habitats (Aguilar *et al*. 2006).

Despite these unequivocal signals of susceptibility in plants, there is a clear gap in the literature of plant population genetics in fragmented habitats that precluded us making further generalizations. Such is the case of the poor representation of short-lived species as study targets and the dearth of studies evaluating contemporary gene flow via pollen and seeds on plant species with different life forms coupled with ecological information on the biotic dispersal vectors. Also, special attention should be given to the study of established progenies (seedlings and saplings) in fragmented habitats. Most of the progeny tissue evaluated up to now comes from non-established seeds (personal observation) and their genetic composition may differ markedly from that of the progeny that is actually being recruited in fragmentation conditions if they are subjected to selective pressures shaped by seed predators and herbivores (e.g. Cascante *et al*. 2002) and/or if they come from seed banks of previous reproductive episodes (Mandák *et al*. 2006; Honnay *et al*. 2008). Increasing these types of studies may allow us to determine whether gene flow mediated by animals is in fact changing and how changes in mating patterns will affect the genetic diversity of future generations of plant populations. Including precise measures and information on the history and characteristics of fragmented systems is particularly important, not only to determine timescales of fragmentation but also to test for possible fragmentation thresholds below which genetic variation is lost (e.g. Prober & Brown 1994; Ezard & Travis 2006). These approaches imply the merging of population genetics, plant–animal interaction ecology, and landscape ecology, a multidisciplinary endeavor that will provide knowledge-based tools for conserving the evolutionary potential of species and for managing ongoing anthropogenic modified landscapes.

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References

Adams DC, Gurevitch J, Rosenberg MS (1997) Resampling tests for meta-analysis of ecological data. *Ecology*, **78**, 1277–1283.

Aguilar R, Ashworth L, Galetto L, Aizen MA (2006) Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecology Letters*, **9**, 968–980.

Aizen MA, Feinsinger P (2003) Bees not to be? Responses of insect pollinator faunas and flower pollination to habitat fragmentation. In: *Disruptions and Variability: The Dynamics of Climate, Human Disturbance and Ecosystems in the Americas* (eds Bradshaw GA, Marquet PA, Mooney HA), pp. 111–129. Springer-Verlag, Berlin, Germany.

Amos W, Balmford A (2001) When does conservation genetics matter? *Heredity*, **87**, 257–265.

Arnqvist G, Wooster D (1995) Meta-analysis: synthesizing research findings in ecology and evolution. *Trends in Ecology & Evolution*, **10**, 236–240.

Barret SCH, Kohn JR (1991) The genetic and evolutionary consequences of small population size in plants: implications for conservation. In: *Genetics and Conservation of Rare Plants* (eds Falk D, Holsinger KE), pp. 3–30. Oxford University Press, Oxford, UK.

Bever JD, Felber F (1992) The theoretical population genetics of autopolyploidy. In: *Oxford Surveys in Evolutionary Biology* (eds Antonovics J, Futuyma D), pp. 185–217. Oxford University Press, Oxford, UK.

Booy G, Hendriks RJJ, Smulders MJM, Van Groenendael JM, Vosman B (2000) Genetic diversity and the survival of populations. *Plant Biology*, **2**, 379–395.

Byers DL, Meagher TR (1992) Mate availability in small populations of plant species with homomorphic sporophytic self-incompatibility. *Heredity*, **68**, 353–359.

Caro TM, Laurenson KM (1994) Ecological and genetic factors in conservation: a cautionary tale. *Science*, **263**, 485–486.

Cascante A, Quesada M, Lobo JJ, Fuchs EA (2002) Effects of dry tropical forest fragmentation on the reproductive success and genetic structure of the tree *Samanea saman*. *Conservation Biology*, **16**, 137–147.

Collevatti RG, Grattapaglia D, Hay JD (2001) Population genetic structure of the endangered tropical tree species *Caryocar brasiliense* based on variability at microsatellite loci. *Molecular Ecology*, **10**, 349–356.

Couvet D (2002) Deleterious effects of restricted gene flow in fragmented populations. *Conservation Biology*, **16**, 369–376.

De Nettancourt D (2001) *Incompatibility and Incongruity in Wild and Cultivated Plants*. Springer-Verlag, Berlin.

Didham RK, Ghazoul J, Stork NE, Davis AJ (1996) Insects in fragmented forest: a functional approach. *Trends in Ecology & Evolution*, **11**, 255–260.

Ehrlén J, Lehtilä K (2002) How perennial are perennial plants? *Oikos*, **98**, 308–322.

Ellstrand NC, Elam DR (1993) Population genetic consequences of small population size: implications for plant conservation. *Annual Review of Ecology and Systematics*, **24**, 217–242.

Endels P, Jacquemyn H, Brys R, Hermy M (2007) Genetic erosion explains deviation from demographic response to disturbance and year variation in relic populations of the perennial *Primula vulgaris*. *Journal of Ecology*, **95**, 960–972.

Ewers RM, Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews*, **81**, 117–142.

Ezard THG, Travis JMJ (2006) The impact of habitat loss and fragmentation on genetic drift and fixation time. *Oikos*, **114**, 367–375.

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution and Systematics*, **34**, 487–515.

Frankham R, Ballou JD, Briscoe DA (2002) *Introduction to Conservation Genetics*. Cambridge University Press, Cambridge, UK.

Fuchs EJ, Lobo JA, Quesada M (2003) Effects of forest fragmentation and flowering phenology on the reproductive success and mating patterns of the tropical dry forest tree *Pachira quinata*. *Conservation Biology*, **17**, 149–157.

García C, Jordano P, Godoy JA (2007) Contemporary pollen and seed dispersal in a *Prunus mahaleb* population: patterns in distance and direction. *Molecular Ecology*, **16**, 1947–1955.

Gaston KJ, Fuller AF (2008) Commonness, population depletion and conservation biology. *Trends in Ecology & Evolution*, **23**, 14–19.

Ghazoul J (2005) Pollen and seed dispersal among dispersed plants. *Biological Reviews*, **80**, 413–443.

Gitzendanner MA, Soltis PS (2000) Patterns of genetic variation in rare and widespread plant congeners. *American Journal of Botany*, **87**, 783–792.

Glémin S, Petit C, Maurice S, Mignot A (2008) Consequences of low mate availability in the rare self-incompatible species *Brassica insularis*. *Conservation Biology*, **22**, 216–221.

Graham CH (2001) Factors influencing movement patterns of keel-billed toucans in a fragmented tropical landscape in Southern Mexico. *Conservation Biology*, **15**, 1789–1798.

Griscom PH, Kalko EKV, Ashton MS (2007) Frugivory by small vertebrates within a deforested, dry tropical region of Central America. *Biotropica*, **39**, 278–282.

Gurevitch J, Hedges LV (2001) Meta-analysis: combining the results of independent experiments. In: *Design and Analysis of Ecological Experiments* (eds Scheiner SM, Gurevitch J), 2nd edn, pp. 378–398. Oxford University Press, New York.

Hamrick JL (2004) Response of forest trees to global environmental changes. *Forest Ecology and Management*, **197**, 323–335.

Hamrick JL, Godt MJW (1989) Allozyme diversity in plants. In: *Population Genetics, Breeding and Genetic Resources* (eds Brown ADH, Clegg MT, Kahler AL, Weir BS), pp. 43–63. Sinauer & Associates, Sunderland, Massachusetts.

Hedges LV, Olkin I (1985) *Statistical Methods for Meta-Analysis*. Academic Press, New York.

Hobbs RJ, Yates CJ (2003) Impacts of ecosystem fragmentation on plant populations: generalizing the idiosyncratic. *Australian Journal of Botany*, **51**, 471–488.

Honnay O, Bossuyt B (2005) Prolonged clonal growth: escape route or route to extinction? *Oikos*, **108**, 427–432.

Honnay O, Jacquemyn H (2007) Susceptibility of common and rare plant species to the genetic consequences of habitat fragmentation. *Conservation Biology*, **21**, 823–831.

Honnay O, Jacquemyn H, Bossuyt B, Hermy M (2005) Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. *New Phytologist*, **166**, 723–736.

Honnay O, Adriaens D, Coart E, Jacquemyn H, Roldan-Ruiz I (2007) Genetic diversity within and between remnant populations of the endangered calcareous grassland plant *Globularia bisnagarica* L. *Conservation Genetics*, **8**, 293–303.

Honnay O, Bossuyt B, Jacquemyn H, Shimono A, Uchiyama K (2008) Can a seed bank maintain the genetic variation in the above ground plant population? *Oikos*, **117**, 1–5.

Huenneke LF (1991) Ecological implications of genetic variation in plant populations. In: *Genetics and Conservation in Rare Plants* (eds Falk DA, Holsinger KE), pp. 31–44. Oxford University Press, New York.

Karron JD (1987) A comparison of levels of genetic polymorphism and self-compatibility in geographically restricted and widespread plant congeners. *Evolutionary Ecology*, **1**, 47–58.

Kettle CJ, Hollingsworth M, Jaffre T, Moran B, Ennos RA (2007) Identifying the early genetic consequences of habitat degradation in a highly threatened tropical conifer, *Araucaria nemorosa* Laubenfels. *Molecular Ecology*, **16**, 3581–3591.

Kunin WE (1997) Population size and density effects in pollination: pollinator foraging and plant reproductive success in experimental arrays of *Brassica kaber*. *Journal of Ecology*, **85**, 225–234.

Lande R (1988) Genetics and demography in biological conservation. *Science*, **241**, 1455–1460.

Leblois R, Estoup A, Streiff R (2006) Genetics of recent habitat contraction and reduction in population size: does isolation by distance matter? *Molecular Ecology*, **15**, 3601–3615.

Leimu R, Mutikainen P, Koricheva J, Fischer M (2006) How general are positive relationships between plant population size, fitness and genetic variation? *Journal of Ecology*, **94**, 942–9452.

Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of the Entomological Society of America*, **15**, 237–240.

Loveless MD, Hamrick JL (1984) Ecological determinants of genetic structure in plant populations. *Annual Review of Ecology and Systematics*, **15**, 60–90.

Lowe AJ, Harris SA, Ashton P (2004) *Ecological Genetics: Design, Analysis and Application*. Blackwell, Oxford, UK.

Lowe AJ, Boshier D, Ward M, Bacles CFE, Navarro C (2005) Genetic resource impacts of habitat loss and degradation; reconciling empirical evidence and predicted theory for neotropical trees. *Heredity*, **95**, 255–273.

Luck GW, Daily GC, Ehrlich PR (2003) Population diversity and ecosystem services. *Trends in Ecology & Evolution*, **18**, 331–336.

MacArthur RH, Wilson EO (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, New Jersey.

Mandák B, Bímová K, Mahelka V, Placková I (2006) How much genetic variation is stored in the seed bank? A study of *Atriplex tatarica* (Chenopodiaceae). *Molecular Ecology*, **15**, 2653–2663.

McGarigal K, Cushman SA (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecological Applications*, **12**, 335–345.

Moody ME, Muellert LD, Soltis DE (1993) Genetic variation and random drift in autotetraploid populations. *Genetics*, **154**, 649–657.

Nason JD, Aldrich PR, Hamrick JL (1997) Dispersal and the dynamics of genetic structure in fragmented tropical tree populations. In: *Tropical Forest Remnants: Ecology, Management and Conservation of Fragmented Communities* (eds Laurance WF, Bierregaard RO), pp. 304–320. University of Chicago Press, Chicago, Illinois.

Nathan R, Muller-Landau HC (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology & Evolution*, **15**, 278–285.

Nei M, Maruyama T, Chakraborty R (1975) The bottleneck effect and genetic variability in populations. *Evolution*, **29**, 1–10.

Oostermeijer JGB, Luijten SH, den Nijs JCM (2003) Integrating demographic and genetic approaches in plant conservation. *Biological Conservation*, **113**, 389–398.

Ouborg NJ, Vergeer P, Mix C (2006) The rough edges of the conservation genetics paradigm for plants. *Journal of Ecology*, **94**, 1233–1248.

Pertoldi C, Bijlsma R, Loeschcke V (2007) Conservation genetics in a globally changing environment: present problems, paradoxes and future challenges. *Biodiversity and Conservation*, **16**, 4147–4163.

Prober SM, Brown AHD (1994) Conservation of the grassy white box woodlands: population genetics and fragmentation of *Eucalyptus albens*. *Conservation Biology*, **8**, 1003–1013.

Rabinowitz D (1981) Seven forms of rarity. In: *The Biology Aspects of Rare Plant Conservation* (ed. Synge H), pp. 205–217. John Wiley, Chichester, UK.

Raudenbush SW (1994) Random effects models. In: *The Handbook of Research Synthesis* (eds Cooper H, Hedges LV), pp. 301–321. Russell Sage Foundation, New York.

Reusch TBH, Hughes AR (2006) The emerging role of genetic diversity for ecosystem functioning: estuarine macrophytes as models. *Estuaries and Coasts*, **29**, 159–164.

Ricketts TH (2001) The matrix matters: effective isolation in fragmented landscapes. *American Naturalist*, **158**, 87–99.

Rosenberg MS (2005) The file-drawer problem revisited: a general weighted method for calculating fail-safe numbers in meta-analysis. *Evolution*, **59**, 464–468.

Rosenberg MS, Adams DC, Gurevitch J (2000) *MetaWin: Statistical Sofware for Meta-analysis*, Version 2.0. Sinauer & Associates, Sunderland, Massachusetts.

Sala OE, Chapin FS III, Armesto JJ *et al.* (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.

Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. *Conservation Biology*, **5**, 18–32.

Sork VL, Smouse PE (2006) Genetic analysis of landscape connectivity in tree populations. *Landscape Ecology*, **21**, 821–836.

Sork VL, Nason J, Campbell DR, Fernandez JF (1999) Landscape approaches to historical and contemporary gene flow in plants. *Trends in Ecology & Evolution*, **14**, 219–224.

Spielman D, Brook BW, Frankham R (2004) Most species are not driven to extinction before genetic factors impact them. *Proceedings of the National Academy of Sciences, USA*, **101**, 15261–15264.

Tewksbury JJ, Levey DJ, Haddad NM *et al*. (2002) Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proceedings of the National Academy of Sciences, USA*, **99**, 12923–12926.

Wright S (1965) The interpretation of population structure by *F*-statistics with special regard to systems of mating. *Evolution*, **19**, 395–420.

Young AG, Clarke GM (2000) *Genetics, Demography and Viability of Fragmented Populations*. Cambridge University Press, Cambridge, UK.

Young AG, Boyle T, Brown T (1996) The population genetic consequences of habitat fragmentation for plants. *Trends in Ecology & Evolution*, **11**, 413–418.

The authors share research interests in the ecology, evolution and genetics of plant reproductive dynamics. They have been evaluating the effects of forest fragmentation and other anthropogenic disturbances on pollinators, sexual reproduction and the genetic structure of flowering plants. They are interested in generating basic and applied knowledge in ecology and conservation biology of plant-animal interactions and their role in preserving the genetic diversity of plant populations in human-altered landscapes. Other research interests involve the study of hybridization processes between genetically modified plants with native relatives, the role of pollinators as ecological service providers for human well-being, and the conservation of tropical and subtropical dry forests.

Supporting Information

Additional supporting information may be found in the online version of this article:

Table S1 List of 102 unique plant species included in the meta-analyses. For each species, we provide the botanical family, the genetic parameters evaluated in the study, the molecular marker used, the compatibility system, mating system, pollination vector, seed dispersal vector, ploidy level, vegetative growth capability, life form, type of rarity, studied tissue, time elapsed in fragmentation conditions and the source publication where information was obtained.

Appendix S1 List of complete references of the studies included in the analyses.

THE SACRAMENTO BEE

HECTOR AMEZCUA PAUL KITAGAKI, JR.

DANIEL KIM JOSÉ LUIS VILLEGAS

The State Worker

Chronicling civil-service life for California state workers

THE STATE WORKER

249 nights away at California fires: Firefighter families cope with a ‘new normal’

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REDDING — Melissa Morgado began 2018 trying to solve an arithmetic problem: How many nights did she and her firefighter husband spend apart because of work in the previous year?

He was gone for the hot summer months, of course, and again for most of October, and then 19 more days in December when deadly fires broke out on the Central Coast.

Her tally hit 249 nights, the most she and her husband spent apart in his 14 years at Cal Fire.

“I don’t like the term ‘fire season’ anymore. It’s a fire year,” said Morgado, 33, who wrote about their long separations in a popular blog post called “A Year in the Life of a Cal Fire Wife.”

The stress on her home and thousands of other firefighter families in California is another sign of the state’s “new normal” of severe, drawn-out wildfires that begin earlier in the year and run almost to the end of it.

Those expansive fires are leading emergency agencies to change their tactics, and they’re also prompting firefighters and their families to rethink how they manage the strains of long months in harm’s way.

Alarming reports of suicides, substance abuse and domestic violence persuaded Cal Fire Director Ken Pimlott to pour resources into firefighter support services.

“We’re responding to unprecedented kinds of fire. We’re doing everything we have to do, so how do we make sure we’re taking care of our employees?” he said.

An April study released by the nonprofit Ruderman Family Foundation reported that firefighters experience a higher suicide rate than the general American population, and that 103 firefighters killed themselves while 93 died on duty. The report followed a 2015 study that found firefighters experienced an “alarmingly high” rate of suicidal thoughts.

Some firefighters are turning to Cal Fire-sponsored support services that offer counseling in the field and at home fire stations. Others are using union-backed counselors to talk through some of the life-changing scenes firefighters are witnessing on the fire lines.

And some, like Morgado’s family, are making a point to schedule time off even in what used to be considered the peak of California’s fire season.

In the past, “you could assume you’d be home for the holidays. Not anymore,” said Cal Fire Deputy Chief Michael Ming, 41, the incoming deputy chief of the department’s employee support program.

He, too, has started scheduling vacation days in the late summer so he’s ready for what might come in the fall, or later.

Giving CPR to a baby

Ming is part of a seven-person team in a department-sponsored unit that aims to improve the emotional and psychological well-being of firefighters and their families. The program, called employee support services, dates back to the 1990s. It swelled to resemble its current state — with seven full-time staff members and trained liaisons throughout the state — about five years ago.

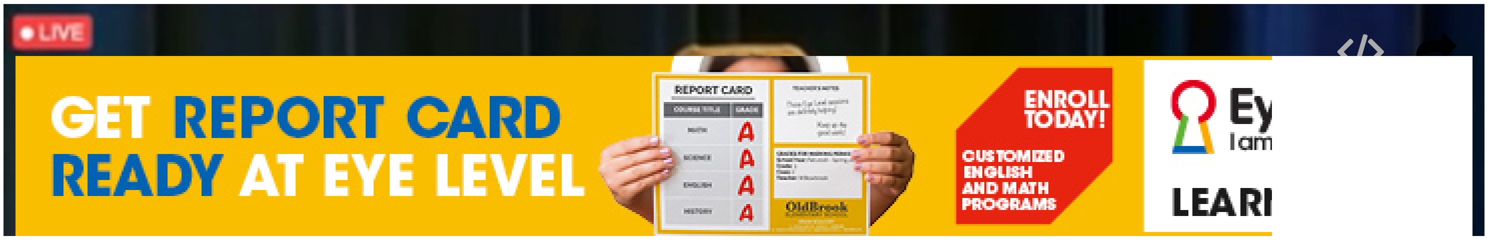
They visit the toughest fires and walk the lines with rank-and-file firefighters. They train firefighters to look for signs of post-traumatic stress in each other, and hold seminars for spouses.

Firefighter unions offer a parallel resource, sending peer counselors to traumatic events, like suicides and firefighter on-duty deaths. California Professional Firefighters, the umbrella organization that advocates for most California fire unions, has trained more than 200 of them.

“What you have to focus on is doing your job and being able to take that experience after it happened, and do some analysis with it,” said California Professional Firefighters President Brian Rice, who can still vividly describe the first death he witnessed on duty in the 1980s.

Their efforts to raise awareness about mental health coincides with growing recognition that firefighters carry vivid memories of traumatic events long after their shifts end.

“This is all still groundbreaking,” said Los Angeles County Fire Capt. Scott Ross, 53, a peer counselor for the International Association of Firefighters who spent the past week in Redding talking with firefighters battling the Carr Fire. “There are still departments that don’t have peer training, but in the last few years, I’ve seen this trend of people understanding and departments understanding that we have to take care of our own.”



A celebration of life was held for the Cal Fire bulldozer operator Braden Varney after he died fighting the Ferguson Fire earlier this month.

By **Kayla Fitzgerald** ✉

Counselors like Ross build connections with on-the-ground firefighters by listening, and by relating the moments that stayed with them for decades. They leave their phone numbers where they can, and follow up weeks and months later.

Ming, for instance, couldn't sleep at times because he worried an electrical fire would strike his house. His partner, Dattalion Chief Robert Ellis, for decades cried when he remembered the time he tried to resuscitate an infant who had died from sudden infant death syndrome. The baby reminded him of his own daughter.

"I thought I would lose it and end up in a straitjacket," Ellis, 65, said. "I couldn't handle the thought that I might go out of my mind. When I found out my mind was working in a normal way, I could handle that. I could handle being normal. It was the abnormal that scared me."

'We're stretched super thin'

This year is shaping up to be another intense one, with massive, deadly wildfires taking off from the North Coast to Yosemite, claiming the lives of three firefighters and a Cal Fire contractor.

“We’re stretched super thin,” Cal Fire firefighter Trevor Pappas said last week in downtown Lakeport, where Cal Fire and U.S. Forest Services battled to check fast-growing blazes. “We have crews everywhere.”

Across the state, firefighters are spending weeks in the field before returning to their homes. Some are confronting life-changing scenes, like the two-day effort to recover Cal Fire firefighter Braden Varney after he tumbled to his death into a steep Mariposa County canyon.

His friends and former colleagues stood watch over him until they could muster up a safe recovery plan that had them lifting his body hand by hand out of the canyon.

“Firefighters knew what was at stake. They knew it was dangerous. The fire was coming. But that’s what firefighters do, and Braden was brought to the road,” Cal Fire’s Nancy Koerperich, Varney’s unit chief, said at his memorial last month.

Exhaustion is setting in for some.

“People are definitely tired. People are working 24 hour shifts: 24 on, 24 off. You can work for 21 days then have two days off and go back out and have 21 days on again,” said Cal Fire spokesman Scott McLean.

Cal Fire last week received permission to hire 300 more seasonal firefighters, who will round out the department’s ranks and help ensure that firefighters can rest as the fires drag on.

“Right now what we’re working on is just trying to get these guys some relief because they’re going nonstop,” said Tim Edwards, the rank and file director for the union that represents Cal Fire firefighters. “These guys have no relief, and that’s what takes a toll, not just their bodies, but their families.”

Taking time

Morgado, the Cal Fire wife, didn’t like what she saw when she realized that her husband was home for only 109 nights last year. Aside from the 249 he spent at fire stations and in the field, he had a week-long elk hunt that kept him away, too.

They have two children with a third on the way. She wanted her kids to have more time with their dad.

"He just missed out on the first year of his son's life and almost all of our daughters "terrific 3's." He missed the ups and downs of our fast growing children. Next time you see a firefighter, know that they don't just risk their lives for the lives of strangers. They also sacrifice being present with their families," Morgado wrote on her blog.

They live in southern Idaho. He commutes for 72-hour shifts at a station in the northeast corner of California. It sounds like a long drive, but many Cal Fire firefighters have similar commutes when they move from station to station as they seek better jobs in the department.

This year, the couple decided they would be better off scheduling more vacation days. That can be complicated for firefighters. They often have to book vacations months, or a year, in advance. Firefighters with more seniority get more leeway.

Her husband has been gone since July 11, but she's looking forward to a break they scheduled later this month.

"I know there's a certain day; there's a light of the end tunnel," she said.

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Human-started wildfires expand the fire niche across the United States

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The economic and ecological costs of wildfire in the United States have risen substantially in recent decades. Although climate change has likely enabled a portion of the increase in wildfire activity, the direct role of people in increasing wildfire activity has been largely overlooked. We evaluate over 1.5 million government records of wildfires that had to be extinguished or managed by state or federal agencies from 1992 to 2012, and examined geographic and seasonal extents of human-ignited wildfires relative to lightning-ignited wildfires. Humans have vastly expanded the spatial and seasonal "fire niche" in the coterminous United States, accounting for 84% of all wildfires and 44% of total area burned. During the 21-y time period, the human-caused fire season was three times longer than the lightning-caused fire season and added an average of 40,000 wildfires per year across the United States. Human-started wildfires disproportionally occurred where fuel moisture was higher than lightning-started fires, thereby helping expand the geographic and seasonal niche of wildfire. Human-started wildfires were dominant (>80% of ignitions) in over 5.1 million km^2, the vast majority of the United States, whereas lightning-started fires were dominant in only 0.7 million km^2, primarily in sparsely populated areas of the mountainous western United States. Ignitions caused by human activities are a substantial driver of overall fire risk to ecosystems and economies. Actions to raise awareness and increase management in regions prone to human-started wildfires should be a focus of United States policy to reduce fire risk and associated hazards.

anthropogenic wildfires | fire starts | ignitions | modern fire regimes | wildfire causes

The United States has experienced some of the largest wildfire years this decade, with over 36,000 km^2 burned in 2006, 2007, 2012, and 2015 (1). There is national and global concern over how fire regimes have changed in the past few decades and how they will change in the future (2–4). In the western United States, there is strong evidence that regional warming and drying, including that directly attributed to anthropogenic climate change, are linked to increased fire frequency and size and longer fire seasons (5–9). However, the role that humans play in starting these fires and the direct role of human-ignitions on recent increases in wildfire activity have been overlooked in public and scientific discourse because of the difficulty in ascribing a cause, either human- or lightning-started (10). Humans primarily alter fire regimes in three ways: changing the distribution and density of ignitions, shifting the seasonality of burning, or altering available fuels (2, 3). Geographic variability in regional and continental-scale fire activity in the United States is strongly tied to proxies for these human-caused changes, including population and road density, and different land-use and development patterns (10–15). Although changing climate and fuels also influence fire regimes across the United States (10, 16, 17), there can be no fire without an ignition source. Here, we explore the role that human-started wildfires play in modern United States fire regimes.

Ignitions are often presumed to be saturated (18, 19), and therefore have limited ability to predict fire activity. However, several studies suggest that humans play an important role in redistributing ignitions (20–22), particularly where lightning rarely occurs or where lightning is not concurrent with dry conditions (23). The human–fire connection in the modern era appears strongest at intermediate levels of development, as fires become less likely in the landscape beyond a certain population density, level of urbanization, or dependence on fossil fuels (11, 13, 24). Overall, humans expand the spatial and temporal "fire niche" by introducing ignitions into landscapes when fuels are sufficiently dry enough to ignite and carry fire, but when lightning is rare. Human ignitions are therefore a critical force acting to expand how the fire niche is realized across United States ecoregions.

National-scale analysis of human alteration of the fire niche is critical given that the annual expense of fighting wildfires has exceeded $2 billion in recent years, and the accrued direct and indirect impacts of wildfire on infrastructure and communities could be 30 times that amount (25). Policies that govern wildfire management and response are also directed at the national level, demanding analysis at a national scale (10, 22, 26). Although recent human influence on fire regimes has been studied at local (13) to regional scales (14), human influence nationally remains poorly understood (10). National policies can strongly influence fire regimes (27) and, with sufficient information on human ignitions, policy directives could target human behavior in ways that remediate increasing trends in wildfire risk.

Here, we ask how human ignitions have altered the spatial extents, seasonality, and temporal trends in wildfire across the coterminous United States. We analyze over 1.5 million records of both human- and lightning-started fires in the United States from

Significance

Fighting wildfires in the United States costs billions of dollars annually. Public dialog and ongoing research have focused on increasing wildfire risk because of climate warming, overlooking the direct role that people play in igniting wildfires and increasing fire activity. Our analysis of two decades of government agency wildfire records highlights the fundamental role of human ignitions. Human-started wildfires accounted for 84% of all wildfires, tripled the length of the fire season, dominated an area seven times greater than that affected by lightning fires, and were responsible for nearly half of all area burned. National and regional policy efforts to mitigate wildfire-related hazards would benefit from focusing on reducing the human expansion of the fire niche.

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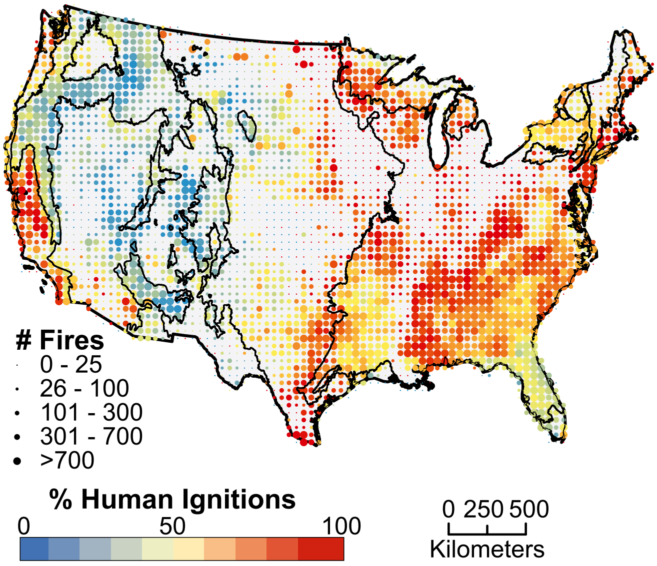

Fig. 1. The total number of wildfires (dot size) and the proportion started by humans (dot color: red indicating greater number of human started fires) within each 50 km × 50-km grid cell across the coterminous United States from 1992 to 2012. Black lines are ecoregion boundaries, as defined in the text.

1992 to 2012 (28). All of these wildfires necessitated an agency response to manage or suppress them, and therefore posed a threat to ecosystems or infrastructure; this record does not include intentionally set prescribed burns or managed agricultural fires. To our knowledge, this is the most comprehensive assessment of the role of human-started wildfires across the United States over the past two decades. We compare: (*i*) the spatial extents of human- vs. lightning-started wildfires, (*ii*) the seasonality of human vs. lightning wildfires, (*iii*) the climate niche for human- vs. lightning-started wildfires, and (*iv*) 21-y trends in large human vs. lightning wildfires. Our analysis documents the pronounced expansion of wildfire extent, seasonality of wildfires, and increasing numbers of large wildfires through time as a result of human-related ignitions across the United States.

Human-Related Ignitions Vastly Expanded the Extent of Wildfire

Human-started wildfires represented 84% of the 1.5 million wildfires included in this analysis (n = 245,446 lightning-started fires; n = 1,272,076 human-started wildfires). The eastern United States and western coastal areas were dominated by human-started wildfires, whereas lightning-started fires dominated the mountainous regions of the western United States (Fig. 1, Table 1 and Table S1). Here we define a fire regime as dominated by either human or lighting ignitions when one cause accounts for more than 80% of the number of fires in a given 50 × 50-km grid cell. Based on this definition, 5.1 million km^2, or 60% of the total land area of the coterminous United States, was dominated by human-started wildfires, whereas only 0.7 million km^2, or 8% of the area, was dominated by lightning-started fires. In addition to expanding the numbers of fires, humans also expanded the total area burned. Human-started wildfires burned a total of 160,274 km^2, or ∼44% of the total area burned from 1992 to 2012 (Table 1).

Human-Related Ignitions More Than Tripled the Length of the Wildfire Season

Human ignitions dramatically expanded the wildfire season in the United States, particularly during spring. The length of the human-started wildfire season [defined as the interquartile range (IQR) of human-ignited fires] was 154 d, more than triple that of the lightning wildfire season (IQR = 46 d) (Fig. 2 and Table 1). This national-scale expansion is driven by earlier (spring) human-started fires in eastern ecoregions coupled with later (late summer or fall) human-started fires in western ecoregions (Table S2). The median discovery date for human-started fires was over 2-mo (May 20th) earlier than lightning-started fires (July 25th). Summed across the 21-y record, the most common day for human-started fires by far was July 4th, US Independence Day, with 7,762 fires starting that day over the course of the record (Fig. 2), whereas, the most common day for lightning-started fires was July 22nd. Of all lightning-ignited fires, 78% occurred in the summer (June–August), 9% in the spring (March–May), and 12% in the fall (September–November). In contrast, human-ignited wildfires were more evenly distributed throughout the year, with 24% in summer, 38% in spring, 19% in fall, and 19% in winter. This pronounced expansion of the wildfire season was also evident spatially (Fig. 3), with human-ignited wildfires occurring predominantly in spring in the eastern United States and in the fall and winter in Texas and the Gulf states. See Table S1 for state-level analysis. When lightning-started fires were rare (<5% and >95% quantile; i.e., before May 13th or after September 16th), humans ignited 842,289 wildfires, effectively increasing the number of wildfires 35-fold compared with the 24,081 lightning-ignited wildfires during these spring, fall, and winter seasons.

Table 1. The number of wildfires, total burned area (ha), and fire season length (IQR, in days), by ecoregion (ordered by percent human-caused fires) and within the coterminous United States from 1992 to 2012

	No. of fires			Area burned (ha)			Length (IQR, days)		
Ecoregion	Human	Light	Human caused (%)	Human	Light	Human caused (%)	Human	Light	Human expansion (%)
MC	87,274	2,855	97	2,143,282	253,210	89	85	45	189
NF	61,673	2,574	96	302,561	82,721	79	51	79	N/A
ETF	815,499	44,859	95	3,827,045	829,293	82	167	66	253
MWCF	14,586	925	94	19,251	27,291	41	67	52	129
GP	134,944	17,586	88	3,992,557	2,564,955	61	148	47	315
SSH	7,504	2,167	78	340,873	254,418	57	55	41	134
TWF	4,832	1,917	72	357,150	350,477	50	98	52	188
NAD	55,422	52,044	52	2,394,677	8,880,691	21	92	40	230
NFM	76,735	94,017	45	1,895,622	5,731,733	25	75	36	208
TS	13,607	26,502	34	754,393	1,152,064	40	85	39	218
CONUS	1,272,076	245,446	84	16,027,412	20,126,852	44	154	46	335

CONUS, Coterminous United States; ETF, Eastern Temperate Forests; GP, Great Plains; MC, Mediterranean California; MWCF, Marine West Coast Forests; NAD, North American Desert; NF, Northern Forests; NFM, Northwest Forested Mountains; SSH, Southern Semiarid Highlands; TWF, Tropical Wet Forests; TS, Temperate Sierras.

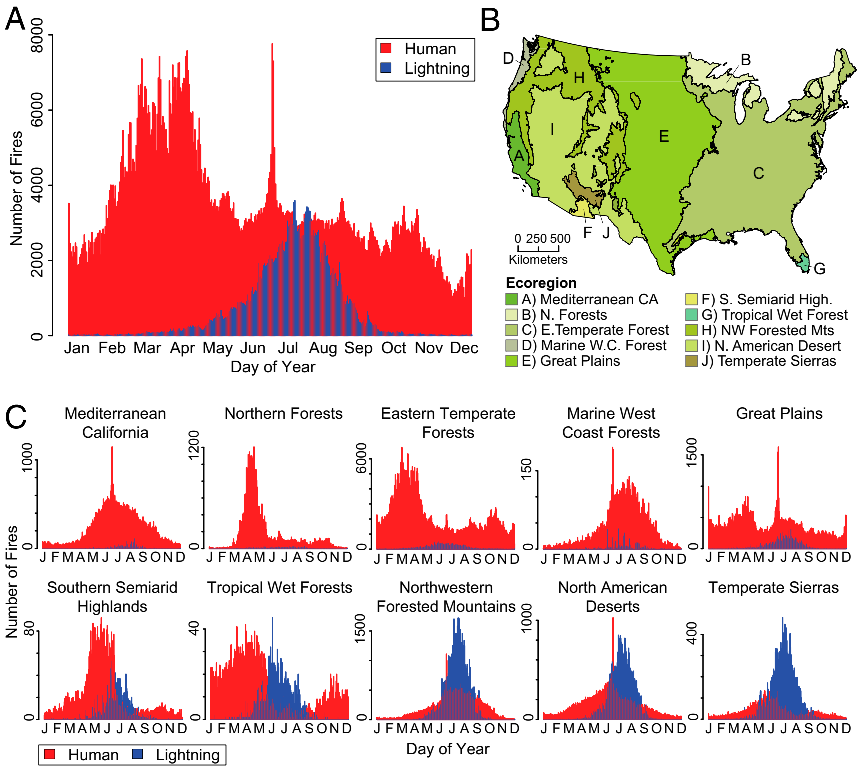

Fig. 2. Frequency distributions of human and lightning-caused wildfires by Julian day of year. (*A*) Frequency distribution of wildfires across the coterminous United States from 1992 to 2012 (n = 1.5 million); (*B*) map of United States ecoregions; (*C*) frequency distributions of wildfires by ecoregions, ordered by decreasing human dominance.

Human-Driven Expansion of the Fire Niche

Humans greatly expanded the natural fire niche (Fig. 4), which we calculated as the co-occurrence of the average monthly lightning density and 1,000-h dead fuel moisture. Regions and seasons of moderate to high lightning-started fire density (>0.4 fires per 1,000 km^2 per month) had a median lightning-strike density of 0.19 (IQR: 0.065–0.57) strikes per square kilometer per month and a median 1,000-h fuel moisture of 11.9% (IQR: 9.25–15.6%) (Fig. 4*A*). In contrast, regions and seasons of moderate to high human-started fire density (>0.4 fires per 1,000 km^2 per month) had a median lightning-strike density of only 0.11 (IQR: 0.025–0.39) strikes per square kilometer per month and a median 1,000-h fuel moisture of 17.8% (IQR: 15.95–19.25%) (Fig. 4*B*). The median fuel moisture and lightning conditions when human-started wildfires occurred were significantly different from those values for lightning-started fires ($P < 0.0001$). Areas and months of moderate to high human-caused fire density had approximately 40% fewer lightning strikes, and nearly 50% higher fuel moisture levels (based on median values) than for moderate to high lightning-caused fire density. Additional exploration of the fire niche for human-started and lightning-started fires relative to lightning density, fuel moisture, and net primary production (NPP), a proxy for fuels, is provided in Figs. S1 and S2.

Increasing Trends in Large Human-Started Wildfires

During the 21-y time period, there were significant increasing trends in large wildfires ignited by both lightning (n = 4,312; Theil-Sen estimated slope = 12.2; P = 0.001) and humans (n = 4,143; Theil-Sen estimated slope = 3.6; P = 0.004) (Fig. S3). There was a strong dichotomy in human vs. lightning trends seasonally (Fig. 5). Overall trends in lightning-caused fires were primarily driven by increasing numbers of large summer fires (Fig. 5*B*), whereas overall trends in human-caused fires were primarily driven by increasing numbers of large spring fires (Fig. 5*D*). Spatially, lightning-caused fires increased the most in the Northwest Forested Mountains ecoregion (Fig. S4*A*), whereas human-caused wildfires increased the most in the Great Plains ecoregion (Fig. S4*B*).

Discussion

Humans, the keystone fire species (29), play a primary role in spatially and temporally redistributing ignitions and resulting wildfires. We document that over 84% of the government-recorded

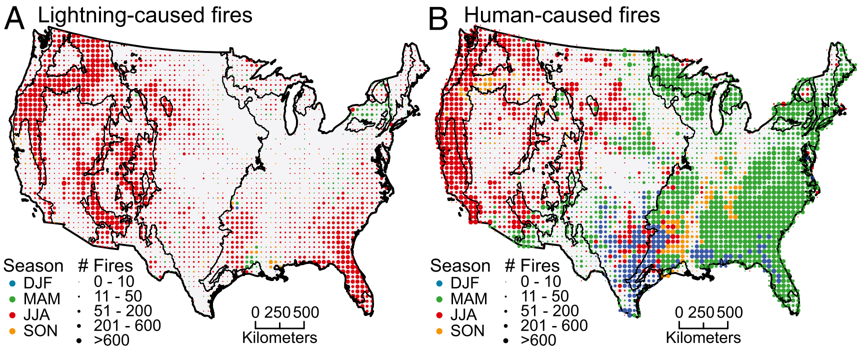

Fig. 3. Comparison of seasonality for (*A*) lightning- vs. (*B*) human-ignited wildfires. Human ignitions expand the seasonal fire niche considerably into spring and fall months. Colors show the season with the maximum ignitions caused by lightning and human within each 50 km × 50-km grid cell. Size of dot indicates the number of unique lightning and human fires between 1992 and 2012. Ecoregion boundaries are overlaid for visualization.

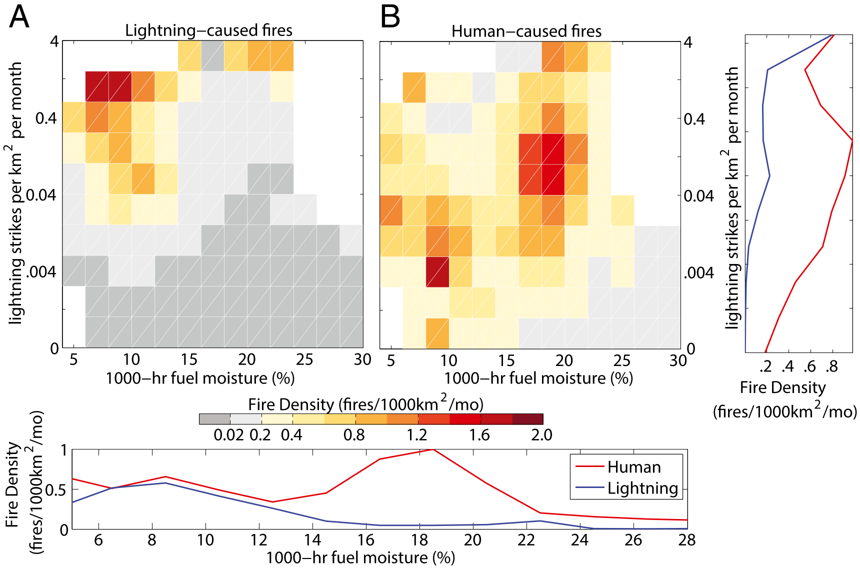

Fig. 4. Human vs. lightning fire niche relative to fuel moisture and lightning density, with greatest resulting wildfire density represented by dark red. (*A*) Lightning-started fires occur in areas with high lightning-strike density and dry fuels. (*B*) Human-started wildfires expand the fire niche to include areas with low lightning-strike density as well as areas with higher fuel moisture. Graphs on the bottom and far right show histograms of 1,000-h dead fuel moisture and lightning strikes, respectively, for human- and lightning-started fires.

wildfires were started by people from 1992 to 2012. Sixty percent of the total land area of the coterminous United States was dominated by human-started wildfires, whereas only 8% of the area was dominated by lightning fires. Humans tripled the length of the wildfire season, extending burning into the spring, fall, and winter months. During the spring, fall, and winter, people added more than 840,000 wildfires, a 35-fold increase over the number of lightning-started fires in those seasons. This expansion of the fire-niche was caused by human-related ignitions under higher fuel moisture conditions, compared with lightning-started fires. Moreover, during this 21-y record, large human-started wildfires increased significantly.

There was a strong national east–west dichotomy in the spatial distribution of human-started wildfires. Although human-started wildfires were pervasive across the United States (Fig. 1), the expansion of human-started wildfires relative to lightning-started fires was most dramatic in the eastern United States and central and southern California (Figs. 1 and 2*C*). Recent work for California confirms the important role of humans, with anthropogenic variables explaining half of the variability in fire probability over the past four decades (30). In contrast, lightning-started fires were found primarily in the intermountain west and Florida and occurred predominantly in the summer, reflecting national lightning strike patterns (31) (Fig. 2*C*). This finding supports other studies of human vs. lightning ignition sources that have found an important distinction between eastern and western United States fire patterns (10, 21) and drivers (32). Some explanations for this distinction include higher population and housing densities, lower proportions of public land, and more extensive land use and development in the eastern United States (33, 34), all of which could lead to more sources of anthropogenic ignitions. Synchrony between lightning activity and the seasonal nadir of fuel moisture in the western United States also likely contributes to these geographic differences. However, even with a projected increase in the number of lightning strikes as a result of anthropogenic climate change (50% by 2100) (35), humans would still remain the dominant ignition source across the majority of the United States land area. The majority of the wildfires requiring agency suppression in the east can be attributed to escaped fires from debris burning occurring in the spring months (or winter in Texas and the Gulf Coast) (Fig. 3). Between 1992 and 2012, wildfires caused by debris burning tended to be small (median

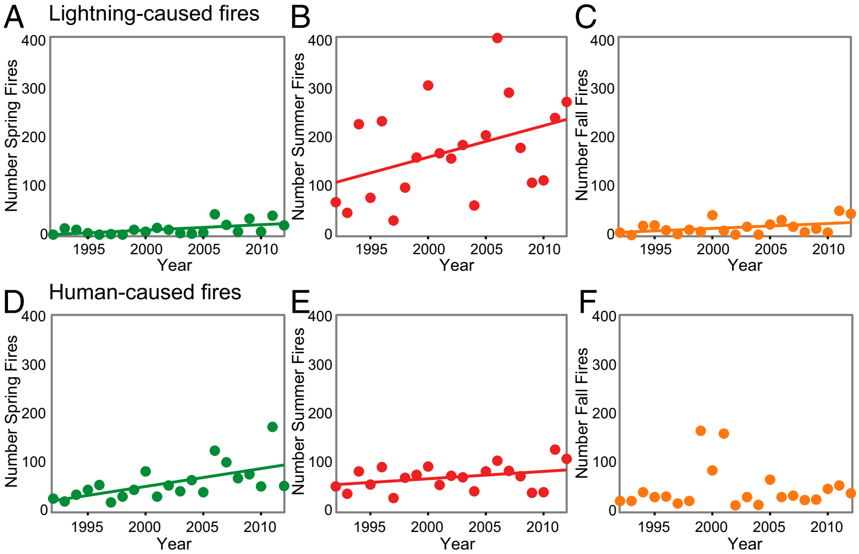

Fig. 5. Trends in the number of large wildfires verified by MTBS records from 1992 to 2012 for lightning-started fires (*A*–*C*) vs. human-started fires (*D*–*F*) in the spring (green: *A* and *D*), summer (red: *B* and *E*), and fall (orange: *C* and *F*). Where trend lines are shown, Theil-Sen estimated slopes are significantly different from zero ($P < 0.05$).

fire size 0.4 ha, IQR: 0.14–1.62 ha), but still an important source of risk to surrounding ecosystems. At finer scales, there are also notable patterns in human- vs. lightning-started wildfires (Fig. S5). Increased wildfires can follow road networks (36), the wildland–urban interface (13), and boundaries between agricultural and forested areas (37), highlighting just a few examples of how human activities and cultural drivers provide ignitions that substantially change the distribution of fire across the United States (38).

Our findings reinforce the strong imprint of people on fire regimes through changes in wildfire seasonality, which has been documented globally (39). In the past few decades, early onset of warmer and drier conditions has promoted greater fire activity across the western United States (6, 7, 40). However, our study highlights the equally important role of human ignitions in changing modern fire regimes by increasing the fire season length to encompass the entire year. The vast majority (78%) of lightning-started fires occurred during the summer months, whereas 76% of human-started fires occurred during the spring, fall, and winter months. Moreover, this trend varies substantially by ecoregion, reflecting again the principle dichotomy between the eastern and western United States (Fig. 3). Human-started fires extend the fire season earlier in the east, and later in the west (Fig. 3 and Table S2). Observations suggest that climate change has extended the duration of the fire weather season across most of the globe, including parts of the United States by a couple of weeks over the past three decades (5, 9), whereas we show that human ignitions in the United States increased the length of the fire season by more than three mo. There was also a notable mark of American culture on the distribution of wildfires, with the peak day of wildfires occurring on July 4th, concurrent with Independence Day fireworks displays (Fig. 2). Indeed, Americans start over twice as many wildfires on July 4th as any other summer day. A similar cultural mark has also been demonstrated globally with a marked decline in wildfires on Sunday compared with other weekdays (41).

Thus, at the national scale, human ignitions dramatically expand the spatial and seasonal niche of fire. The key components that define the fire niche are ignition sources, fuel mass, and desiccation. By exploring the fire niche along these axes, our results show that lightning fires are primarily constrained to areas with a lightning-strike density of greater than 100 strikes per grid cell per month (0.04 strikes/km^2 per month) and are concurrent with drier fuels ($< 15\%$ fuel moisture) (Fig. 4). Human ignitions expand fires into regions with higher fuel moisture (Fig. 4) and higher NPP (Figs. S1 and S2), suggesting that humans create sufficient ignition pressure for wetter fuels to burn. As a consequence, human ignitions have expanded the fire niche into areas with historically low lightning-strike density, such as Mediterranean California, or low concurrence of lightning and dry conditions, such as Eastern Temperate Forests (Fig. 1).

Over the past two decades, there was a significant increase across the United States for both human- and lightning-caused large fires (Fig. S3). The significant increase in large lightning fires is driven primarily by fires in summer months (Fig. 5) in the Northwest Forested Mountains ecoregion of the western United States (Fig. S4). This finding is consistent with other studies that have demonstrated an increase in large fires across the western United States (6, 7, 40), likely as a consequence of changes in climate and fuels rather than ignitions. In contrast, the significant trend in human-caused fires is primarily driven by an increase in large fires during spring months (Fig. 5) in the Great Plains ecoregion of the United States (Fig. S4). This increasing trend suggests that earlier springs as a result of climate change (42, 43) may be interacting with human ignition sources to increase the risk of large fires in the central United States.

The strong year-to-year variability in human ignitions (Fig. S3 and S4) may reflect the degree to which human choices can affect fire regimes. However, interannual climate variability also influences fuel moisture, NPP, and short-term weather conditions that enable the spread of human-ignited wildfires (44). There was a significant temporal correlation between large human- and lightning-started fires ($R = 0.75$). This pattern has been observed previously in the western United States (23) and suggests that large-scale climate drivers affect the frequency of both human- and lightning-caused fires. It is unknown how human actions will be affected by hotter and drier conditions, potentially increasing or decreasing ignitions from land use, recreation, and other sources. Increased public awareness and focused policy and management, particularly in years with elevated fire risk associated with climatic anomalies, are needed to reduce the number of human-caused ignitions.

In conclusion, we demonstrate the remarkable influence that humans have on modern United States wildfire regimes through changes in the spatial and seasonal distribution of ignitions. Although considerable fire research in the United States has rightly focused on increased fire activity (e.g., larger fires and more area burned) because of climate change, we demonstrate that the expanded fire niche as a result of human-related ignitions is equally profound. Moreover, the convergence of warming trends and expanded ignition pressure from people is increasing the number of large human-caused wildfires (Fig. 5). Currently, humans are extending the fire niche into conditions that are less conducive to fire activity, including regions and seasons with wetter fuels and higher biomass (Figs. 3 and 4). Land-use practices, such as clearing and logging, may also be creating an abundance of drier fuels, potentially leading to larger fires even under historically wetter conditions. Additionally, projected climate warming is expected to lower fuel moisture and create more frequent weather conditions conducive to fire ignition and spread (45), and earlier springs attributed to climate change are leading to accelerated phenology (42). Although plant physiological responses to rising CO_2 may reduce some drought stress (46), climate change will likely lead to faster desiccation of fuels and increased risk in areas where human ignitions are prevalent.

Uncertainty remains regarding how anthropogenic climate change will alter wildfire activity geographically and seasonally (47, 48), particularly in areas where human-caused fires dominate. Moreover, the current wildland–urban interface, where houses intermingle with natural areas, constitutes 9% of the United States total land area (33) but is projected to double by 2030, predominantly in the intermountain West (49). This expected development expansion will increase not only ignition pressure, but also the vulnerability of new infrastructure. Human-driven expansion of the spatial and temporal distribution of ignitions makes national- and regional-scale policy interventions and increased public awareness critical for reducing national wildfire risk.

Materials and Methods

For this analysis, we used the publically available US Forest Service Fire Program Analysis-Fire Occurrence Database (FPA-FOD) (28). This comprehensive dataset includes United States federal, state, and local records of wildfires (both on public and private lands) that were suppressed from 1992 to 2012, a total of ~1.6 million records. Previous studies have focused on the western United States (20), federal lands (22), or records from just one agency (21). Each entry includes at minimum the location, discovery date, and cause of the wildfire. We excluded 114,191 wildfires with an unknown cause and analyzed the spatial, seasonal, and temporal patterns of human- vs. lightning-started wildfires. In total, 1,517,522 wildfires were included in the analysis. Human-started wildfires were caused by a variety of sources, including the US Forest Service-designated categories of equipment use, smoking, campfire, railroad, arson, debris burning, children, fireworks, power line, structure, and miscellaneous fires (28). Spatially, we calculated the proportion of human- vs. lightning-caused wildfires within equal-area 50 × 50-km grid cells across the coterminous United States. This grid size corresponds roughly to the size of an average United States county. For each grid cell, we calculated the season (winter, spring, summer, or fall) when the majority of human-caused and lightning-caused wildfires were started. All spatial analyses were conducted in the Albers-Conical equal-area projection. To determine the seasonal distribution of wildfires, we plotted the distribution of human- and lightning-started fires by the day of year for the coterminous United States and for individual ecoregions. We used the level 1 ecological regions of North America, developed by the Commission for Environmental Cooperation (50). We calculated the length of the human- and lightning-caused fire seasons as the IQR of the Julian day of recorded fire ignition: that is, the difference between the first and third quartiles.

We determined how humans expanded the fire niche by comparing the lightning-strike density (i.e., natural ignition pressure) and fuel-moisture conditions under which actual human- and lightning-started fire events occurred. We obtained daily 1,000-h dead fuel moisture data from the surface meteorological data (51) on a 4-km grid from 1992 to 2012, and computed monthly averages across the 21-y study period. We obtained 4-km gridded monthly lightning-strike data from the Vaisala National Lightning Detection Network (https://www.ncdc.noaa.gov/data-access/severe-weather/lightning-products-and-services) and averaged the data over the 21-y study period. To account for fuel limitations, we also explored the fire niche as a function of fuel amount (approximated by NPP). We used MODIS mean annual NPP data (1-km resolution, from 2002 to 2015) (52) for this purpose. These three datasets were aggregated to the common 50 × 50-km grid cell. We calculated the number of human- and lightning-started fires by grid cell using the FPA-FOD dataset (28). We excluded any grid cells from subsequent analyses that did not report at least one lightning-caused or human-caused wildfire over the period of record. We tested whether fire niche expansion (as determined by fuel moisture and lightning-strike density) caused by human ignitions was significant based on Mann–Whitney tests between human- vs. lightning-started fires.

To assess trends in human- vs. lightning-caused wildfires through time, we used only large fires that were independently verified by the Monitoring Trends in Burn Severity (MTBS) project (53). We specifically focused on these large fires (>400 ha in the west, >200 ha in the east; $n = 8{,}455$) for comparability with previous research, which has examined temporal trends in the western United States and the link to climate warming (6, 7, 40), but has not investigated the relative contribution of human-started fires at a national scale. In addition to overall temporal trends, we tested for significant trends by ignition source versus season (spring, summer, fall) and versus ecoregion based on the level I ecological regions of North America (50). We explored a similar analysis using all available FPA-FOD data, but changes in reporting frequency through time for some states precluded a robust temporal analysis. We tested for trends in wildfire numbers through time using the nonparametric Theil-Sen estimator (54) and tested for trend significance using nonparametric Mann–Kendall tests (55).

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1. NIFC (2015) Total Wildland Fires and Acres (1960–2015) and Current Year-to-Date by State. *National Interagency Fire Center Statistics*. Available at https://www.nifc.gov/. Accessed October 7, 2016.
2. Bowman DM, et al. (2011) The human dimension of fire regimes on Earth. *J Biogeogr* 38(12):2223–2236.
3. Bowman DMJS, et al. (2009) Fire in the Earth system. *Science* 324(5926):481–484.
4. Stephens SL, et al. (2013) Land use. Managing forests and fire in changing climates. *Science* 342(6154):41–42.
5. Abatzoglou JT, Williams AP (2016) Impact of anthropogenic climate change on wildfire across western US forests. *Proc Natl Acad Sci USA* 113(42):11770–11775.
6. Westerling AL, Hidalgo HG, Cayan DR, Swetnam TW (2006) Warming and earlier spring increase western U.S. forest wildfire activity. *Science* 313(5789):940–943.
7. Westerling AL (2016) Increasing western US forest wildfire activity: Sensitivity to changes in the timing of spring. *Philos Trans R Soc Lond B Biol Sci* 371(1696): 20150178, erratum in *Philos Trans R Soc Lond B Biol Sci* 371(1707):20160373.
8. Williams AP, Abatzoglou JT (2016) Recent advances and remaining uncertainties in resolving past and future climate effects on global fire activity. *Curr Clim Change Rep* 2(1):1–14.
9. Jolly WM, et al. (2015) Climate-induced variations in global wildfire danger from 1979 to 2013. *Nat Commun* 6:7537.
10. Hawbaker TJ, et al. (2013) Human and biophysical influences on fire occurrence in the United States. *Ecol Appl* 23(3):565–582.
11. Bistinas I, et al. (2013) Relationships between human population density and burned area at continental and global scales. *PLoS One* 8(12):e81188.
12. Parisien M-A, et al. (2016) The spatially varying influence of humans on fire probability in North America. *Environ Res Lett* 11(7):075005.
13. Syphard AD, et al. (2007) Human influence on California fire regimes. *Ecol Appl* 17(5):1388–1402.
14. Fusco EJ, Abatzoglou JT, Balch JK, Finn JT, Bradley BA (2016) Quantifying the human influence on fire ignition across the western USA. *Ecol Appl* 26:2390–2401.
15. Calef MP, McGuire AD, Chapin FS (2008) Human influences on wildfire in Alaska from 1988 through 2005: An analysis of the spatial patterns of human impacts. *Earth Interact* 12(1):1–17.
16. Morton DC, et al. (2013) Satellite-based assessment of climate controls on US burned area. *Biogeosci Disc* 10:247–260.
17. Littell JS, McKenzie D, Peterson DL, Westerling AL (2009) Climate and wildfire area burned in western U.S. ecoprovinces, 1916-2003. *Ecol Appl* 19(4):1003–1021.
18. Krawchuk MA, Moritz MA, Parisien M-A, Van Dorn J, Hayhoe K (2009) Global pyrogeography: The current and future distribution of wildfire. *PLoS One* 4(4):e5102.
19. Thonicke K, Venevsky S, Sitch S, Cramer W (2001) The role of fire disturbance for global vegetation dynamics: Coupling fire into a dynamic global vegetation model. *Glob Ecol Biogeogr* 10(6):661–677.
20. Bartlein PJ, Hostetler SW, Shafer SL, Holman JO, Solomon AM (2008) Temporal and spatial structure in a daily wildfire-start data set from the western United States (198696). *Int J Wildland Fire* 17(1):8–17.
21. Malamud BD, Millington JDA, Perry GLW (2005) Characterizing wildfire regimes in the United States. *Proc Natl Acad Sci USA* 102(13):4694–4699.
22. Stephens SL (2005) Forest fire causes and extent on United States Forest Service lands. *Int J Wildland Fire* 14:213–222.
23. Abatzoglou JT, Kolden CA, Balch JK, Bradley BA (2016) Controls on interannual variability in lightning-caused fire activity in the western US. *Environ Res Lett* 11(4):045005.
24. Balch JK, et al. (2016) Global combustion: The connection between fossil fuel and biomass burning emissions (1997-2010). *Philos Trans R Soc Lond B Biol Sci* 371(1696):371.
25. Schoennagel T, et al. (2016) Insights from wildfire science: A resource for fire policy discussions. *Headwaters Economics*, pp 1–9. Available at https://headwaterseconomics.org/wildfire/insights. Accessed January 20, 2017.
26. Stephens SL, Ruth LW (2005) Federal forest-fire policy in the United States. *Ecol Appl* 15(2):532–542.
27. North MP, et al. (2015) Environmental science. Reform forest fire management. *Science* 349(6254):1280–1281.
28. Short KC (2014) A spatial database of wildfires in the United States, 1992–2011. *Earth Syst Sci Data* 6(1):1–27.
29. Pyne SJ (2014) Fire creature. *Fire on Earth: An Introduction*, eds Scott AC, Bowman DMJS, Bond WJ, Alexander ME (John Wiley and Sons, West Sussex, UK), pp 195–230.
30. Mann ML, et al. (2016) Incorporating anthropogenic influences into fire probability models: Effects of human activity and climate change on fire activity in California. *PLoS One* 11(4):e0153589.
31. Orville RE, Huffines GR (2001) Cloud-to-ground lightning in the United States: NLDN results in the first decade, 1989–98. *Mon Weather Rev* 129(5):1179–1193.
32. Pyne SJ (2015) *Between Two Fires: A Fire History of Contemporary America* (Univ of Arizona Press, Tucson, AZ).
33. Radeloff VC, et al. (2005) The wildland-urban interface in the United States. *Ecol Appl* 15(3):799–805.
34. Riitters KH, et al. (2002) Fragmentation of continental United States forests. *Ecosystems* 5(8):815–822.
35. Romps DM, Seeley JT, Vollaro D, Molinari J (2014) Climate change. Projected increase in lightning strikes in the United States due to global warming. *Science* 346(6211):851–854.
36. Cardille JA, Ventura SJ, Turner MG (2001) Environmental and social factors influencing wildfires in the Upper Midwest, United States. *Ecol Appl* 11(1):111–127.
37. McCarty JL, Korontzi S, Justice CO, Loboda T (2009) The spatial and temporal distribution of crop residue burning in the contiguous United States. *Sci Total Environ* 407(21):5701–5712.
38. Pyne SJ (1982) *Fire in America* (Univ of Washington Press, Seattle, WA), p 654.
39. Le Page Y, Oom D, Silva JMN, Jönsson P, Pereira JMC (2010) Seasonality of vegetation fires as modified by human action: Observing the deviation from eco-climatic fire regimes. *Glob Ecol Biogeogr* 19(4):575–588.
40. Dennison PE, Brewer SC, Arnold JD, Moritz MA (2014) Large wildfire trends in the western United States, 1984–2011. *Geophys Res Lett* 41(8):2928–2933.
41. Earl N, Simmonds I, Tapper N (2015) Weekly cycles of global fires—Associations with religion, wealth and culture, and insights into anthropogenic influences on global climate. *Geophys Res Lett* 42(21):9579–9589.
42. Schwartz MD, Ahas R, Aasa A (2006) Onset of spring starting earlier across the Northern Hemisphere. *Glob Change Biol* 12(2):343–351.
43. Melillo JM, Richmond T, Yohe GW (2014) *Climate Change Impacts in the United States: The Third National Climate Assessment* (US Global Change Research Program, Washington, DC), 10.7930/J0Z31WJ2.
44. Jin Y, et al. (2014) Contrasting controls on wildland fires in Southern California during periods with and without Santa Ana winds. *J Geophys Res Biogeosci* 119(3):432–450.
45. Flannigan M, et al. (2013) Global wildland fire season severity in the 21st century. *For Ecol Manage* 294:54–61.
46. Swann ALS, Hoffman FM, Koven CD, Randerson JT (2016) Plant responses to increasing CO2 reduce estimates of climate impacts on drought severity. *Proc Natl Acad Sci USA* 113(36):10019–10024.
47. Barbero R, Abatzoglou JT, Larkin NK, Kolden CA, Stocks B (2015) Climate change presents increased potential for very large fires in the contiguous United States. *Int J Wildland Fire* 24(7):892–899.
48. Luce CH, et al. (2016) Contributing factors for drought in United States forest ecosystems under projected future climates and their uncertainty. *For Ecol Manage* 380:299–308.
49. Theobald DM, Romme WH (2007) Expansion of the US wildland–urban interface. *Landsc Urban Plan* 83(4):340–354.
50. Wiken E, Nava FJ, Griffith G (2011) *North American Terrestrial Ecoregions—Level III* (Commission for Environmental Cooperation, Montreal).
51. Abatzoglou JT (2013) Development of gridded surface meteorological data for ecological applications and modelling. *Int J Climatol* 33(1):121–131.
52. Zhao M, Heinsch FA, Nemani RR, Running SW (2005) Improvements of the MODIS terrestrial gross and net primary production global data set. *Remote Sens Environ* 95(2):164–176.
53. Eidenshink J, et al. (2007) A project for monitoring trends in burn severity. *Fire Ecol* 3(1):3–21.
54. Wilcox RR (2012) *Introduction to Robust Estimation and Hypothesis Testing* (Academic, San Diego).
55. Mann HB (1945) Nonparametric tests against trend. *Econometrica* 13(3):245–259.

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Systematic review

The impacts of roads and other infrastructure on mammal and bird populations: A meta-analysis

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ABSTRACT

Biodiversity is being lost at an increased rate as a result of human activities. One of the major threats to biodiversity is infrastructural development. We used meta-analyses to study the effects of infrastructure proximity on mammal and bird populations. Data were gathered from 49 studies on 234 mammal and bird species. The main response by mammals and birds in the vicinity of infrastructure was either avoidance or a reduced population density. The mean species abundance, relative to non-disturbed distances (MSA), was used as the effect size measure. The impact of infrastructure distance on MSA was studied using meta-analyses. Possible sources of heterogeneity in the results of the meta-analysis were explored with meta-regression.

Mammal and bird population densities declined with their proximity to infrastructure. The effect of infrastructure on bird populations extended over distances up to about 1 km, and for mammal populations up to about 5 km. Mammals and birds seemed to avoid infrastructure in open areas over larger distances compared to forested areas, which could be related to the reduced visibility of the infrastructure in forested areas. We did not find a significant effect of traffic intensity on the MSA of birds. Species varied in their response to infrastructure. Raptors were found to be more abundant in the proximity of infrastructure whereas other bird taxa tended to avoid it. Abundances were affected at variable distances from infrastructure: within a few meters for small-sized mammals and up to several hundred meters for large-sized mammals.

Our findings show the importance of minimizing infrastructure development for wildlife conservation in relatively undisturbed areas. By combining actual species distributions with the effect distance functions we developed, regions sensitive to infrastructure development may be identified. Additionally, the effect distance functions can be used in models in support of decision making on infrastructure planning.

1. Introduction

Global biodiversity is changing at an unprecedented rate as a result of several human-induced changes in the global environment (Vitousek, 1994; Pimm et al., 1995; Sala et al., 2000; MEA, 2005). Biodiversity loss at the species level tends to result in the so-called homogenisation process (Lockwood and McKinney, 2001). This process is generally characterised by a decrease in the abundance of many species, culminating into an increase in the number of threatened species and the extinction of others, in combination with a simultaneous increase in the abundance of a few species. The main drivers of biodiversity change are land-use and land-cover change, climate change, pollution, fragmentation and infrastructure development (UNEP, 2001; Sala et al., 2000; Sanderson et al., 2002; Alkemade et al., 2009).

The ubiquity of road networks and the growing body of evidence of the negative impacts that roads and other linear infrastructure have on wildlife and ecosystems suggest that infrastructure represents a major driving factor of biodiversity loss. The most commonly reported impacts from roads and utility corridors include habitat loss, intrusion of edge effects in natural areas, isolation of populations, barrier effects, road mortality and increased human access (Andrews, 1990; Forman and Alexander, 1998; Spellerberg, 1998; Trombulak and Frissell, 2000; Forman et al., 2003). Road construction leads to habitat destruction and creates open spaces in otherwise closed forests (Gullison and Hardner, 1993; Reed et al., 1996; Santos and Tabarelli, 2002). The open spaces may fragment populations (barrier effect), attract light-demanding species and may be avoided by others (edge effect)

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(Kroodsma, 1984; Vos and Chardon, 1998; Bolger et al., 1997; Ortega and Capen, 1999). Additionally, the use of infrastructure by cars or trains increases the risk of collisions with wildlife and the stress on (breeding) individuals (due to noise and visual stimuli), both of these risks affecting animal populations (Van der Zande et al., 1980; Reijnen et al., 1996; Romin and Bissonette, 1996; Boarman and Sazaki, 2005; Parris and Schneider, 2009).

Besides roads, other types of infrastructure, such as railways, powerlines, pipelines, hydroelectric developments, oil wells, seismic lines and wind parks, have an impact on wildlife populations (Dunthorn and Errington, 1964; McLellan and Shackleton, 1989; Cameron et al., 1992; Van Dyke and Klein, 1996; Mahoney and Schaefer, 2002; Nellemann et al., 2003a; Barrios and Rodriguez, 2004). All these impacts may influence the long-term viability of populations and, eventually, biodiversity.

Qualitative reviews provide a broad understanding of the ecological effects of infrastructure that affect a range of taxa and ecosystems, but lack quantitative evidence (Trombulak and Frissell, 2000; Forman et al., 2003). However, the few attempts to quantify the effects of infrastructure (UNEP, 2001; Nellemann et al., 2003b; Fahrig and Rytwinski, 2009), or to model the vulnerability of animal populations to road effects (Jaeger et al., 2005), are not based on meta-analysis, which is the statistical procedure for combining the results of independent studies in a quantitative way (Arnqvist and Wooster, 1995). In this study, we aim at estimating the decline of animal populations in relation to proximity to infrastructure by using a meta-analytical approach.

Among all animal taxa, mammal and bird populations were chosen for our analysis since both have been widely reported to be declining in relation to their distance from infrastructure. However, large differences in disturbance sensitivity seem to exist between and within these groups. Bird populations seem to be affected within a few hundred metres from infrastructure, whereas a reduction in mammal populations has been found at distances of a few hundred metres up to several kilometres from infrastructure (McLellan and Shackleton, 1989; Cameron et al., 1992; Ortega and Capen, 1999; Nellemann et al., 2003a). Additionally, traffic intensity seems to play a role in the decline of both bird and mammal populations close to roads (Van der Zande et al., 1980; Reijnen et al., 1995, 1996; Dyer et al., 2001; Rheindt, 2003; Gagnon et al., 2007).

To quantify the patterns of reduced population densities in relation to infrastructural development, we searched the scientific and non-scientific literature for quantitative data on mammal and bird populations at varying distances from infrastructure. As the metric of effect size, we calculated the ratio between the species abundance at varying distances to infrastructure (Disturbance or Effect distance) relative to the species abundance at the largest (control) distance reported in the study. This ratio is a form of the biodiversity indicator mean species abundance (MSA) which represents the mean abundance of (remaining) original species in an area related to an undisturbed situation (Alkemade et al., 2009). Meta-analysis was used to combine the effect sizes (MSA values) across all studies for several distance intervals and test their level of significance. Furthermore, meta-regression was applied to model the relationship between distance to infrastructure and MSA for birds (MSA_B) and mammals (MSA_M) (infrastructure–distance effect), and to examine sources of heterogeneity in this relationship.

2. Methods

2.1. Search and selection of published studies on infrastructural effects

Relevant studies were searched by using the following electronic databases: Ebsco, ISI Web of Knowledge, JSTOR, Omega (Utrecht University Digital Publications Search Machine), Science Direct, Scopus, Springer Link and Wiley InterScience. The search terms were: road∗ AND impact∗ AND biodiversity OR mammal, bird; infrastructure AND impact∗ AND biodiversity OR mammal, bird; road∗ AND distance AND biodiversity OR mammal, bird; road-effect zone AND mammal abundance, bird abundance; road∗ AND disturbance∗ and biodiversity OR mammal, bird; powerline AND impact AND biodiversity OR mammal, bird; wind park AND biodiversity OR mammal, bird; road traffic∗ AND impact∗ AND biodiversity∗ OR mammal, bird; infrastructure AND disturbance AND biodiversity OR mammal, bird. An Internet search was also performed using the meta-search engine Google scholar. Bibliographies of articles viewed at full text were searched for relevant secondary articles. Authors and recognized experts in the field of infrastructure development, road establishment and effects on biodiversity (Christian Nellemann, UNEP-Grid Arendal, and Rien Reijnen, Alterra) were also contacted for further recommendations, and for provision of any unpublished material or missing data that may be relevant (grey literature). Foreign language searches were undertaken by using cross-reference.

2.2. Study inclusion criteria

From this bulk of literature we selected those studies of which title and keywords were associated to the objective of this review. Subsequently, information contained in the abstracts was examined to further narrow down the selection to those studies that met the following criteria:

- Relevant study objects: Populations of any mammal or bird species. Studies were included irrespective of habitat or spatial scale.
- Types of intervention: Disturbance distances or distances close to infrastructure at which mammal and bird populations might be reduced compared to larger distances or control distances (see Types of comparator).
- Types of outcome: Species abundance (density and/or counts) at varying distances to infrastructure.
- Types of comparator: Control distances or distances at which mammal and bird populations are unaffected by infrastructure and roads.

2.3. Data extraction

Finally, 49 studies met the selection criteria for data extraction, from which 90 datasets were extracted and stored in a database, resulting in 2107 data points. The data included the mean abundance at disturbance distances close to infrastructure and at a larger control distance; furthermore we recorded the sample size, the variance, and standard deviation or standard error, depending on the study. These data were used to estimate an effect size and its variance as required in meta-analysis (Osenberg et al., 1999). Additionally, we stored data on location, habitat, infrastructure type, taxon (order) and traffic intensity to explore sources of heterogeneity (see Table 2 in Supplementary material, available at http://www.environmentalevidence.org/SR68.html). These variables are considered biologically meaningful and could affect the way different taxa respond to infrastructure. Thus, we expected that different taxa would respond differently to different infrastructure types (linear and clustered) and in different habitat types according to varying visibility of infrastructure, while traffic intensity could affect the response due to the influence of noise and visual stimuli.

2.4. Effect size calculation: Mean Species Abundance (MSA)

For each study, individual effect sizes were calculated as the ratio between the abundance of each species close to the infrastructure

(Disturbance distance) and the abundance of the same species at the largest (control) distance, as reported in the study. Individual effect sizes were aggregated for each study and distance, resulting in an estimate of the mean species abundance (MSA), which is the metric of effect size for the meta-analysis (see Eq. (1))

$$\mathrm{MSA}_{sd} = \frac{\sum_i R_{isd}}{N_s}; \tag{1}$$

where MSA_{sd} is the relative mean species abundance estimated in study s at a distance d; R_{isd} is the ratio between the abundance or density of species i at distance d and the abundance or density of species i at the control distance, calculated as: A_{isd}/A_{isc} for $A_{isc} > 0$. N_s is the number of species considered in study s. MSA values ranged from 0 to 1 and declined at shorter distances from infrastructure. For species with higher densities at short distances from infrastructure compared to the control distance, the MSA value was truncated to 1; therefore, if $A_{isd} > A_{isc}$, then $R_{isd} = 1$.

2.5. Estimation of variation in MSA values

The variance of the MSA value for each distance and study was estimated by calculating the variance of the external error (2), and of the internal error (3), which are both forms of the variance of a sample mean (Mood et al., 1973). The largest variance was used in the meta-analysis, thus taking into account the largest error associated with each data point (DerSimonian and Laird, 1986). For single species' studies, only the variance of the internal error could be calculated.

The variance of the external error was calculated as:

$$\sigma^2_{ext} = \frac{\sum (MSA_{sd} - R_{isd})^2}{N_s(N_s - 1)} \tag{2}$$

The variance of the internal error was calculated as:

$$\sigma^2_{int} = \frac{\sum \sigma^2_{R_{isd}}}{N_s^2}; \tag{3}$$

where $\sigma^2_{R_{isd}}$ is the individual variance for each ratio, which was calculated by using the Delta Method (4), a first-order approximation of the variance of a ratio of two random variables (Oehlert, 1992; Winzer, 2000).

$$\sigma^2_{R_{isd}} = \frac{A^2_{isd}}{A^2_{isc}}\left[\frac{A^2_{isd}}{\sigma^2_{A_{isd}}} + \frac{A^2_{isc}}{\sigma^2_{A_{isc}}} - \frac{2\rho \cdot \sigma_{A_{isd}} \cdot \sigma_{A_{isc}}}{A_{isd} \cdot A_{isc}}\right] \tag{4}$$

In this equation $\sigma^2_{A_{isd}}$ and $\sigma^2_{A_{isc}}$ are the variances of A_{isd} and A_{isc}, respectively, and ρ their correlation coefficient. We assume A_{isd} and A_{isc} to be independent and, therefore, the correlation coefficient ρ to be zero. Variances of A_{isd} and A_{isc} were obtained from studies, when available; where this was not the case, the data was assumed to follow a Poisson distribution, in which $\mu = \sigma^2$ and, therefore, $A_{isd} = \sigma^2_{A_{isd}}$, and $A_{isc} = \sigma^2_{A_{isc}}$ (Sokal and Rohlf, 1981).

Finally, as some species had a density of zero at the disturbance distance ($A_{isd} = 0$), a continuity correction factor ($k = 1/2$) was added to the numerator and denominator of the ratio of all species, resulting in slightly higher variance estimates (Cox, 1970; Sweeting et al., 2004).

2.6. Study quality assessment

Study characteristics were summarized and experimental design (control and treatment plots) and data availability for extraction (means, standard errors and sample sizes) were used as criteria for determining study quality (low; medium–low; medium; medium–high; high) (Supplementary material available at http://www.environmentalevidence.org/SR68.html). A sensitivity analysis was done by removing studies scoring "medium–low" or "low".

2.7. Data analyses

Meta-analyses were performed separately for mammal and bird studies by using the package "metafor" in R 2.9.1 software (Viechtbauer, 2009). A random effects meta-analysis was done to derive a pooled effect size for all datasets allowing pseudoreplication. Additionally, meta-analyses were done per distance interval containing non-duplicated independent datasets.

Heterogeneity was assessed by inspection of Forest plots and formal tests of heterogeneity Q and I^2 (Thompson and Sharp, 1999). Publication bias was also assessed using Funnel plots of asymmetry along with formal tests (Egger et al., 1997; Supplementary material available at http://www.environmentalevidence.org/SR68.html).

To explore factors introducing heterogeneity we built several Generalized Linear Mixed Models (GLMM), accounting for several alternative nested ecological hypotheses that included the following a priori selected explanatory variables: distance to infrastructure (DIST or LOGDIST when log-transformed), presence of forest cover (FOR), infrastructure type (INFTYP) and traffic intensity (TRAF). All GLMM were built in S-Plus 7.0 and fit by restricted penalised quasi-likelihood (Pinheiro and Bates, 2000). Each MSA value was weighed by its variance. Study was introduced as random effect since we expected similar but not identical effects of infrastructure across studies.

Models were compared and selected by means of information theoretic criteria, including Akaike's Information Criterion corrected for sample size (AICc) and Akaike weights. AIC corrected for overdispersion (QAIC) was not needed since the random effects of the GLMM accommodate any possible overdispersion in the data. This was *ad hoc* checked by calculating a scale parameter (sigma) for our models using package "lme4" in R 2.9.1. (Bates and Maechler, 2009). The model selected was that minimizing the loss of Kullback–Leibler information.

Additionally data was disaggregated and GLMM were built to examine differences in the relationship between MSA and distance for different habitats, for forested and non-forested habitats, for different infrastructure types (linear and clustered) and for different taxa.

3. Results

3.1. Data availability and selected studies: review statistics

More than 600 studies contained relevant titles and abstracts. Of these, 50 studies corresponded to the selected criteria for data extraction. Two studies referred to the same data and were treated as one (Noel et al., 2004; Joly et al., 2006), resulting in 49 studies used for the meta-analysis. Some geographical bias was found since most of the studies were from either North America (21) or Europe (23), while a few studies from Africa (3) and Oceania (2) were found.

Twenty-seven studies included 201 bird species, and 49 independent datasets were extracted for the meta-analysis. The other 22 studies included 33 mammal species, and 41 independent datasets were extracted. Some species were repeated more than once (Appendix 3, Supplementary material available at http://www.environmentalevidence.org/SR68.html). Of the 49 datasets for birds, 10 contained relevant information on traffic intensities. Of the 41 datasets for mammals, five included information on traffic intensity, which was considered insufficient for the inclusion of this variable in the analysis (Supplementary material available at http://www.environmentalevidence.org/SR68.html).

Bird datasets frequently included a large number of species (mean = 9.1 (1–54)), compared to mammal datasets, which (with some exceptions, e.g. Newmark et al., 1996; Goosem and Marsh, 1997; Yost and Wright, 2001) usually focused on a single species (mean = 3.7 (1–11)). The most represented habitat types within the bird datasets were grasslands and agricultural lands (each of them in 15 datasets), and the least represented was boreal forests (1 dataset). The most represented habitat type in the mammal datasets was arctic tundra (12 times) and the least represented habitat types were grasslands and semi-arid habitats (1 time each).

The most represented bird taxon was Passeriformes (21 datasets) and the least represented bird taxa were Coraciiformes, Psittaciformes and Trochiliformes (1 dataset each). The most represented mammal taxon was Artiodactyla (25 datasets) and the least represented mammal taxa were Lagomorpha and Perissodactyla (1 dataset each).

Reported distances in bird datasets were in the range of 0–2580 m whereas data points for mammals were obtained within a range of 0–17,000 m.

3.2. Meta-analysis

3.2.1. Combination of all distances with pseudorreplication

The pooled effect size derived from an all-encompassing meta-analysis of MSA values for birds indicated that bird abundance declined within ca. 2600 m from infrastructure ($\mathrm{MSA_B} = 0.678$; 95% CI 0.636–0.720, $P < 0.0001$; Table 1). Likewise for mammals, $\mathrm{MSA_M}$ decreased within 17,000 m from infrastructure ($\mathrm{MSA_M} = 0.675$; 95% CI 0.608–0.742, $P < 0.0001$). However, for both meta-analyses there was large heterogeneity and publication bias within the datasets ($Q_B = 16938.28$, $P < 0.0001$; Egger $\mathrm{test_B} = 5.785$, $P < 0.0001$; $Q_M = 3466.80$, $P < 0.0001$; Egger $\mathrm{test_M} = 3.684$, $P < 0.0001$; Tables 1 and 2). Fail-safe numbers indicated that a large number of studies reporting neutral or positive effects of the proximity of infrastructure on species abundance would be needed to overturn these results and so even with some publication bias, the results for mammals and birds can be considered a reliable estimate of the true effect (Rosenthal, 1979).

Sensitivity analyses were performed and the results remained similar after removing studies that scored "medium–low" in the study quality assessment. The pooled effect size for bird data increased slightly, heterogeneity was lower but still statistically significant and there was evidence of publication bias ($\mathrm{MSA_B} = 0.683$; 95% CI 0.627–0.740, $P < 0.0001$; $Q = 2653.70$, $P < 0.0001$; Egger test = 4.699, $P < 0.0001$; Appendix 4, Supplementary material available at http://www.environmentalevidence.org/SR68.html). For mammals the pooled effect size was similar, heterogeneity decreased slightly and there was publication bias ($\mathrm{MSA_M} = 0.678$; 95% CI 0.6086–0.7472, $P < 0.0001$; $Q = 3401.70$, $P < 0.0001$; Egger test = 4.006, $P < 0.0001$; Appendix 4, Supplementary material available at http://www.environmentalevidence.org/SR68.html).

3.2.2. Effect size per distance interval

Pooled effect sizes calculated per distance interval for independent datasets were significant for mammal and bird data, but considerable heterogeneity and publication bias existed for most of the intervals. Lower MSA values were obtained at shorter distance intervals to infrastructure for both mammals and birds.

Table 1
Results of the meta-analysis for bird species at different distance intervals.

Distance (m)	*n*	Effect size (MSA)	SE	CI (lb)	CI (ub)	*P* (e.size)	*Q*	*P*(*Q*)	I^2 (%)	Egger's test intercept	*P*(*t*) Egger	Fail-safe *N*
0–2580	288[a]	0.6777	0.0215	0.6355	0.7200	**<0.0001**	16938.28	**<0.0001**	96.6	5.785	**<0.0001**	**11,23,452**
<10	10	0.3983	0.1290	0.1455	0.6512	**0.002**	62.7322	**<0.0001**	94.4	2.625	**0.0026**	**245**
15–35	18	0.4855	0.0893	0.3105	0.6605	**<0.0001**	223.89	**<0.0001**	93.3	4.336	**<0.0001**	**2233**
38–65	20	0.5339	0.0905	0.3566	0.7112	**<0.0001**	370.28	**<0.0001**	95.2	3.639	**<0.0001**	**1939**
70–80	16	0.5923	0.0896	0.4165	0.7680	**<0.0001**	33.19	**0.007**	54.5	2.561	**0.0002**	**689**
90–100	16	0.6218	0.0722	0.4802	0.7634	**<0.0001**	38.42	**0.0004**	68.4	3.993	**0.0003**	**1494**
110–125	13	0.6673	0.1022	0.4671	0.8676	**<0.0001**	40.99	**<0.0001**	65.7	3.072	**0.0001**	**577**
130–140	5	0.7070	0.1592	0.3950	1.0190	**<0.0001**	45.79	**<0.0001**	85	4.981	**0.0222**	**225**
150–160	16	0.5978	0.0788	0.4434	0.7522	**<0.0001**	79.12	**<0.0001**	83.8	4.874	**0.0002**	**1946**
170–180	10	Fisher scoring algorithm did not converge										
190–200	13	0.6292	0.0908	0.4512	0.8072	**<0.0001**	301.50	**<0.0001**	95.7	6.786	**0.0015**	**2864**
210–240	12	0.6734	0.1281	0.4223	0.9246	**<0.0001**	428.83	**<0.0001**	95.3	5.434	**0.0124**	**1560**
250–280	17	0.6676	0.0963	0.4789	0.8563	**<0.0001**	331.47	**<0.0001**	96.5	9.347	**0.0122**	**9320**
300–320	15	0.7454	0.1062	0.5374	0.9535	**<0.0001**	8769.78	**<0.0001**	99.4	15.540	0.202	**20,053**
340–375	10	0.6432	0.0943	0.4583	0.8281	**<0.0001**	34.74	**0.0001**	75.2	4.828	**0.0161**	**851**
380–480	16	0.7495	0.0888	0.5755	0.9236	**<0.0001**	1052.78	**<0.0001**	96.9	8.952	**0.0003**	**7820**
490–550	14	0.6946	0.1004	0.4978	0.8914	**<0.0001**	86.19	**<0.0001**	87	5.331	**0.0073**	**2013**
565–645	9	0.7182	0.0929	0.5361	0.9003	**<0.0001**	27.72	**0.0005**	75.8	6.594	**0.0436**	**1294**
650–785	11	0.7564	0.1203	0.5206	0.9921	**<0.0001**	581.18	**<0.0001**	94.1	5.980	**0.0451**	**1588**
800–860	3	0.6869	0.1968	0.3011	1.0728	**<0.0001**	12.75	**<0.0001**	81.1	4.640	**0.0124**	**69**
900–915	4	0.9152	0.1043	0.7108	1.1196	**<0.0001**	0.2687	0.9658	0	4.1168	**0.0189**	**97**
1000–1075	11	0.8363	0.0791	0.6812	0.9913	**<0.0001**	17.23	0.0695	46.7	4.585	**0.0050**	**930**
1100–1175	3	0.9696	0.1275	0.7198	1.2195	**<0.0001**	0.0722	0.9645	0	4.052	0.0780	**52**
1200–1290	4	0.8308	0.1097	0.6158	1.0459	**<0.0001**	5.011	0.171	47	5.426	**0.0344**	**171**
1300	1	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
1400	2	0.9098	0.0515	0.8090	1.0107	**<0.0001**	0.0398	0.842	0	10.941	0.321	**176**
1500–1505	7	0.8511	0.0677	0.7183	0.9838	**<0.0001**	13.894	**0.0308**	71.7	10.572	0.0516	**2018**
1600	1	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
1700–1750	4	0.9294	0.0992	0.7349	1.1239	**<0.0001**	0.5252	0.9133	0	4.4439	**0.0148**	113
1800–2000	4	1.0000	0.0483	0.9053	1.0947	**0.0000**	0	1.0000	0	7.868	0.136	362
2150	1	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
2365	1	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
2580	1	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.

[a] Total number of MSA values included in the meta-analysis for bird species. The total number of studies is 27, from which 49 datasets were extracted containing 288 MSA calculated values for different distances.

Table 2
Results of the meta-analysis for mammal species at different distance intervals.

Distance (m)	*n*	Effect size (MSA)	SE	CI (lb)	CI (ub)	*P* (e.size)	*Q*	*P*(*Q*)	I^2 (%)	Egger's test intercept	*P*(*t*) Egger	Fail-safe *N*
0–17,000	151[a]	0.6746	0.0342	0.6076	0.7415	**<0.0001**	3466.80	**<0.0001**	90.7	3.6843	**<0.0001**	**114,151**
1	6	0.1528	0.1005	−0.0442	0.3498	>0.1	12.74	**0.0259**	71.9	1.0862	0.0937	10
10–25	11	0.7110	0.0451	0.6227	0.7993	**<0.0001**	4.38	0.9284	0	4.300	**<0.0001**	**816**
30–50	16	0.5651	0.0726	0.4229	0.7073	**<0.0001**	28.65	0.0178	55.8	2.9972	**<0.0001**	**834**
75–100	7	0.3957	0.1831	0.0369	0.7545	**<0.05**	10.87	0.0925	47.7	1.4193	**0.0016**	**362**
110–180	16	0.8374	0.0520	0.7354	0.9394	**<0.0001**	7.42	0.9448	0	3.4069	**<0.0001**	**1083**
200	2	0.6104	0.2382	0.1435	1.0774	**0.0104**	0.02	0.878	0	1.464	0.402	2
250–300	9	0.8470	0.0627	0.7241	0.9698	**<0.0001**	7.78	0.4557	7.8	4.059	**0.0037**	**485**
350–600	19	0.6222	0.1115	0.4035	0.8408	**<0.0001**	206.68	**<0.0001**	91.9	3.3561	**<0.0001**	**1485**
750–1000	6	0.8669	0.1052	0.6608	1.0731	**<0.0001**	9.23	0.1002	50.2	4.8430	**0.0036**	**307**
1050–2200	20	0.5786	0.0806	0.4207	0.7366	**<0.0001**	75.49	**<0.0001**	74.1	3.0049	**<0.0001**	**1316**
2500	8	0.8233	0.2098	0.4121	1.2345	**<0.0001**	0.9453	0.9957	0	1.2516	**0.0020**	30
3500–4000	7	0.9807	0.1276	0.7307	1.2308	**<0.0001**	0.2907	0.9995	0	1.9095	0.0775	**60**
4500–5000	8	0.8666	0.1099	0.6512	1.0820	**<0.0001**	6.06	0.5323	30.8	3.395	**0.0255**	**265**
5500–7000	8	0.8049	0.1983	0.4163	1.1936	**<0.0001**	0.8083	0.9974	0	1.2467	**0.0039**	29
7500	2	0.8730	0.0118	0.8498	0.8962	**<0.0001**	0.0084	0.9272	0	37.35	0.494	**2047**
8500	1	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
9500–11,000	4	1.0000	0.0131	0.9744	1.0256	**<0.0001**	0	1	0	76.122	**<0.0001**	**2527**
17,000	1	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.

[a] Total number of observations points or MSA values included in the meta-analysis for mammal species. The total number of studies is 22, from which 41 datasets were extracted containing 151 MSA calculated values for different distances.

The number of datasets per distance interval decreased as the distance from infrastructure increased (Tables 1 and 2).

Sensitivity analyses for mammal and bird data resulted in similar MSA values per distance interval with the exception of the distance intervals 300–320, 340–375 and 380–490 m for the bird data, which had larger MSA values (Appendix 4, Supplementary material available at http://www.environmentalevidence.org/SR68.html). Heterogeneity was not statistically significant in these intervals, but there was publication bias.

3.2.3. Exploration of reasons for heterogeneity: meta-regression

The relationship between MSA and distance to infrastructure was positive for both mammals and birds (Fig. 1 and 2). When the data was subgrouped per habitat, all relationships were also positive except for temperate forests in the case of mammal species, and Mediterranean forests in the case of bird species (Tables 6 and 7). In forests both bird and mammal species abundances were affected in the proximity of infrastructure whereas in non-forested areas the effect extended over a larger distance (Tables 6 and 7). All relationships had lower AICc when "LOGDIST" was chosen as explanatory variable, except for Tundra.

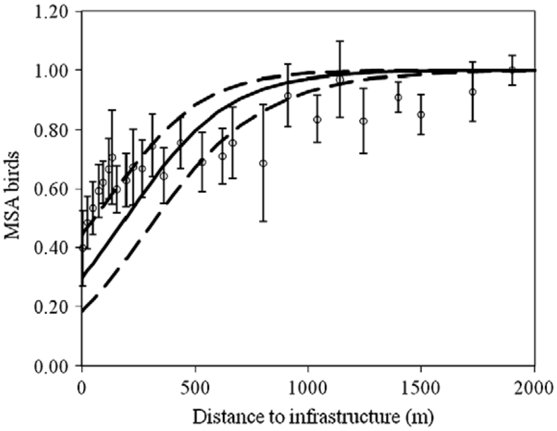

Fig. 1. Logistic regression between mean species abundance of birds and distance from infrastructure. Open dots represent the pooled results of the meta-analysis per distance interval ± S.E. The black line denotes the estimated curve for the decline of MSA, related to distance. Dashed lines are the 95% upper and lower limits of the confidence bands of the curve.

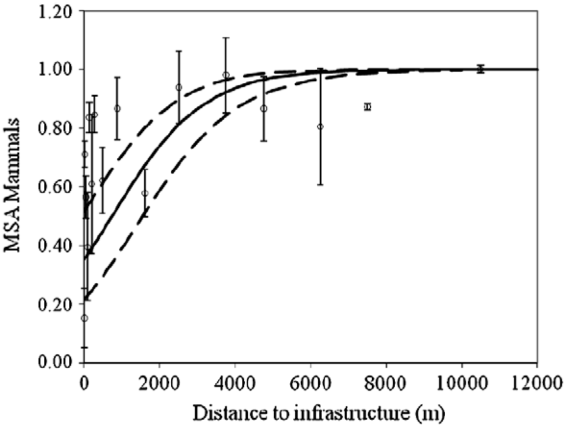

Fig. 2. Logistic regression between mean species abundance of mammals and distance from infrastructure. Open dots represent the pooled results of the meta-analysis per distance interval ± S.E. The black line denotes the estimated curve for the decline of MSA, related to distance. Dashed lines are the 95% upper and lower limits of the confidence bands of the curve.

There existed also differences in the relationship between MSA and distance to infrastructure for different taxa. Accitriformes and Falconiformes were the only bird taxa which were unaffected or positively affected by the presence of infrastructure, whereas for other bird taxa proximity to infrastructure seemed to exert a negative effect on species abundance, or the magnitude of the effect was unknown due to low sample size (Supplementary material available at http://www.environmentalevidence.org/SR68.html). From all mammal taxa, a positive relationship between MSA and distance to infrastructure could only be found for Artiodactyla and Rodentia, but abundances of the latter were only reduced at short distances from infrastructure while this effect extended over a large distance for the former.

Several *ad hoc* models were built to explore the high heterogeneity between effect sizes. We worked on several biological hypotheses to explain the variability in the relationship between MSA and distance to infrastructure. For bird species the most parsimonious model was that containing only the explanatory variable "LOGDIST" (Akaike weight: 0.78, Table 3). For mammal

Table 3
Models expressing different biological hypotheses on the influence of infrastructure distance, infrastructure type and infrastructure visibility (forest) on the mean species abundance of birds. The selected model appears in bold.

Model (birds)	AICc	K	n	Δ_iAICc	w_i
LOGDIST + FOR + INFTYP + LOGDIST ∗ INFTYP + LOGDIST ∗ FOR + FOR ∗ INFTYP + LOGDIST ∗ INFTYP ∗ FOR	No model convergence				
LOGDIST + FOR + LOGDIST ∗ FOR	1630.78	6	288	3.04	0.17
LOGDIST + INFTYP + LOGDIST ∗ INFTYP	1636.04	6	288	8.30	0.01
LOGDIST + FOR	1633.96	5	288	6.21	0.03
LOGDIST + INFTYP	1637.29	5	288	9.54	0.01
LOGDIST	**1627.75**	**4**	**288**	**0.00**	**0.78**
FOR	1647.18	4	288	19.43	<0.01
INFTYP	1646.40	4	288	18.65	<0.01
DIST + FOR + DIST ∗ FOR	1762.19	6	288	134.45	<0.01
DIST + FOR	1744.61	5	288	116.86	<0.01
DIST	1739.98	4	288	112.23	<0.01

AICc = Akaike Information Criterion corrected for sample size;
K = No. of estimable parameters: Intercept, log (effect distance), effect distance, forest, infra type, interaction term, study and error term;
n = No. of data points;
Δ_iAICc = Delta AICc value;
w_i = Akaike weight.

Table 4
Models expressing different biological hypotheses on the influence of infrastructure distance, infrastructure type and infrastructure visibility (forest) on the mean species abundance of mammals. The selected model appears in bold. See Table 3 for explanation of coefficients.

Model (mammals)	AICc	K	n	Δ_iAICc	w_i
LOGDIST + FOR + INFTYP + LOGDIST ∗ INFTYP + LOGDIST ∗ FOR + FOR ∗ INFTYP + LOGDIST ∗ INFTYP ∗ FOR	889.18	10	151	3.59	0.14
LOGDIST + INFTYP + LOGDIST ∗ INFTYP	963.06	6	151	77.50	<0.01
LOGDIST + FOR + LOGDIST ∗ FOR	900.02	6	151	14.46	<0.01
LOGDIST + LOGDIST	919.67	5	151	34.12	<0.01
LOGDIST + FOR	911.34	5	151	25.79	<0.01
LOGDIST	923.42	4	151	37.87	<0.01
INFTYP	896.93	4	151	11.38	<0.01
FOR	899.30	4	151	13.75	<0.01
DIST + FOR + INFTYP + DIST ∗ INFTYP + DIST ∗ FOR + FOR ∗ INFTYP + DIST ∗ INFTYP ∗ FOR	1081.87	10	151	196.28	<0.01
DIST + FOR + DIST ∗ FOR	964.56	6	151	79.01	<0.01
DIST + INFTYP	893.28	5	151	7.73	0.02
DIST + FOR	**885.54**	**5**	**151**	**0.00**	0.84
DIST	897.99	4	151	12.45	<0.01

Table 5
Models expressing different biological hypotheses on the influence of infrastructure distance, traffic intensity (noise) and infrastructure visibility (forest) on the mean species abundance of birds. The selected model appears in bold. See Table 3 for explanation of coefficients.

Model (birds)	AICc	K	n	Δ_iAICc	w_i
LOGDIST + FOR + TRAF + LOGDIST ∗ TRAF + LOGDIST ∗ FOR + FOR ∗ TRAF + LOGDIST ∗ TRAF ∗ FOR	583.52	10	87	10.87	<0.01
LOGDIST + TRAF + LOGDIST ∗ TRAF	512.30	6	87	31.65	<0.01
LOGDIST + TRAF	503.06	5	87	22.40	<0.01
TRAF	537.10	4	87	56.44	<0.01
LOGDIST	**480.66**	**4**	**87**	**0.00**	**0.99**

species the most parsimonious model was that including the explanatory variables “DIST” and “FOR” (Akaike weight: 0.84, Table 4).

The most parsimonious model for the subset of bird data containing information on traffic intensity was that including only “LOGDIST” as explanatory variable (Akaike weight: 0.99, Table 5).

4. Discussion

4.1. Effect of distance from infrastructure on bird and mammal species abundance

Our analyses suggest that infrastructure can have a negative impact on bird and mammal abundance and that this impact is more evident in the proximity of the infrastructure. Pooled results for pseudorreplicated data indicated a decline in species abundance of 28–36% and 25–38% for birds and mammals within 2.6 km and 17 km from infrastructure, respectively. Pooled results per distance interval showed that MSA of birds and of mammals became higher for distance intervals far away from infrastructure. The meta-regression also indicated a positive relationship between MSA of birds and mammals and distance to infrastructure. A second conclusion that can be obtained from these results is that bird populations are likely to be more affected at short distances from infrastructure while the effect on mammal populations seems to extend over larger distances. These results confirm the effect distances reported in other studies, which were larger for mammals (Cameron et al., 1992; Newmark et al., 1996; Nellemann et al., 2003a; Joly et al., 2006) than for birds (Van der Zande et al., 1980; Madsen, 1985; Reijnen et al., 1996; Rheindt, 2003). However, considerable heterogeneity was found in our results, especially for birds, and also publication bias, both limiting the robustness of these conclusions.

Table 6
Univariate meta-regression coefficients for the relationship between MSA and distance for bird species in different habitats. Models with log-transformed distance as explanatory variable are more parsimonious than without transformation for all habitats.

Bird species							
Explanatory variable	Habitat	*b*	Intercept	*k*	*n*	*K*	AICc
LOGDIST	Agricultural lands	1.523	−7.933	15	109	4	626.29
	Temperate forests	0.761	−2.868	8	35	4	192.57
	Boreal forests	No model convergence		1	2		
	Mediterranean forests	27.020	−136.950	2	4	4	−12.28
	Grasslands	1.014	−5.193	15	97	4	417.24
	Scrublands	1.174	−4.853	5	35	4	200.84
	Tropical forests	18.834	−61.705	3	6	4	80.13
	All forests	0.826	−2.770	14	47	4	263.04
	Non-forested habitats	1.333	−6.712	35	241	4	1361.75
DIST	Agricultural lands	0.005	−1.777	15	109	4	779.75
	Temperate forests	No model convergence		8	35	4	
	Boreal forests	No model convergence		1	2		
	Mediterranean forests	0.046	3.222	2	4	4	0.45
	Grasslands	0.002	−0.759	15	97	4	488.01
	Scrublands	No model convergence		5	35	4	
	Tropical forests	0.522	−17.254	3	6	4	97.57
	Forests	0.011	−0.894	14	47	4	301.93
	Non-forested habitats	0.004	−1.218	35	241	4	1478.68

Table 7
Univariate meta-regression coefficients for the relationship between MSA and distance for mammal species in different habitats. Models with log-transformed distance as explanatory variable are more parsimonious than without transformation for all habitats except for tundra.

Mammal species							
Explanatory variable	Habitat	*b*	Intercept	*k*	*n*	*K*	AICc
LOGDIST	Agricultural lands	No model convergence		2	9		
	Temperate forests	0.260	0.103	4	15	4	67.99
	Boreal forests	1.526	−7.742	9	34	4	162.23
	Grasslands	Only 1 dataset		*1*	*5*		
	Scrublands	2.133	−6.773	3	11	4	59.19
	Tropical forests	0.681	−1.136	5	22	4	81.39
	Semi-arid lands	Only 1 dataset		*1*	*8*		
	Arctic tundra	2.854	−21.429	12	52	4	364.50
	All except for Tundra	0.978	−3.670	25	104	4	528.05
	Forests	0.860	−3.151	18	71	4	313.90
	Non-forested habitats	1.142	−7.089	19	85	4	548.28
DIST	Agricultural lands	No model convergence		2	9		
	Temperate forests	0.002	0.850	4	15	4	75.91
	Boreal forests	No model convergence					
	Grasslands	Only 1 dataset		*1*	*5*		
	Scrublands	No model convergence		4			
	Tropical forests	0.003	0.592	5	22	4	107.21
	Semi-arid lands	Only 1 dataset		*1*	*8*		
	Arctic tundra	0.001	−1.832	12	52	4	332.68
	All except for Tundra	0.004	−0.478	25	104	4	614.09
	Forests	0.003	−0.026	18	71	4	397.21
	Non-forested habitats	0.001	−1.659	19	85	4	561.76

The sensitivity analyses resulted in a slightly (but not statistically significant) larger pooled effect size for pseudorreplicated data in the case of bird species. Sensitivity analyses per distance interval showed similar results to the full meta-analyses except for the distance intervals between 300 and 480 m from infrastructure, with larger effect sizes. Yet, fail-safe numbers indicate that a large number of non-significant studies would be needed to overturn the pooled effect sizes calculated for these distance intervals. Thus, we decided to maintain these studies in the meta-regression following Wolf and Guevara (2001), who advocate for the use of all available data when doing meta-analysis.

The high heterogeneity underlying the results of our meta-analysis indicates that infrastructure development can have negative impacts on bird and mammal abundance within a certain distance depending on a number of factors which we further explore in Section 4.2.

4.2. Exploration of sources of heterogeneity

Meta-regression helped us to elucidate that “LOGDIST” was the main explanatory variable for the decline in abundance of bird populations due to infrastructure. For mammals, “DIST” was the main variable but the variable “FOR” seemed to add important information to the model. Meta-regression on subgroups divided by habitat type and taxa indicated that in open habitats, both mammal and bird populations seem to avoid infrastructure over larger distances, compared to those in forested biomes, which could probably be related to reduced visibility of infrastructure. Forman and Deblinger (2000) showed similar results for breeding birds in open grasslands and in woodlands (data adapted from Reijnen et al. (1995, 1996)).

For the subset of bird data including information on traffic intensity, the most parsimonious model was that which contained only "LOGDIST" as explanatory variable. Therefore it seems that traffic intensity has no effect on the reduction of bird populations nearby roads. These results are contrary to the findings of a number of authors that have highlighted the pernicious effects of traffic intensity and noise on bird populations (Reijnen and Foppen, 1994; Reijnen et al., 1995, 1996, 1997; Forman et al., 2002; Rheindt, 2003). However, there are other studies which found a decline in bird populations near roads with low traffic intensity (Räty, 1979; Madsen, 1985; Develey and Stouffer, 2001) and others which found no clear relationship (Peris and Pescador, 2004). Finally, some authors claim that there exists a trade-off between traffic intensity and velocity, with low traffic intensity being related to higher velocities (Martínez-Abraín, 1994; Drews, 1995). Yet, traffic velocity seems to be related to bird mortality, which occurs on the road itself. To the best of our knowledge, studies that deal with this topic usually do not report on bird densities at increasing distances from roads (or include a control distance for comparison). As none of the studies included in our analysis contained data on traffic velocity, the influence of this variable could not be evaluated.

Not all species showed a decline in abundance nearby infrastructure: species abundance of Accipitriformes and Falconiformes was larger in the proximity of infrastructure. This was not a surprising outcome since other studies have reported the presence of raptors nearby roads searching roadkill carrion (Forman and Alexander, 1998; Lambertucci et al., 2009) and hunting (Dónazar et al., 1993; Fajardo et al., 1998; Dean and Milton, 2003), with some exceptions during the breeding season (Martínez-Abraín et al., 2008).

In the case of mammals, we could detect that Rodentia populations were slightly affected within few meters from infrastructure. By contrast, Artiodactyla species were affected up to distances of several hundred meters. Within Artiodactyla wild reindeer (*Rangifer tarandus*) was one of the most studied and sensitive species, with their population abundance being reduced up to several kilometres from infrastructure (Nellemann and Cameron, 1996; Nellemann et al., 2001, 2003a,b). These outcomes are consistent with the fact that small-sized mammals usually have smaller home ranges and migration distances compared to medium- and large-sized mammals, the latter being more sensitive to infrastructure development and habitat fragmentation (Harestad and Bunnel, 1979; Buskirk, 2009).

4.3. Review limitations

Only some of the included studies used Before-After-Control-Impact (BACI) experimental designs, so we decided to use the largest reported distance in the study as control distance. Although the sensitivity analyses allowed us to remove some of the studies of lower quality and indeed the results did not vary in most of the cases, we acknowledge that our conclusions are restricted by the lack of proper comparators in some of the studies.

The identified publication bias is another of the weaknesses of our review. A few studies did not find negative effects of infrastructure on bird and mammal populations and were not included due to lack of proper data on the selected variables (e.g. Adams, 1984; Evans and Gates, 1997; Ballard et al., 2000); and there may exist many others that were never published due to non-significant results or that we were unable to obtain (grey literature). However, fail-safe numbers indicated that our results are sufficiently robust.

Many of the studies initially considered in our systematic review lacked suitable data for extraction and had to be left out of the analysis. Therefore we may have excluded potentially relevant studies and included lower quality studies due to availability of data on the selected variables.

The scope of the study was intended to be global and covered different types of biomes and habitats; nevertheless there is a geographical bias in the studies included in our review. Most studies were done in Europe and North America and therefore the applicability of the results to other geographic areas remains unknown.

4.4. Conclusions and management implications

Changes in wildlife populations in the proximity of infrastructure have been reported for decades in a number of studies (see Table 2 in Supplementary material, available at http://www.environmentalevidence.org/SR68.html), and have been pointed out in relevant authors' reviews (Spellerberg, 1998; Trombulak and Frissell, 2000; Forman et al., 2003). Additionally, there have been previous attempts to quantify wildlife population decline in relation to distance from infrastructure, either locally (Forman and Deblinger, 2000) or at the global scale (UNEP, 2001; Nellemann et al., 2003b; Fahrig and Rytwinski, 2009), but none of them followed the guidelines for systematic reviews (Pullin and Stewart, 2006) or summarized the information by means of a meta-analysis. Our study represents a step forward within the field of road ecology research that may contribute to the understanding of the magnitude of the pernicious effects of infrastructure development on animal populations. Reported effects for most bird populations extend over distances up to about 1 km, and for most mammal populations up to about 5 km, with variation according to taxa and habitat type (Fig. 1 and 2). However, the evidence shown by our results is somewhat hampered by the limitations mentioned in Section 4.3. We therefore encourage researchers to perform BACI studies whenever possible and make their data available for researchers pursuing a systematic review. Should new studies that include these recommendations be released in the future, the review can be updated by including the new available evidence.

Although the patterns found in our analysis are clear, we would like to emphasise that these only represent a partial estimate of the actual effect of infrastructure on wildlife. Therefore, we highlight the importance of broadening the analysis to other taxonomic groups, such as herpetofauna, plants and invertebrates (e.g. Przybylski, 1979; Angold, 1997; Auerbach et al., 1997; Haskell, 2000; Shine et al., 2004; Barrows et al., 2006). Further research on these taxonomic groups would add up to the current models presented in this study, contributing to eventually produce a model that would provide an accurate estimate of the effects of infrastructure development on biodiversity.

The results of our meta-analysis will be implemented in the next version of the GLOBIO3 model, which is used to estimate the biodiversity loss at global, regional and national level at current state and for possible future scenarios and policy options (Alkemade et al., 2009). The results of the GLOBIO3 model have been reported in global assessments such as the second Global Biodiversity Outlook and the fourth Global environmental Outlook and are aimed to support policy makers on the elaboration of biodiversity conservation policies (sCBD and MNP, 2007; UNEP, 2007). The method is also used at the regional level (Verboom et al., 2007) and at the country level (e.g. in Viet Nam, Ecuador and Nicaragua).

Our study shows the importance of minimizing infrastructure development for wildlife conservation in relatively undisturbed areas. By combining actual species distributions with the effect distance functions we developed as a form of dose–effect relationship, regions sensitive to infrastructure development may be identified. More specifically, the effect distance functions can be used in models in support of decision making on infrastructure planning. This would mean a substantial improvement of the current situation in which, in most cases, results of previous studies on ecological impacts are barely taken into account (OECD, 2002; Roedenbeck et al., 2007).

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Supplementary material

Supplementary material available at http://www.environmentalevidence.org/SR68.html. Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.02.009.

References

**References of studies included in the meta-analysis.*

Adams, L.W., 1984. Small mammal use of an interstate highway median strip. Journal of Applied Ecology 21, 175–178.

Alkemade, R., van Oorschot, M., Miles, L., Nellemann, C., Bakkenes, M., ten Brink, B., 2009. GLOBIO3: a framework to investigate options for reducing global terrestrial biodiversity loss. Ecosystems 12, 374–390.

Andrews, A., 1990. Fragmentation of habitat by roads and utility corridors: a review. Australian Zoologist 26, 130–141.

Angold, P.G., 1997. The impact of a road upon adjacent heathland vegetation: effects on plant species composition. Journal of Applied Ecology 34, 409–417.

Arnqvist, G., Wooster, D., 1995. Meta-analysis: synthesizing research findings in ecology and evolution. Trends in Ecology and Evolution 10, 236–240.

Auerbach, N.A., Walker, M.D., Walker, D.A., 1997. Effects of roadside disturbance on substrate and vegetation properties in Arctic Tundra. Ecological Applications 7, 218–235.

Ballard, W.B., Cronin, M.A., Rodrigues, R., Skoog, R.O., Pollard, R.H., 2000. Arctic fox, *Alopex galopus*, den densities in the Prudhoe Bay Oil Field, Alaska. Canadian Field-Naturalist 114, 453–456.

*Ballasus, H., Sossinka, R., 1997. The impact of power lines on field selection and grazing intensity of wintering White-fronted- and Bean Geese *Anser albifrons*, *A. fabalis*. Journal für Ornithologie 138, 215–228.

Barrios, L., Rodriguez, A., 2004. Behavioural and environmental correlates of soaring-bird mortality at on-shore wind turbines. Journal of Applied Ecology 41, 72–81.

Barrows, C.W., Allen, M.F., Rotenberry, J.T., 2006. Boundary processes between a desert sand dune community and an encroaching suburban landscape. Biological Conservation 131, 486–494.

Bates, D., Maechler, M., 2009. lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-31. <http://CRAN.R-project.org/package=lme4>.

*Bautista, L.M., García, J.T., Calmaestra, R.G., Palacin, C., Martín, C.A., Morales, M.B., Bonal, R., Viñuela, J., 2004. Effect of weekend road traffic on the use of space by raptors. Conservation Biology 18, 726–732.

Boarman, W.I., Sazaki, M., 2005. A highway's road-effect for desert tortoises (*Gopherus agasazii*). Journal of Arid Environments 65, 94–101.

Bolger, D.T., Scott, T.A., Rotenberry, J.T., 1997. Breeding bird abundance in an urbanizing landscape in coastal Southern California. Conservation Biology 11, 406–421.

Buskirk, S., 2009. Keeping an eye on the neighbours. Science 306, 238–239.

Cameron, R.D., Reed, D.J., Dau, J.R., Smith, W.T., 1992. Redistribution of calving caribou in response to oil field development on the Arctic Slope of Alaska. Arctic 45, 338–342.

*Carbaugh, B., Vaughan, J.P., Bellis, E.D., Graves, H.B., 1975. Distribution and activity of white-tailed deer along an interstate highway. Journal of Wildlife Management 39, 570–581.

*Clark, W.D., Karr, J.R., 1979. Effects of highways on Red-winged Blackbird and Horned Lark populations. Wilson Bulletin 81, 143–145.

Cox, D.R., 1970. The Analysis of Binary Data. Methuen & Co. Ltd., London.

*Cronin, M.A., Amstrup, S.C., Durner, G.M., Noel, L.E., McDonald, T.L., Ballard, W., 1998. Caribou distribution during the post-calving period in relation to infrastructure in the Prudhoe Bay oil field, Alaska. Arctic 51, 85–93.

Dean, W.R.J., Milton, S.J., 2003. The importance of roads and road verges for raptors and crows in the Succulent and Nama-Karoo, South Africa. Ostrich 74, 181–186.

*Delgado, J.D., Arévalo, J.R., Fernández-Palacios, J.M., 2004. Consecuencias de la fragmentación viaria: efectos de borde de las carreteras en la laurisilva y el pinar de Tenerife. In: Fernández-Palacios, J.M., Morici, C. (Eds.), Ecología Insular/Island Ecology. Asociación Española de Ecología Terrestre (AEET)-Cabildo Insular de La Palma, pp. 181–225.

DerSimonian, R., Laird, N., 1986. Meta-analysis in clinical trials. Controlled Clinical Trials 7, 177–188.

Develey, P.F., Stouffer, P.C., 2001. Effects of roads on movements by understorey birds in mixed-species flocks in Central Amazonian Brazil. Conservation Biology 15, 1416–1422.

*Devereux, C.L., Denny, M.J.H., Whittingham, M.J., 2008. Minimal effects of wind turbines on the distribution of wintering farmland birds. Journal of Applied Ecology 45, 1689–1694.

Dónazar, J.A., Ceballos, O., Travaini, A., Hiraldo, F., 1993. Roadside raptor surveys in the Argentinean Patagonia. Journal of Raptor Research 27, 106–110.

Drews, C., 1995. Road kills of animals by public traffic in Mikumi National Park, Tanzania, with notes on baboon mortality. African Journal of Ecology 33, 89–100.

Dunthorn, A.A., Errington, F.P., 1964. Casualties among birds along a selected road in Wiltshire. Bird Study 11, 168–182.

Dyer, S.J., O'Neill, J.P., Wasel, S.M., Boutin, S., 2001. Avoidance of industrial development by woodland caribou. Journal of Wildlife Management 65, 531–542.

Egger, M., Davey-Smith, G., Schneider, M., Minder, C., 1997. Bias in meta-analysis detected by a simple graphical test. British Medical Journal 315, 629–634.

Evans, D.R., Gates, E.J., 1997. Cowbird selection of breeding areas: the role of habitat and bird species abundance. Wilson Bulletin 109, 470–480.

Fahrig, L., Rytwinski, T., 2009. Effects of roads on animal abundance: an empirical review and synthesis. Ecology and Society 14, 21. <http://www.ecologyandsociety.org/vol14/iss1/art21/>.

Fajardo, I., Pividal, V., Trigo, M., Jimenez, M., 1998. Habitat selection, activity peaks and strategies to avoid road mortality by the little owl, a new methodology on owls research. Alauda 66, 49–60.

Forman, R.T.T., Alexander, L.E., 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29, 207–231.

Forman, R.T.T., Deblinger, R.D., 2000. The ecological road-effect zone of Massachusetts (USA) suburban highway. Conservation Biology 14, 36–46.

Forman, R.T.T., Reineking, B., Hersperger, A.M., 2002. Road traffic and nearby grassland bird patterns in a suburbanizing landscape. Environmental Management 29, 782–800.

Forman, R.T.T., Sperling, D., Bissonette, J.A., Clevenger, A.P., Cutshall, C.D., Dale, V.H., Fahrig, L., France, R., Goldman, C.R., Heanue, K., Jones, J.A., Swanson, F.J., Turrentine, T., Winter, T.C., 2003. Road Ecology: Science and Solutions. Island Press, Washington, Covelo, London.

Gagnon, J.W., Theimer, T.C., Dodd, N.L., Boe, S., Schweinsburg, R.E., 2007. Traffic volume alters elk distribution and highway crossings in Arizona. Journal of Wildlife Management 71, 2318–2323.

*Gill, J.A., Sutherland, W.J., Watkinson, A.R., 1996. A method to quantify the effects of human disturbance on animal populations. Journal of Applied Ecology 33, 786–792.

Goosem, M., Marsh, H., 1997. Fragmentation of a small-mammal community by a powerline corridor through tropical rainforest. Wildlife Research 24, 613–629.

Gullison, R.E., Hardner, J.J., 1993. The effects of road design and harvest intensity on forest damage caused by selective logging: empirical results and a simulation model from the Bosque Chimanes, Bolivia. Forest Ecology and Management 59, l–14.

Harestad, A.S., Bunnel, F.L., 1979. Home range and body weight—a reevaluation. Ecology 60, 389–402.

Haskell, D.G., 2000. Effects of roads on macroinvertebrate soil fauna of the Southern Appalachian Mountains. Conservation Biology 14, 57–63.

*Hüppop, V.O., Hüppop, K., 1995. The influence of agriculture and road usage on the distribution of coastal bird nests on saltmarshes in Schleswig-Holstein (Germany). Die Vogelwarte 38, 76–88.

Jaeger, J.A.G., Bowman, J., Brennan, J., Fahrig, L., Bert, D., Bouchard, J., Charbonneau, N., Frank, K., Gruber, B., von Toschanowitz, K.T., 2005. Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. Ecological Modeling 185, 329–348.

Joly, K., Nellemann, C., Vistnes, I., 2006. A reevaluation of caribou distribution near an oilfield road on Alaska's North Slope. Wildlife Society Bulletin 34, 866–869.

*Keller, V.E., 1991. The effect of disturbance from roads on the distribution of feeding sites of geese (*Anser brachyrhynchus, A. anser*), wintering in North-Scotland. Ardea 79, 229–232.

Kroodsma, R.L., 1984. Effect of edge on breeding forest bird species. Wilson Bulletin 96, 426–436.

*Kuitunen, M., Rossi, E., Stenroos, A., 1998. Do highways influence density of land birds? Environmental Management 22, 297–302.

Lambertucci, S.A., Speziale, K.L., Rogers, T.A., Morales, J.M., 2009. How do roads affect the habitat use of an assemblage of scavenging raptors? Biodiversity and Conservation 18, 2063–2074.

*Lane, S.J., Alonso, J.C., Martín, C.A., 2001. Habitat preferences of great bustard *Otis tarda* flocks in the arable steppes of central Spain: are potentially suitable areas unoccupied? Journal of Applied Ecology 38, 193–203.

*Larsen, J.K., Madsen, J., 2000. Effects of wind turbines and other physical elements on field utilization by Pink-footed Geese (*Anser brachyrhynchus*): a landscape perspective. Landscape Ecology 15, 755–764.

*Laurance, W.F., Croes, B.M., Tchignoumba, L., Lahm, S.A., Alonso, A., Lee, M.E., Campbell, P., Ondzeano, C., 2006. Impacts of roads and hunting on central African rainforest mammals. Conservation Biology 20, 1251–1261.

Lockwood, J.L., McKinney, M.L., 2001. Biotic Homogenization. Kluwer Academic/Plenum Publishers.

Madsen, J., 1985. Impact of disturbance on field utilization of Pink-footed Geese in West Jutland, Denmark. Biological Conservation 33, 53–63.

Mahoney, S.P., Schaefer, J.A., 2002. Hydroelectric development and the disruption of migration in caribou. Biological Conservation 107, 147–153.

*Malcolm, J.R., Ray, J.C., 2000. Influence of timber extraction routes on Central African small-mammal communities, forest structure and tree diversity. Conservation Biology 14, 1623–1638.

Martínez-Abraín, A., 1994. Mortalidad estacional de aves en una carretera del P.N. de l'Albufera de Valencia (E. España). Doñana, Acta Vertebrata 21, 90–95.

Martínez-Abraín, A., Oro, D., Jiménez, J., Stewart, G., Pullin, A., 2008. What are the Impacts of Human Recreational Activity on the Distribution, Nest-occupancy Rates and Reproductive Success of Breeding Raptors? Systematic Review No. 27. Collaboration for Environmental Evidence.

McLellan, B.N., Shackleton, D.M., 1989. Grizzly bear and resource extraction industries: habitat displacement in response to seismic exploration, timber harvesting and road maintenance. Journal of Applied Ecology 26, 371–380.

Millennium Ecosystem Assessment, 2005. Ecosystems and Human Well-being: Biodiversity Synthesis. Island Press, Washington, DC.

*Meunier, F.D., Verheyden, C., Jouventin, P., 1999. Bird communities of highway verges: influence of adjacent habitat and roadside management. Acta Oecologica 20, 1–13.

*Meunier, F.D., Verheyden, C., Jouventin, P., 2000. Use of roadsides by diurnal raptors in agricultural landscapes. Biological Conservation 92, 291–298.

Mood, A.M., Graybill, F.A., Boes, D.C., 1973. Introduction and Theory of Statistics, third ed. McGraw-Hill, Auckland.

Nellemann, C., Cameron, R.D., 1996. Effects of petroleum development on terrain preferences of calving caribou. Arctic 49, 23–28.

Nellemann, C., Vistnes, I., Jordhøy, P., Strand, O., 2001. Winter distribution of wild reindeer in relation to powerlines, roads and resorts. Biological Conservation 101, 351–360.

Nellemann, C., Jordhøy, P., Vistnes, I., Strand, O., Newton, A., 2003a. Progressive impacts of piecemeal development. Biological Conservation 113, 307–317.

Nellemann, C., Vistnes, I., Ahlenius, H., Rekazewicz, P., Kaltenborn, B.P., Magomedova, M., Udovyk, O., Furuhovde, T., 2003b. Environment and security: 2050 scenarios. In: Rasmussen, R.O., Koroleva, N.E. (Eds.), Social and Environmental Impacts in the North. Kluwer Academic Publishers, pp. 129–148.

Newmark, W.D., Boshe, J.I., Sariko, H.I., Makumbule, G.K., 1996. Effects of a highway on large mammals in Mikumi National Park, Tanzania. African Journal of Ecology 34, 15–31.

Noel, L.E., Parker, F.R., Cronin, M.A., 2004. Caribou distribution near an oilfield road on Alaska's North Slope, 1978–2001. Wildlife Society Bulletin 32, 757–771.

OECD, 2002. OECD Guidelines Towards Environmentally Sustainable Transport. OECD Publications, Paris.

*Oehler, J.D., Litvaitis, J.A., 1996. The role of spatial scale in understanding responses of medium-sized carnivores to forest fragmentation. Canadian Journal of Zoology 74, 2070–2079.

Oehlert, G.W., 1992. A note on the Delta Method. The American Statistician 46, 27–29.

Ortega, Y.K., Capen, D.E., 1999. Effects of forest roads on habitat quality for Ovenbirds in a forested landscape. Auk 116, 937–946.

Osenberg, C.W., Sarnelle, O., Cooper, S.D., Holt, R.D., 1999. Resolving ecological questions through meta-analysis: goals, metrics, and models. Ecology 80, 1105–1117.

Parris, K.M., Schneider, A., 2009. Impacts of traffic noise and traffic volume on birds of roadside habitats. Ecology and Society 14, 29. <http://www.ecologyandsociety.org/vol14/iss1/art29/>.

*Paruk, J.D., 1987. Habitat utilization by bald eagles wintering along the Mississippi River. Transactions or the Illinois Academy of Science 80, 333–342.

Peris, S.J., Pescador, M., 2004. Effects of traffic noise on passerine populations in Mediterranean wooded pastures. Applied Acoustics 65, 357–366.

Pimm, S.L., Russell, G.H., Gittleman, J.H., Brooks, T.M., 1995. The future of biodiversity. Science 269, 347–350.

Pinheiro, J.C., Bates, D.M., 2000. Mixed-effects Models in S and S-PLUS. Springer Verlag, New York.

*Piper, S.D., Catterall, C.P., 2006. Impacts of picnic areas on bird assemblages and nest predation activity within Australian eucalypt forests. Landscape and Urban Planning 78, 251–262.

Przybylski, Z., 1979. The effects of automobile exhaust gases on the arthropods of cultivated plants, meadows and orchards. Environmental Pollution 19, 157–161.

Pullin, A.S., Stewart, G.S., 2006. Guidelines for systematic review in conservation and environmental management. Conservation Biology 20, 1647–1656.

Räty, M., 1979. Effect of highway traffic on tetraonid densities. Ornis Finnica 56, 169–170.

Reed, R.A., Johnson-Barnard, J., Baker, W.L., 1996. Contribution of roads to forest fragmentation in the Rocky Mountains. Conservation Biology 10, 1098–1106.

Reijnen, R., Foppen, R., 1994. The effects of car traffic on breeding bird populations in woodland. I. Evidence of reduced habitat quality for Willow Warblers (*Phylloscopus trochilus*) breeding close to a highway. Journal of Applied Ecology 31, 85–94.

Reijnen, R., Foppen, R., Ter Braak, C., Thissen, J., 1995. The effects of car traffic on breeding bird populations in woodland. III. Reduction of density in relation to the proximity of main roads. Journal of Applied Ecology 32, 187–202.

Reijnen, R., Foppen, R., Meeuwsen, H., 1996. The effect of traffic on the density of breeding bird populations in Dutch agricultural grasslands. Biological Conservation 75, 255–260.

Reijnen, R., Foppen, R., Veenbaas, G., 1997. Disturbance by traffic as a threat to breeding birds: evaluation of the effect and considerations in planning and managing road corridors. Biodiversity and Conservation 6, 567–581.

Rheindt, F.E., 2003. The impact of roads on birds: does song frequency play a role in determining susceptibility to noise pollution? Journal für Ornithologie 144, 295–306.

*Rich, A.C., Dobkin, D.S., Niles, L.J., 1994. Defining forest fragmentation by corridor width: the influence of narrow forest-dividing corridors on forest-nesting birds in southern New Jersey. Conservation Biology 8, 1109–1121.

*Roedenbeck, I.A., Voser, P., 2008. Effects of roads on spatial distribution, abundance and mortality of brown hare (*Lepus europaeus*) in Switzerland. European Journal of Wildlife Research 54, 425–437.

Roedenbeck, I.A., Fahrig, L., Findlay, C.S., Houlahan, J.E., Jaeger, J.A.G., Klar, N., Kramer-Schadt, S., Van der Grift, E.A., 2007. The Rauischholzhausen agenda for road ecology. Ecology and Society 12 (1), 11. <http://www.ecologyandsociety.org/vol12/iss1/art11/>.

Romin, L.A., Bissonette, J.A., 1996. Deer-vehicle collisions: status of state monitoring activities and mitigation efforts. Wildlife Society Bulletin 24, 276–283.

Rosenthal, R., 1979. The "file drawer problem" and tolerance for null results. Psychological Bulletin 86, 638–641.

*Rost, G.R., Bailey, J.A., 1979. Distribution of mule deer and elk in relation to roads. Journal of Wildlife Management 43, 634–641.

Sala, O.E., Chapin III, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Irzo, R., Huber-Samwald, E., Huenneke, K.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. Science 87, 1770–1774.

Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V., Woolmer, G., 2002. The Human footprint and the last of the wild. BioScience 52, 891–904.

Santos, A.M., Tabarelli, M., 2002. Distance from roads and cities as a predictor of habitat loss and fragmentation in the Caatinga vegetation of Brazil. Brazilian Journal of Biology 62, 897–905.

sCBD, MNP, 2007. Cross-roads of Life on Earth—Exploring Means to Meet the 2010 Biodiversity Target. Solution-oriented Scenarios for Global Biodiversity Outlook 2. Technical Series No. 31. Secretariat of the Convention on Biological Diversity, Montreal. pp. 90.

Shine, R., Lemaster, M., Wall, M., Langkilde, T., Mason, R., 2004. Why did the snake cross the road? Effects of roads on movement and location of mates by garter snakes (*Thamnophis sirtalis parietalis*). Ecology and Society 9, 9. <http://www.ecologyandsociety.org/vol9/iss1/art9/>.

Sokal, R.R., Rohlf, F.J., 1981. Biometry: The Principles and Practice of Statistics in Biological Research, second ed. Freeman, New York.

Spellerberg, I.F., 1998. Ecological effects of roads and traffic: a literature review. Global Ecology and Biogeography Letters 7, 317–333.

Sweeting, M.J., Sutton, A.J., Lambert, P., 2004. What to add to nothing? Use and avoidance of continuity corrections in meta-analysis of sparse data. Statistics in Medicine 23, 1351–1375.

Thompson, S.G., Sharp, S.J., 1999. Explaining heterogeneity in meta-analysis: a comparison of methods. Statistics in Medicine 18, 2693–2708.

*Tigas, L.A., Van Vuren, D.H., Sauvajot, R.M., 2002. Behavioral responses of bobcats and coyotes to habitat fragmentation and corridors in an urban environment. Biological Conservation 108, 299–306.

Trombulak, S.C., Frissell, C.A., 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14, 18–30.

UNEP, Nellemann, C., Kullerud, L., Vistnes, I., Forbes, B.C., Husby, E., Kofinas, G.P., Kaltenborn, B.P., Rouaud, J., Magomedova, M., Bobiwash, R., Lambrechts, C., Schei, P.J., Tveitdal, S., Grøn, O., Larsen, T.S., 2001. GLOBIO. Global Methodology for Mapping Human Impacts on the Biosphere. UNEP/DEWA/TR.01-3.

UNEP, 2007. Global Environmental Outlook 4. Environment for Development. United Nations Environmental Programme, Nairobi, Kenya.

Van der Zande, A.N., TerKeurs, W.J., van der Weijden, W.J., 1980. The impact of roads on the densities of four bird species in an open field habitat–evidence of a long-distance effect. Biological Conservation 18, 299–321.

Van Dyke, F., Klein, W.C., 1996. Response of elk to installation of oil wells. Journal of Mammalogy 77, 1028–1041.

Verboom, J., Alkemade, R., Klijn, J., Metzger, M.J., Reijnen, R., 2007. Combining biodiversity modeling with political and economical development scenarios for 25 countries. Ecological Economics 62, 267–276.

Viechtbauer, W., 2009. metafor: Meta-analysis package for R. R package version 0.5-4. <http://CRAN.R-project.org/package=metafor>.

*Vistnes, I., Nellemann, C., 2001. Avoidance of cabins, roads, and power lines by reindeer during calving. Journal of Wildlife Management 65, 915–925.

Vitousek, P.M., 1994. Beyond global warming: ecology and global change. Ecology 75, 3–15.

Vos, C.C., Chardon, J.P., 1998. Effects of habitat fragmentation and road density on the distribution pattern of the moor frog *Rana arvalis*. Journal of Applied Ecology 35, 44–56.

Winzer, P.J., 2000. Accuracy of error propagation exemplified with ratios of random variables. Review of Scientific Instruments 71, 1447–1454.

Wolf, F., Guevara, J., 2001. Imputation of missing data in systematic reviews: so what is the standard deviation? Cochrane 1, 7.

Yost, A.C., Wright, R.G., 2001. Moose, caribou and grizzly bear distribution in relation to road traffic in Denali National Park, Alaska. Arctic 54, 41–48.

Relationships between Human Population Density and Burned Area at Continental and Global Scales

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Abstract

We explore the large spatial variation in the relationship between population density and burned area, using continental-scale Geographically Weighted Regression (GWR) based on 13 years of satellite-derived burned area maps from the global fire emissions database (GFED) and the human population density from the gridded population of the world (GPW 2005). Significant relationships are observed over 51.5% of the global land area, and the area affected varies from continent to continent: population density has a significant impact on fire over most of Asia and Africa but is important in explaining fire over < 22% of Europe and Australia. Increasing population density is associated with both increased and decreased in fire. The nature of the relationship depends on land-use: increasing population density is associated with increased burned are in rangelands but with decreased burned area in croplands. Overall, the relationship between population density and burned area is non-monotonic: burned area initially increases with population density and then decreases when population density exceeds a threshold. These thresholds vary regionally. Our study contributes to improved understanding of how human activities relate to burned area, and should contribute to a better estimate of atmospheric emissions from biomass burning.

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Introduction

Fire is a natural process that has played a key role in the maintenance of natural ecosystems for millions of years, and regulates plant and animal population dynamics [1-3]. However, fire is also a tool used by people to transform the natural environment [4-6]. Humans are the dominant influence over most of the land surface today [7]. Prior to the industrial revolution only ca 5 % of the ice free land surface was used for agriculture and settlement. However, between 1700 and 2000 AD, the terrestrial biosphere transitioned from being mostly wild to mostly anthropogenic, passing the 50% threshold early in the 20th century [8]. This transformation makes it important to consider human influence on modern fire regimes [9].

Guyette et al. (2002) [9] identified four ways in which human influence the amount of land burnt (or the burned area fraction): anthropogenic ignitions, fuel production, fuel fragmentation and cultural behaviour. All these factors are linked to population density. Many regional studies show a single-peaked relationship between human population and fire extent and/or numbers of fires, with intermediate populations at the peak of this parabola, after which different land use activities and land cover types attenuate fire frequency and reduces burnt area fraction [10-13].

The objective of this study is to investigate the influence of population density on burnt area by exploring its spatial variability using Geographically Weighted Regression, and try to detect existence of critical thresholds in population density for fire behaviour using quantile regression. We then interpret the findings in the light of differences in major land use management classes.

Data and Methods

Data

Satellite-derived burned area maps covering 13 years (1997-2009) are available from the Global Fire Emissions Database version 3 (GFED3: [14]) at 0.5° cell resolution for the whole globe (Fig. 1a), available at: http://www.globalfiredata.org/. This spatial resolution can reveal first-order global and continental-scale patterns in burnt area [15]. Giglio et al. (2010) [14] demonstrated that the GFED v3 data used in this study has improved accuracy over version 2 in Canada and the USA. Since active fire detection can capture mush smaller events (sub-pixel) than burned area products, GFED may indeed better represent area burned in small fires than products that do not rely on active fire data. For 0.5° spatial resolution burned area, GFED v3 uses either VIRS or ATSR world fire atlas fire counts [14]. The input data for a GWR are the centroids of the 0.5° cells. Cells that intersect water bodies, ice and artificial surfaces are considered to be non-combustible areas and were removed using a mask from the Global Land Cover 2000 database [16]. The global combustible area extent was calculated from the area of each cell using a latitude correction. The annual mean burned area (km^2) for the 13 years of observations was used as the response variable. Population density (persons per square kilometre: p/km^2) was obtained from the Gridded Population of the World version 3 [17] at 0.5° spatial resolution (Fig. 1b) available at: http://sedac.ciesin.columbia.edu/data/collection/gpw-v3, and is used as the predictor variable. As both burned area and population density are highly skewed toward small values, we applied a decimal logarithmic transformation to both variables.

To support the interpretation of our analyses of the human influence on burned area, we use the anthropogenic biomes (Anthromes) of the world [18] available at: http://ecotope.org/anthromes/v1/guide/. This dataset classifies terrestrial biomes based on the level of human influence, estimated as a function of population density, land use and land cover. The 21 anthromes are grouped into 6 major anthrome types in the original publication (Table 1; Figure 1c) and we use these major types here to simplify interpretation of the GWR results.

Statistical Analyses

We initially computed the global linear relationship between burned area and population density using Ordinary Least Squares (OLS). The global OLS regression model assumes that the studied relationship is stationary, i.e. the estimated parameters do not vary spatially. To test the hypothesis that the relationship varies spatially, we use Geographically Weighted Regression (GWR). GWR estimates local parameter values as in (Eq. 1) [19,20].

$$y=\beta_o(\mu,\nu)+\sum_{j=1}^{p}\beta_j(\mu,\nu)X_j+\varepsilon \qquad \textbf{(1)}$$

Where (μ,v) is the coordinate location and j is the number of the explanatory variables of the X matrix, β is a matrix with the regression coefficients and ε is a random error whose distribution is N(0, σ^2I) [20].

We initially ran the GWR at 0.5° spatial resolution, which is the original resolution of both the burned area and population data sets, but also the resolution used by several Dynamic Global Vegetation Models (DGVM). Other than such pragmatic criteria, the choice of an appropriate level of spatial aggregation for analyses of spatial relationships is essentially arbitrary [21]. The basic assumption of the GWR is that observations closer to a target point have more impact on the modelled relationship at that point than more distant observations. A distance decay function centered on each observation is used for this purpose, and this makes it important to choose an appropriate level of aggregation. The GWR procedure includes a step that assesses whether the selected scale is appropriate. However, to assess the sensitivity of the spatial relationship between population density and burned area to the choice of spatial resolution, we used Africa as a test case and re-ran the analyses for this continent using 0.25° and 1.0° cells. The distance-decay depends on the bandwidth of the spatial kernel used, which is the radius or the number of observations around each point [19]. Here, we used a continental space scale, defining the continents according to political borders (M. Charlton, personal communication). We used an adaptive Gaussian kernel, whose bandwidth varies according to the density of the data, an approach usually adopted when there is no prior knowledge of the studied relationship [19]. The optimal bandwidth for each continent was determined by minimizing the Akaike information criterion (AIC) [22,23]. Due to the different extent of land of each continent and the minimization of the AIC coefficient for the highest adjusted R^2, the bandwidth varies, but remains proportional at 5.1% of the total observations in all cases. The use of the AIC ensures that we use the appropriate level of spatial aggregation for each continent. The analysis is performed with GWR version 3.0. (see 20).

A Monte Carlo permutation test is used to test the significance of the spatial variability of local coefficient estimates. We only map the statistically significant values of the GWR output parameters (slope coefficients and intercept), as determined by a t-test. As multiple hypotheses tests are used, an alpha correction is employed to reduce type I errors [23]. The parameter coefficients were tested for significance according to the family-wise error rate ξ_m by choosing

$$a=\frac{\xi_o}{1+p_e-\frac{p_e}{np}} \qquad \textbf{(2)}$$

where p_e is the effective number of parameters, n is the total number of observations and p is the number of parameters in each model [23,24].

The relationship between population density and burned area is expected to be non-linear and non-monotonic. To examine whether there are abrupt changes in the nature of the relationship switches, we fit a linear "broken stick" version of quantile regression [25-28], using the package "quantreg" in R (http://cran.r-project.org/web/packages/quantreg/index.html). This technique makes no prior assumption of abruptness [29]. Since there could be more than a single slope in rate of change because of interactions between factors [30], we consider the 50th and 90th burned area percentiles, to explore the impact of human activities on area burnt.

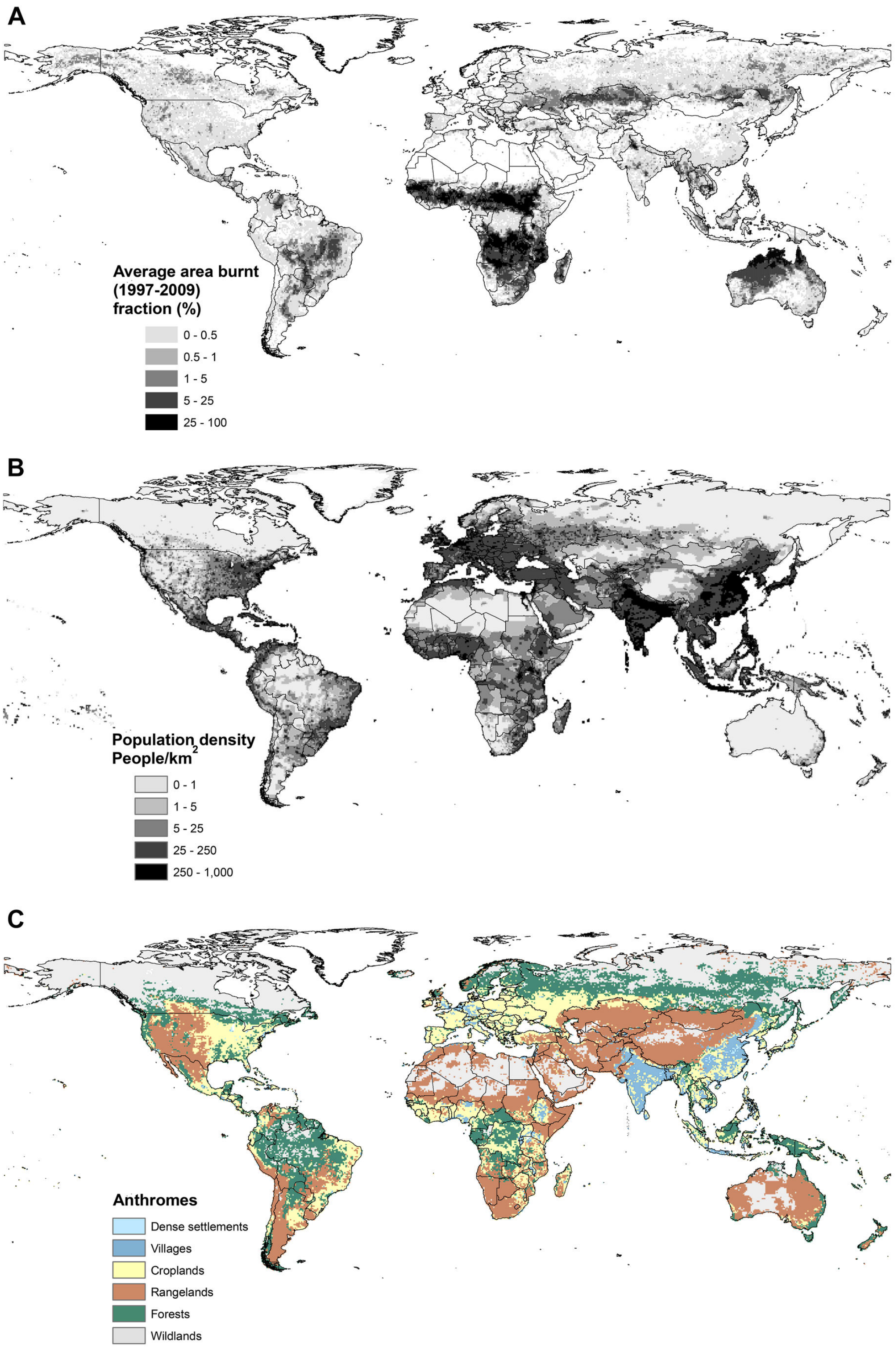

Figure 1. Input data sets. Average mean annual burned area (showed in cell area fraction instead of km^2 in order to help the interpretation), based on data from the Global Fire Emissions Database version 3 (GFED3: Giglio et al., 2010) for the period 1997-2009; (B) Population density (persons per square kilometre: p/km^2) from the Gridded Population of the World version 3 (Ciesin, 2005); and (C) The anthropogenic biomes (anthromes) of the world, mapped as the six major anthrome types (see Table 1) defined by Ellis and Ramankutty (2008).

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Table 2. Percentage of statistically significant values per continent, AIC coefficients and adjusted R² for the OLS and the GWR model.

Continent	Number of observations	% significant slopes	% positive slopes	AIC (OLS)	AIC (GWR)	Adjusted R^2 (OLS)	Adjusted R^2 (GWR)
Africa	10647	61.3	75.5	52871.22	39362.11	0.27	0.80
Asia	23799	65.7	78.3	115337.97	101721.13	0.04	0.46
N. America	17192	42.9	55.1	76372.24	67573.16	0.24	0.55
S. America	6551	46.8	81.8	31317.89	26493.67	0.07	0.56
Europe	6899	21.44	68	32402.14	27009.41	0.11	0.60
Australia	3038	20.51	76.4	14508.43	11947.93	0.001	0.58

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Table 1. Anthromes and major anthrome types defined by Ellis and Ramankutty (2008).

Anthrome	Major anthrome type
Urban	Dense Settlement
Dense settlements	Dense Settlement
Rice villages	Villages
Irrigated villages	Villages
Cropped and pastoral villages	Villages
Pastoral villages	Villages
Rainfed villages	Villages
Rainfed mosaic villages	Villages
Residential irrigated cropland	Croplands
Residential rainfed mosaic cropland	Croplands
Populated irrigated cropland	Croplands
Populated rainfed cropland	Croplands
Remote croplands	Croplands
Residential rangelands	Rangelands
Populated rangelands	Rangelands
Remote rangelands	Rangelands
Populated forest	Forest
Remote forest	Forest
Wild forest	Wildlands
Sparse trees	Wildlands
Barren	Wildlands

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Results

OLS versus GWR comparison

The relationship between log-transformed population density and burned area estimated using OLS is poor, with R^2 values varying from 0.001 (Australia) to a maximum of 0.27 (Africa). The relation between the log-transformed population density and burned area using the GWR models at 0.5° resolution is significant for all continents; the proportion of variability in burned area explained varies from 46% (Asia) to 80% (Africa). Thus, GWR performs much better than OLS for every continent. The GWR models also have lower AIC coefficients than OLS model and much higher adjusted R^2 values (Table 2), showing that the local model (GWR) is a significant improvement on the global (OLS) model for all continents.

The GWR analysis shows that there is no significant relationship between population density and burned area over 48.5% of the total area of the globe. A significant relationship between population density and burned area is found for ca 66% of the total area of Asia, ca 61% of Africa, ca 47% of South America and 43% of North America. Less than 22% of Europe and Australia are characterised by a significant relationship between burned area and population density.

Spatial patterns

The relationship between population density and burned area is non-stationary and shows patterns that differ both in sign and magnitude (Figure 2a). The relationship can be positive or negative, where positive relationships indicate that human activities increase burned area and negative relationships indicate that human activities have negative influence on fire. The magnitudes of the slope coefficients are different in different continents, so we focus on the sign in regions showing significant relationships between population density and burned area. The intercept can be an estimate of the area burnt when population density is small (1 p/km^2), although absolute values are influenced by the slope coefficient. However, for regions displaying similar slopes, the intercept can be interpreted as a measure of the fire-proneness of the landscape, where positive intercepts indicate that the region is fire-prone and negative intercepts indicate that the region is less likely to burn.

Africa

On average over the period 1997-2009, 69% of the global area burned is in Africa. This is comparable to Tansey et al.'s (2004) [31] estimate that Africa accounted for 64% of the total area burned in 2000. The relationship between population density and burned area is statistically significant over nearly 61% of the continental area, with positive relationships in the Maghreb, the Sahel, the Horn of Africa, central Africa, and south-western Africa (Figure 2a) and negative relationships in the Sudanian savannah region and parts of eastern Africa (Figure 2a). Over most of these areas, the slope coefficients are >1 (or < -1), indicating that the impact of people becomes progressively larger at higher population densities. Regions with positive relationships between burned area and population density generally occur in rangelands (Figure 1c), while the areas with negative relationships have a higher incidence in

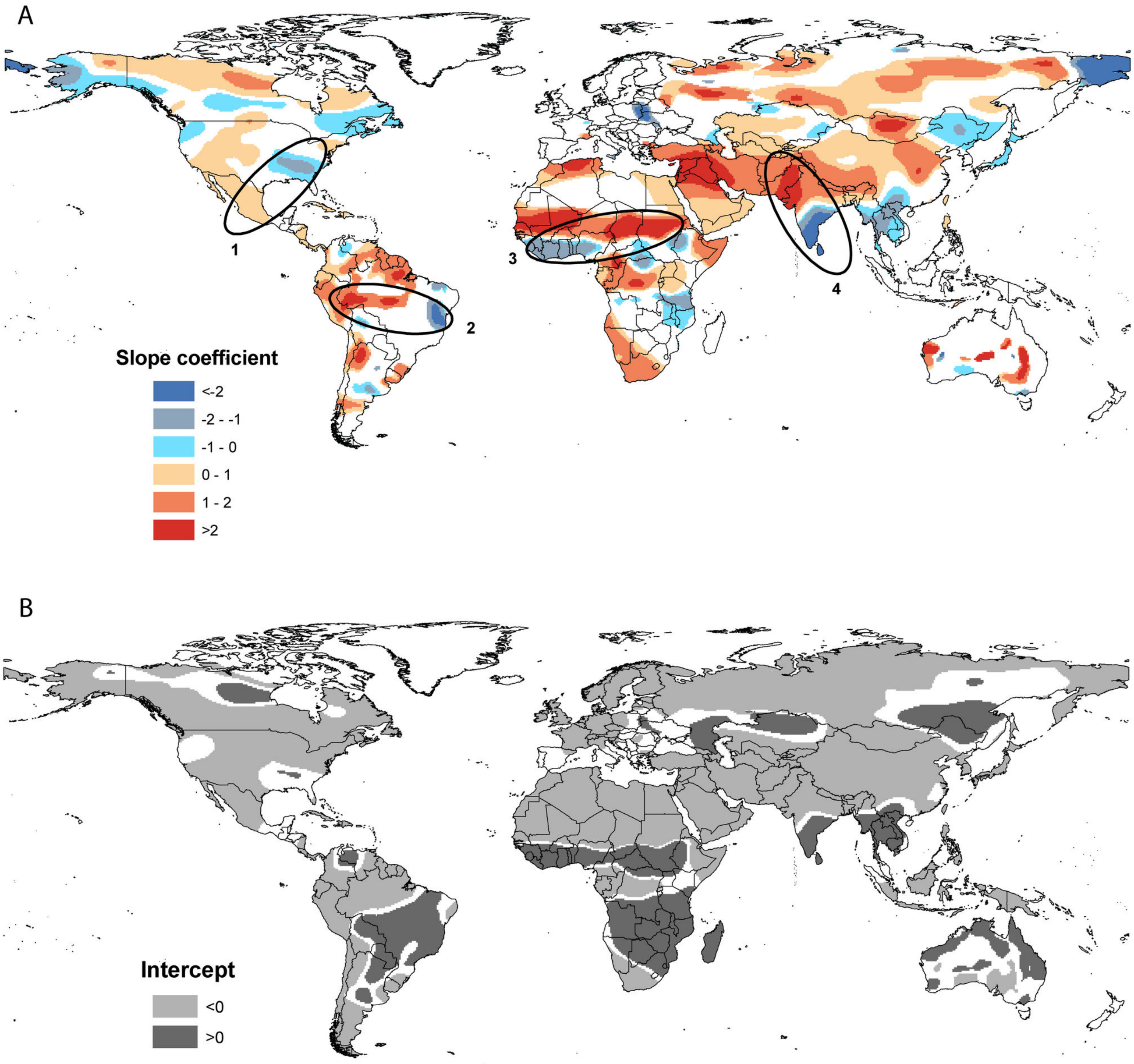

Figure 2. Output parameters and local R^2. The upper panel (A) shows results from the GWR analysis, showing the nature of the relationship between population density and burned area for those regions where the relationship is significant at the 95% level (red shows a positive relationship, blue shows a negative relationship). The slope coefficient classes are defined separately for each continent; (B) Mapped patterns in the sign and magnitude of the statistically significant intercept values from the GWR analysis of population density and burned area. Dark grey shows positive intercept values, where the area burned is large even at negligible population density (i.e. where the landscape is naturally fire-prone), while light grey shows negative intercept values where climatic or vegetation factors do not favour fire; (C) Showing the significant patterns for both intercept and slopes according to the sign of the relationship, thus the four combinations show both out being positive (red), positive slopes and negative intercept (green), negative slopes and positive intercept (yellow) and both being negative (blue) ;(D) Mapped patterns of the local R^2 for the regions where the relationship between population density and burned area is statistically significant.

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areas of croplands and villages, and in forests. Absence of fire (because of lack of fuel) explains the absence of significant relationships in the Sahara, but the absence of any significant relationship associated with the high burned area (Figure 1a) in the Angola-Congo-Zambia region is perhaps more surprising (Figure 2a), given the general view that Miombo woodlands are highly susceptible to anthropogenic fires (e.g. 32) and has been identified as one of the highest fire incidence in the world [15]. Population density in this region is rather low (5-15 people per km^2) and shows little spatial variability. This could partly explain the lack of a significant relationship between burned area and population. However, the region is characterised by a mosaic of open, fire-prone savannah vegetation and it is likely that both the high incidence and variability of fire is mainly determined by variability in climate and vegetation.

About 40.1% of the regions showing a significant relationship between burned area and population density have positive values for the intercept (Figure 2b), most particularly the Sudanian savannah region and parts of eastern Africa, where the relationship between fire and population density is inverse (Figure 2a). The positive intercept values indicate that these regions are naturally fire-prone, and help to explain why increasing population density should lead to lower area burnt. In contrast, the regions with negative intercepts can be interpreted suggesting that low fuel loads would normally limit fire and human modification of the vegetation cover is responsible for the relatively high levels of fire in these regions. This is consistent with the finding that burned area increases strongly (values > 1) with population density, because landscape modification will also increase with population density.

Asia

Asia is the continent with the largest area (over 49 million km^2) and the highest percentage (66%) of statistically significant slope values (Table 2). There are three regions that show a positive effect of population. The first extends from Turkey and Saudi Arabia through Iran and across to Afghanistan, Pakistan and northern India, the second is the rangelands of Mongolia and northern China, and the third occurs in the boreal parklands of Russia. Whereas the slope coefficients of the first two regions are always >1 (Figure 2a), a large part of the Russian parklands has slope coefficients <1, showing that the largest effects on fire occur for small population increments. Regions with significant negative slope coefficients occur in southern India, Southeast Asia and southern China, north-eastern China and Chukotka (north-eastern Siberia). As in the case of Africa, the regions showing positive relationships between burned area and population density tend to be predominantly characterised by rangelands. Regions characterised by villages and croplands, rangelands with extremely high population densities (e.g. in northern India and Pakistan, where populations densities are >250 p/km^2) and forested areas tend to show positive relationships between burned area and population density.

About 14% of the area of the total significant intercept values are positive (Figure 2b). Positive intercepts occur in southern India, Southeast Asia and north-eastern China – all areas where the relationship between burned area and population density is negative (i.e. an increase in population leads to suppression of fire). Areas with negative intercept values in the region stretching from Turkey through northern India to Mongolia show positive relationships between burned area and population density. The relationship in the boreal parklands is more complex, since although areas with positive slope coefficients mostly have negative intercept values, there are some limited areas with positive slope coefficients. However, the R^2 values (Figure 2d) in these regions are low (< 0.25), and the difference in the signals may not be robust. A different relationship occurs in Chukotka (and indeed in parts of Alaska), where negative relationships between burned area and population density are characterised by negative intercepts. Thus, in this not particularly fire-prone tundra region, increasing population density can significantly reduce fire incidence.

North America

The relationship between population density and burned area is statistically significant for over 43% of the area of North America (Table 2a). Positive relationships are found in the semi-arid (and mostly rangeland areas) of northern Mexico and the Great Basin, and in the boreal parkland regions of Canada and north-eastern Alaska. Negative relationships are found in the forested and cropped landscapes of south-eastern U.S.A (Alabama, Georgia, South Carolina), the forested regions of the Pacific Northwest and southern Alaska, and the boreal forest zone of central and eastern Canada (Figure 2a). Across virtually all of North America, slope coefficients are between 1 and -1, a feature that is consistent with the high technological levels of agriculture and contrasts strongly with regions of more traditional agricultural practices, such as Africa.

Only 4.1% of the regions showing statistically significant intercept have positive values. Positive intercept values (Figure 2b) are found in the south-eastern U.S.A., where the relationship between burned area and population density is negative, and in the boreal parklands of northern Canada where the slope of the relationship is positive. Areas with negative intercepts are characteristic of the southern boreal forest in eastern Canada and southern Alaska, and the semi-arid rangelands of the Great Basin and northern Mexico. The relationship between slope and intercept in the rangeland areas (positive slope coefficients, negative intercepts) is consistent with what is observed in semi-arid rangelands in other parts of the world; the relationship in the southern boreal forests (negative slopes, negative intercepts) is distinctive.

South America

The relationship between population density and burned area is statistically significant for 47% of the area of South America (Table 2). The relationship is positive around the margins of Amazonia, and in northern Argentina (Figure 2a). Negative relationships are found in the Bahia state in Brazil and, somewhat anomalously, in the rangeland area of central Argentina. The areas characterised by negative relationships between burned area and population density have positive intercepts (Figure 2b), i.e. these are fire-prone areas where increasing population leads to a reduction in fire. Most of the regions where the relationship between burned area and population density is positive are characterised by negative intercept values. However, in some parts of the so-called “arc of deforestation” on the southern side of the Amazon forest the positive relationship between fire and population density is associated with positive intercept values (Figure 2b), indicating

Table 3. Summary statistics of the GWR analysis for Africa, comparing the results obtained using 0.25°, 0.5° and 1.0° grid cell resolutions.

Continent	Number of observations	% significant slopes	% positiveslopes	AIC (OLS)	AIC (GWR)	Adjusted R^2 (OLS)	Adjusted R^2 (GWR)
Africa (0.25)	40864	67.7	65.5	189463.45	138841.26	0.21	0.77
Africa (0.5)	10647	61.3	75.5	52871.22	39362.11	0.27	0.80
Africa (1)	2557	52.4	97.8	12261.02	8188.66	0.36	0.87

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fire-prone landscapes where human activity is increasing the amount of burning.

Europe and Australia

The relationship between population density and area burned is significant in < 22% of Europe and Australia (Table 2). In Europe, the only areas showing statistically significant negative relationships are in Poland, Ukraine and Belarus. However, intercept values in this region are positive, indicating some level of landscape susceptibility to fire. This feature most likely reflects a pattern dominated by the forested landscapes of e.g. the Carpathians, where natural forest fire regimes are suppressed with increasing population. Positive relationships between population density and burned area are found in some forested parts of north-western Russia; the intercept values are negative.

There are no significant relationships between area burned and population density in the savannah and rangeland areas of northern and western Australia characterised by the highest incidence of fire in the continent (Figure 1a). Areas showing a positive relationship between burned area and population density are in the rangelands of the Murray-Darling basin, on the northern margin of the Lake Eyre basin and to the south of the Hamersley Range in Western Australia. These regions are all associated with positive intercept values. Small areas showing a negative relationship between burned area and population density occur on rangelands of the Nullarbor Plain and in the densely-settled region (Figure 2a) around Melbourne in southern Victoria. The Nullarbor is characterised by negative intercept values (Figure 2b), presumably because of the very low vegetation cover and hence fuel loads in this region. In contrast, the area around Melbourne is characterised by positive intercept values – this is a fire-prone area where human activities work to suppress fire.

Sensitivity to spatial resolution

As expected, the GWR is sensitive to the choice of spatial resolution (Table 3). The extent of the area with significant relationships decreases with spatial resolution, from 68% at 0.25° resolution to 52% at 1° resolution. Changing resolution does not affect the conclusion that most of the relationships between burned area and population density are positive, but the proportion of positive values increases with increasing resolution, reaching an unrealistically high value of 98% at 1° resolution. This presumably reflects the increasing homogenisation of grid cell values of burnt area and/or population density with increasing resolution. The geographical patterns of significant values, and positive and negative relationships, are not impacted by the change from 0.25° resolution to 0.5° resolution, although areas showing negative relationships between population density and burned area have virtually disappeared in the analyses at 1° resolution. These sensitivity tests suggest that the overall conclusions of our GWR analysis would not be affected by running at finer than 0.5° resolution, but clearly information is likely to be lost in analyses at coarser resolution.

Impact of land-use on the relationship between burned area and population density

Both positive and negative relationships between burned area and population density are found in every type of anthrome (Figure 3). Wild lands represent a significant proportion of the regions where there is a significant correlation between burned area and population density, but nevertheless the proportion showing positive or negative correlations is about the same (29% of the total area showing positive, 31% showing negative correlations). However, croplands and rangelands are not equally represented in the two classes of relationship: 37% of the area where there is a negative relationship between burned area and population density is cropland and only 10% is rangelands. Conversely, rangelands account for nearly 40% of the area where there is a positive relationship between burned area and population density, while croplands account for only 11% of these regions.

Quantile regression analysis

Although regions may show an overall positive or negative relationship between burned area and population density, the nature and strength of the relationship is not necessarily constant at different levels of population [33]. We examine whether there are critical thresholds in population density at which the relationship between population density and the burned area extent changes using quantile regression, focusing on four different regions in Africa, Asia and the Americas (Figure 2a). Each region is characterised by close bipolar patterns, thus displaying areas with both strongly positive and strongly negative slope coefficients (Figure 2a).

In Asia, the relationship between population density and burned area is monotonic (Figure 4, case 4): as population density increases the impact on fire, whether positive or negative, increases. This is true for regions with moderate levels (50%) and at higher levels of burned area. In Africa and South America, the relationship between population density and burned area is non-monotonic: burnt area increases up to

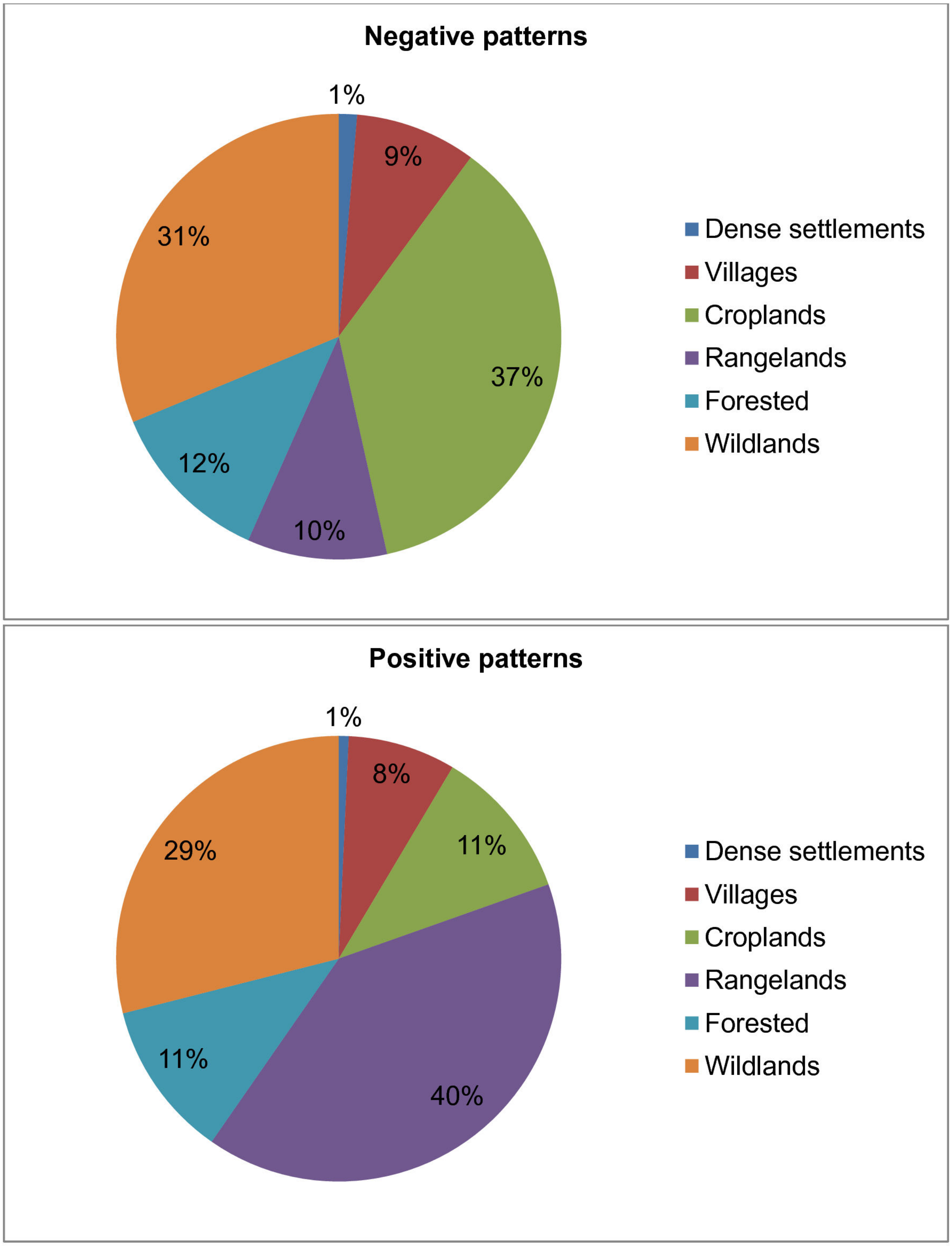

Figure 3. Proportion of Anthromes showing negative and positive relationship. Pie-charts showing the relative proportion of the total area showing (A) positive and (B) negative significant relationships between burned area and population density, classified according to the six major anthrome types defined by Ellis and Ramankutty (2008).

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a given threshold, reaches a peak and then declines (Figure 4, cases 2-3). In both regions, the change point in the nature of the relationship occurs at about 7 p/km^2 in both regions with moderate and high levels of fire. The impact of changes in population density on burned area becomes negligible at population densities greater than ca 10 p/km^2 in both regions. The relationship between burned area and population density in North America is also non-monotonic (Figure 4, case 1). In regions with only moderate levels of fire (as shown by the 50% quantile regression), the relationship is similar to that observed in South America and Africa: increasing population density leads to increasing impact on burned area up population densities of 7 p/km^2 and then becomes negative and the slope becomes more gentle at population densities of > 12 p/km^2. However, in regions with higher levels of fire (as shown by the 90% regressions), the negative relationship at population densities > 7 p/km^2 is reversed and becomes positive at population levels > 30 p/km^2.

Discussion and Conclusions

This study quantifies the spatial variability in the relationship between human activities (as measure by population density) and fire (as measured by burned area). There is no statistically significant relationship between burned area and population density over more than 50% of the global land area. The univariate relationship between population density and area burnt is relatively unimportant in Australia and Europe: in the case of Australia this supports the idea of a strong climate control on fire regimes, while in Europe the lack of relationship most likely reflects the closely managed nature of the landscape. At a sub-continental scale, there are regions where population density has little or no impact on burned area. In Kazakhstan, for example, variability in burning shows no relationship with population density despite the fact that this is one of the biggest agricultural areas in the world [34] and the country that contributes with highest amount of area burnt in dry land ecosystems in central Asia [35]. A similar situation pertains in the Miombo woodlands region of Angola-Congo-Zambia, where variability in burned area is unrelated to population density. The absence of a relationship between population density and burned area over much of the globe does not imply that human activities have no influence on fire regimes. Several studies have shown, for example, that humans can alter the timing [36] or the number of fires [13,37]. However, since it is burned area (rather than timing or number) that is most important for the carbon cycle and pyrogenic emissions, the lack of a strong relationship between human activities and burned area over much of the globe, including areas characterised by high levels of burning, is noteworthy.

In areas where there is a statistically significant relationship, this relationship is positive (i.e. burned area increases with population density) over 73.3% of the global land area. However, there are substantial parts of the world, where the relationship between burned area and population density is negative (i.e. increasingly human activity leads to fire attenuation). The relative proportion of the land area showing positive/negative relationships varies from continent to continent. There has been considerable focus on the positive relationship between human activities and burned area, through using fire to clear land and as part of the agricultural regime [34,38]. The impact of landscape fragmentation on reducing fire in agricultural area has also been documented [16,39,40].

About 30% of the regions where a significant relationship between population density and burned area are classified as wild lands, but the relative proportion of wild lands in the areas showing positive or negative relationships between fire and human activity is approximately the same. This is not the case for all anthromes. Rangelands are over-represented in the regions showing positive relationships between fire and population, while croplands are over-represented in the regions showing negative relationships between fire and population. The distribution of rangelands is to some extent a reflection of climate controls, with most rangeland areas occurring in semi-arid regions and croplands occurring in more well-watered regions, nevertheless these tendencies suggest that land-use practices can have a significant impact of fire regimes.

The GWR analysis shows that, in general, regions which display a negative relationship between burned area and population density generally have positive intercept values, and vice versa. In other words, in regions where climate and/or vegetation create conditions where fires are likely (i.e. fire prone landscapes), people tend to supress fire whereas in regions that are less fire-prone because of e.g. lack of fuel, people tend to increase the area burned. However, there are regions where there is both a positive relationship between population and burned area and the intercept is also positive. One of these regions is the arc of deforestation on the southern border of Amazonia, suggesting that deforestation is exploiting a landscape that is already susceptible to the impact of fire. This is not a new suggestion; Le Page et al. (2010) [41] pointed out that this region experiences three to five months of low precipitation which facilitates extended periods of burning.

In most regions of the world, the nature of the relationship between population density and burned area is non-monotonic: increasing human activity (as measured by population density) initially lead to an increase in burned area but this peaks at intermediate levels of population density and then declines. The critical value in three of the case studies regions examine here is around 7 p/km^2 and above values of 12 p/km^2 there is no further impact of population density changes on fire. Our results for Africa support previous findings [13,42] that suggest that fire extent in this region displays a non-monotonic relationship with anthropogenic variables. However, in areas of North America characterised by high fire, there is a second threshold at ca > 30 p/km^2 where increasing population density leads to increasing burned area. The situation in Asia seems anomalous in that increasing population density always leads to an increased impact in burned area.

The GWR approach allows an appropriate spatial scale of comparison to be selected continent by continent through the choice of bandwidth combined with use of the AIC. Fotheringham et al. (2002) [20] showed that the GWR approach was more robust to the choice of spatial resolution than models that do not take spatial non-stationarity into

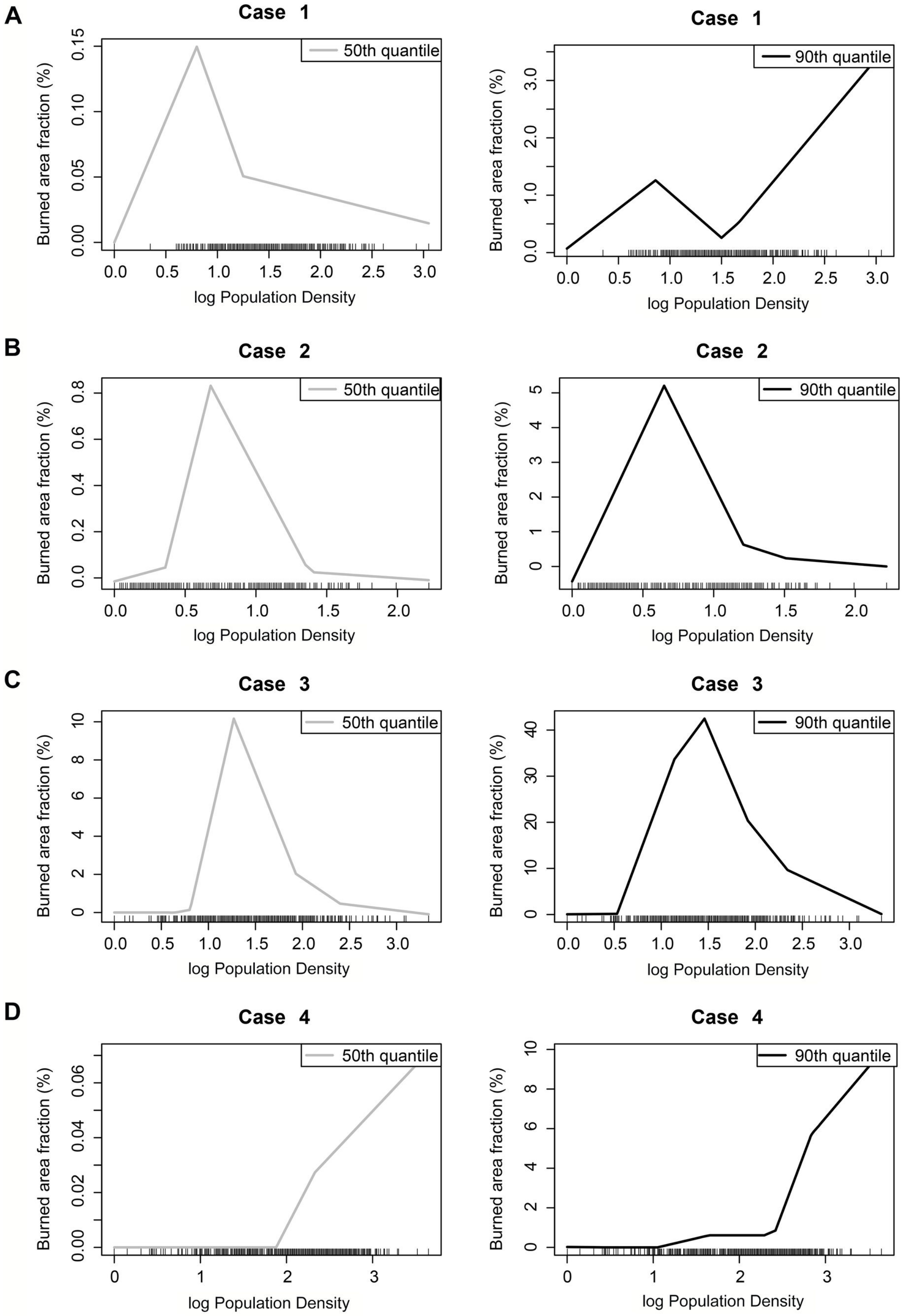

Figure 4. The relationship between burned area and population density at different levels of burned area (50 and 90%) for the 4 case studies. (A) Case 1 in North America. (B) Case 2 in South America. (C) Case 3 in Africa. (D) Case 4 in Asia.
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account. Nevertheless, we examined the impact of the choice of spatial resolution using Africa as a test case. The use of a higher resolution than our baseline of 0.5° produces no change in the geographic patterns of regions showing significant positive or negative relationships between population density and burnt area, although the percentage of grid cells showing positive values declines slightly (and the percentage showing negative values correspondingly increases). The overall impact of increasing the resolution is slight, and this suggests that our regional findings are robust. Most other studies of the controls on burnt area have used coarser spatial resolutions (e.g. 12,43). Our sensitivity analyses show that decreasing the resolution has a larger impact on the geographic patterns, and particularly on the recognition of areas where the relationship between population density and burnt area is negative. This suggests that these earlier studies may miss important aspects of the relationship between population density and burnt area because of their choice of spatial scale. The selection of spatial scale is can affect the conclusions about the nature of spatial relationships, making it important to use a technique (such as the AIC optimization) that allows this choice to be made objectively.

Understanding the complexity of the relationships between people and fire is important in a modelling context. Fire-enabled dynamic vegetation models can be used to predict the consequences of projected changes in climate on fire regimes (see e.g. 44-46). However, those models that explicitly include anthropogenic fire generally focus on human impacts on ignitions and furthermore employ either a universal population density value as a threshold for anthropogenic fire ignitions [47], or single-peaked global function of population density [48]. Other fire-enabled DGVMs (e.g. LPX: [49]) ignore anthropogenic ignitions, although they allow for human suppression of fire in agricultural areas. No extant model incorporates spatially varying relationships between burned area and population density that are dependent on vegetation types, land-use and cultural practices – which our analyses show a non-negligible influence on regional fire regimes. However, this study has not exhausted the analyses necessary to arrive at a complete understanding of the biogeography of fire.

Author Contributions

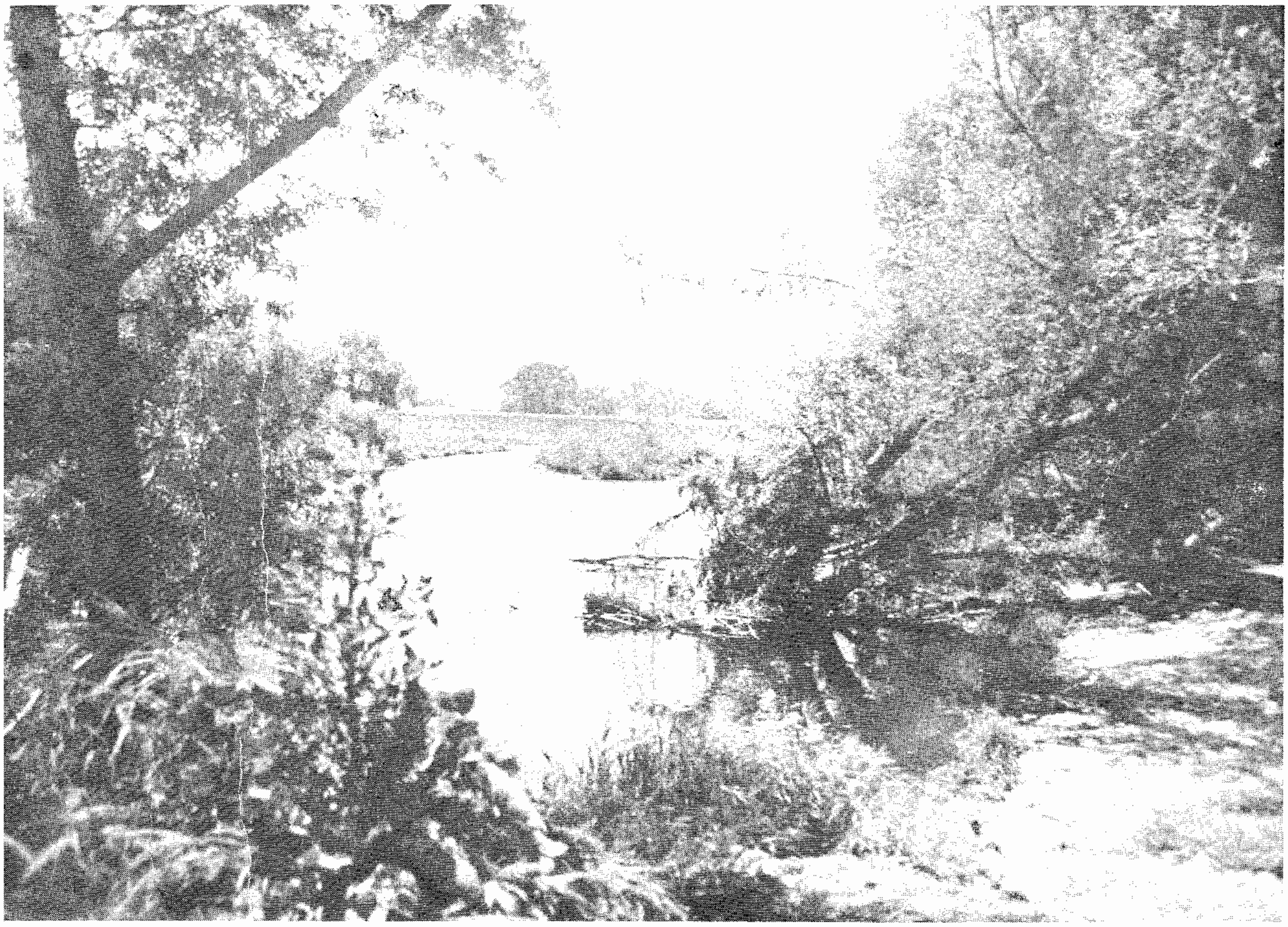
Conceived and designed the experiments: IB DO ACLS JMCP. Performed the experiments: IB DO. Analyzed the data: IB DO ACLS SPH ICP JMCP. Contributed reagents/materials/analysis tools: IB DO ACLS JMCP. Wrote the manuscript: IB DO ACLS SPH ICP JMCP.

References

1. Bond WJ, Wilgen B (1996) Fire and plants. Chapman and Hall. London. UK.
2. Johnson E (1996) Fire and Vegetation Dynamics: Studies from the North American Boreal Forest. Cambridge University Press. Cambridge.
3. Pyne SJ, Andrews PL, Laven RD (1996) Introduction to wildland fire. New York, John Wiley and Sons. p.769.
4. Pyne SJ (2009) The human geography of fire: a research agenda. Progress in Human Geography. 33(4): 443–446. doi: 10.1177/0309132508101598.
5. Flannigan MD, Stocks BJ, Wotton BM (2000) Climate Change and Forest Fires. 1–9. Sci Total Environ 262(3): 221-229. doi:10.1016/S0048-9697(00)00524-6. PubMed: 11087028.
6. IPCC (2007) Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [S SolomonD QinM ManningZ ChenM Marquis. Cambridge University Press, Cambridge, UK and New York, NY, USA.
7. Sanderson EW, Jaiteh M, Levy MA, Redford KH, Wannebo AV et al. (2002) The Human Footprint and the Last of the Wild. BioScience, 52(10): 891-904.
8. Ellis EC, Goldewijk K, Siebert S, Lightman D, Ramankutty N (2010) Anthropogenic transformation of the biomes, 1700 to 2000. Global Ecology and Biogeography 19(5). doi:10.1111/j.1466-8238.2010.00540.x.
9. Guyette RP, Muzika RM, Dey DC (2002) Dynamics of an anthropogenic fire regime. Ecosystems 5: 472-486. doi:10.1007/s10021-002-0115-7.
10. Barbosa PM, Stroppiana D, Gregoire J-M, Pereira JMC (1999a) An assessment of vegetation fire in Africa (1981–1991): burned areas, burned biomass, and atmospheric emissions. Glob Biogeochem Cycles 13(4): 933–950. doi:10.1029/1999GB900042.
11. Syphard AD, Radeloff VC, Keeley JE, Hawbaker TJ, Clayton MK et al. (2007) Human influence on California fire regimes. Ecol Appl 17(5): 1388–1402. doi:10.1890/06-1128.1. PubMed: 17708216.
12. Aldersley A, Murray SJ, Cornell SE (2011) Global and regional analysis of climate and human drivers of wildfire. Sci Total Environ 409(18): 3472–3481. doi:10.1016/j.scitotenv.2011.05.032. PubMed: 21689843.
13. Archibald S, Roy DP, vanWilgen BW, Sholes RJ (2009) What limits fire? An examination of drivers of burnt area in Southern Africa. Glob Change Biol 15(3): 613–630. doi:10.1111/j.1365-2486.2008.01754.x.
14. Giglio L, Randerson JT, van der Werf GR, Kahsibhatla PS, Collatz GJ et al. (2010) Assessing variability and long term trends in burned area by merging multiple satellite fire products. Biogeosciences 7: 1171–1186. doi:10.5194/bg-7-1171-2010.
15. Oom D, Pereira JMC (2013) Exploratory spatial data analysis of global MODIS active fire data. International Journal of Applied Earth Observation and Geoinformation 21: 326–340. doi:10.1016/j.jag.2012.07.018.
16. Bartholomè E, Belward AS (2005) A new approach to global land cover mapping from Earth observation data. International Journal of Remote Sensing 26(9): 1959–1977. doi:10.1080/01431160412331291297.
17. Center for International Earth Science Information Network (CIESIN), Columbia University, Centro Internacional de Agricultura Tropical (CIAT) (2005) Gridded population of the World version 3 (GPWv3): population density grids. Socioeconomic Data and Applications Center (SEDAC), Columbia University, Palisades.
18. Ellis EC, Ramankutty N (2008) Putting people in the map: anthropogenic biomes of the world. Frontiers in Ecology and the Environment 6(8): 439–447. doi:10.1890/070062.
19. Brunsdon CA, Fotheringham AS, Charlton ME (1998) Geographically weighted regression–modelling spatial non-stationarity. Stat 47(3): 431–443.
20. Fotheringham S, Brunsdon C, Charlton M (2002) Geographically Weighted Regression: the analysis of spatially varying relationships. John Wiley & Sons, UK.
21. Openshaw S, Taylor PJ (1981) The modifiable areal unit problem. in: Quantitative geography: a British View, (eds) N. Wrigley and R.J. Bennett, (Routledge and Kegan Paul: London), p. 60-70
22. Akaike H (1981) Likelihood of a model and information criteria. J Econ 16(1): 3–14. doi:10.1016/0304-4076(81)90071-3.
23. Byrne G, Charlton M, Fotheringham S (2009) Multiple dependent hypothesis tests in geographically weighted regression. In: BG LeesSW Laffan. 10th International conference on geocomputation. UNSW, Sydney November-December
24. Brunsdon C, Charlton M (2011) An assessment of the effectiveness of multiple hypothesis testing for geographical anomaly detection. Environment and Planning B: Planning and Design 38(2): 216 - 230. doi:10.1068/b36093.
25. Toms JD, Lesperance ML (2003) Piecewise Regression: A tool for identifying ecological thresholds. Ecology 84(8): 2034-2041. doi: 10.1890/02-0472.

26. Koenker R, Basset G (1978) Regression Quantiles. Econometrica 46(1): 33-50. doi:10.2307/1913643.
27. Koenker R (2005) Quantile Regression. Cambridge University Press. Cambridge. UK.
28. Sankaran M, Hanan NP, Scholes RJ, Ratnam J, Augustine DJ et al. (2005) Determinants of woody cover in African savannas. Nature 438(7069): 846–849. doi:10.1038/nature04070. PubMed: 16341012.
29. Chiu GS (2003) Bent cable Regression for Assesing Abruptness of Change. PhD Thesis, University of British Columbia: Canada.
30. Cade SB, Noon BR (2003) A gentle introduction to quantile regression for ecologists. Front Ecol Environment 1(8): 412-420. Available online at: doi:10.1890/1540-9295(2003)001[0412:AGITQR]2.0.CO;2
31. Tansey K, Gregoire J-M, Stroppiana D, Sousa A, Silva J, et al. (2004) Vegetation burning in the year 2000: global burned area estimates from SPOT VEGETATION data. J Geophys Res 109: D14S03 DOI 10.1029/2003JD003598.
32. Ryan CM, Williams M (2011) How does fire intensity and frequency affect miombo woodland tree populations and biomass? Ecol Appl 21: 48-60. doi:10.1890/09-1489.1. PubMed: 21516887.
33. Archibald S, Staver AC, Levin SA (2012) Evolution of human-driven fire regimes in Africa. Proc Natl Acad Sci U S A 109(3): 847-852. doi: 10.1073/pnas.1118648109. PubMed: 22184249.
34. Leff B, Ramankutty N, Folley JA (2004) Geographic distribution of major crops across the world. Global Biogeochemical Cycles 18.
35. Loboda TV, Giglio L, Boschetti L, Justice CO (2012) Regional fire monitoring characterization using global NASA MODIS fire products in dry lands of Central Asia. Front. Earth Sci. 6(2): 196-205. doi:10.1007/s11707-012-0313-3.
36. Page Le Y, Oom D, Silva JMN, Jonsson P, Pereira JMC (2009) Seasonality of vegetation fires as modified by human action: Observing the deviation from eco-climatic fire regimes. Global Ecology and Biogeography 19: 575-588.
37. Gralewicz NJ, Nelson TA, Wulder MA (2011) Spatial and temporal patterns of wildfire ignitions in Canada from 1980 to 2006. International Journal of Wildland Fire 21(3): 230-242.
38. Silva JMN, Carreiras JMB, Rosa I, Pereira JMC (2011) Greenhouse gas emissions from shifting cultivation in the tropics, including uncertainty and sensitivity analysis. Journal of Geophysical Research, 116(D20) DOI 10.1029/2011JD016056.
39. Laris P (2002) Burning the seasonal mosaic: Preventive burning strategies in the wooded savanna of southern Mali. Human Ecology 30: 155-186. doi:10.1023/A:1015685529180.
40. Marlon JR, Bartlein PJ, Carcaillet C, Gavin DG, Harrison SP et al. (2008) Climate and human influences on global biomass burning over the past two millennia. Nature Geoscience, 1(10): 697–702. doi: 10.1038/ngeo313.
41. Page Le Y, van der Werf GR, Morton DC, Pereira JMC (2010) Modelling fire-driven deforestation potential in Amazonia under current and projected climate conditions. Journal of Geophysical Research 115: 11
42. Sá ACL, Pereira JMC, Charlton ME, Mota B, Barbosa PM et al. (2010) The pyrogeography of sub-Saharan Africa: a study of the spatial non-stationarity of fire–environment relationships using GWR. Journal of Geographical Systems 13(3): 227–248. doi:10.1007/s10109-010-0123-7.
43. Krawchuk MA, Moritz MA, Parisien M-A, Van Dorn J, Hayhoe K (2009) Global Pyrogeography: the Current and Future Distribution of Wildfire. PLOS ONE 4(4): e5102. doi:10.1371/journal.pone.0005102. PubMed: 19352494.
44. Scholze M, Knorr W, Arnell NW, Prentice IC (2006) A climate change risk analysis for world ecosystems. Proc of the Natl Acad of Sciences of the USA 103: 13116–13120. doi:10.1073/pnas.0601816103. PubMed: 16924112.
45. Lenihan J, Bachelet D, Neilson R, Drapek R (2008) Response of vegetation distribution, ecosystem productivity, and fire to climate change scenarios for California. Clim Change 87: 215–230. doi: 10.1007/s10584-007-9362-0.
46. Harrison SP, Marlon J, Bartlein PJ (2010) Fire in the Earth System. Changing Climates, Earth Systems and Society. International Year of Planet Earth 2010, Climate Change Theme, 21-48.
47. Venevsky S, Thonicke K, Sitch S, Cramer W (2002) Simulating fire regimes in human-dominated ecosystems: Iberian Peninsula case study. Global Change Biology 8(10): 984–998. doi:10.1046/j.1365-2486.2002.00528.x.
48. Thonicke K, Spessa A, Prentice IC, Harrison SP, Dong L et al. (2010) The influence of vegetation, fire spread and fire behavior on biomass burning and trace gas emissions: results from a process-based model. Biogeosciences 7(6): 1991–2011. doi:10.5194/bg-7-1991-2010.
49. Prentice IC, Kelley DI, Foster PN, Friendlingstein P, Harrison SP et al. (2011) Modeling fire and the terrestrial carbon balance. Global Biogeochemical Cycles 25. doi:10.1029/2010GB003906.

ENDANGERED PLANT COMMUNITIES
OF
SOUTHERN CALIFORNIA



PROCEEDINGS OF THE 15th ANNUAL SYMPOSIUM

SOUTHERN CALIFORNIA BOTANISTS

SPECIAL PUBLICATION No. 3

ALLAN A. SCHOENHERR, EDITOR

RIPARIAN WOODLAND: AN ENDANGERED HABITAT IN SOUTHERN CALIFORNIA

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INTRODUCTION

There is no precise inventory of North American wetlands prior to European contact, but it has been estimated that wetland resources covered over 200 million acres (80 million ha) in the lower 48 states when European settlement began (Frayer, et. al., 1983). By the mid-1970s over half of the total had been eliminated, and only an estimated 99 million acres (40 million ha) remained. Destruction of wetlands over the previous two decades had proceeded at 400,000 to 500,000 acres (160-200 thousand ha) per year. By 1975 California had lost 91% of its wetland habitats (The Conservation Foundation, 1989). A dramatic example of riparian woodland loss occurred in the Sacramento Valley, where there were an estimated 800,000 acres (325,000 ha) of riparian habitat in 1850 (Roberts, Howe and Major, 1980). In 1952 this resource had shrunk to 20,000 acres (8000 ha) and by 1972 there were an estimated 12,000 acres (5000 ha) - or 1.5% of the original habitat - remaining. By 1980, the rate of national wetland "alteration" had slowed to an estimated average of 275,000 acres (111,000 ha) per year (Office of Technology Assessment, 1984), although in some areas, such as rapidly developing southern California, habitat loss continued at a high rate. Between the mid-1950s and mid-1970s an estimated 14,877,000 acres (6,023,000 ha) of freshwater wetlands were eliminated (Office of Technology Assessment and U.S.F.W.S. National Wetlands Trends Study, 1982). During this era, draining of wetlands for agricultural purposes dominated freshwater wetland habitat destruction of 11,720,000 acres (4,750,000 ha), or 79% of total losses - but rationales for converting wetlands to other land uses ranged from urban development of 925,000 acres (375,000 ha), or 6%, to flooding them behind hydroelectric projects, stream channelization, and filling them for agricultural use, among many others (Table 1). Current estimates of riparian habitat reduction in southern California floodplain areas have been as high as 95% -97% (Faber, et. al., 1989), a regional loss exceeding that of the endemic coastal sage scrub plant community. There is no question that riparian habitat in southern California is endangere. Global warming and a rising sea level in the next 150 years will claim another heavy toll for wetlands, particularly along the coasts. A few of the anticipated global warming impacts that will change riparian habitat distribution and perhaps even community structure to some extent, as summarized by Tonnessen (1988) and others, include:

- Air temperatures will be higher year-round which will increase evaporation and transpiration.

- It will be drier in the fall, drought will occur in the summer and there will be

Table 1.
Methods of altering wetlands (from The Conservation Foundation, 1989).

Physical

1. Filling:
   - adding any material to change the bottom level of a wetland or to replace the wetland with dry land;
2. Draining:
   - removing the water from a wetland by ditching, tiling, pumping, etc.;
3. Excavating:
   - dredging and removing soil and vegetation from a wetland;
4. Diverting water away:
   - preventing the flow of water into a wetland by removing water upstream, lowering lake levels, or lowering groundwater tables;
5. Clearing:
   - removing vegetation by burning, digging, application of herbicide, scraping, mowing or otherwise cutting;
6. Flooding:
   - raising water levels, either behind dams or by pumping or otherwise channeling water into a wetland;
7. Diverting or withholding sediment:
   - trapping sediment, through construction of dams, channelization or other types of projects; thereby inhibiting the regeneration of wetlands in natural areas of deposition, such as deltas;
8. Shading:
   - placing pile-supported platforms or bridges over wetlands, causing vegetation to die;
9. Conducting activities in adjacent areas:
   - disrupting the interactions between wetlands and adjacent land areas, or incidentally impacting wetlands through activities at adjoining sites;

Chemical

1. Changing nutrient levels:
   - increasing or decreasing levels of nutrients within the local water and/or soil system, forcing changes in the wetland plant community;
2. Introducing toxics:
   - adding toxic compounds to a wetland either intentionally (e.g. herbicide treatment to reduce vegetation) or unintentionally, adversely affecting wetland plants and animals;

Biological

1. Grazing:
   - consumption and compaction of vegetation by either domestic or wild animals;
2. Disrupting natural populations:
   - reducing populations of existing species, introducing exotic species or otherwise disturbing resident organisms.

Selected riparian habitat alterations in southern California (including most impacts reviewed in Faber, et.al., 1989).

1. Channelization:
   - "... eliminates all riparian habitat and wildlife values" (Faber, et.al, 1989); breaks continuity and connectedness of riparian corridor, fragmenting riparian habitat within a watershed; eliminates the wildlife corridor function of stream courses - whether lined or unlined channelization is employed; reduces habitat diversity and distribution within watersheds;
2. Increased sediment loading:
   - caused by logging, clearing habitat for development, construction-related sediment generation, agriculture, road-building, overgrazing, and altering the fire cycle in natural upland vegetation, among other practices which generate sediment and increase vulnerability to erosion;

Table 1 (Continued)

3. Domestic or agricultural wells, ditching and draining of wetland sites:
   - lowers water table, reduces wetted areas available to riparian vegetation;
4. Man's recreational activities:
   - off-road vehicle (both motorcycle and four-wheel drive vehicle) and mountain bicycle use of streamchannels, riparian habitat and adjacent uplands as trails denudes habitat, increases erosion, and so forth; use of riparian trees and shrubs for firewood; camping and picnicing impacts; trash accumulation; graffiti and carvings on trees; shooting (glass, damaged vegetation); trails, roads, and human and pet waste in riparian habitat -among many other recreational impacts;
5. Gravel mining:
   - disrupts the streambed, increases downstream sediment loads, alters the water table, and requires roading through riparian habitat;
6. Proliferation of exotic species:
   - non-native plant species, such as castor bean, tamarisk, Indian tree tobacco, ice plant species, Pampas grass, and many other exotics are abundant in riparian settings (for example, there are 73 exotic plant species in the San Joaquin Marsh; also see Faber, et.al., 1989); non-native snails (Helix aspersa) consume vegetation;
7. Grazing:
   - eliminates riparian habitat, degrades aquatic ecosystem values, increases sedimentation and erosion, and so forth;
8. Altering natural flooding and flow regimes:
   - flood control, water storage, diurnal water level fluctuation impacts below hydroelectric facilities, and so forth (see Faber, et. al., 1989, for a discussion of flood-triggered seed production and dispersal);
9. Mitigation banking:
   - allows regional elimination of riparian habitat, simplifies regional habitat diversity, promotes "all your eggs in one basket" syndrome by allowing consolidated offsite mitigation (for example, see the U.S. Army Corps of Engineers, 1989, proposal to mitigation bank 27 riparian sites averaging 2 acres each at a single mitigation project on Aliso Creek); loss of diversity of riparian habitat by focusing on establishing target species (willow-woodland, for example); utilization of non-local genetic stock in plantings;
10. Failed attempts at mitigation:
    - lack of successful establishment of replacement communities, low species richness, lack of mitigation for wetland habitat altered to allow a site for target species (mitigation) plantings (for example, elimination of sedge or Baccharis for replacement with willow- woodland); long time spans between habitat destruction and functional replacement (see Kusler, 1989; 1990);
11. Impacts of lowered water quality:
    - though not clearly understood for all forms of pollution, "first flush" runoff from streets and freeways; herbicide, fungicide, pesticide and fertilizer laden runoff from golf courses, agricultural fields, nurseries, and to a lesser degree urban residential areas; industrial pollution; reclaimed sewage water (nutrient and salt rich) runoff from cities using it for city and large development landscape watering; chlorinated or chloraminated runoff; seepage from septic tanks or systems, all degrade water with varying potential impacts upon aquatic ecosystems and riparian communities (especially herbs and water quality-sensitive under story species). Synergistic and cumulative impacts as pollutants accumulate in sediments;
12. Urban development, creation of golf courses, flooding behind water storage or flood control projects, conversion to agricultural uses, freeway and other road building in riparian corridors all directly contribute to habitat loss and alteration (see the first portion of Table 1).

greater than average precipitation and runoff in the winter and spring.

- The Sierran snowline will be found at higher elevations and winter rain will be more frequent at intermediate elevations.

- There will be greater air pollution (ozone, acidic pollutants) transported to higher elevations.

- There will be a northward shift of storms, resulting in more monsoonal storms reaching into the southern Sierra during the summer.

- Major climatic zones could shift as much as 30-60 km northward and in mountainous areas the shift would be in elevation not latitude (see Ferren, 1989, and Byron, Jassby and Goldman, 1989, for numerous additional potential future influences on freshwater wetland systems and other references in this burgeoning area of research).

Increased need for water by agriculture and urban requirements will stress systems, and will make riparian habitat preservation planning extremely important. With lower water volumes pollution will be less diluted which will also cause an increased impact on riparian and aquatic habitat. As Ferren (1989) stated, "In urban areas, the likely increased need for water, increased levels of ozone, and the potential need to create new reservoirs in rivers and canyons all could contribute to the loss and degradation of riparian communities." In short, global warming is not good news for riparian habitats and will exacerbate the current situation.

CHARACTERISTICS OF RIPARIAN ZONES

There are many anthropocentric as well as biocentric "benefits" afforded by wetland habitats (Table 2). Not the least of these is that nearly 35% of our endangered species depend upon wetland habitats although they comprise less than 5% of our lands (The Conservation Foundation, 1989).

Riparian zones usually have two essential characteristics: laterally flowing water that rises and falls at least once during the growing season, and a strong connectedness with other ecosystems (Ewel, 1978). They are buffers and filters between man's development and water resources. Riparian habitat is ecotonal in nature with an elongate shape and very high edge to area ratio (Odum, 1978). Riparian areas can range in width from less than a meter to hundreds of meters or more in a floodplain. Riparian habitat has a large energy, nutrient and biotic interchange with the aquatic systems on the one hand and with the upland terrestrial ecosystem on the outer margin. It exhibits the "edge effect"; the density and diversity of species tends to be higher at the land/water ecotone than in the adjacent uplands. Many animal species are riparian habitat obligates and large mammals that require access to water use the band of riparian habitat as a wildlife corridor. Hydroperiod and a natural hydrologic cycle are keys in determining vegetative composition and productivity. Riparian habitat when viewed at any point in a drainage is somewhat of an ecosystemic snapshot, and it's important to understand a site's context in terms of what lies below and above. Although botanists often don't think much about it, riparian vegetation in various stream sections in a watershed plays a large role in the energy flow in stream ecosystems (Figure 1). While this approach is diagrammatic, it is useful as long as one keeps in mind that these generalities

Table 2. Wetlands functions, including biocentric and anthropocentric elements (from The Conservation Foundation, 1989, as adapted from Kusler, 1983)

A. *Flood conveyance* - Riverine wetlands and adjacent floodplain lands often form natural floodways that convey flood waters from upstream to downstream points.

B *Barriers to waves and erosion* - Coastal wetlands and those inland wetlands adjoining larger lakes and rivers reduce the impact of storm tides and waves before they reach upland areas.

C. *Flood storage* - Inland wetlands may store water during floods and slowly release it to downstream areas, lowering flood peaks.

D. *Sediment control* - Wetlands reduce flood flows and the velocity of flood waters, reducing erosion and causing flood waters to release sediment.

E. *Fish and shellfish* - Wetlands are important spawning and nursery areas and provide sources of nutrients for commercial and recreational fin and shellfish industries, particularly in coastal areas.

F. *Habitat for waterfowl and other wildlife* - Both coastal and inland wetlands provide essential breeding, nesting, feeding, and predator escape habitats for many forms of waterfowl, other birds (see Zenbal's chapter), mammals, and reptiles.

G. *Habitat for rare and endangered species* - Almost 35 percent of all rare and endangered animal species are either located in wetland areas or are dependent on them, although wetlands constitute only about 5 percent of the nation's lands.

H. *Recreation* - Wetlands serve as recreation sites for fishing, hunting, and observing wildlife.

I. *Water supply* - Wetlands are increasingly important as a source of ground and surface water with the growth of urban centers and dwindling ground and surface water supplies.

J. *Food production* - Because of their high natural productivity, both tidal and inland wetlands have unrealized food production potential for harvesting of marsh vegetation and aqua-culture.

K. *Timber production* - Under proper management, forested wetlands are an important source of timber, despite the physical problems of timber removal.

L. *Historic, archaeological values* - Some wetlands are of archaeological interest. Indian settlements were located in coastal and inland wetlands, which serve as sources of fish and shellfish.

M. *Education and research* - Tidal, coastal, and inland wetlands provide educational opportunities for nature observation and scientific study.

N. *Open space and aesthetic values* - Both tidal and inland wetlands are areas of great diversity and beauty and provide open space for recreational and visual employment.

O. *Water quality* - Wetlands contribute to improving water quality by removing excess nutrients and many chemical contaminants. They are sometimes used in tertiary treatment of wastewater.

aren't hard and fast.

There are four primary factors governing stream ecosystems (modified from Cummins, 1979; Bowler, 1988):

- The annual hydrographic pattern (flooding cycles, low flow cycles, and seasonal variation), which determines scouring rate and the rate of hydrologic pruning, nutrient and sediment flow a riparian setting receives; hydroperiod determines the resilience of a riparian community.

- The geomorphic setting(the geology, gradient, and shape of the channel), which defines the slope and influences the non-sediment edaphic factors.

- The vegetative setting (riparian vegetation characteristics, particularly in the headwater reach), which can influence colonization rates, species diversity and the composition of communities which survive heavy seasonal floods and scouring.

- Stream order (the size of the stream).

In discussing riparian habitat it is useful to review briefly some of the characteristics of streams and drainages in headwater, mid-reach and lower river sections because it's important to realize that the often distinct settings in different reaches of a stream or river directly influence the kinds of riparian habitat found in each. Tables 3 and 4 show some of the characteristic plants from riparian woodlands in southern California and from Orange County, broken down into stream reaches. Faber, et. al. (1989) present examples of community dominants in riparian settings at various elevations at sites throughout southern California, though stream reaches are not identified.

The concept of the river as an energetic and ecosystemic continuum, as developed by Vannote, Cummins and others (Vannote, et. al., 1980; Knight and Bottorf, 1984), stresses the role that headwater vegetation plays in providing the coarse particulate organic matter which supports the predominantly heterotrophic community in the headwater reaches (Figure 1). Faber, et. al. (1989) presented an excellent synopsis of this relationship in southern Californian settings, although there is little data to fill out the broad ecosystemic functions known in other regions. As Faber, et. al. (1989) summarized, "Detritus provided by riparian vegetation is a source of up to 90 percent of the nutrients consumed by instream aquatic communities (Hubbard, 1977; Cummins, 1975; Merritt, 1978; Hart, 1975)." Furthermore, upland fire-adapted plant communities such as chaparral and coastal sage scrub may contribute nutrients to adjacent aquatic ecosystems through post-fire runoff (Faber, et. al., 1989).

The concept of connectedness (Ewel, 1978) plays a significant role in resilience, ensuring inflow of species after disturbance, but also exposes a system to the battering of impacts from above. In stream headwaters there is usually a heavy riparian cover, often with a closed canopy over the stream which limits the light reaching the streambed. This cover produces a heavy litter load and serves as the source for large quantities of coarse particulate organic matter, enhanced by deciduous trees and shrubs if the headwater elevation is great. The coarse particulate organic matter derived from riparian habitat becomes the primary foodsource for the predominantly heterotrophic community in light-limited, heavily shaded headwater situations. Headwater shading can also have a profound influence on water temperature. As is evident in Table 4, many of the

TABLE 3. Selected species occurring in Southern California riparian habitat in headwater, mid-drainage and floodplain settings. The abbreviations are keyed as follows: Deciduous = D; Evergreen = E; Headwater reach = HW; Mid-drainage = M; Floodplain = FP. (Adapted from Roberts, et.al., 1977 by Fred Roberts.)

1. Trees

A. Common:

Alnus rhombifolia	M (-FP)	D
Platanus racemosa	M - FP	D
Populus fremontii	FP	D
Quercus agrifolia	HW - M	E
Salix laevigata	FP	D
Salix lasiandra	FP	D

B. Uncommon:

Acer macrphyllum	HW	D
Juglans californica	M	D
Populus trichocarpa	M - FP	D
Umbellularia californica	HW - M	E

2. **Shrubs**

A. Common

Artemesia douglasiana	M - FP	E
Baccharis emoryi	FP	E
Baccharis glutinosa	M - FP	E
Baccharis pilularis subsp. *consanguineus*		E
Cornus occidentalis	HW	D
Phoradendron tomentosum subsp. *macrophyllum*	M	
Rosa californica	M - FP	D
Salix hindsiana	FP	D
Salix lasiolepis	HW - FP	D
Sambucus mexicana		D

TABLE 4. Riparian communities in headwater, mid-drainage and floodplain settings in Orange County, California. The abbreviations are keyed as follows: E = Evergreen; D = Deciduous. These "communities" are not formally named, and are based on observation. (Compiled by Fred Roberts.)

1. Headwater Settings, 800-1700 meters
Montane Riparian Woodland

Acer macrophyllum	D
Quercus chrysolepis	E
Quercus agrifolia	E
Umbellularia californica	E

2. Midreach Settings, 180-800 meters
Riparian Woodland

Quercus agrifolia	E
Alnus rhombifolia	D
Platanus racemosa	D
Salix lasiolepis	D
Populus trichocarpa	D
Fraxinus velutina	D

3. Floodplain Settings, 0-180 meters
Sycamore Alluvial Woodland

Platanus racemosa (widely scattered)	D
Quercus agrifolia	E
Sambucas mexicana	D

4. Lowland Riparian Forest

Populus trichocarpa	D
Populus fremontii	D
Salix lasiolepsis	D
Salix laevigata	D

Toxicodendron and Artemesia douglasiana are not uncommon, and less frequently Platanus racemosa and Quercus agrifolia.

5. Willow Woodland

Salix lasiolepsis	D
Salix laevigata	D
Salix goodingii	D

Mugwort often common in this communtiy as well.

6. Mulefat Scrub

Baccharis glutinosa	E

Often there is a little Salix lasiolepsis and Salix goodingii, but there isn't a real overstory development.

7. Willow Scrub

Salix hindsiana	D

Some other willows as well.

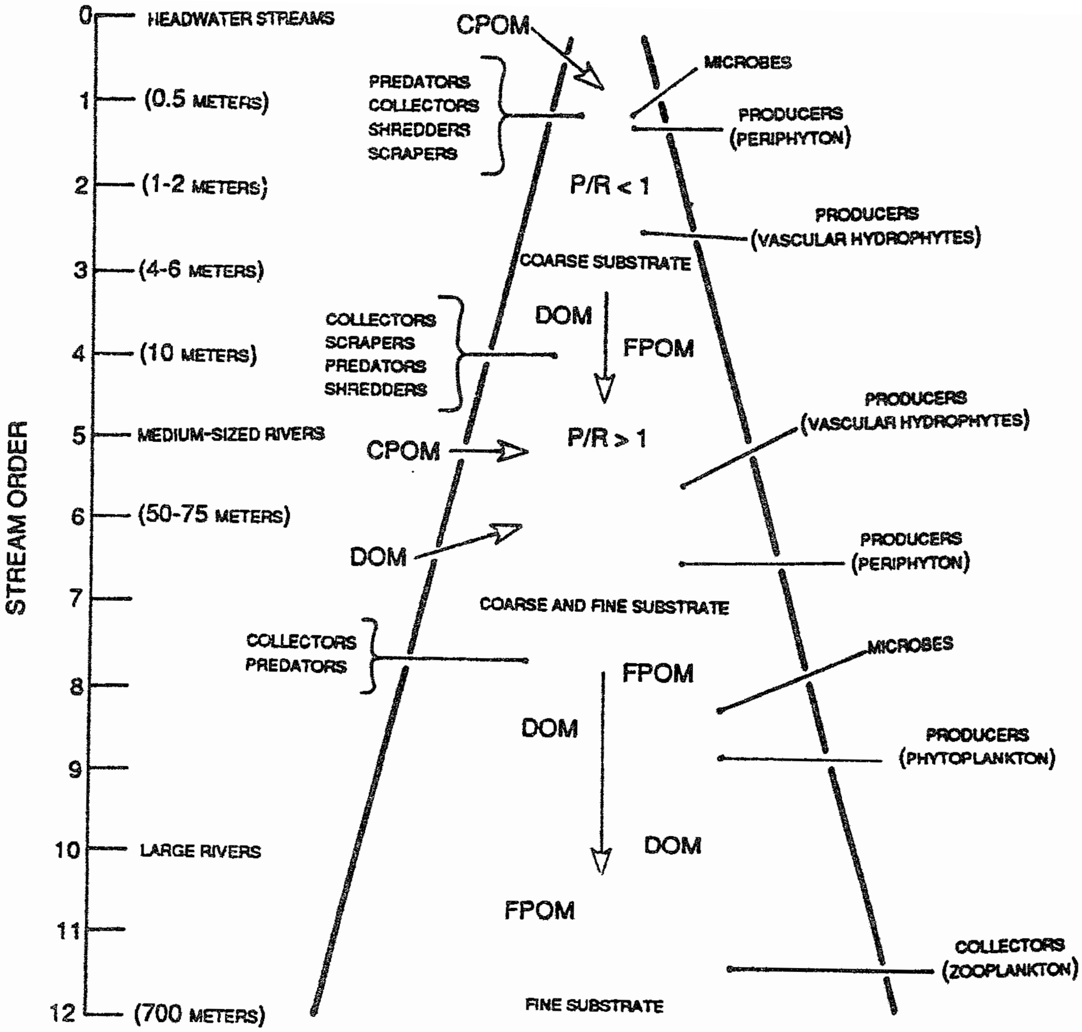

Figure 1. Schematic representation of a Sierran stream shown as an expanding continuum from headwaters (0.5-6m wide; order = 1) to a medium-sized river (50-75m wide; order = 4-6), to a large river (up to 700m wide; order = 12). Abbreviations: P/R = ratio of gross photosynthesis to community respiration; CPOM = coarse particulate organic matter; FPOM = fine particulate organic matter; DOM = dissolved organic matter. Headwaters and large rivers are heterotrophic (P/R < 1), medium-sized rivers are shown as autotrophic (P/R > 1). (From Bowler, 1988, as adapted from Cummins, 1975, 1979; Knight and Bottorff, 1984; Vannote, et al, 1980.)

dominant woody species characteristic of headwater sites in Orange County are not deciduous, an interesting situation somewhat in contrast with other California settings.

In the mid-river reaches, the aquatic ecosystem shifts from a heterotrophic to an autotrophic community due, among other reasons, to a widening of the river valley and lack of a light-limited aquatic setting. There is usually relatively little shading by riparian vegetation in the middle sections of river systems, and there are higher nutrient and fine particulate organic matter levels from the upstream vegetation sources, which shifts the invertebrate community from shredders to grazers (Figure 1). The gradient is usually much flatter than headwaters and a well configured flood plain is often developed. The stereotypic "riparian forest" is often present in this section of the streamcourse.

The lower reaches of rivers near the mouth reflect a flat gradient with a broad floodplain. Under natural conditions this portion of a drainage would see seasonal flooding and blanketing with layers of soil and nutrients.

HUMAN IMPACT ON RIPARIAN HABITAT

As anyone living in southern California is aware, humans have dramatically altered, if not mangled, nearly every watershed in our region (Figure 2). It has been said that the third largest perennial freshwater tributary entering the ocean in California and the largest in southern California is the Hyperion sewage treatment plant outfall. Water diversions reduce riparian potential and dams similarly alter natural drainage processes. In southern California, the Sweetwater River, Tijuana River and San Diego River were all perennial streams before water storage projects altered their natural hydrologic cycle.

By and large, dams produce half-lakes with depauperate terrestrial species diversity compared with free-flowing river reaches. As can be seen, for example, in San Diego County at Loveland Dam on the Sweetwater River near El Cajon, riparian vegetation is scoured out of the area below the dam. Residents familiar with the Sweetwater River in the reach below Loveland Dam recall white alder, <u>Alnus rhombifolia</u>, as a riparian community dominant, however, this species is now absent due to the altered stream flows caused by the water storage project (William Bretz, pers. comm.). Above the dam there is virtually no "riparian" vegetation, but a bathtub ring series of water level marks etched into a sterile hillside with emergent vegetation at the water's edge.

Though not a southern California situation, a site on the upper Middle Snake River in Idaho which my students and I studied, exhibited this phenomenon well (Jensen and Verhovek, 1980). In this study area within the Columbia Plateau and dominated by great basin sage associations and deciduous riparian forest along the river, we identified 158 vascular plant species, though only 78 species actually occurred within our transects. The Lower Salmon Falls Dam impoundment study site had a total of only 55 species, 34.5% of which were introduced. Along this impoundment there had been very little shoreline revegetation since the present water level was established around 40 years ago (the original riparian valley bottom was inundated in 1910 with a lower dam which was subsequently raised). The great basin sagebrush community came nearly to the water's edge and there was a discontinuous, thin band of a few meters

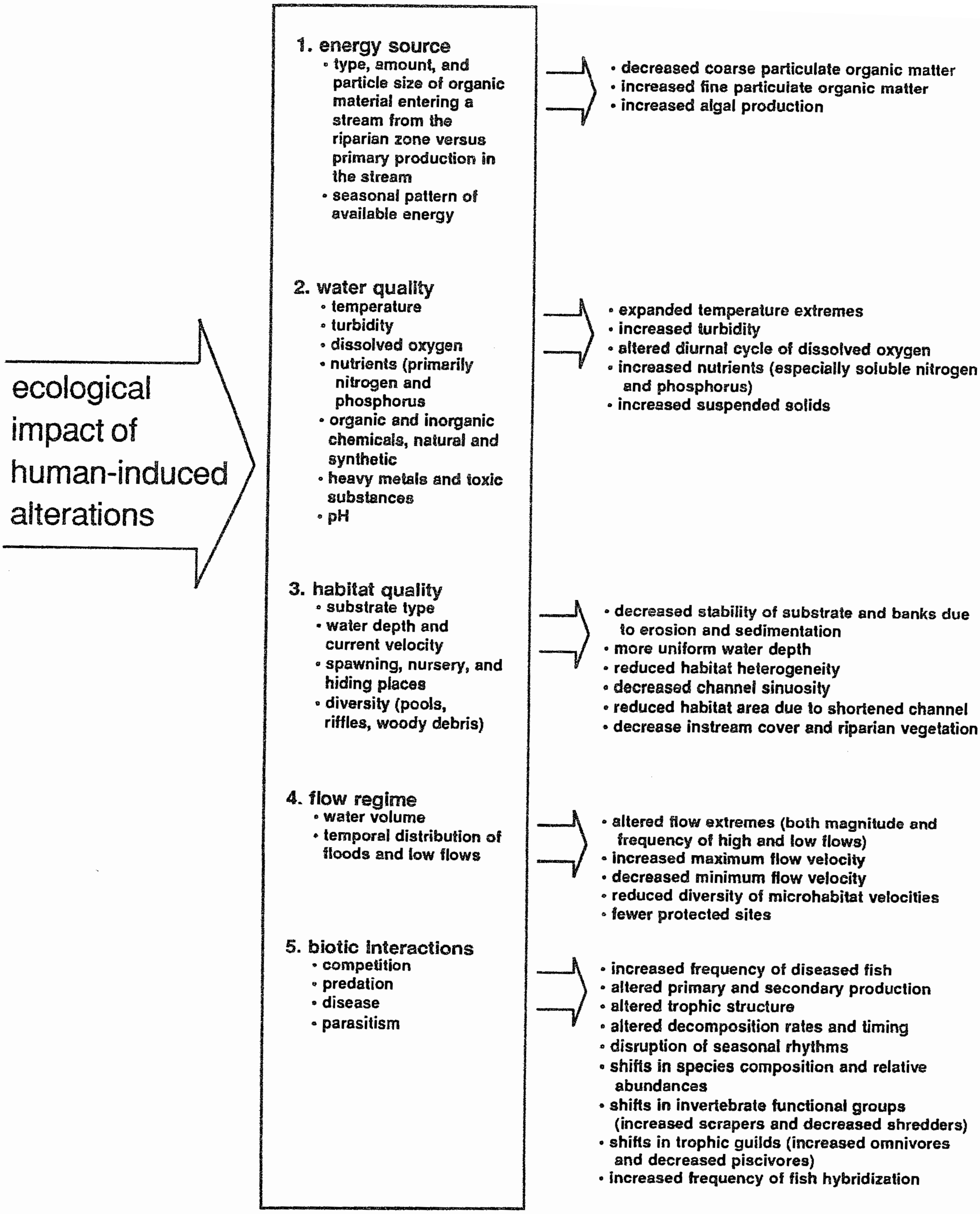

Figure 2. Five major classes of environmental factors that affect aquatic biota. The arrows indicate the kinds of effects that can be expected from human activities, in this case the alteration of headwater streams, excluding small impoundments (from Karr, et al., 1986, as modified from Karr, et al., 1983).

of low riparian vegetation. At three sample sites along the tailwaters below the dam, however, there was a very different species diversity and community composition, with 80 to 90 species present, a non-native percentage of 27%, and with large groves of hackberry (Celtis reticulata), river birch (Betula occidentalis), and squawbush (Rhus trilobata) - dominants of a rare deciduous riparian forest formation. In this study area riparian vegetation ranged between 0.5 and 75 meters from the water, and was typified by inconsistent distribution of species, mosaics of suitable habitat and many species which were infrequent or rare along the reach.

These results aren't surprising, since virtually all terrestrial, as well as aquatic, conditions are different before and after closing a water project. It's intuitively easy to see how eliminating habitat conditions along a natural streambed and raising the waterline to a height along a canyon wall normally dominated by sagebrush, chaparral or some other slope-inhabiting upland plant community, would produce a sterile shoreline.

Flood control projects - designed to capture water during flooding events and are therefore kept drained - are different in attendant vegetation from run-of-the-river hydroelectric impoundments, which are designed to store and release much smaller quantities of water. As Zembal documents elsewhere in this volume, the Prado Dam basin, designed as a storage facility for flood control, is a unique situation which has unintentionally created an interesting riparian situation with a simple community comprised of a few dominant species (Zembal, 1984a; see also Zembal, 1984b for data on the Santa Margarita River, still a natural riparian setting).

Another fundamental hydrologic character which has been transformed in southern California is that of the natural flooding cycle and the scouring effect experienced in mid-river and lower reach areas. While diversion of instream flow has reduced the quantity of water available for natural processes in a drainage, water storage has similarly altered the timing of waterflow in a stream - occasionally altering the seasonal streamflow regime to suit perennial percolation requirements and inadvertently providing a water supply more dependable during the dry season than would occur without dams and impoundments. In this context, a number of models have been designed to examine instream flow needs for aquatic ecosystems, but in reality not much is known about longterm impacts of altered instream flows upon riparian vegetation and terrestrial ecology.

A summary of data from California basins by the U.S.F.W.S. WELUT team indicated that:

- 10% of average annual streamflow is the absolute minimal to sustain short-term survival of most aquatic life forms.

- 40% of average annual streamflow is required as a base flow to sustain an adequate habitat for (aquatic) survival.

- 60% of average annual streamflow is required to provide excellent habitat protection for most aquatic life forms and the majority of recreational needs.

Even if this controversial and simplistic "rule of thumb" for aquatic habitat is accepted, there is little real idea of how reducing streamflow to these degrees would alter riparian habitat, but it would likely be profound.

While water storage and streamflow diversion cause changes, flood control causes others. As is intuitively obvious, flooding impacts increase progressively down a drainage, and the successional aspect of riparian communities caused by streamside scouring, similarly, is often most conspicuous in the floodplain reaches below headwaters. Flood control projects capture runoff and hold back the scouring, sediment, and nutrient-transporting flows which normally would flush out stream channels and thin vegetation. In a sense, the lower areas of southern California drainages are more advanced and denser in riparian formation (as much as streamflow allows, so that these are like the riparian formations of smaller streams) than they would have been without flood interruption, when succession would have been a more rapid process. The historic canyons and floodplains are overfit for the reduced flows in them today. Channelization, another element of flood control, is habitat evisceration, leaving vegetation and stream ecology with segmented, sterile breaks in connectedness (see Faber, et. al., 1989, for an excellent treatment of this ubiquitous habitat gutting in southern California).

In this context, riparian vegetation can be characterized in areas of flooding as having many of the opportunistic features of plants entering disturbed areas - rapid colonization, high productivity, good dispersal, and so forth. Especially at lower elevations, if a reach is not flooded and scoured, species diversity drops and woody species, especially willows, become dominant. This is particularly true in urban or agricultural runoff situations, in which water is continuous during otherwise dry seasons for natural streams of comparable size. This "urban slobber" or "nuisance flow" has created a "new" category of riparian habitats, which are particularly important in southern California. Since the drainage capture of the Owens and Colorado Rivers, availability of water has resulted in runoff through drains, ditches and streamcourses which otherwise wouldn't occur. The U. S. Fish and Wildlife Service is in the process of inventorying California wetlands. The results of their survey will provide the first quantitative insight into the distribution and acreage of runoff-induced riparian habitat. In Orange County, the San Diego Creek and Laguna Lakes drainages are case histories that illustrate this phenomenon.

The San Diego Creek drainage as it exists today is an artifact of man's urban and agricultural needs. The broad contour of the drainage reflects an ancient and abandoned Santa Ana River channel; however, prior to the 1880s it was not a drainage emptying in the sense it does today into Upper Newport Bay. The end of the 1880s saw a gradual change from a pastoral land use to one more agriculturally based, rapidly leading to the need to drain and ditch the "Cienga de las Ranas," an extensive marshy wetland that formerly covered the Tustin Plain. The transition from range to fields occurred in a 20-year period, and the water table under the Tustin Plain, which had been ditched and drained beginning in 1906, dropped 10.2 meter between 1904 and 1928. Ditches became the watershed channels for storm flow, and by 1932 these channels connected with Upper Newport Bay. In 1942 the 47-acre (19 ha) Sand Canyon Reservoir was constructed and is currently owned and operated by the Irvine Ranch Water District. In the late 1960s San Diego Creek was channelized. The areas of the drainage that illustrate the effects of agricultural runoff and channelization particularly well are the sections below Sand Canyon Reservoir to MacArthur Bridge.

Over the past forty, but especially

during the last twenty years, the "stream" segment below Sand Canyon Reservoir has developed a lush closed-canopy willow habitat, which now extends all the way through Mason Regional Park to Culver Drive. Sunset Magazine recently touted the bicycle trail through the corridor as being one of the best touches of nature available to cyclists. While this is an excellent example of low elevation, willow-dominated habitat, it is actually a fairly simple community. The dominant willows are Salix goodingii, S. laevigata and S. lasiolepis. This cohort of willows has grown into trees of 5 or more meters in height. A few cottonwoods and a sycamore or two have been planted, so that the prospect is good for developing a multi-story habitat along the creek in future decades. Nonetheless, it is a skeleton, species-poor community compared with analogous elevational settings in natural streamcourses, such as the Santa Margarita River (Zembal, 1984b), though the scale in instream flow is significantly different between these sites.

The flood control channel between Campus Drive Bridge and MacArthur Bridge includes a sediment capture basin and the channelized creekbed with drop structures at both bridges. The sediment basin is cleared roughly each 5 years, and in the interim an interesting mosaic of plant communities develops. The flood control channel downstream of the sediment basin is also cleared, but less frequently. This site supports 59 species of plants, of which 59% are introduced. A majority of these species are rapid colonizers and are weedy.

Contrast this with the species-poor and simpler community in the Sand Canyon Wash above the "Christ College" reach. This riparian community is watered largely by agricultural runoff and has a poor herb and understory species representation - perhaps due to chemicals used on the fields. In these sites there is a climax willow situation, where the tall and dense stands of only a couple of Salix species become dominant. In a sense this is almost a senescent community, while the flood control channel supports a more diverse but early successional group of species.

The Laguna Canyon complex of vernal pools, lakes, perched drainage habitat and the riparian corridor provides a different insight to artificially enhanced watersheds. At this site a vernal pool has been severely degraded by cattle and the proliferation of Eucalyptus in the pool basin. Overflow of the lake receiving urban runoff from a portion of Leisure World (a local retirement community) enters a perched groundwater lens and supports a rich and diverse riparian community - primarily watered by subsurface sources. A channel on the opposite side of Laguna Canyon Road has a large willow corridor - not unlike that in Mason Park. In this mosaic of wetland communities there are approximately 75 species, 61% of which are native.

Data on Table 5 suggest how selected local habitats rank in terms of introductions and disturbance. Though Table 5 represents only a few sites, it's interesting to consider the degrees to which local communities have been invaded by non-native species. One could hypothesize from these data that local lightly to moderately disturbed coastal sage scrub and chaparral communities have somewhat fewer introductions (around 21-17%) than heavily grazed grasslands (around 40%), and that ruderal habitats could have the highest proportions of introduced species (58%). Riparian habitat seems variable, but supports a substantial suite of non-native species (between 28 and 38%). An advanced growth flood-control channel

Table 5. An analysis of some selected habitats (data are summarized from the University of California, Irvine, 1989 EIR record; Zembal, 1984a; Laguna Canyon EIR record; the Natural Reserve System database on the San Joaquin Marsh; and Jensen and Verhovek, 1980 for the Snake River sites).

Site	Habitat Type	No. of Sp.	% Native	% Exotic
UCI	C. Sage Scrub	120	68%	32%
Lag. Canyon	C. Sage Scrub	110	79%	21%
Quail Hill	Grassland	67	57%	43%
Lag. Canyon	Grassland	133	62%	38%
Lag. Canyon	Chaparral	93	79%	21%
UCI SD CR.	Riparian	59	41%	59%
UCI	Riparian pockets	26	62%	28%
Lag. Canyon	Riparian/mixed Wetlands	75	61%	39%
Lag. Canyon	So. Oak Wdl.	122	70%	30%
Lag. Canyon	"Ruderal Habitats"	91	42%	58%
San Joaquin Freshwater Marsh		159	54%	46%
Prado Dam Basin & Environs.		311	68%	32%
Riparian/Dam Basin Only		143	63%	37%
Snake River				
Impoundment	Riparian	55	65%	35%
Freeflowing	Riparian	155	73%	27%

had a percentage of around 59% non-natives, on a par with "ruderal habitats." If true, this could be because bulldozed "ruderal" area habitat is similar to the periodically pruned flood control channel in providing "habitat" most suitable to rapidly invading introduced weedy species.

Finally, any discussion of riparian habitat would not be complete without at least mentioning the impact of cattle upon western stream habitats. Grazing has been one of the most profound degraders of riparian habitat on public lands in the west, and the wreckage associated with cattle, such as trampling and subsequent increased runoff, destroys not only streamside vegetation but the instream ecology as well.

In conclusion, there is no question that riparian habitat is endangered in southern California. Wherever "natural" stands occur along historic watercourses they should be protected, and we should not be too proud as botanists to also demand "no net loss" standards for the fragments of habitat developing along urban and agricultural runoff areas (See Kusler, 1989; 1990, for a thorough review of the successes and failures of the "no net loss" strategy of wetland preservation or replacement.

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LITERATURE CITED

Bowler, P.A. 1988. Thoughts about Subtle Impact Potentials of Headwater Sited Small Hydroelectric Devlopments on River Processes. Pp. 13-18 in Bradley, E. (ed.). Proceedings of the State of the Sierra Symposium, 1985-1986. Pacific Publications Co., San Francisco, California.

Byron, E.R., A. Jassby, and R. Goldman. 1989. The Ecological Effects of Global Climate Change on Freshwater Lakes and Streams. Prepared for the Workshop on Global Climate Change and Its Effect on California, University of California, Davis, 10-12 July, 1989. Draft manuscript.

Cummins, K.W. 1975. The Ecology of Running Water: Theory and Practice. Pp. 277-293 in Hynes, H. B. (ed.). Proceedings of the Sandusky River Basin Symposium. International Joint Commission of the Great Lakes. Heidleberg College, Tiffin, Ohio.

Cummins, K.W. 1979. The Natural Stream Ecosystem. Pp. 7-24 in Ward, J.V. and J.A. Ward. International Symposium on Regulated Streams, lst. The Ecology of Regulated Streams.

Ewel, K.C. 1978. Riparian Ecosystems: Conservation of Their Unique Characteristics. Pp. 56-61 in Johnson, R.R. and J.F. McCormick, tech. coords. Symposium Proceedings: Strategies for Protection and Management of Floodplain Wetlands and Other Riparian Ecosystems, Callaway Gardens, Georgia. U.S. For. Serv. Gen. Tech. Rep. WO-12.

Faber, P.A., E. Keller, A. Sands, and B.M. Massey. 1989. The Ecology of Riparian Habitats of the Southern California Coastal Region: A Community Profile. U.S. Fish Wildl. Serv. Biol. Rep. 85(7.27). 152 pp.

Ferren, W. R., Jr. 1989. Climate Change and Its Potential Effects on Wetlands in California. Prepared for the Workshop on Global Climate Change and Its Effect on California, University of California, Davis, 10-12 July, 1989. Draft manuscript.

Frayer, W.E., et al. 1983. Status and Trends of Wetlands and Deepwater Habitats in the Conterminus United States, 1950's to 1970's. Colorado State University, Fort Collins, Colorado.

Hart, S.D. 1975. The Decomposition of Leaves in Two Southern California Streams. Master's Thesis. University of California, Santa Barbara.

Hubbard, J.P. 1977. Importance of Riparian Ecosystems: Biotic Considerations. Pp. 14-18 in Johnson, R.R. and D.A. Jones, (eds.). Symposium Proceedings; Importance, Preservation and Management of Riparian Habitat. U.S. For. Serv. Gen. Tech. Rep. RM-43.

Jensen, D. and L. Verhovek. 1980. Vegetation Analysis. In Studies of Water Use on the Snake River Drainage, Southern Idaho. National Science Foundation Student Originated Studies Program, Grant SPI-7905344.

Karr, J.R., K.D. Fausch, P.L. Angermeier, P.R. Yant, and I.J. Schlosser. 1986. Assessing biological integrity in running waters: a method and its rationale. Illinois Natural History Survey Special Publication 5. 28 pp.

Karr, J.R., L.A. Toth, and G.D. Garman. 1983. Habitat preservation for midwest stream fishes: principles and guidelines. EPA-600/3-83-006. U.S. Environmental Protection Agency, Corvallis, Oregon.

Knight, A.W. and R.L. Bottorff. 1984. The importance of riparian vegetation to stream ecosystems. Pages 160-167 in Warner, R. F. and K.M. Hendrix, (eds.). California Riparian Systems: Ecology, Conservation and Productive Management. University of California Press, Berkeley, California.

Kusler, J.A. 1983. Our National Wetlands Heritage: A Protection Guidebook. Environmental Law Institute, Washington, D.C.

Kusler, J.A. 1989. No Net Loss and the Role of Wetlands Restoration/Creation in a Regulatory Context. Association of Wetland Managers. Unpublished manuscript.

Kusler, J.A. 1990. Viewson Scientific Issues Relating to the Restoration and Creation of Wetlands. pp. 217-230. In Bingham, E. H. Clark, II, L.V. Haygood, and M. Leslie (eds.). Issues in Wetlands Protection: Background Papers Prepared for the National Wetlands Policy Forum. The Conservation Foundation, Washington, D.C.

Merritt, R.W. and D.L. Lawson. 1978. Leaf litter processing in floodplain and stream communiities. In Johnson, R.R. and J.F. McCormick, tech. coords. Symposium Proceedings: Strategies for Protection and Management of Floodplain and Other Riparian Ecosystems, Callaway Gardens, Georgia. U.S. For. Serv. Rep. WO-12.

Odum, E.P. 1978. Ecological importance of the riparian zone. Pages 2-4 In R.R. Johnson and J.F. McCormick, tech. coords. Symposium Proceedings: Strategies for Protection and Management of Floodplain Wetlands and Other Riparian Ecosystems. Callaway Gardens, Georgia. U.S. For. Serv. Gen. Tech. Rep. WO-12.

Orange County Environmental Management Agency. August 28, 1989. Draft Supplemental EIR No. 502. Laguna Laurel Planned Community. State Clearinghouse No. 88113025.

Roberts, W.G., J.G. Howe, and J. Major. A Survey of Riparian Forest Flora and Fauna in California. pp. 3 - 20, In Sands, A. (ed.). Riparian Forests in California: Their Ecology and Conservation. Institute of Ecology Publication No. 15.

The Conservation Foundation. 1988. Protecting America's Wetlands: An Action Agenda. The Final Report of the National Wetlands Policy Forum. Harper Graphics, Waldorf, Maryland.

Tonnessen, K.A. 1989. Implications of

Global Warming for Watersheds of the Sierra Nevada. Prepared for the Workshop on Global Climate Change and Its Effects on California, University of California, Davis, 10-12, 1989. Draft manuscript.

University of California, Irvine. 1989. Long Range Development Plan Environmental Impact Report. State Clearinghouse No. 8805212. (Including submissions by P.A. Bowler summarizing data on campus habitats; incorporated by reference.)

U.S. Army, Corps of Engineers, Los Angeles District. December 10, 1989. Mission Viejo Company and Orange County EMA Clean Water Act Section 404 Permit Application (Applic. No. 90-057-MD).

U.S. Congress, Office of Technology Assessment. 1984. Wetlands: Their Use and Regulation. OTA-0-206. U.S. Government Printing Office, Washington, D.C.

Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37: 130-137.

Wilson, E.O. 1989. Threats to Biodiversity, Scientific American 261 (3): 108-116.

Zembal, R. 1984a. Survey of vegetation and vertebrate fauna in the Prado Basin and the Santa Ana River Canyon, California. U.S. Army Corps of Engineers, Los Angeles.

Zembal, R.A. 1984b. Fish and Wildlife Coordination Act Report, Santa Margarita River Project, San Diego County, California. U.S. Bureau of Reclamation, Lower Colorado Region, Boulder City, Nevada. Biol. Op. 1-1-86-F-9.

The New York Times

As Carr Fire Kills 2 in California, Firefighters Reflect on a Job Now ‘Twice as Violent’

By Scott Bransford, Jennifer Medina and Jose A. Del Real

July 27, 2018

REDDING, Calif. — When Brian Rice fought wildfires in the 1990s, his time on the line was intense during the summer fire season, followed by months to recharge during the cooler winter. But fighting wildfires is no longer seasonal work in California.

“There used to be a rhythm to this, and you could at least count on that rhythm,” he said. “It’s a year-round cycle now.”

Since 2012, according to state emergency management officials, there has not been a month without a wildfire burning — a stark contrast to previous decades, when fire officials saw the fall and winter as a time to plan and regroup. The recent historic drought and rising temperatures have heightened an already serious risk for widespread fires in the state.

Just this month, there have been three firefighters killed on the front lines, including two who died during a rapidly expanding wildfire in Northern California in the last two days. Dry conditions and triple-digit temperatures added fuel to that fast-moving blaze, known as the Carr Fire, as it marched eastward, swept over the Sacramento River and pushed into the outskirts of Redding, the largest city in the region. It continued to grow on Friday, burning dozens of buildings and prompting emergency officials to issue an urgent plea for people in parts of Redding and the surrounding areas to evacuate immediately.

“This fire is extremely dangerous and moving with no regard for what’s in its path,” said Bret Gouvea, the incident commander for the California Department of Forestry and Fire Protection.

Gov. Jerry Brown has called this the new normal and set aside more than $440 million in the state budget for emergency wildfires. But beyond the costs, the year-round fires have taken a heavy toll on thousands of firefighters in the state.

[*Read more about why experts are saying this summer's destructive wildfire season is "the new normal."*]

In the town of Corning, about an hour south of Redding, the Rolling Hills Casino offered shelter to about 200 evacuees, opening its doors for people and animals fleeing flames for the second time this year. Evacuees slept in a ballroom off the main casino Friday, talking to family members on cellphones and watching for fire updates on a big-screen television.

For Michelle Hickok, 30, a graphic designer at the casino, the start of each fire brings the fear that her husband, a local firefighter, will be in harm's way. The longer fire seasons have exacerbated that worry, she said. "With summer being hotter and longer, you have tons of dry fuel up here," she said.

Firefighters had long looked at the area now burning and saw the dry vegetation as a disaster waiting to happen, she said. "They were afraid that when that day came it would be bad, and they were right," she said.

The fires in 2017 were among the most destructive in California's history, causing nearly $12 billion in damage and leaving 46 people dead.

"This job has gotten twice as busy and twice as violent," said Mr. Rice, who retired from fighting fires in 2011 and is based in Sacramento, and is now president of California Professional Firefighters, a statewide union. "I was down in Ventura and realized, holy smokes, we have firefighters on the fire line on Christmas Day. In my 30 years, I've never heard of that.

COMMENT OF THE MOMENT

K

Kathy Lollock **Times Pick**
Santa Rosa, CA | July 27

This is a nightmarish replay of what my county went through last year. I pray for those people and their homes. How can there be any doubt of global warming and climate change? Over my long years of life here in CA, I have recently witnessed too many hot summers, fierce and destructive winds, and dry winters. Yet the powers that be deny us the means to at the very least assuage the wrath of Mother Nature. We can do something about this. But this administration sacrifices the many for the few who are parasites off the land in the name of greed.

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"This is the first year for me that I really feel like one fire season has connected itself to the next 12 months," he added. "Is that going to be the new normal or the new reality? I don't know."

In addition to the Carr Fire, wildfires are burning in Central and Southern California. The Ferguson Fire caused the largest closing of Yosemite National Park in 30 years, and the Cranston Fire is only 5 percent contained in the San Jacinto Mountains in Southern California. After evacuating thousands of tourists and residents near Yosemite earlier this week, officials on Friday were closely monitoring the flames as they crept toward groves of dry, dead trees.

“Now we really are having to look into a crystal ball, not only in terms of fires we’re fighting already, but also fires that haven’t even started yet,” said Kelly Huston, a spokesman for California’s Office of Emergency Services. “In the past there was some logic, some time to plan, but we don’t have that time any more because these fires are so hot and so fast they are getting away from us more quicker than they used to.”

A firefighter at a home that was destroyed in Redding, Calif., on Friday. Temperatures in the region were predicted to reach 110 degrees. Justin Sullivan/Getty Images

The constant fires have also made it more difficult to get enough firefighters up and down the state, with officials constantly scrambling to make sure there are enough people available, Mr. Huston said.

Often, the stretched resources have meant more firefighters working longer hours for longer stretches of time, leaving many of them exhausted. Experts and state officials said they all worry about short- and long-term fatigue, which can lead to mistakes.

“They still love it and they are still dedicated, but it takes a huge toll on them,” said Nancy Bohl-Penrod, a psychologist who has worked with firefighters across the country for 30 years and who is currently supervising therapists working with firefighters in Yosemite. “When they get home, some of them don’t talk to their families about it. Some it is just the mere fact that they are exhausted and that impacts their emotion and, their personality.”

Dr. Penrod said far more fire departments are carrying out wellness and support programs and she has also seen a significant spike in the number of spouses and parents of firefighters attending workshops to learn how to cope with fires lasting for weeks on end.

Standing in a parking lot on the outskirts of Redding, where firefighters from multiple agencies had gathered, Anthony Romero, with the Kern County Fire Department, said the dynamics of present-day fire seasons also throws firefighters off by taking them further from their home bases, calling upon them to fight fires in parts of California where the terrain and weather patterns are unfamiliar. Mr. Romero, dripping with sweat and flecked in ash, noted that many firefighters from coastal California were not accustomed to Redding’s notoriously intense sun, its parched and radiating grasslands, or its warm downslope winds.

“We can just stand here and we’re dripping,” Mr. Romero said. But, he added, “We still adapt to what’s going on.”

Scientists say that severe wildfire seasons in California may occur more frequently because of climate change. Since the 1970s, temperatures have risen by two degrees Fahrenheit in the western United States. And trees and grasses — the fuel of wildfires — are more dry and for longer periods of the year. That means fire season now lasts three months longer than it used to, starting earlier and often going on through the fall, said Jennifer Balch, a fire ecologist at the University of Colorado at Boulder.

“What’s going on in the background is we’ve got warmer conditions. It’s making our fuels drier earlier and for longer,” Dr. Balch said. “Wildfires are a real in-your-face way we’re seeing evidence of a warming climate.”

California is feeling the brunt. Seven of the state’s largest forest fires have come in the last decade, including one every year since 2012.

From Thursday night to Friday morning, the Carr Fire raged out of control and scorched an additional 16,000 acres, bringing the total area burned to more than 44,000 acres. By Friday night, an additional 4,000 acres had been burned. Firefighters struggled to contain its growth; the blaze was 5 percent contained on Friday night.

The weather was not expected to offer any relief through the weekend, according to the National Weather Service. The high temperature in Redding was in the hundreds on Friday and was expected to rise the next two days. Wind gusts could reach 25 miles an hour in areas where the fire continues to rage.

Fire officials said it was too early to account for the total damage caused by the Carr Fire, but said that at least 500 structures had been destroyed and additional 75 damaged. Nearly 5,000 structures in its path were threatened.

On Friday, the roads leading into downtown Redding, usually teeming with the traffic of summertime tourism, were largely deserted except for emergency vehicles.

Sundial Bridge, a popular stop for motorists on their way to Mount Shasta and points north, was closed because of the fire, and its parking lot, often filled close to capacity on weekend travel days, was mostly empty.

Flecks of ash checkered the blue uniform of Robert Valente, 61, a security guard for the facility, as he halted a stray group of tourists from the San Francisco area. Mr. Valente said it is frightening to see a fire this close to Redding. “You could lose everything,” he said.

Erick Mattson, a captain with the Redding Fire Department, was battling out-of-control flames encroaching on homes in the Old Shasta community just outside Redding on Friday morning. Mr. Mattson, who has been a firefighter for over 20 years, said that his fire season used to end in October or November, but now stretches across the entire year.

“It’s a situation where we just have to keep going. Those that have been in the fire service for a long time, they develop the skills necessary to cope with your body shutting down,” he said. “That’s kind of what we do. We encourage each other. We understand what the job is and what the end goal is. It’s about serving the public and that’s what pushes us, even when the fire seasons go longer.”

Scott Bransford reported from Redding, Calif.; and Jennifer Medina and Jose A. Del Real from Los Angeles. Reporting was contributed by Matthew Haag, Somini Sengupta, Daniel Victor, Inyoung Kang and Terence McGinley in New York.

A version of this article appears in print on July 27, 2018, on Page A10 of the New York edition with the headline: Fire Kills Two In California, As It Reaches Urban Areas

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Conservation Biology

Contributed Paper

Permeability of Roads to Movement of Scrubland Lizards and Small Mammals

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Abstract: *A primary objective of road ecology is to understand and predict how roads affect connectivity of wildlife populations. Road avoidance behavior can fragment populations, whereas lack of road avoidance can result in high mortality due to wildlife-vehicle collisions. Many small animal species focus their activities to particular microhabitats within their larger habitat. We sought to assess how different types of roads affect the movement of small vertebrates and to explore whether responses to roads may be predictable on the basis of animal life history or microhabitat preferences preferences. We tracked the movements of fluorescently marked animals at 24 sites distributed among 3 road types: low-use dirt, low-use secondary paved, and rural 2-lane highway. Most data we collected were on the San Diego pocket mouse (*Chaetodipus fallax*), cactus mouse (*Peromyscus eremicus*), western fence lizard (*Sceloporus occidentalis*), orange-throated whiptail (*Aspidoscelis hyperythra*), Dulzura kangaroo rat (*Dipodomys simulans*) (dirt, secondary paved), and deer mouse (*Peromyscus maniculatus*) (highway only). San Diego pocket mice and cactus mice moved onto dirt roads but not onto a low-use paved road of similar width or onto the highway, indicating they avoid paved road substrate. Both lizard species moved onto the dirt and secondary paved roads but avoided the rural 2-lane rural highway, indicating they may avoid noise, vibration, or visual disturbance from a steady flow of traffic. Kangaroo rats did not avoid the dirt or secondary paved roads. Overall, dirt and secondary roads were more permeable to species that prefer to forage or bask in open areas of their habitat, rather than under the cover of rocks or shrubs. However, all study species avoided the rural 2-lane highway. Our results suggest that microhabitat use preferences and road substrate help predict species responses to low-use roads, but roads with heavy traffic may deter movement of a much wider range of small animal species.*

Keywords: avoidance, connectivity, conservation planning, habitat fragmentation, heteromyid, reptiles, road ecology, urban ecology

Resumen: *Un objetivo principal de la ecología de caminos es entender y predecir como afectan los caminos la conectividad de las poblaciones silvestres. El comportamiento de evitación de caminos puede fragmentar poblaciones, mientras que la falta de evitación puede resultar en alta mortandad debido a colisiones. Muchas especies animales pequeñas enfocan sus actividades a microhábitats particulares dentro de su hábitat mayor. Buscamos estudiar como los diferentes tipos de caminos afectan el movimiento de pequeños vertebrados y conocer si ciertas respuestas hacia los caminos pueden ser predecibles basándose en la historia de vida del animal o el microhábitat. Rastreamos los movimientos de animales marcados con fluorescencia en 24 sitios distribuidos entre 3 tipos de caminos: tierra de bajo uso, camino secundario pavimentado de bajo uso, y carretera rural de 2 carriles. La mayoría de los datos que colectamos fueron sobre* Chaetodipus fallax, Peromyscus eremicus, Sceloporus occidentalis, Aspidoscelis hyperythra, Dipodomys simulans *(tierra, pavimentación secundaria), y* P. maniculatus *(solamente en carretera).* C. fallax *y* P. eremicus *se movían hacia los caminos de tierra pero no hacia una carretera de baja pavimentación de anchura similar o hacia la carretera, indicando que evitan los caminos con sustrato pavimentado.* S. occidentalis *y* A. hyperythra *se movían hacia la tierra y los caminos secundarios pavimentados pero evitaban la carretera rural de 2 carriles, indicando que pueden evitar el ruido, las vibraciones o el disturbio visual de un constante flujo de tráfico.* D. simulans *no evitaba el camino de tierra ni los caminos secundarios con pavimento. En general, el camino de tierra y los caminos*

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secundarios fueron más permeables para las especies que prefieren forrajear o tomar el sol en áreas abiertas de su hábitat en lugar de bajo rocas o arbustos. D. simulans *no evitó el camino de tierra ni los caminos secundarios pavimentados. Sin embargo todas las especies estudiadas evitaron la carretera de 2 carriles. Nuestros resultados sugieren que las preferencias de uso de microhábitat y sustrato de caminos ayudan a predecir las respuestas de las especies hacia caminos de bajo uso, pero los caminos con tráfico pesado pueden disuadir el movimiento de un rango mucho mayor de especies animales pequeñas.*

Palabras Clave: conectividad, ecología de caminos, ecología urbana, evitación, fragmentación de hábitat, heterómido, planificación de la conservación, reptiles

Introduction

Terrestrial and aquatic areas have become increasingly permeated by roads. Roads affect movement patterns, demographics, and spatial distribution of local species. They can adversely affect wildlife by fragmenting habitats, creating population sinks, and acting as conduits for the spread of invasive species (e.g., Forman et al. 2003; Fahrig & Rytwinski 2009; Taylor & Goldingay 2010). They can positively affect wildlife by increasing connectivity between suitable habitat patches and food resources (e.g., Huey 1941; Getz et al. 1978; Forman et al. 2003).

A current need in the field of road ecology is to understand and predict how roads affect the probability wildlife populations will persist (Roedenbeck et al. 2007; Fahrig & Rytwinski 2009; Rytwinski & Fahrig 2012). This will likely require the development of demographic and spatial-movement models that incorporate behavioral responses to roads (e.g., Jaeger et al. 2005; Tracey 2006; Frair et al. 2008). Roads are highly variable, ranging from rarely traveled dirt roads to multilane highways with heavy traffic. Correspondingly, the responses of animals to different road types are expected to be highly variable.

To address variation in animal responses to different road attributes and traffic patterns, Jaeger et al. (2005) incorporated 3 types of road-specific avoidance behavior (road-surface avoidance related to road substrate and width, and, noise and car avoidance related to traffic) in their model for predicting when animal populations are at risk from roads. However, data to test these models are lacking because much of the current literature on road-related movement behavior typically focuses on either a single species or road type (e.g., Fahrig & Rytwinski 2009; Taylor & Goldingay 2010). There are also relatively few data available on reptiles, although this taxon is thought to be substantially and negatively affected by roads (Andrews et al. 2008). Finally, few researchers have incorporated both multiple road types and taxonomic classes in their studies to ascertain how animal communities respond to these linear features of the landscape.

Scrublands are distributed throughout mid-latitude deserts and areas with Mediterranean-type climates. Scrublands are characterized by low-growing shrubs adapted to arid conditions and range from open habitats with sparse vegetation cover to areas with dense vegetation (Kellman 1980). Our study area was in coastal sage scrubland of southern California (U.S.A.). Much of this area is fragmented by urbanization, disturbed, or permeated with highways, secondary roads, dirt roads, and trails (O'Leary 1995; Noss et al. 2000).

We sought to understand how roads affect habitat connectivity for small vertebrate populations within these scrublands. We assessed the movement patterns of 4 small-mammal species and 2 lizard species relative to 3 types of roads: low-use dirt roads, a secondary paved road, and a primary paved highway. We also examined whether animal responses to roads differed among species with different life-history strategies and whether species' microhabitat-use preferences could be used to predict their responses to roads.

Methods

Study Site

Our study area was in San Diego County, California, within the San Diego National Wildlife Refuge (Otay-Sweetwater Unit) and in Rancho Jamul, a 1915-ha ecological preserve managed by the California Department of Fish and Game. The coastal sage scrub (CSS) vegetation was dominated by California sagebrush (*Artemisia californica*), buckwheat (*Eriogonum fasciculatum*), and a variety of herbs and grasses. The region has a Mediterranean-type climate characterized by hot, dry summers and cool, wet winters. Average annual precipitation is 350 mm, and approximately 95% of the annual mean rainfall occurs from November through April. The CSS vegetation averaged 63% shrub cover, 30% grass and herb cover, and 28% open ground (total greater than 100% due to measures at multiple height categories [Brehme 2003]). There were 3 road types in the study area: 1.8 km of low-use unimproved dirt roads with an average width of 4.7 m (SD 1.3) and traffic volume of 0–20 vehicles/day; a 1.6-km low-use, secondary, 2-lane paved road (Millar Ranch Road) with an average width of 6.6 m (SD 0.2) and traffic volume of 200–500 vehicles/day (Traffic Section of San Diego County Public Works); and over 24 km of high-use, primary, 2-lane paved highway (State Highway 94) with an average width of 11.2 m (SD 0.9) and traffic volume of 7,400–18,000 vehicles/day

(California Department of Transportation). Road widths were measured as the width of grading for dirt roads and width of pavement for paved roads. Native soil or vegetation extended to the road edge for all unimproved and improved road types. During the study, there was no evidence of mowing or other vegetation-management activities.

Data Collection

Eight linear trapping arrays were installed along the length of each of the 3 road types. We chose sites where CSS vegetation extended at least 50 m from both sides of the road to avoid confounding the presence of a road with any other edge. Linear trapping arrays consisted of 3, 9-L pitfall traps connected by a 15-m drift fence (7.5 m between each bucket), 4 Sherman live traps (along both sides of fence halfway between each bucket), and one funnel trap. We baited all traps with birdseed and rolled oats. Arrays were diagonal to the road to increase effectiveness of intercepting animals moving both parallel and perpendicular to the road. At one end of the array, the pitfall trap was 1 m from the road edge, and at the other end, the pitfall trap was 11 m from the road edge. The middle pitfall trap was 5 m from the road edge. Pitfall-array materials and installation procedures are described in Fisher et al. (2008). Trap arrays remained open during each trapping period and were checked every morning at sunrise. We conducted ten 3-night trapping sessions at each array from April to December of 2001.

We used fluorescent-powder tracking (Lemen & Freeman 1985; Fellers & Drost 1989) to track the movements of small mammals and reptiles captured in the trap arrays. The fluorescent powder (Radiant Color, Richmond, California, U.S.A.) is nontoxic and is a safe and effective means of tracking small-scale animal movements (Stapp et al. 1994). The powder-tracking technique allowed us to study species' direct responses to roads. Tracking movements over longer distances and periods of time (e.g., with radiotelemetry) would better document infrequent crossings, but the use of fluorescent dye allows for documentation of fine-scale movement activity that telemetry does not (Lemen & Freeman 1985).

To differentiate among individuals, we dusted each animal released from an array with 1 of 20 base colors or unique mixtures of base colors. We were careful to dust only the body and to avoid the head area to prevent the animal from breathing in the powder (Stapp et al. 1994). Prior to their natural activity period, we placed it on the lid of the center bucket 5 m from the road edge. This allowed for a standard release distance from the road for all animals without the drift fence acting as a barrier to movement in any direction. When releasing an animal, the handler crouched down parallel to the animal and the road, released the animal, slowly backed away staying parallel to the road, and then left the area. This release strategy was to prevent the handler from scaring the animal toward or away from the road. We traced the fluorescent powder tracks at night with a portable 12-watt long-wave ultraviolet lamp. We laid a 50-m measuring tape over the trail until the powder could no longer be traced. For each animal, we recorded the total distance of the fluorescent track and made a diagram of the animal's movements in relation to the road. We recorded locations of burrows where tracks ended at burrow entrances. We tracked the movement of most individuals only one time to avoid problems with pseudoreplication (Hurlbert 1984). We traced a small number of animals on several occasions to examine the variability of results for individuals. For these animals, only the result of their first tracking occasion was used in statistical analyses.

We categorized all movements as either road use or habitat use. Road use was when an animal moved over the road for any distance of the track length. Habitat use was when an animal stayed in the scrubland during the entire tracking period. We included in our analyses only animals tracked for a minimum of 10 m. For the Dulzura kangaroo rat (*Dipodomys simulans*), we included 2 movements of approximately 9.5 m because there were a low number of total tracks. Because all animals were released within 5 m of the road, this minimum track distance allowed us to document movements relative to the road or well away from the array in any direction. We calculated permeability as the number of animals that exhibited road use divided by the total numbers of animals tracked for each species and road type.

Analyses

To test whether animals avoided or used the roads more than expected by chance, we compared observed species movement paths with paths simulated from species-specific correlated random walk (CRW) models. The CRW models represent predicted movement without any behavioral response to the roads. We parameterized CRW models with tracking data from at least 3 individuals of each species. We used only paths within the interior scrubland and well away from the road to represent typical movements within an animal's habitat. We used recorded spatial coordinates at 1.0-m intervals along the path to calculate move and turn angles. The move angle was the direction of movement, and the turn angle was the angle of the current move step minus the angle of the previous move step.

We parameterized the simulations in 2 stages. First, for each individual animal's movement path, we estimated the mean turn angle and concentration parameter that determined the dispersion of a von Mises distribution (Fisher 1993). Second, we fitted a von Mises distribution to the mean turn angles for all paths and a gamma distribution to the concentration parameter of the turn angles for all paths. When simulating a path, we randomly drew a mean turn angle from the von Mises distribution and a concentration parameter from the gamma distribution. We added the turn angle to the move angle of the previous move step to obtain the move angle for the current move step. The move-step length was 1.0 m, and the total length was constrained to the average length of the observed paths for each species. We simulated 1000 paths for each species. To determine the expected number of animal movements onto roads if there was no barrier effect, we determined the number of CRW paths that transected a line 5 m from the start point. We parameterized and simulated all CRW models with a program written in R (R Development Core Team 2010). We compared the number of observed versus expected road movements with Fishers' exact tests. A significant result suggested the animals moved onto roads more or less than expected under the null hypothesis.

Individual animal movement behavior may be affected by population density (Swihart & Slade 1984; Hanski 1999). Therefore, we determined whether relative abundance differed among the roadside habitats with one-way analysis of variation for each species. For our index of species abundance, we used the minimum number of animals known alive. We calculated this index by removing all recaptures within each 3-day trapping session at each array. Although minimum number known alive can be biased as an abundance estimator, it is proportional to population sizes and is thus a reasonable index of abundance (Slade & Blair 2012).

Results

We dusted 306 animals with fluorescent powder and released them 5 m from the road edge. One-third of the animals were not included in our analyses because their track lengths were <10 m. Most of the small mammals that were not used in the analyses were tracked to a nearby burrow on the side of the road on which they were released, and there were no obvious tracks coming out of the burrow. Small reptiles and those with smooth scales (many snakes, skinks, side-blotched lizards [*Uta stansburiana*], and whiptails [*Aspidoscelis* spp.]) did not retain the powder dye well; thus, many of their tracks were lost within several meters. Some species were excluded due to too few captures. The 181 individuals we used in the analyses (125 small mammals, 56 lizards) were followed an average of 20.7 m (SE 0.8).

We also tracked 19 animals on a second occasion to test the repeatability of individual results. All these animals repeated their initial movement types. Seventeen (12 mammals and 5 lizards) stayed within the scrubland on both tracking occasions, whereas 2 (1 mammal and 1 lizard) repeatedly crossed the road. We present the results for 4 small mammal species and 2 lizard species. These species represent movements of 54 San Diego pocket mice (*Chaetodipus fallax*), 57 cactus mice (*Peromyscus eremicus*), 6 Dulzura kangaroo rats (dirt and secondary paved road only), 8 deer mice (*Peromyscus maniculatus*) (highway only), 26 western fence lizards (*Sceloporus occidentalis*), and 30 orange-throated whiptail lizards (*Aspidoscelis hyperythra*) (secondary paved road and highway only).

Small Mammals

San Diego pocket mice were tracked an average distance of 25.1 m (SE 1.6) from the point of release. Species-specific movement simulations predicted a permeability of 42% (percentage of animals moving onto road) if the roads had no effect on movement. Twenty-seven percent of San Diego pocket mice movements were tracked onto the dirt roads (Fisher's exact test, $n = 22$, $p = 0.194$). The majority of these movements (4 out of 5) were crossing events to the habitat on the other side of the road. The percentage of movements onto the secondary road was significantly lower than expected at 9.5% ($n = 21$, $p = 0.003$). The 2 movements onto the secondary road were not crossings, but along the edge of the road returning to the habitat on the same side of the road. There were no movements of San Diego pocket mice onto the primary highway ($n = 11$, $p = 0.004$) (Fig. 1). The relative abundance of pocket mice did not differ significantly among the 3 road types ($F_{2,21} = 1.493, p = 0.248$).

Cactus mice were tracked an average distance of 19.0 m (SE 1.2). Species-specific movement simulations predicted an expected road permeability of 30%. All the movements onto the dirt road were direct crossing events to the other side of the road (Fig. 2). Although 25% of the individuals went onto the dirt road (meaning there was no significant barrier effect [$n = 20$, $p = 0.626$]), no individuals were tracked onto the secondary paved road or primary highway ($n = 18$, $p = 0.003$ and $n = 19$, $p = 0.002$, respectively). Relative abundance of cactus mice did not differ significantly among the 3 road types ($F_{2,21} = 0.676, p = 0.522$).

Dulzura kangaroo rats were tracked an average of 14.6 m (SE 2.4). Movement simulations for this species predicted a road permeability of 41%. Although there were few animals tracked, most of them went onto the roadways. Of the 3 individuals tracked near the dirt road, all went onto the road ($n = 3, p = 0.070$), which indicates the road was more permeable to this species than the surrounding habitat. One individual's burrow entrance was in the middle of the roadway. Two out of 3 individuals tracked went onto the secondary paved road ($n = 3, p = 0.572$), which indicates this road was not a barrier to movement. One individual ran along the length of the road and the other crossed the road (Fig. 3).

Deer mice were tracked adjacent to the highway for an average length of 19.9 m (SE 2.3). Species-specific

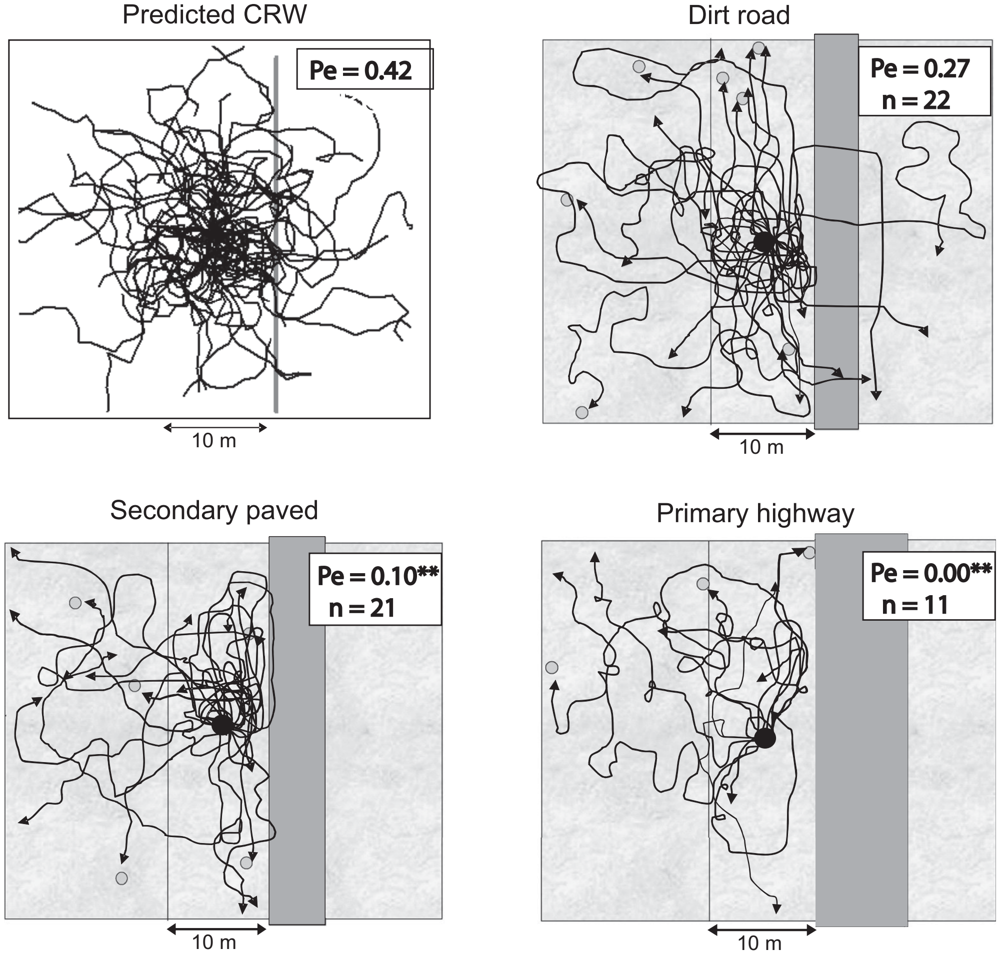

Figure 1. Predicted (correlated random walk, CRW) and observed permeability (Pe) of road types to movement of the San Diego pocket mouse (Chaetodipus fallax). Each drawing shows movements tracked at multiple independent release sites superimposed onto a single frame (gray circles, burrows; $^{**}p < 0.01$).

movement simulations predicted a road permeability of 37%. No deer mice went out onto the road, which indicates the rural highway was a significant barrier for this species ($n = 8, p = 0.030$). Many individuals were tracked to burrow entrances that were within a few meters of the road.

Lizards

Western fence lizards were tracked an average distance of 17.4 m (SE 2.2) from point of release. Species-specific movement simulations predicted an expected road permeability of 31%. The permeability of the dirt roads to movement of western fence lizards was higher than expected; 66% of lizards went onto the dirt road ($n = 9$, $p = 0.030$). These were a mixture of crossing events and movement along the road. A high percentage (56%) of individuals also went onto the secondary paved road ($n = 9$, $p = 0.146$). These movements were all along the road and no crossing events were recorded. However, most of these tracks were lost on the pavement, so we could not determine which side of the road the animal went to. In comparison, not a single western fence lizard went onto the highway (Fig. 4). Although permeability between the expected and observed values for the highway was not significant ($n = 6, p = 0.186$), the permeability of the highway to fence lizard movements was significantly lower than permeability of the dirt ($p = 0.028$) and secondary paved roads ($p = 0.044$) to movements of fence lizards. Their relative abundance did not differ among road types ($F_{2,21} = 0.006, p = 0.994$).

Movement simulations predicted road permeability of 31% for orange-throated whiptail if the roads had no effect on movement behavior. The average track length was 17.0 m (SE 1.3) by the secondary and primary paved roads. Although 33.3% of orange-throated whiptails crossed the secondary paved road ($n = 6$, $p = 1.00$), none were tracked out onto the highway ($n = 24$, $p \leq 0.001$) (Fig. 5). Only one whiptail was captured by the dirt road, and its track length was <10 m. Whiptail abundance next to the paved road and highway did not differ significantly ($t_{14} = 1.612, p = 0.129$). However, the

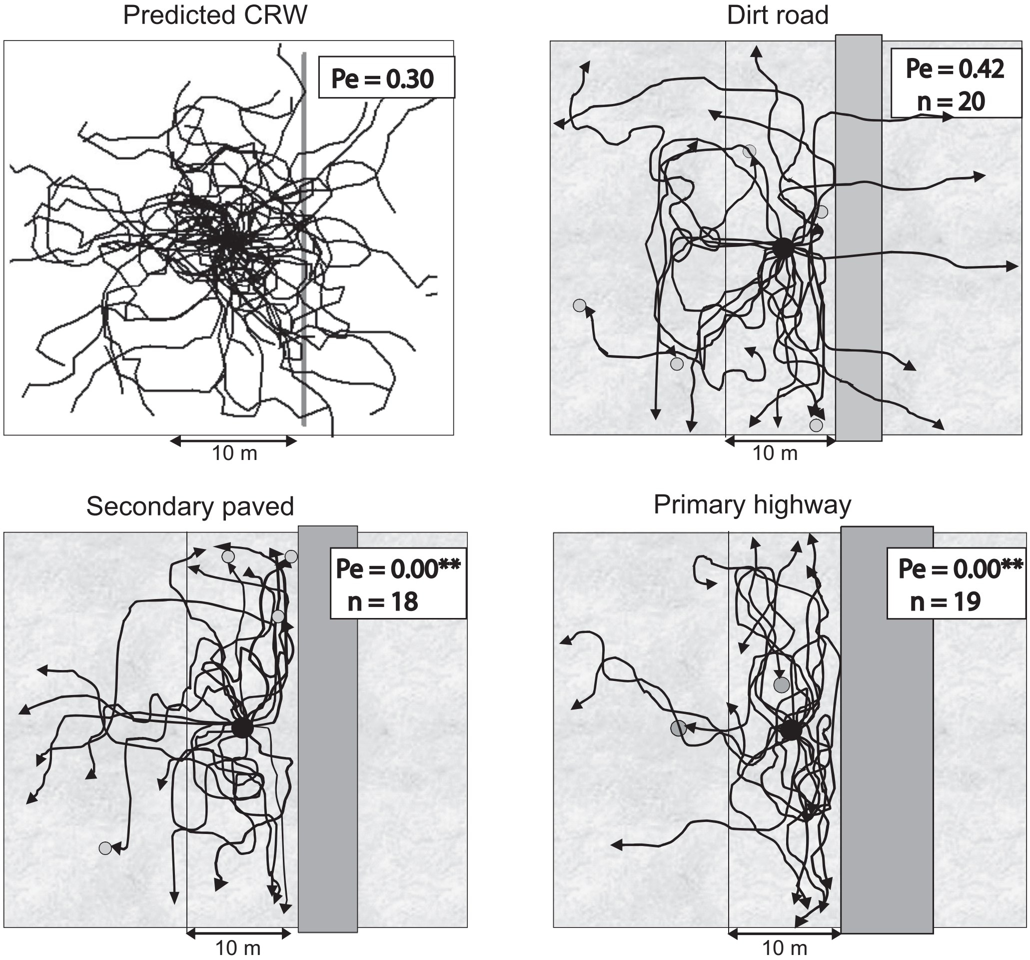

Figure 2. Predicted (correlated random walk, CRW) and observed permeability (Pe) of road types to movement of the cactus mouse (Peromyscus eremicus). Each drawing shows movements tracked at multiple independent release sites superimposed onto a single frame (gray circles, burrows; $^{**}p < 0.01$).

success rate in tracking the whiptail for distances >10 m was significantly greater by the highway (24/32) than by the paved road (6/20, $p = 0.002$).

Discussion

Although they live in open scrub habitats, San Diego pocket mice and cactus mice prefer to move and forage under microhabitats of shrub and rock cover rather than open areas (Meserve 1976; Price & Kramer 1984). Thus, they may quickly pass through or avoid areas of open ground. This is consistent with their movements relative to the dirt road, which were primarily direct crossings to shrub and rock cover on the other side of the road. One cactus mouse crossed the dirt road on 2 occasions. This result indicates the dirt road was within its home range. In contrast to the dirt road, there were no documented movements of either species across the secondary paved road or highway even though the distances required to cross either road were well under the average tracked distances of the species. The secondary road differed from the dirt roads by an average added width of 1.9 m, the addition of pavement, and an increased traffic volume averaging one vehicle every 5 minutes. It is unknown which of these factors or combination thereof resulted in their avoidance of this road. However, because of the low traffic volume and little difference in width, it is likely that these species were avoiding the road substrate. White-footed mice (*Peromyscus leucopus*) and eastern chipmunks (*Tamias striatus*) avoid crossing paved roads regardless of traffic volume (McGregor et al. 2008). By comparing roads with different substrates and traffic volumes, our results support the hypothesis that many small mammal species avoid paved road substrates. The reasons for this are not understood and deserve further study. However, mammals are particularly sensitive to odors in their environment. Road pavement surfaces, such as asphalt and coal tar, contain complex mixtures of volatile and non-volatile compounds. Even very minute concentrations of smells and chemicals that mimic pheromones may elicit instinctive behavioral

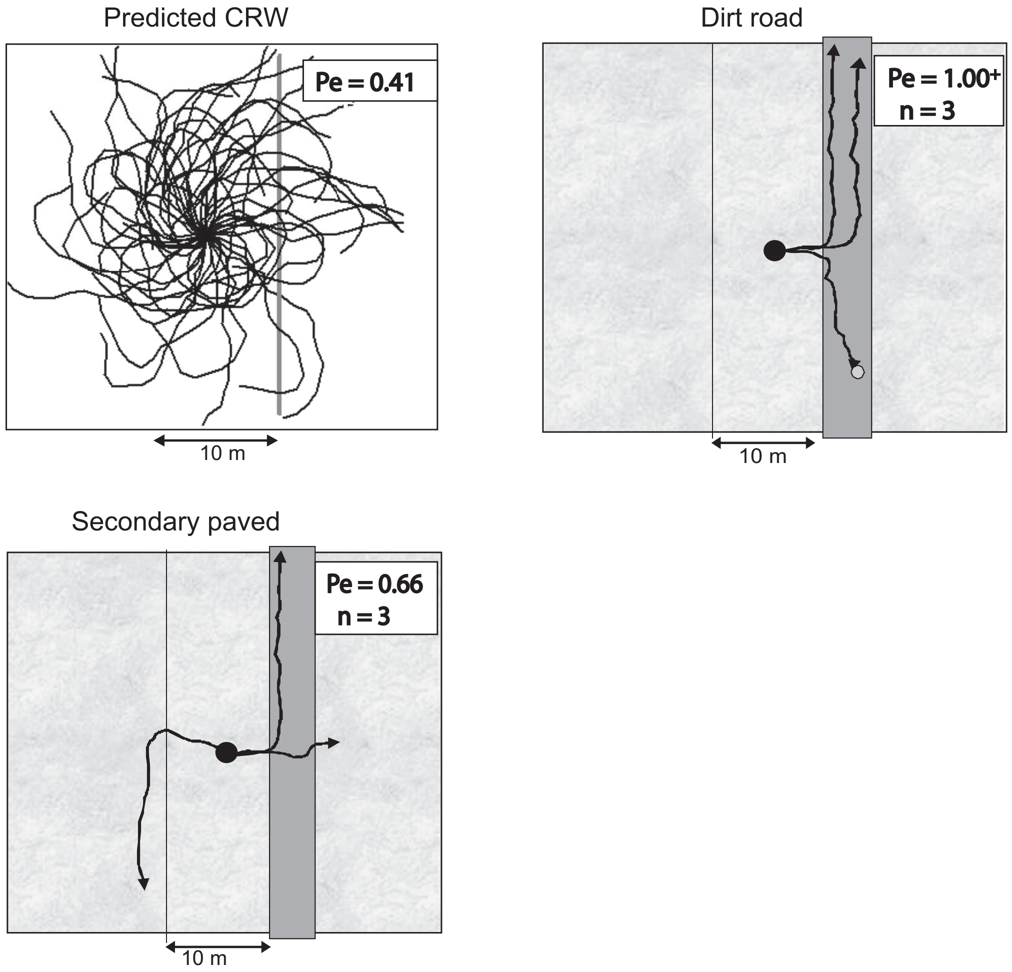

Figure 3. Predicted (correlated random walk, CRW) and observed permeability (Pe) of road types to movement of Dulzura kangaroo rat (Dipodomys simulans). Each drawing shows movements tracked at multiple independent release sites superimposed onto a single frame (gray circle, burrows; +$p < 0.10$).

responses in some species (e.g., Leinders-Zufall et al. 2000).

However, the avoidance of pavement is not generalizable to all species of small mammals. The yellow-necked mouse (*Apodemus flavicollis*) regularly crossed both dirt and paved roads of similar width (Rico et al. 2007). In our study, 2 out of 3 Dulzura kangaroo rats went out onto the secondary paved road. Although we did not capture any Dulzura kangaroo rats by the highway, this species accounted for the majority of dead animals we observed on the highway (3 out of 7) (Brehme 2003), which indicates the highway was also somewhat permeable to movement for this species. The higher than expected permeability of dirt roads to movements of the Dulzura kangaroo rat is consistent with results of a previous study on the Stephens' kangaroo rat (*D. stephensi*) (Brock & Kelt 2004). Kangaroo rats may preferentially use dirt roads for movement within their habitat. These bipedal heteromyids prefer to move and forage within open-ground areas of scrub habitats and respond positively to disturbances such as fire (e.g., Meserve 1976; Price & Kramer 1984; Brehme et al. 2011). In areas with denser vegetation, low-use dirt roads and trails may provide an increased opportunity for kangaroo rats to disperse to open scrub habitats. Alternately, we would expect negative effects from high-traffic roads on kangaroo rats. Traffic noise can disrupt communication in kangaroo rats (Shier et al. 2012) and nonavoidance of these roads would very likely result in increased mortality rates from vehicular traffic.

Because many reptiles may be attracted to open spaces and paved surfaces for thermoregulatory purposes, it is often hypothesized that these animals do not avoid roads (e.g., Klauber 1939; Jochimsen et al. 2004; Andrews et al. 2008). The dirt and secondary paved roads in our study were highly permeable to movement of western fence lizards (67% and 56%, respectively). Their movements on the dirt roads consisted of crossings and movements along the road; thus, the road was in part used as a conduit for movement. In contrast, their

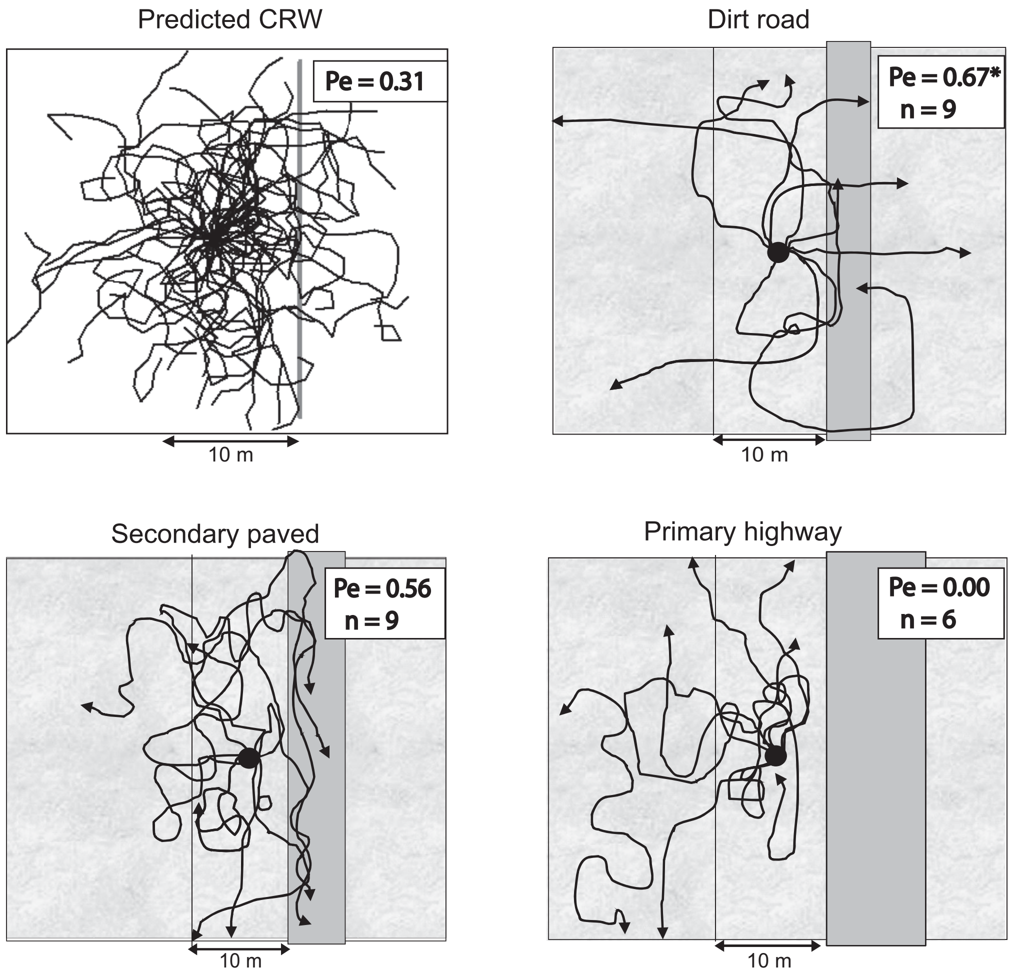

Figure 4. Predicted (correlated random walk, CRW) and observed permeability (Pe) of road types to movement of the western fence lizard (Sceloporus occidentalis). Each drawing represents movements tracked at multiple independent release sites that are superimposed onto a single frame ($^{*}p < 0.05$*).*

movements on the secondary road were often erratic and irregular along the road edge. This suggests the paved road was used for basking which was regularly observed during the study. The complete absence of movements onto the highway was in stark contrast to their response to the dirt and secondary paved roads. Similarly, although the secondary road was permeable to movement of the orange-throated whiptail, this species also completely avoided the highway.

Delaney et al (2010) found that genetic diversity is lower in populations of western fence lizards that are separated by a highway than in populations in continuous habitat. Because of the high permeability of the secondary paved road to these 2 species, we think it is unlikely that the additional width of the highway (4.6 m) alone adequately explains their marked avoidance of the highway. However, the level of traffic (average 1 vehicle/7 seconds) was 40-fold higher on the highway than on the secondary paved road; thus, the constant stream of vehicular traffic and corresponding noise and vibration may have been sufficient to deter use of the highway. On the basis of our own literature search and recent reviews on responses of reptiles to roads (Andrews et al. 2008; Rytwinski & Fahrig 2012), we believe ours is the first study to document behavioral road avoidance in lizards.

All the study species exhibited increased road avoidance and thus experienced decreased connectivity as road improvement and traffic increased. By studying both small mammals and reptiles we were able to make direct comparisons of behavior between taxa with different microhabitat preferences and life-history strategies. Species microhabitat-use preferences within their habitat may be an important predictive factor for road permeability (Fig. 6). Animals that are more likely to focus their activities in open areas within their habitat were more likely to venture out onto low-use roads. In our study, the 3 species (Dulzura kangaroo rat, western fence lizard, orange-throated whiptail) that use open areas for foraging

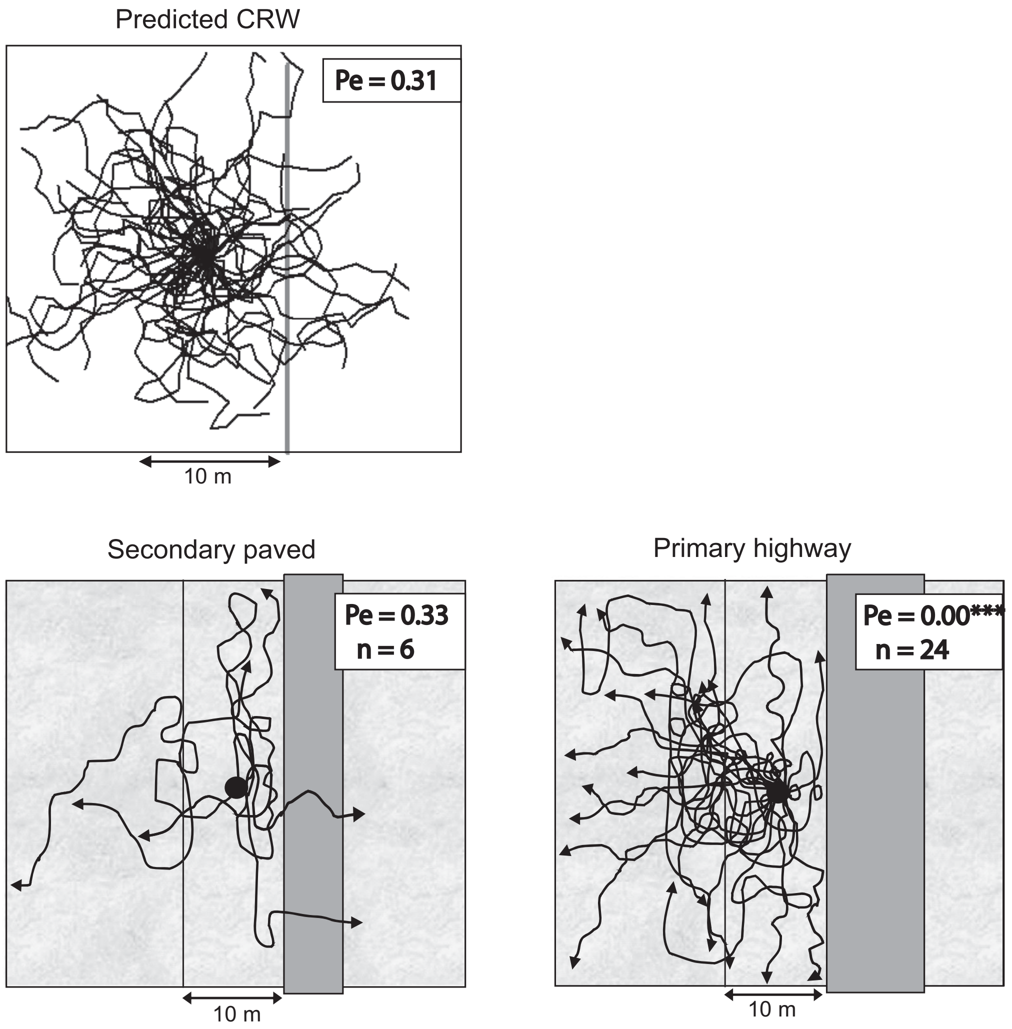

Figure 5. Predicted (correlated random walk, CRW) and observed permeability (Pe) of road types to movement of orange-throated whiptail lizard (Aspedoscelis hyperythra). Each drawing shows movements tracked at multiple independent release sites superimposed onto a single frame ($^{***}p < 0.001$*).*

or thermoregulation ventured onto dirt and secondary paved roads more than the species (San Diego pocket mouse, cactus mouse) that prefer to forage within or under the cover of rocks and shrubs.

Thus, one would predict that the populations of small animals with closed microhabitat preferences would be in most danger of becoming fragmented by any type of road. For instance, small mammal and reptile species that avoid open ground, such as the cotton rat (*Sigmodon hispidus*), prairie vole (*Microtus ochrogaster*), Eastern massasauga rattlesnake (*Sistrurus c. catenus*), rosy boa (*Lichanura trivirgata*), and many rainforest species, avoid crossing even narrow dirt roads (Swihart & Slade 1984; Weatherhead & Prior 1992; Goosem 2001; Rochester et al. 2005). Whereas generalist species and those with open microhabitat preferences would be more likely to cross roads, use roads for activity, and as conduits for movement. However, even these species may avoid roads with heavy traffic due to the constant disturbance from noise, vibrations, and lights. Therefore, roads with moderate traffic would be expected to pose the greatest risk of vehicular mortality for generalists and open microhabitat specialists due to the use of roads by both animals and vehicles (Seiler 2003). Our results pertain to small mammals and lizards with home ranges that are small relative to the road matrices within the study area. It is expected that movements onto roads would be more common for animals that make long migratory movements or that have large home ranges relative to the road matrices within their habitat.

Our results show that a 2-lane rural highway through open scrubland can create a significant movement barrier for species of small mammals and reptiles. Behavioral mechanisms appear to be road surface avoidance for some small mammal species and traffic avoidance for lizard species. Avoidance of improved roads may be a beneficial response in that mortality from vehicular traffic is avoided or minimized. However, networks of

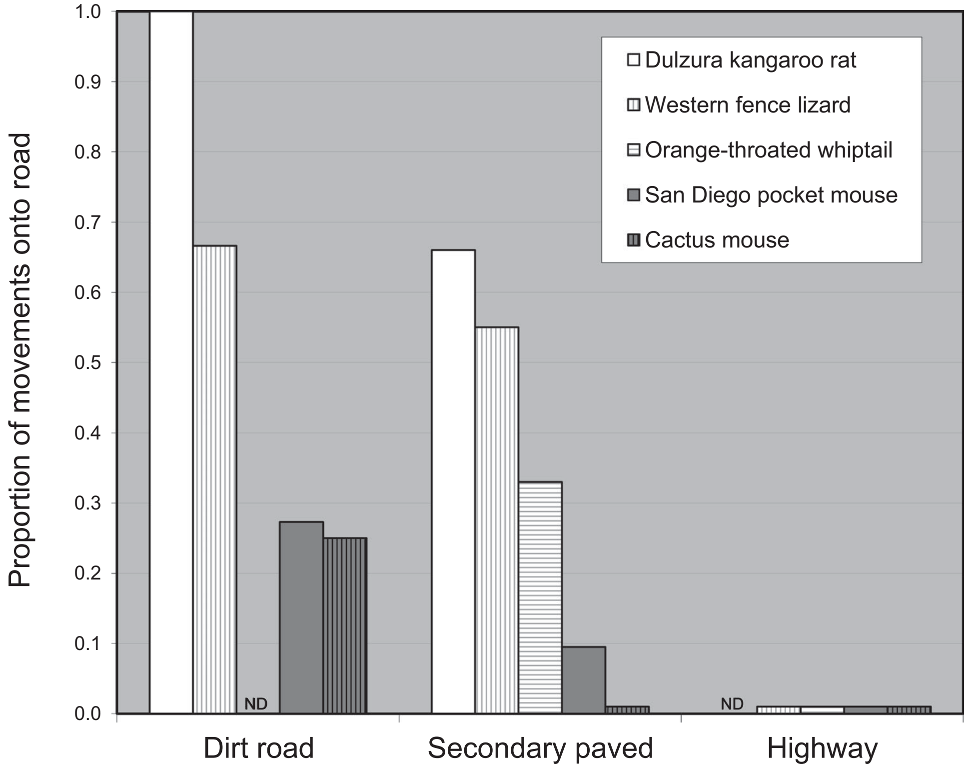

Figure 6. Road permeability relative to species microhabitat-use preferences (white bars, species that typically forage in and use open areas of their habitat; gray bars, species that primarily forage under vegetation cover; ND, no data for species at specific road type). Expected permeability range 0.30–0.41 with no road response.

roads throughout a landscape may divide habitat into fragments that are too small to sustain some populations over the long term. Barrier fencing and safe-crossing structures may reduce the effects of habitat fragmentation for species that avoid roads and reduce road mortality for species that do not avoid roads (e.g., Boarman & Sazaki 1996; Dodd et al. 2004).

More research is needed to determine whether road response patterns are consistent across other habitats and small animal species, whether microhabitat-use preferences can also help predict the use of road-crossing structures, and to further understand the population-level effects of movement-behavior decisions (Fahrig 2007; Rytwinski & Fahrig 2012). If generalizations are found, they will help us to identify vulnerable species and potentially detrimental roads within their habitat, inform population and spatial-movement models, and inform management decisions and mitigation measures for both studied and unstudied species.

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Literature Cited

Andrews, K. M., J. W. Gibbons, and D. M. Jochimsen. 2008. Ecological effects of roads on amphibians and reptiles: a literature review. Pages 121–143 in J. C. Mitchell, R. E. Jung Brown, and B. Bartholomew, editors. Urban herpetology. Society for the Study of Amphibians and Reptiles, Salt Lake City, Utah.

Boarman, W. I., and M. Sazaki. 1996. Highway mortality in desert tortoises and small vertebrates: success of barrier fences and culverts. Pages 169–173 in G. Evink, D. Ziegler, P. Garret, and J. Berry, editors. Highways and movement of wildlife. Report FHWA-PD-96–041. Florida Department of Transportation, Orlando.

Brehme, C. S. 2003. Responses of terrestrial vertebrates to roads in a coastal sage scrub ecosystem. MS thesis. San Diego State University, San Diego, California.

Brehme, C. S., D. R. Clark, C. J. Rochester, and R. N. Fisher. 2011. Wildfires alter rodent community structure across four vegetation types in southern California, USA. Fire Ecology **7**:81–98.

Brock, R. E., and D. A. Kelt. 2004. Influence of roads on the endangered Stephens' kangaroo rat (*Dipodomys stephensi*): Are dirt and gravel roads different? Biological Conservation **118**:633–640.

Delaney, K. S., S. P. D. Riley, and R. N. Fisher. 2010. A rapid, strong, and convergent genetic response to urban habitat fragmentation in four divergent and widespread vertebrates. PLoS ONE 5(9): e12767. DOI: 10.1371/journal.pone.0012767.

Dodd, N., W. J. Barichivich, and L. L. Smith. 2004. Effectiveness of a barrier wall and culverts in reducing wildlife mortality on a heavily traveled highway in Florida. Biological Conservation **118:**619–631.

Fahrig, L. 2007. Non-optimal animal movement in human-altered landscapes. Functional Ecology **21:**1003–1015.

Fahrig, L., and T. Rytwinski. 2009. Effects of roads on animal abundance: an empirical review and synthesis. Ecology and Society **14**. Available from http://www.ecologyandsociety.org/vol14/iss1/art21/ (accessed May 2013).

Fellers, G. M., and C. A. Drost. 1989. Fluorescent powder- a method for tracking reptiles. Herpetological Review **20:**91–92.

Fisher, N. I. 1993. Statistical analysis of circular data. Cambridge University Press, Cambridge, United Kingdom.

Fisher, R., D. Stokes, C. Rochester, C. Brehme, S. Hathaway, and T. Case. 2008. Herpetological monitoring using a pitfall trapping design in southern California. Techniques and methods 2-A5. U.S. Geological Survey, Reston, Virginia. Available from http://pubs.usgs.gov/tm/tm2a5/ (accessed January 2013).

Forman, R. T., et al. 2003. Road ecology: science and solutions. Island Press, Washington, D.C.

Frair, J. L., E. H. Merrill, H. L. Beyer, and J. M. Morales. 2008. Thresholds in landscape connectivity and mortality risks in response to growing road networks. Journal of Applied Ecology **45:**1504–1513.

Getz, L. L., F. R. Cole, and D. L. Gates. 1978. Interstate roadsides as dispersal routes for *Microtus pennsylvanicus*. Journal of Mammology **59:**208–212.

Goosem, M. 2001. Effects of tropical rainforest roads on small mammals: inhibition of crossing movements. Wildlife Research **28:**351–364.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, Oxford, United Kingdom.

Huey, L. M. 1941. Mammalian invasion via the highway. Journal of Mammology **22:**383–385.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs **54:**187–211.

Jaeger, J. A. G., J. Bowman, J. Brennan, L. Fahrig, D. Bert, J. Bouchard, N. Charbonneau, K. Frank, B. Gruber, and K. Tluk von Toschanowitz. 2005. Predicting when animal populations are at risk from roads: an interactive model of road avoidance behaviour. Ecological Modeling **185:**329–348.

Jochimsen, P. M., C. R Peterson, K. M. Andrews, and J. W. Gibbons. 2004. A literature review of the effects of roads on amphibians and reptiles and the measures used to minimize those effects. Idaho Fish and Game Department, Boise; U.S. Department of Agriculture Forest Service, Washington, D.C.

Kellman, M. C. 1980. Plant geography. 2nd edition. Palgrave Macmillan, New York.

Klauber, L. M. 1939. Studies of reptile life in the arid southwest. Bulletin of the Zoological Society of San Diego **14:**2–64.

Leinders-Zufall, T., A. P. Lane, A. C. Puche, W. Ma, M. Novotny, M. T. Shipley, and F. Zufall. 2000. Ultrasensitive pheromone detection by mammalian vomeronasal neurons. Nature **405:**792–796.

Lemen, C. A., and P. W. Freeman. 1985. Tracking mammals with fluorescent pigments: a new technique. Journal of Mammology **66:**134–136.

McGregor, R. L., D. J. Bender, and L. Fahrig. 2008. Do small mammals avoid roads because of traffic? Journal of Applied Ecology **45:** 117–123.

Meserve, P. L. 1976. Habitat and resource utilization by California rodents. Journal of Animal Ecology **45:**647–666.

Noss, R. F., E. T. LaRoe III, and M. J. Scott. 2000. Endangered ecosystems of the United States: a preliminary assessment of loss and degradation. 28. National Biological Service, Washington, D.C.

O'Leary, J. F. 1995. Coastal sage scrub: threats and current status. Fremontia **23:**27–31.

Price, M. V., and K. A. Kramer. 1984. On measuring microhabitat affinities with special reference to small mammals. Oikos **42:**349–354.

R Development Core Team. 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rico, A., P. Kindlmann, and F. Sedlacek. 2007. Barrier effects of roads on movements of small mammals. Folia Zoologica **56:**1–12.

Rochester, C. J., R. N. Fisher, and J. E. Diffendorfer. 2001. Natural history of the rosy boa (Charina trivergata). U.S. Geological Survey Technical Report. San Diego, California.

Roedenbeck, I. A., L. Fahrig, C. S. Findlay, J. E. Houlahan, J. A. G. Jaeger, N. Klar, S. Kramer-Schadt, and E. A. Van der Grift. 2007. The Rauischholzhausen agenda for road ecology. Ecology and Society **12**. Available from http://www.ecologyandsociety.org/vol12/iss1/art11/. (accessed May 2013)

Rytwinski, T., and L. Fahrig. 2012. Do species life history traits explain population responses to roads? A meta-analysis. Biological Conservation **147:**87–98.

Seiler, A. 2003. The toll of the automobile: wildlife and roads in Sweden. PhD dissertation. Swedish University of Agricultural Sciences, Uppsala.

Shier, D. M., A. J. Lea, and M. A. Owen. 2012. Beyond masking: endangered Stephens' kangaroo rats respond to traffic noise with footdrumming. Biological Conservation **160:**63–68.

Slade, N. A., and S. M. Blair. 2012. An empirical test of using counts of individuals captured as indices of population size. Journal of Mammalogy **81:**1035–1045.

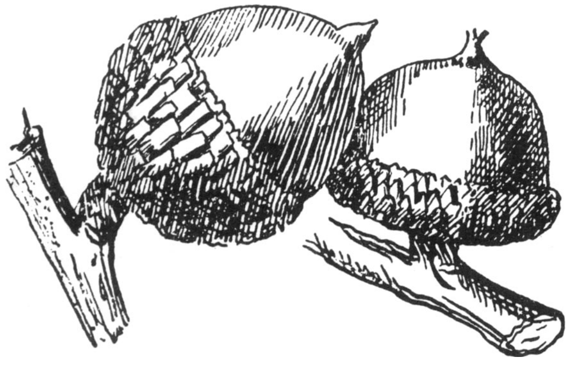
Stapp, P., J. K. Young, S. Vandewoude, and B. Van Horne. 1994. An evaluation of the pathological effects of fluorescent powder on deer mice (*Peromyscus maniculatus*). Journal of Mammalogy **75:**704–709.

Swihart, R. K., and N. A. Slade. 1984. Road crossing in *Sigmodon hispidus* and *Microtus ochrogaster*. Journal of Mammalogy **65:**357–360.

Taylor, B. D., and R. L. Goldingay. 2010. Roads and wildlife: impacts, mitigation and implications for wildlife management in Australia. Wildlife Research **37:**320–331.

Tracey, J. A. 2006. Individual-based modeling as a tool for conserving connectivity. Pages 343–368 in K. R. Crooks and M. Sanjayan, editors. Connectivity conservation. Cambridge University Press, Cambridge, United Kingdom.

Weatherhead, P. J., and K. A. Prior. 1992. Preliminary observations of habitat use and movements of the eastern massasauga rattlesnake (*Sistrurus c. catenatus*). Journal of Herpetology **26:** 447–452.



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RESEARCH ARTICLE

An objective road risk assessment method for multiple species: ranking 166 reptiles and amphibians in California

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Abstract
Context Transportation and wildlife agencies may consider the need for barrier structures and safe wildlife road-crossings to maintain the long-term viability of wildlife populations. In order to prioritize these efforts, it is important to identify species that are most at risk of extirpation from road-related impacts.
Purpose Our goal was to identify reptiles and amphibians in California most susceptible to road mortality and fragmentation. With over 160 species and a lack of species-specific research data, we developed an objective risk assessment method based upon road ecology science.
Methods Risk scoring was based upon a suite of life history and space-use characteristics associated with negative road effects applied in a hierarchical manner from individuals to species. We evaluated risk to both aquatic and terrestrial connectivity and calculated buffer distances to encompass 95% of population-level movements. We ranked species into five relative categories of road-related risk (very-high to very-low) based upon 20% increments of all species scores.
Results All chelonids, 72% of snakes, 50% of anurans, 18% of lizards and 17% of salamander species in California were ranked at high or very-high risk from negative road impacts. Results were largely consistent with local and global scientific literature in identifying high risk species and groups.
Conclusions This comparative risk assessment method provides a science-based framework to identify species most susceptible to negative road impacts. The results can inform regional-scale road mitigation planning and prioritization efforts and threat assessments for special-status species. We believe this approach is applicable to numerous landscapes and taxonomic groups.

Keywords Reptile · Amphibian · Road mortality · Habitat fragmentation · Road ecology · Risk assessment · Road

Introduction

There have been many attempts to better characterize and quantify threat criteria in order to classify species at higher risk of extinction at state, national, and global levels (Congress 1973 (U.S. Endangered Species Act); Mace et al. 2008; Hobday et al. 2011; Thomson et al. 2016; IUCN 2017). Roads are a significant threat to wildlife populations (e.g., Forman et al. 2003;

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Andrews et al. 2015a; van der Ree et al. 2015), causing both barrier (habitat fragmentation) and depletion (road mortality) effects. Barrier effects occur when animals avoid crossing roads, in which case roads essentially fragment species habitat. Barrier effects include reduced size and quality of available habitat, reduced effective population size, reduced ability to find mates and resources, increased genetic structuring, and increased probability of local extirpation (e.g., Forman et al. 2003; Fahrig and Rytwinski 2009; D'Amico et al. 2016). Depletion effects occur when animals attempt to cross roads and are killed by vehicles. Depletion effects include all of the risks from barrier effects as well as reduced survivorship, making high road mortality an even greater concern (Jackson and Fahrig 2011). Among other stressors, such as habitat loss and fragmentation, invasive species, pesticide use, changing climate, and disease, the negative impacts from roads may independently or cumulatively threaten the persistence of populations and even species.

Amphibians and reptiles have been identified as being particularly susceptible to the negative effects of roads within their habitat (e.g., Klauber 1931; Forman et al. 2003; Rytwinski and Fahrig 2012; Andrews et al. 2015a, b; D'Amico et al. 2015). Many are slow moving, do not avoid roads, and are simply too small for drivers to see and avoid. During rains many amphibians make long linear terrestrial movements regardless of the presence of intersecting roadways (Glista et al. 2008), and because paved roads typically absorb and retain more heat than the surrounding habitat, snakes and lizards are often attracted to roads for thermoregulation (Case and Fisher 2001; Jochimsen et al. 2004). In fact, road surveys are one of the most common methods for surveying these reptiles (e.g., Sullivan 2012). Many herpetofauna species utilize both aquatic and terrestrial habitat for breeding, development, foraging, and overwintering and therefore require connectivity within and between both aquatic and terrestrial habitats to support basic life history requirements.

The primary goal of this study was to provide information to transportation and other planning agencies in California to assist them in prioritizing road mitigation efforts for amphibian and reptile species. Although there is still a lot to learn about the effectiveness of different designs of road mitigation systems, the use of barrier systems, underpasses, and overpasses can reduce road mortality and help to maintain connectivity and safe passage across roads for herpetofauna and other wildlife (Jochimsen et al. 2004; Colino-Rabanal and Lizana 2012; Langton 2015; Langen et al. 2015b). Because it is currently unrealistic and cost prohibitive to mitigate all roadways for all species, it is vital to identify species most susceptible to road-related impacts. Within species ranges, risks to populations and need for mitigation can then be evaluated based upon local road densities and matrix, road-types, traffic, and road locations in relation to species habitat and movement corridors (e.g., Jaeger 2000; Litvaitis and Tash 2008; Langen et al. 2015b; Zimmermann Teixeira et al. 2017).

Here we describe a road risk assessment methodology applied to native amphibian and reptile species in California, a global biodiversity hotspot (Myers et al. 2000). We also included analysis of subspecies if they had special federal or state protection status. This includes 166 species and subspecies of frogs, toads, salamanders, snakes, lizards, turtles, and tortoise. Rankings and prioritizations such as these can be very subjective. In order to avoid including low risk species that may be favored by the assessors or to unintentionally overlook species that are at high risk, it was important for this be done in an objective manner informed by current road ecology literature.

Very few quantitative data are available on the impact of roads on population persistence. Jaeger et al. (2005) were the first to develop a relative ranking system to compare the impact of roads on wildlife populations. Their ranking system was largely based upon behavioral responses of animal species to the road surface, road size, traffic noise, and vehicles with varying road sizes and traffic volumes. However, knowledge of these detailed behavioral responses to ranges in road and traffic characteristics is rarely found in literature and the link between individual behavior and population-level effects has not been clearly established (Rytwinski and Fahrig 2012, 2013).

Rytwinski and Fahrig (2012) performed a meta-analysis of wildlife groups to test whether certain life history characteristics were related to negative responses to roads. High reproductive rate (fecundity) was negatively associated with the magnitude of population-level effects for amphibians. No associations were significant in reptiles, although there were few studies to inform this analysis. However, a strong link was shown between body size, greater mobility, lower reproductive rates and the magnitude of negative road effects in mammals, the most studied wildlife group. Conversely, simulations predicted populations of species with small home ranges and high reproductive rates were the least likely to be affected by roads (Rytwinski and Fahrig 2013).

We used these findings as a basis for creating a multi-tiered system to rank and identify reptile and amphibian species that may be most susceptible to road impacts. We based our ranking upon a suite of species life history and space-use characteristics associated with negative road effects, as well as including species distribution and conservation status. We evaluated risk to both aquatic and terrestrial connectivity and include buffer distances that were calculated to encompass 95% of population movements. Relative confidence in these distances is given for each species based upon the amount of support from scientific studies. We solely focused on the direct effects of roads as barriers and sources of road mortality and not impacts from road construction and maintenance or indirect effects from increased human use of the landscape once a road is in place (see review by Langen et al. 2015a).

Because we based the risk assessment solely upon space-use and life history characteristics, this represents a species relative susceptibility to road impacts. It is understood that circumstances associated with particular populations (e.g., local road types, locations, densities) may elevate or reduce the risk for certain populations and species.

Methods

Road risk assessment (overview)

We assessed the relative risk of California herpetofauna species to negative road-related impacts at three scales in a hierarchical fashion. We first assessed risk at the scale of an individual animal and then expanded the risk to the population and then to species (Fig. 1).

At the individual-level, we based road risk primarily upon the likelihood that an individual would encounter one or more roads. We considered this a product of movement distance (home range, seasonal migrations) and movement frequency (e.g., active foragers, seasonal migrants, sit-and-wait predators vs. sedentary species) (e.g., Bonnet et al. 1999; Carr and Fahrig 2001). Because many species are semi-aquatic, movement distance and frequency were scored separately for both aquatic and terrestrial habitats.

There is a theorized higher risk associated with depletion effects (i.e., road mortality) in comparison to barrier effects (Fahrig and Rytwinski 2009; Jackson and Fahrig 2011). Therefore, we gave additional weight to those species more likely to go out onto a road surface and be killed by vehicular traffic. For this we considered factors of habitat preference (e.g., open vs. closed), roads as potential attractants (e.g., for basking), and movement speed (e.g., slow vs. fast). However, individuals within and among species may respond differently to roads (attraction vs. avoidance) based upon local landscape features, road width, traffic volume, and perceived danger (Forman et al. 2003; Andrews 2005; Brehme et al. 2013; Jacobson et al. 2016). Because a state-wide analysis encompasses extreme variation in landscape and road characteristics, the extent to which roads act as barriers or sources of direct mortality within a species range is unknown. The risk disparity between depletion and barrier effects could also be highly variable. Therefore, we limited the additional weight for potential depletion effects to twenty percent of the individual risk score.

We assessed population-level road risk by multiplying individual risk with scores representing: (1) the relative proportion of the population at risk; and (2) the species ability to sustain higher rates of mortality. For instance, the proportion of the population at risk was expected to be higher for migratory species than for territorial species. Highly fecund species were expected to better withstand (or more quickly recover from) higher mortality in comparison to those with few annual offspring.

Finally, we assessed species-level road risk by multiplying population road risk with scores for range size (both within and outside of California) and conservation status according to the U.S. Fish and Wildlife Service (USFWS 2016) and the California Department of Fish and Wildlife (CDFW 2016a; Thomson et al. 2016). Species with smaller ranges typically have fewer populations and are thus less resilient to population-level stressors. Endangered, threatened, and special concern species have already been designated at risk of extirpation, often due to

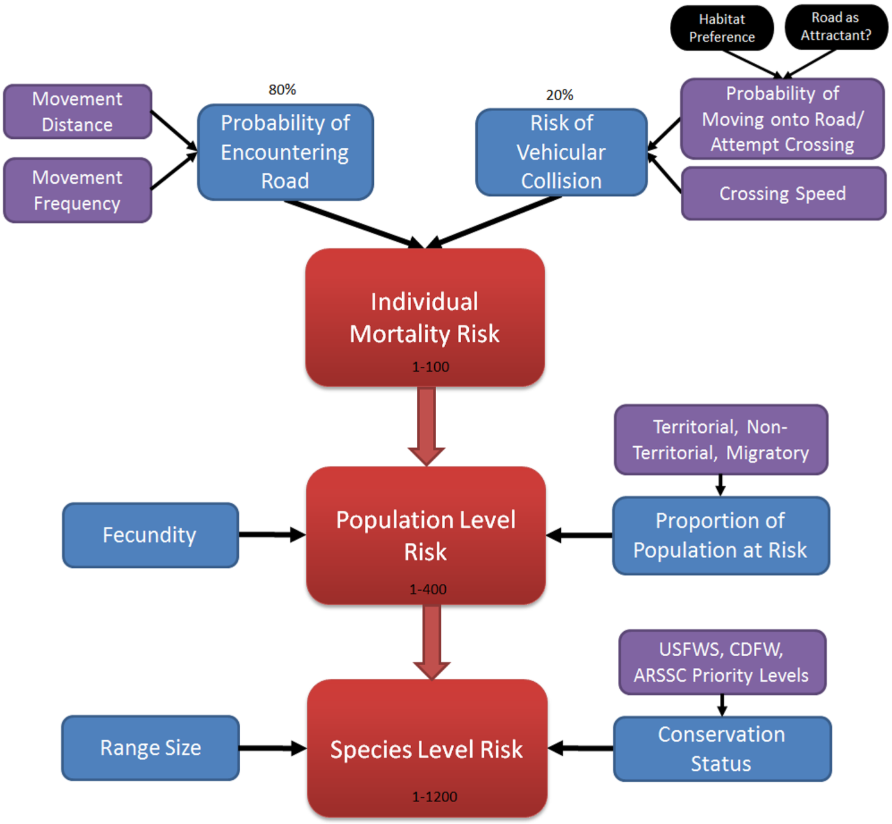


Fig. 1 California reptile and amphibian road risk assessment conceptual model (*ARSSC* Amphibian and Reptile Species of Special Concern (Thomson et al. 2016))

multiple stressors, and are thus thought to be less likely to be resilient to additional road impacts.

Although we present both aquatic and terrestrial risk scores for semi-aquatic species, we used the higher of the two scores for the overall risk ranking.

Literature review

Species life history data were primarily taken from and cross-checked among the following species account review sources;

1. U.S. Fish and Wildlife Service (USFWS) Recovery Plans and 5-year Reviews https://www.fws.gov/endangered/.
2. California Amphibian and Reptile Species of Special Concern (ARSSC; Thomson et al. 2016).
3. A Field Guide to Amphibians and Reptiles of California (Stebbins and McGinnis 2012)
4. Amphibian declines: the conservation status of United States species (Lannoo 2005).
5. Conservation Status of Amphibians and Reptiles on USDA National Forests, Pacific Southwest Region, 2012 (Evelyn and Sweet 2012).
6. Natureserve Explorer (natureserve.org): Species Accounts largely authored by G. Hammerson (2003–2016).

When these reviews were lacking life history information needed for the road risk assessment, we then searched for supplementary peer-reviewed literature using the Google Scholar search engine. Because movement distances (terrestrial, aquatic, home range, migratory) were so important for the risk assessment, we acquired referenced articles from the species accounts and independently searched the literature to acquire these data. Search terms included the species common name, scientific name, or genus and terms such as “movement”, “home-range”, “spatial”, and “telemetry”. We also reviewed articles for citations of other studies to find more recent information on movement. This literature included published articles, book chapters, M.S. Theses, Ph.D. dissertations, agency reports, and consultant reports. In the case that specific life history or movement information was not found for a species, we chose a surrogate species based upon phylogeny, habitat, and body size. We first looked for the closest related species within the genus or family and chose a closely related surrogate based upon similar habitat and body size. If surrogates were used, these are clearly reported.

Road risk metrics

The following section describes in detail the rank scoring used for Individual-level Road Risk, Population-level Road Risk, and Species-level Road Risk. All rank values are meant to represent the relative contribution of each attribute to either additive or multiplicative road risk.

Individual-level risk (100 points possible)

Table 1 Individual-level Road Risk (IRR): Score criteria for risk of individuals encountering a road

Risk of individuals encountering a road = Movement distance × frequency

Movement distance (m)	Score	Frequency	Score
> 1200	40	Active throughout home range	2
901–1200	32	Migratory (2–4 × per year)/ non-migratory sit and wait foragers	1.5
601–900	24	Sedentary, confined to specialized habitat	1
451–600	16		
301–450	12		
201–300	8		
101–200	5		
51–100	3		
0–50	1		

Out of a total of 100 points for individual road mortality risk, we attributed up to 80 points (80%) to the risk of encountering a road and up to 20 points (20%) for the risk of an individual moving onto a road and being killed by a motor vehicle.

The risk of encountering a road was based on a combination of movement distance and general movement frequency. Movement distance was ranked 1–40 based upon home range movement distances (diameter) for non-migrants or migration distances for seasonal migrants that spanned from 0 to > 1200 m (Table 1). The scores are linearly correlated with increasing movement distance.

For species that use both terrestrial and wetland/stream/riverine habitats, such as frogs, toads, aquatic snakes and turtles, we scored aquatic and terrestrial movement distances and frequencies separately. This was necessary as some species move much larger distances and at different frequencies in one habitat versus the other. This also informs the type(s) of mitigation structures that may be warranted based upon habitat type, buffer distances and risk scores for each species. Aquatic movement distances were not calculated for pond-breeding amphibians. Ponds are typically small ephemeral bodies of water and terrestrial movements of amphibians to and among ponds account for the majority of movement for these species.

The calculations and rankings for movement distances were well considered and deserve further explanation. Our original thinking was that maximum distances should reflect relative movement distances across species and these data were commonly reported in species accounts. However, it became increasingly difficult to determine whether maximum distances reported were seasonal migration movements, home range movements or rarer dispersal events. We believed this assessment should reflect annual movement distances and not rare dispersal events. We considered using average/median movement distances; however, these often underestimate the movement of seasonal migrants because in many cases a sizeable portion of the population may remain close to a breeding site, while another sizable portion make longer distance migrations causing an average or median to be uninformative. Therefore, we decided to use a buffer distance that incorporates the movement distances of 95% of the population studied. A 95% population movement distance is commonly accepted for the delineation of terrestrial buffer zones for amphibians (i.e., Semlitsch 1998; Semlitsch and Bodie 2003) and we believe it was the most biologically meaningful and useful measure for this study. This measure, which we will refer to as Maximum Population Movement Distance (MPMD), should include almost all population movements, such as seasonal migration distances and annual home ranges (diameter), but not rare dispersal events. The MPMD should also be useful for local risk assessments as these distances can be used to aide in mapping and mitigation decisions.

The calculation we used for MPMD is commonly known as the 95% upper tolerance interval (Vangel 2015). A tolerance interval is an interval that is meant to contain a specified percentage of individual population measurements. This should not be confused with a confidence interval, which is an interval that is meant to contain the population mean. We chose a 50% confidence level for the upper 95% confidence limit of movement distances which is equal to the 95% prediction interval for future observations and is the mean + 1.645 × standard deviation. In cases where a standard deviation was not reported, we back calculated standard deviation from the standard error and sample size, calculated it from the individual data, or estimated it based on the methods recommended by Hozo et al. (2005). Although non-parametric tolerance intervals would be more appropriate for non-normally distributed movement data, the data required to calculate these is rarely reported in the published literature. In the case of non-normally distributed data where medians, sample sizes and ranges are reported, Hozo et al. (2005) methods allow for approximation of means and standard deviations with no assumption of the underlying data distribution. We found the resulting MPMDs to be reasonable in excluding large outliers but including multiple long distance movements below the maximum movement distance.

We recognize that for any species there can be substantial variability in movement distances that depend upon varying local, landscape, and climatic factors. This was often reflected in studies with sometimes widely varying estimates of home range and migration distances. We attempted to be conservative by using the study data for calculation of MPMD in which the largest population movement distances were observed. For studies where movement distance significantly varied between females and males, we used the information from the wider ranging sex. For migratory distances, we did not use distances from extreme environments, such as Canada, where suitable overwintering sites are typically much farther away from breeding and summer activity areas than in milder California climates (e.g., Gregory 1984). We did use study data from adjacent states or lower estimates of migration distances from those reported in Midwestern states. In some cases where little information was available, we made an educated guess based upon limited study data and/or closely related species and noted these in the tables. For all MPMDs, we report a relative confidence level based upon the number and quality of studies, sample sizes, and locations in or adjacent to California. It is intended that the scores be adjusted as new information becomes available.

To compute the risk of encountering a road, the MPMD was multiplied by a relative index of the expected frequency of longer distance movements (1–2 points; Table 1). We defined three frequency categories largely based upon annual migratory movements or foraging strategies for non-migratory species. The highest category included actively foraging predators which are characterized by frequent wandering movements throughout their home range (Pianka 1966). Less frequent movers included seasonal migrants traveling among breeding, summer foraging, and/or overwintering sites and non-migratory 'sit-and-wait' predators that remain still for long periods of time to ambush prey (Pianka 1966). Finally, low frequency included highly sedentary species with high site fidelity, particularly specialized rock, crevice, soil, or tree dwellers that may rarely traverse terrestrial or aquatic habitats.

The risk of an individual moving onto a road and being killed by a moving vehicle was ranked by attributes of habitat preference, road use, and movement speed (Table 2). Habitat preference represents the degree to which an individual is expected to go out onto or avoid an open road as predicted from their habitat and microhabitat preferences. Open habitat specialists and generalists were expected to more readily move onto a road than species that prefer cover (e.g., Forman et al. 2003; Brehme et al. 2013). Although many amphibians are closed habitat specialists, most readily move through open habitats during rain events, when most overland migratory movements tend to occur (Glista et al. 2008). Therefore, amphibians were considered open habitat specialists for this ranking. An additional factor that may increase road use is for thermoregulation for lizards

Table 2 Individual-level Road Risk (IRR): Score criteria for risk of road mortality

Risk of road mortality = Habitat preference + road use + movement speed

Habitat preference	Score	Road use	Score	Movement speed	Score
Open habitat specialist/amphibians	10	Thermoregulation (snakes/lizards)	4	Slow (< 0.6 m/s)	6
Generalist	8	Other	0	Medium (0.6–2.0 m/s)	3
Edge specialist	4			Fast (> 2.0 m/s)	0
Closed habitat or aquatic specialist	0				

Table 3 Population-level Road Risk (PRR): Score criteria for population level road risk

PRR = IRR × (Fecundity + Proportion of population at risk)

Fecundity	Ave. potential offspring/year	Score	Proportion of population at risk	Score
Low	0–10	2	Seasonal migrants (Migratory)	2
Med	11–25	1.5	Wandering	1.5
High	26–100	1	Territorial	1
Very high	> 100	0		

and snakes, as roads often retain more heat than the surrounding environment (Colino-Rabanal and Lizana 2012; Mccardle and Fontenot 2016). Finally, there is an increased risk of road mortality for slow versus fast moving species (see Andrews and Gibbons 2005; Mazerolle et al. 2005; Andrews et al. 2015b).

Population-level Road Risk (400 points possible)

To assess the risk of negative road impacts on the persistence of a population we incorporated scores for population-level movement behavior and fecundity (Table 3). For the proportion of a population expected to encounter a road, we scored the greatest risk to species that seasonally migrate to overwintering and breeding areas (Jackson et al. 2015). For those that do not migrate, we expected higher proportions of non-territorial or loosely territorial species (“wandering”) to encounter roads than species that defend distinct territories.

Species with low fecundity are less resilient to road mortality impacts than highly fecund species (Rytwinski and Fahrig 2013). Relative fecundity was simply calculated from the average number of potential offspring per year whether the animals were oviparous or live-bearing. For egg-laying species, the number of potential offspring was calculated by multiplying the average clutch size by the average number of clutches per year.

Individual mortality risk (1–100 points) was multiplied by the sum of these population-level factors (1–4 points) to calculate population-level road risk.

Species-level road risk (1200 points possible)

In comparison to population-level risk, we considered the overall risk of roads to species to be negatively associated with species range and conservation status. Although some populations may be at high risk, species with a wide distribution and many populations should be more resilient to localized declines and extirpations. Therefore, we assigned a range isolation score ranging from 0 to 1 that considered species distributions range-wide (North America) and within California (CA) (Table 4). Range-wide distribution varied from “CA only” to “widespread” (> 4 states). If the species range extended into Mexico and/or Canada, these countries were counted as another state for calculation of the index. California-wide distribution was calculated based upon the number of CA geographic regions occupied out of twelve regions defined by Hickman (1993) and used in Stebbins and

Table 4 Species-level Road Risk (SRR): Score criteria for species-level road risk

SRR[a] = PRR × ((Range isolation score + Conservation status score)/2)

(a) Range isolation score = (North America range + CA range)/2

North America range	Rank/score
CA only	1.00
2 states (very restricted distribution)	1.00
2 states (restricted)	0.67
2–3 states	0.33
Widespread (4 + states)	0.00

California range (No. of geographic regions occupied)	Rank/score
1	0.92
2	0.83
3	0.75
4	0.67
5	0.58
6	0.50
7	0.42
8	0.33
9	0.25
10	0.17
11	0.08
12	0.00

(b) Conservation status score

Conservation status	Rank/score[a]
CA or federal threatened/endangered	1.00
SSC priority 1	0.75
SSC priority 2	0.50
SSC priority 3	0.25
None	0.00

[a] Population-level risk > 80 only

McGinnis (2012). These two scores (Range-wide isolation, CA isolation) were summed and divided by two in order to normalize the overall range isolation score to a 0 to 1 scale.

At the species-level, we also incorporated conservation status (Table 4). Some species are declining and are at higher risk of extinction often due to multiple stressors. Federal and State Threatened and Endangered Species were given the highest score (1.0). In California, forty-five species are designated “Species of Special Concern (SSC)” with a ranking of 1, 2, or 3 based upon severity and immediacy of threats affecting each taxon (Thomson et al. 2016). SSC species were given a conservation status score ranging from 0.25 to 0.75 based upon their SSC ranking. Population-level Road Risk (score range 1–400) was multiplied by (1 + Range Isolation Score + Conservation Status Score; score range 1–3) to calculate the final Species-level Road Risk.

Range and conservation status were only used as a multiplier for species-level road risk if the population-level road risk was greater than 80 (20% of possible population score). This helped to prevent false inflation of the road risk metrics for low road susceptible species.

Because all members of the genus *Batrachoseps* (slender salamanders) are similar in body size, range size and general life history characteristics, we scored

Table 5 Species-level frequency distributions and road risk rankings

Percentile	Scores	Relative ranks
81–100	322–710	Very high
61–80	213–321	High
41–60	63–212	Medium
21–40	53–62	Low
1–20	0–52	Very Low

the genus as whole with the most conservative estimates and conservation status but included all 20 species in the final count and calculations.

Once all 166 species (including subspecies with conservation status) were scored for species-level road risk within both terrestrial and aquatic habitats, we took the maximum score for each species and sorted them from the highest to lowest scores. We grouped species into categories of risk (Very high, high, medium, low, and very low) based upon ranges of values that represented frequency distributions in 20% increments of all species scores (Table 5, Fig. 2).

As a way to support the results of our ranking model with species literature, we focused on special status species. We reviewed recovery plans and 5-year reviews for federally listed species and state species accounts for California listed species and species of special concern (collectively referred to as special status species). For each rank group (i.e., "very low" to "very high"), we calculated the percentage of special status species where roads were specifically listed as a threat. Similarly, we tallied the number of species identified in a recent California preliminary road risk assessment (Levine 2013, Amy Golden pers. comm.) and compared the number of species that fell within each of our road risk categories.

Results

All chelonids, 72% of snakes, 50% of anurans, 18% of lizards and 17% of salamander species were ranked as high or very high risk from negative road impacts. (Table 6, Fig. 3).

Review of species accounts, recovery plans, and 5-year reviews for all special status species showed

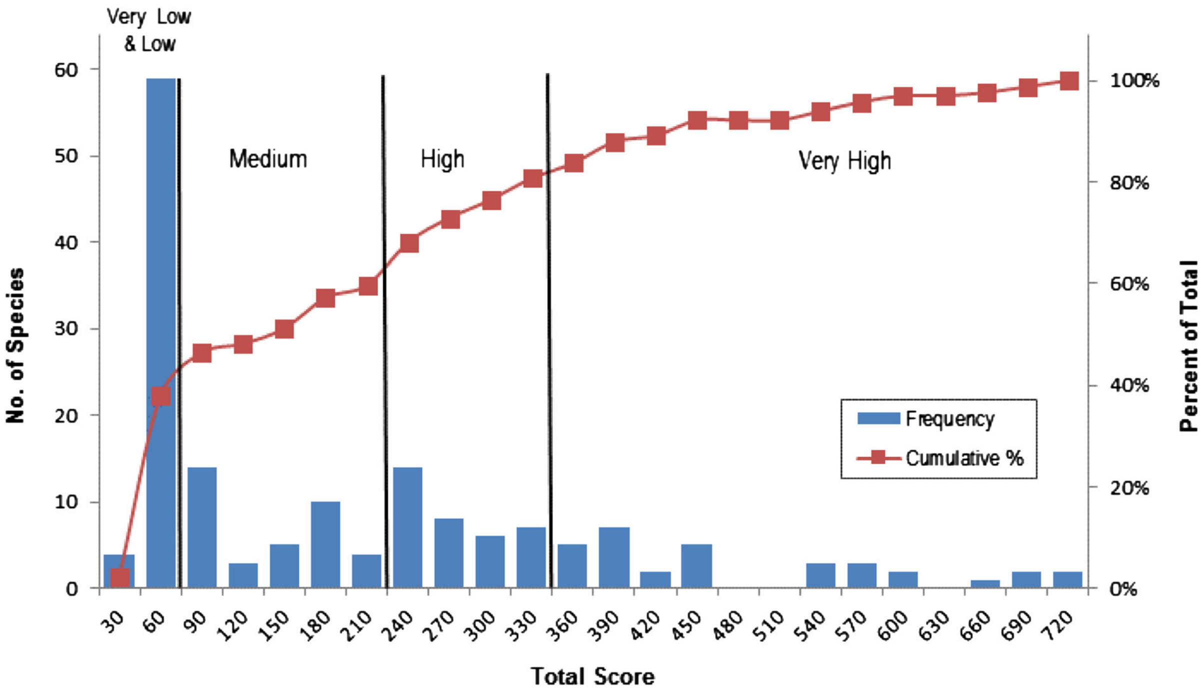


Fig. 2 Histogram of species-level scores and approximate 20 percentile road risk categories

Table 6 Numbers of species by taxa within each risk category

Species group	Species-level rankings				
	Very high	High	Med	Low	Very low
Salamander	4	4	3	26	9
Lizard	5	3	8	7	21
Anuran	5	6	6	4	1
Snake	15	21	13	0	1
Tortoise	1	0	0	0	0
Turtle	3	0	0	0	0

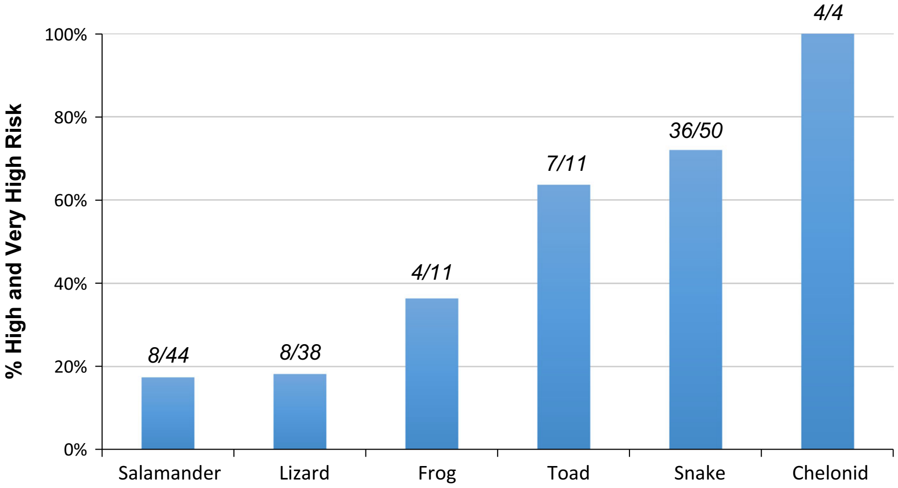


Fig. 3 Percentages of species by taxa in high and very high road risk categories

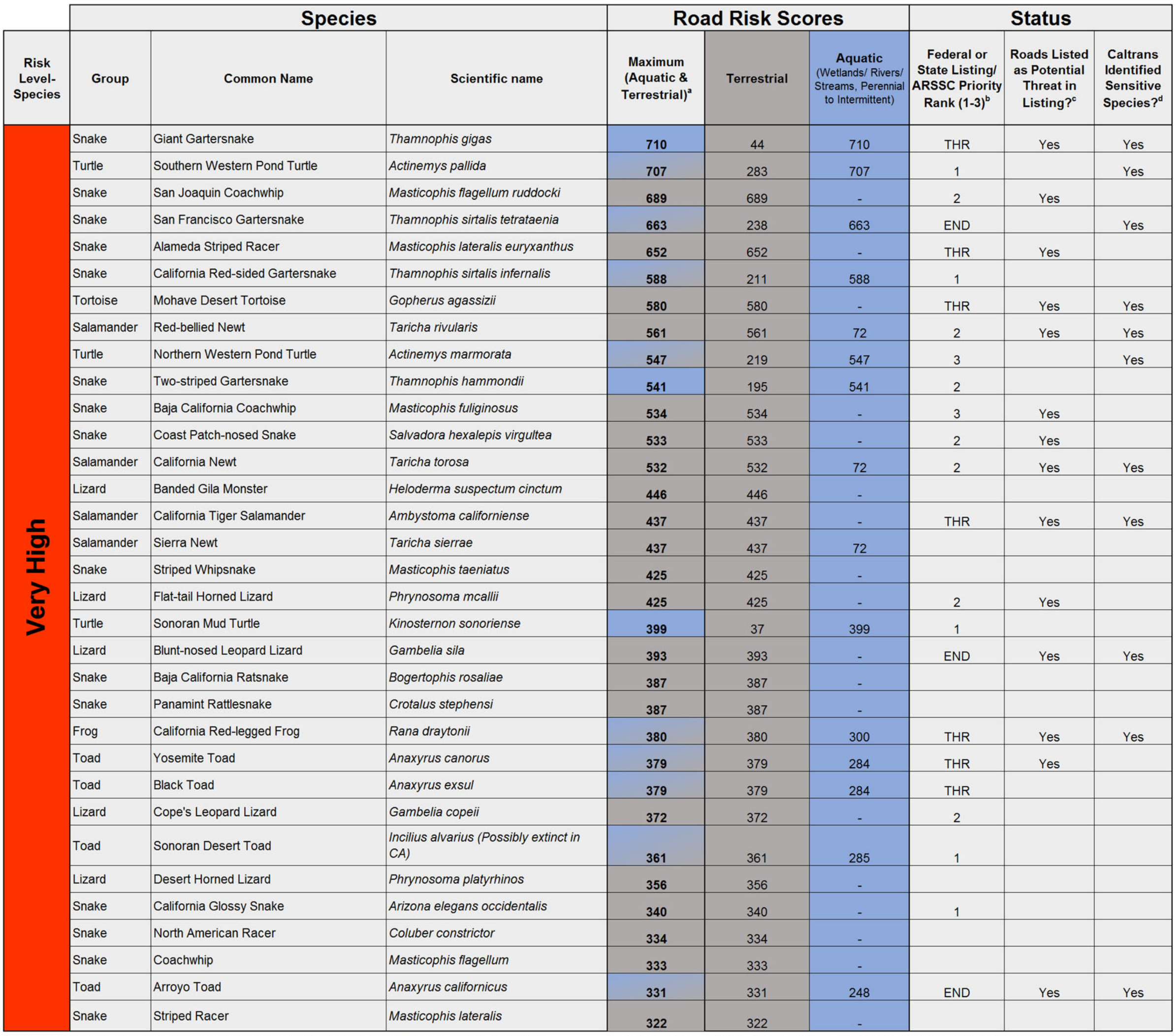
that 94% (17/18) of species accounts that referenced roads as a threat to the species were ranked as "high" or "very high" in our risk assessment (Table 7). Of the special status species that ranked 'high' and 'very high', close to fifty percent (17/35) had road-related threats referenced in their listing literature. In comparison, only 4% (1/27) of 'medium' to 'very low' risk special status species accounts mentioned roads as a potential threat. In addition, 79% (15/19) of species of concern recommended in a recent Caltrans preliminary road risk assessment scored as 'high' or 'very high' risk in our analysis (Levine 2013, Amy Golden pers. comm.).

Table 7 Comparison of road risk results and number of special status species with roads listed as threat

Road risk level	Special status species			Caltrans PI[a]
	No. species in road risk level	No. species with roads listed as threat	% of Total	No. Spp in road risk level
Very high	25	14	56	11
High	11	3	27	4
Medium	5	1	20	3
Low	10	0	0	1
Very low	7	0	0	0

[a] Caltrans PI are Caltrans identified sensitive species

Table 8 Amphibian and reptile road risk assessment: very high risk species (80–100% percentile), high risk species (60–80% percentile), medium risk species (40–60% percentile range), low risk species (20–40% percentile) and very low risk species (0–20% percentile)



	Species			Road Risk Scores			Status		
Risk Level-Species	Group	Common Name	Scientific name	Maximum (Aquatic & Terrestrial)[a]	Terrestrial	Aquatic (Wetlands/ Rivers/ Streams, Perennial to Intermittent)	Federal or State Listing/ ARSSC Priority Rank (1-3)[b]	Roads Listed as Potential Threat in Listing?[c]	Caltrans Identified Sensitive Species?[d]
Very High	Snake	Giant Gartersnake	*Thamnophis gigas*	**710**	44	710	THR	Yes	Yes
	Turtle	Southern Western Pond Turtle	*Actinemys pallida*	**707**	283	707	1		Yes
	Snake	San Joaquin Coachwhip	*Masticophis flagellum ruddocki*	**689**	689	-	2	Yes	
	Snake	San Francisco Gartersnake	*Thamnophis sirtalis tetrataenia*	**663**	238	663	END		Yes
	Snake	Alameda Striped Racer	*Masticophis lateralis euryxanthus*	**652**	652	-	THR	Yes	
	Snake	California Red-sided Gartersnake	*Thamnophis sirtalis infernalis*	**588**	211	588	1		
	Tortoise	Mohave Desert Tortoise	*Gopherus agassizii*	**580**	580	-	THR	Yes	Yes
	Salamander	Red-bellied Newt	*Taricha rivularis*	**561**	561	72	2	Yes	Yes
	Turtle	Northern Western Pond Turtle	*Actinemys marmorata*	**547**	219	547	3		Yes
	Snake	Two-striped Gartersnake	*Thamnophis hammondii*	**541**	195	541	2		
	Snake	Baja California Coachwhip	*Masticophis fuliginosus*	**534**	534	-	3	Yes	
	Snake	Coast Patch-nosed Snake	*Salvadora hexalepis virgultea*	**533**	533	-	2	Yes	
	Salamander	California Newt	*Taricha torosa*	**532**	532	72	2	Yes	Yes
	Lizard	Banded Gila Monster	*Heloderma suspectum cinctum*	**446**	446	-			
	Salamander	California Tiger Salamander	*Ambystoma californiense*	**437**	437	-	THR	Yes	Yes
	Salamander	Sierra Newt	*Taricha sierrae*	**437**	437	72			
	Snake	Striped Whipsnake	*Masticophis taeniatus*	**425**	425	-			
	Lizard	Flat-tail Horned Lizard	*Phrynosoma mcallii*	**425**	425	-	2	Yes	
	Turtle	Sonoran Mud Turtle	*Kinosternon sonoriense*	**399**	37	399	1		
	Lizard	Blunt-nosed Leopard Lizard	*Gambelia sila*	**393**	393	-	END	Yes	Yes
	Snake	Baja California Ratsnake	*Bogertophis rosaliae*	**387**	387	-			
	Snake	Panamint Rattlesnake	*Crotalus stephensi*	**387**	387	-			
	Frog	California Red-legged Frog	*Rana draytonii*	**380**	380	300	THR	Yes	Yes
	Toad	Yosemite Toad	*Anaxyrus canorus*	**379**	379	284	THR	Yes	
	Toad	Black Toad	*Anaxyrus exsul*	**379**	379	284	THR		
	Lizard	Cope's Leopard Lizard	*Gambelia copeii*	**372**	372	-	2		
	Toad	Sonoran Desert Toad	*Incilius alvarius (Possibly extinct in CA)*	**361**	361	285	1		
	Lizard	Desert Horned Lizard	*Phrynosoma platyrhinos*	**356**	356	-			
	Snake	California Glossy Snake	*Arizona elegans occidentalis*	**340**	340	-	1		
	Snake	North American Racer	*Coluber constrictor*	**334**	334	-			
	Snake	Coachwhip	*Masticophis flagellum*	**333**	333	-			
	Toad	Arroyo Toad	*Anaxyrus californicus*	**331**	331	248	END	Yes	Yes
	Snake	Striped Racer	*Masticophis lateralis*	**322**	322	-			

[a] Maximum scores color-coded for toad risk type; terrestrial (gray), aquatic (blue), or both (gray/blue)

[b] END=Endangered, THR= Threatened, 1-3= ARSSC Priority Ranking

[c] Federal Recovery plans, 5-year reviews, California species accounts for special status species

[d] California Amphibian and Reptile Crossing Preliminary Investigation

Risk scores and relative rankings for California reptile and amphibian species in both terrestrial and aquatic habitats are presented in Tables 8. Terrestrial and Aquatic rankings are provided separately in Tables 9 and 10 and also include population-level risk scores, 95% population buffer distances, confidence levels, and identification of any surrogate species used for the distance calculations. Species scores for all ranking criteria and life history and movement references are provided in Appendices 1 and 2.

Discussion

To our knowledge, this is the first attempt to objectively assess the relative risk of roads at a species level using a logical and scientifically based framework and apply it across a large array of species and habitats. We believe this approach could be useful for assessing and comparing susceptibility of species to negative road impacts within and among all taxonomic groups. To date, such risk assessments have been based largely upon expert opinion, limited information available on

Table 8 continued

	Species			Road Risk Scores			Status		
Risk Level-Species	Group	Common Name	Scientific name	Maximum (Aquatic & Terrestrial)[a]	Terrestrial	Aquatic (Wetlands/ Rivers/ Streams, Perennial to Intermittent)	Federal or State Listing/ ARSSC Priority Rank (1-3)[b]	Roads Listed as Potential Threat in Listing?[c]	Caltrans Identified Sensitive Species?[d]
High	Snake	Red Diamond Rattlesnake	*Crotalus ruber*	**321**	321	-	3	Yes	
	Snake	Speckled Rattlesnake	*Crotalus mitchellii*	**317**	317	-			
	Frog	Oregon Spotted Frog	*Rana pretiosa (Possibly extinct in CA)*	**315**	41	315	THR		
	Salamander	Santa Cruz Long-toed Salamander	*Ambystoma macrodactylum croceum*	**308**	308	-	END	Yes	Yes
	Salamander	Rough-skinned Newt	*Taricha granulosa*	**304**	304	72			
	Snake	Sierra Gartersnake	*Thamnophis couchii*	**304**	44	304			
	Snake	Regal Ring-necked Snake	*Diadophis punctatus regalis*	**298**	298	-	2		Yes
	Snake	California Lyresnake	*Trimorphodon lyrophanes*	**293**	293	-			
	Frog	Northern Red-legged Frog	*Rana aurora*	**291**	291	230	2		Yes
	Snake	Mojave Rattlesnake	*Crotalus scutulatus*	**276**	276	-			
	Snake	Western Patch-nosed Snake	*Salvadora hexalepis*	**276**	276	-			
	Snake	Common Gartersnake	*Thamnophis sirtalis*	**271**	165	271			
	Snake	Aquatic Gartersnake	*Thamnophis atratus*	**266**	40	266	0		
	Snake	Sidewinder	*Crotalus cerastes*	**263**	263	-			
	Salamander	California Giant Salamander	*Dicamptodon ensatus*	**260**	260	72	3	Yes	
	Snake	Sonoran Lyresnake	*Trimorphodon lambda*	**260**	260	-			
	Snake	Western Rattlesnake	*Crotalus oreganus*	**250**	250	-			
	Snake	Northwestern Gartersnake	*Thamnophis ordinoides*	**245**	138	245			
	Snake	Desert Nightsnake	*Hypsiglena chlorophaea*	**241**	241	-			
	Snake	Western Terrestrial Gartersnake	*Thamnophis elegans*	**240**	75	240			
	Lizard	Switak's Banded Gecko	*Coleonyx switaki*	**236**	236	-	THR		
	Toad	Western Spadefoot	*Spea hammondii*	**234**	234	-	1		Yes
	Snake	Coast Nightsnake	*Hypsiglena ochrorhyncha*	**233**	233	-			
	Lizard	Long-nosed Leopard Lizard	*Gambelia wislizenii*	**226**	226	-			
	Toad	Great Plains Toad	*Anaxyrus cognatus*	**222**	222	175			
	Toad	Woodhouse's Toad	*Anaxyrus woodhousii*	**222**	222	175			
	Lizard	Coastal Whiptail	*Aspidoscelis tigris stejnegeri*	**219**	219	-	2		
	Snake	Western Shovel-nosed Snake	*Chionactis occipitalis*	**218**	218	-			
	Snake	Spotted Leaf-nosed Snake	*Phyllorhynchus decurtatus*	**218**	218	-			
	Salamander	Southern Long-toed Salamander	*Ambystoma macrodactylum sigillatum*	**217**	217	-	2		
	Frog	Cascades Frog	*Rana cascadae*	**217**	217	72	2		
	Snake	Western Diamond-backed Rattlesnake	*Crotalus atrox*	**214**	214	-			
	Snake	Western Groundsnake	*Sonora semiannulata*	**212**	212	-			

[a] Maximum scores color-coded for toad risk type; terrestrial (gray), aquatic (blue), or both (gray/blue)

[b] END=Endangered, THR= Threatened, 1-3= ARSSC Priority Ranking

[c] Federal Recovery plans, 5-year reviews, California species accounts for special status species

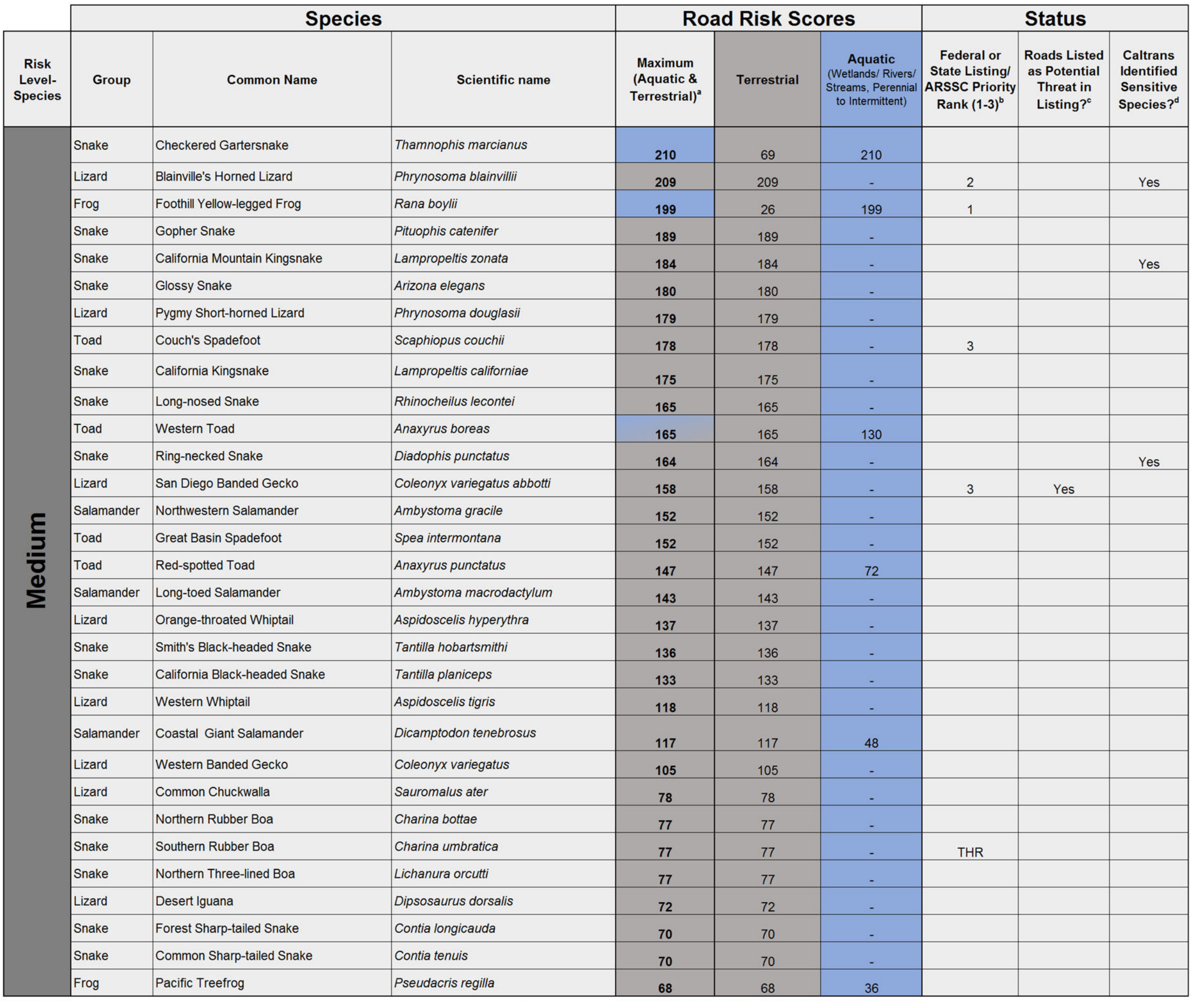
[d] California Amphibian and Reptile Crossing Preliminary Investigation

road mortality, and even less information available on population or species-level road effects (Levine 2013; Rytwinski and Fahrig 2015).

Overall, this is meant to be a first step in highlighting reptile and amphibian species that may be at highest risk from roads transecting their habitat. These species may deserve consideration for further study and for implementing mitigation solutions to reduce mortality and to maintain or enhance connectivity. The risk assessment was done for both terrestrial and aquatic habitats to further inform mitigation. Some aquatic species may greatly benefit from fish passages while others may better benefit from terrestrial barriers and wildlife crossings or both.

Although data are currently lacking to validate completely the scoring and results of the risk assessment, our review of species accounts, recovery plans, 5-year reviews for federal and state-listed species and California species of special concern show a strong association between elevated road risk from our

Table 8 continued



	Species			Road Risk Scores			Status		
Risk Level-Species	Group	Common Name	Scientific name	Maximum (Aquatic & Terrestrial)[a]	Terrestrial	Aquatic (Wetlands/ Rivers/ Streams, Perennial to Intermittent)	Federal or State Listing/ ARSSC Priority Rank (1-3)[b]	Roads Listed as Potential Threat in Listing?[c]	Caltrans Identified Sensitive Species?[d]
Medium	Snake	Checkered Gartersnake	*Thamnophis marcianus*	**210**	69	210			
	Lizard	Blainville's Horned Lizard	*Phrynosoma blainvillii*	**209**	209	-	2		Yes
	Frog	Foothill Yellow-legged Frog	*Rana boylii*	**199**	26	199	1		
	Snake	Gopher Snake	*Pituophis catenifer*	**189**	189	-			
	Snake	California Mountain Kingsnake	*Lampropeltis zonata*	**184**	184	-			Yes
	Snake	Glossy Snake	*Arizona elegans*	**180**	180	-			
	Lizard	Pygmy Short-horned Lizard	*Phrynosoma douglasii*	**179**	179	-			
	Toad	Couch's Spadefoot	*Scaphiopus couchii*	**178**	178	-	3		
	Snake	California Kingsnake	*Lampropeltis californiae*	**175**	175	-			
	Snake	Long-nosed Snake	*Rhinocheilus lecontei*	**165**	165	-			
	Toad	Western Toad	*Anaxyrus boreas*	**165**	165	130			
	Snake	Ring-necked Snake	*Diadophis punctatus*	**164**	164	-			Yes
	Lizard	San Diego Banded Gecko	*Coleonyx variegatus abbotti*	**158**	158	-	3	Yes	
	Salamander	Northwestern Salamander	*Ambystoma gracile*	**152**	152	-			
	Toad	Great Basin Spadefoot	*Spea intermontana*	**152**	152	-			
	Toad	Red-spotted Toad	*Anaxyrus punctatus*	**147**	147	72			
	Salamander	Long-toed Salamander	*Ambystoma macrodactylum*	**143**	143	-			
	Lizard	Orange-throated Whiptail	*Aspidoscelis hyperythra*	**137**	137	-			
	Snake	Smith's Black-headed Snake	*Tantilla hobartsmithi*	**136**	136	-			
	Snake	California Black-headed Snake	*Tantilla planiceps*	**133**	133	-			
	Lizard	Western Whiptail	*Aspidoscelis tigris*	**118**	118	-			
	Salamander	Coastal Giant Salamander	*Dicamptodon tenebrosus*	**117**	117	48			
	Lizard	Western Banded Gecko	*Coleonyx variegatus*	**105**	105	-			
	Lizard	Common Chuckwalla	*Sauromalus ater*	**78**	78	-			
	Snake	Northern Rubber Boa	*Charina bottae*	**77**	77	-			
	Snake	Southern Rubber Boa	*Charina umbratica*	**77**	77	-	THR		
	Snake	Northern Three-lined Boa	*Lichanura orcutti*	**77**	77	-			
	Lizard	Desert Iguana	*Dipsosaurus dorsalis*	**72**	72	-			
	Snake	Forest Sharp-tailed Snake	*Contia longicauda*	**70**	70	-			
	Snake	Common Sharp-tailed Snake	*Contia tenuis*	**70**	70	-			
	Frog	Pacific Treefrog	*Pseudacris regilla*	**68**	68	36			

[a] Maximum scores color-coded for toad risk type; terrestrial (gray), aquatic (blue), or both (gray/blue)

[b] END=Endangered, THR= Threatened, 1-3= ARSSC Priority Ranking

[c] Federal Recovery plans, 5-year reviews, California species accounts for special status species

[d] California Amphibian and Reptile Crossing Preliminary Investigation

objective analysis and the probability that roads are listed as a potential threat to the species in the species listing literature.

Although more than 40% of special status species are semi-aquatic, roads were rarely considered a threat to aquatic connectivity in the species literature. This may be accurate if bridges or large culverts currently exist for water flow that also provide permeability to aquatic movement. Bridges are generally considered to be completely passable by all aquatic species. Bridges are more likely to be constructed adjacent to or over large water bodies and rivers, presumably resulting in less risk to aquatic movement of populations that inhabit lake and river systems. However, culverts that are more commonly constructed under roads in streams and wetlands vary in passability depending on factors such as diameter, length, slope, outlet configuration, and other characteristics (Furniss et al. 1991; Clarkin et al. 2005; Kemp and O'Hanley 2010). In fact, Januchowski-Hartley et al. (2013) found that only 36% of road crossings were fully passable to fish in the Great Lakes basin. In addition, many low water crossings in arid regions of the state are simply a dip in the road that allows water to flow

Table 8 continued

	Species			Road Risk Scores			Status		
Risk Level-Species	Group	Common Name	Scientific name	Maximum (Aquatic & Terrestrial)[a]	Terrestrial	Aquatic (Wetlands/ Rivers/ Streams, Perennial to Intermittent)	Federal or State Listing/ ARSSC Priority Rank (1-3)[b]	Roads Listed as Potential Threat in Listing?[c]	Caltrans Identified Sensitive Species?[d]
Low	Salamander	Scott Bar Salamander	*Plethodon asupak*	**62**	62	-	THR		
	Salamander	Dunn's Salamander	*Plethodon dunni*	**62**	62	-			
	Salamander	Del Norte Salamander	*Plethodon elongatus*	**62**	62	-			
	Salamander	Siskiyou Mountains Salamander	*Plethodon stormi*	**62**	62	-	THR		
	Frog	California Treefrog	*Pseudacris cadaverina*	**61**	61	26			
	Salamander	Southern Torrent Salamander	*Rhyacotriton variegatus*	**61**	61	5	1		
	Lizard	Peninsula Leaf-toed Gecko	*Phyllodactylus nocticolus*	**60**	60	-			
	Lizard	Northern Alligator Lizard	*Elgaria coerulea*	**60**	60	-			
	Frog	Coastal Tailed Frog	*Ascaphus truei*	**59**	59	30	2		Yes
	Lizard	Common Side-blotched Lizard	*Uta stansburiana*	**59**	59	-			
	Lizard	Coachella Fringe-toed Lizard	*Uma inornata*	**56**	56	-	THR		
	Lizard	Colorado Desert Fringe-toed Lizard	*Uma notata*	**56**	56	-	2		
	Lizard	Mohave Fringe-toed Lizard	*Uma scoparia*	**56**	56	-	3		
	Frog	Lowland Leopard Frog	*Lithobates yavapaiensis (Possibly extinct in CA)*	**54**	31	54	1		
	Frog	Southern Mountain Yellow-legged Frog	*Rana muscosa*	**54**	26	54	END		
	Lizard	Zebra-tailed Lizard	*Callisaurus draconoides*	**54**	54	-			
	Salamander	Wandering Salamander	*Aneides vagrans*	**53**	53	-			
	Salamander	Slender Salamanders	*Batrachoseps (genus: 20 spp.)*	**53**	53	-	END[e]		
Very Low	Salamander	Ensatina	*Ensatina eschscholtzii*	**51**	51	-			
	Salamander	Yellow-blotched Ensatina	*Ensatina eschscholtzii croceater*	**51**	51	-			
	Salamander	Large-blotched Ensatina	*Ensatina eschscholtzii klauberi*	**51**	51	-			
	Lizard	Southern Alligator Lizard	*Elgaria multicarinata*	**51**	51	-			
	Lizard	Panamint Alligator Lizard	*Elgaria panamintina*	**51**	51	-	3		
	Frog	Sierra Nevada Yellow-legged Frog	*Rana sierrae*	**51**	51	36	THR		
	Lizard	Western Fence Lizard	*Sceloporus occidentalis*	**49**	49	-			
	Salamander	Limestone Salamander	*Hydromantes brunus*	**48**	48	-	THR		
	Salamander	Mount Lyell Salamander	*Hydromantes platycephalus*	**48**	48	-			
	Salamander	Clouded Salamander	*Aneides ferreus*	**44**	44	-			
	Salamander	Arboreal Salamander	*Aneides lugubris*	**44**	44	-			
	Lizard	Granite Spiny Lizard	*Sceloporus orcutti*	**43**	43	-			
	Snake	Western Blind Snake	*Rena humilis*	**42**	42	-			
	Lizard	Desert Spiny Lizard	*Sceloporus magister*	**41**	41	-			
	Lizard	Common Sagebrush Lizard	*Sceloporus graciosus*	**39**	41	-			
	Lizard	Gilbert's Skink	*Plestiodon gilberti*	**39**	39	-			
	Lizard	Western Skink	*Plestiodon skiltonianus*	**39**	39	-			
	Lizard	California Legless Lizard	*Anniella pulchra*	**35**	39	-	2		
	Salamander	Black Salamander	*Aneides flavipunctatus*	**35**	35	-			
	Salamander	Santa Cruz Black Salamander	*Aneides flavipunctatus niger*	**35**	35	-			
	Lizard	Baja California Collared Lizard	*Crotaphytus vestigium*	**35**	35	-			
	Lizard	Sandstone Night Lizard	*Xantusia gracilis*	**33**	33	-	3		
	Lizard	Granite Night Lizard	*Xantusia henshawi*	**33**	33	-			
	Lizard	Island Night Lizard	*Xantusia riversiana*	**33**	33	-	THR		
	Lizard	Sierra Night Lizard	*Xantusia sierrae*	**33**	33	-	1		
	Lizard	Desert Night Lizard	*Xantusia vigilis*	**33**	33	-			
	Lizard	Wiggins' Night Lizard	*Xantusia wigginsi*	**33**	33	-			
	Lizard	Long-tailed Brush Lizard	*Urosaurus graciosus*	**27**	27	-			
	Lizard	Baja California Brush Lizard	*Urosaurus nigricaudus*	**27**	27	-			
	Lizard	Ornate Tree Lizard	*Urosaurus ornatus*	**27**	27	-			
	Lizard	Mearns' Rock Lizard	*Petrosaurus mearnsi*	**21**	21	-			

[a] Maximum scores color-coded for toad risk type; terrestrial (gray), aquatic (blue), or both (gray/blue)

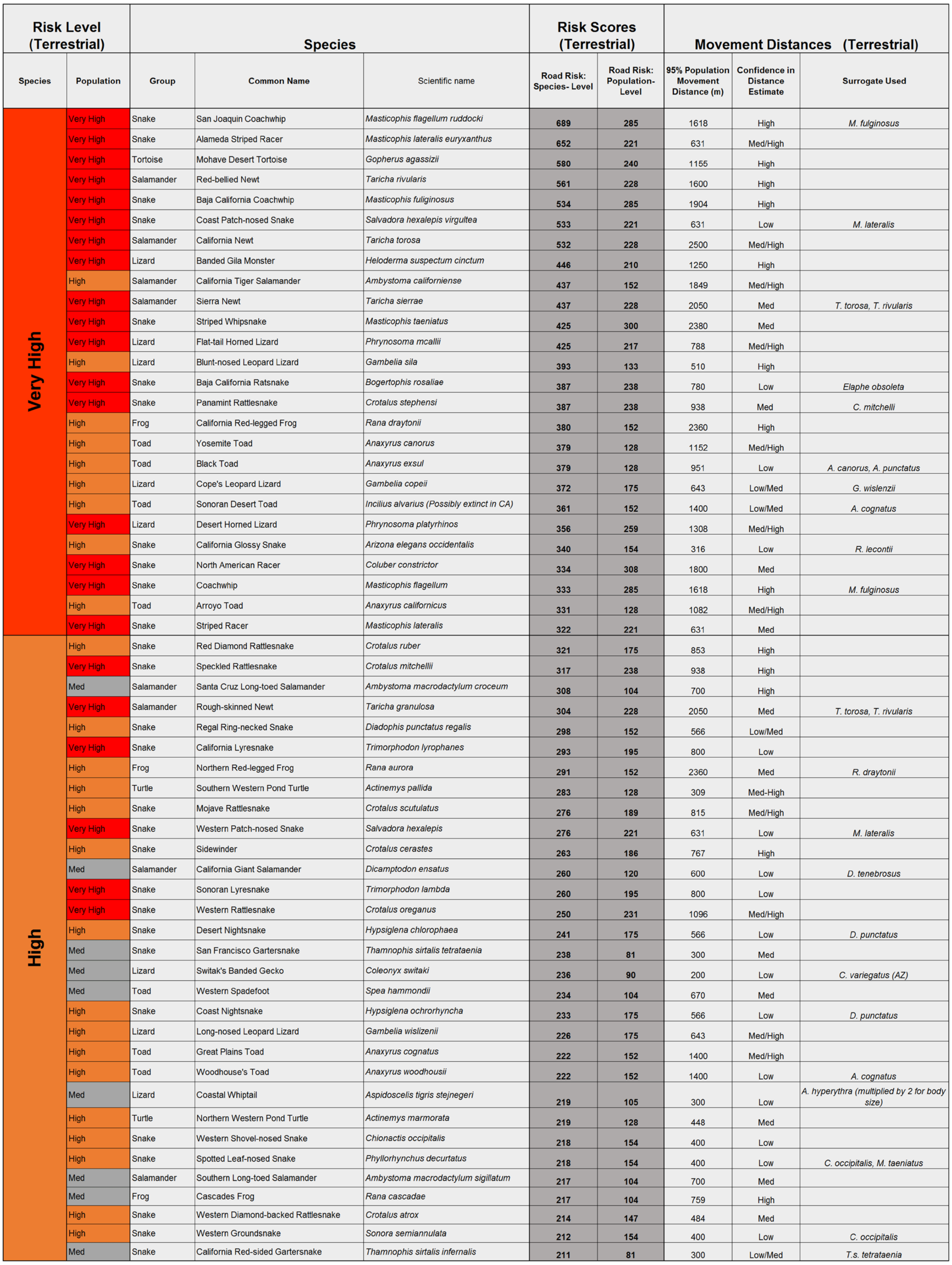
[b] END=Endangered, THR= Threatened, 1-3= ARSSC Priority Ranking

[c] Federal Recovery plans, 5-year reviews, California species accounts for special status species

[d] California Amphibian and Reptile Crossing Preliminary Investigation

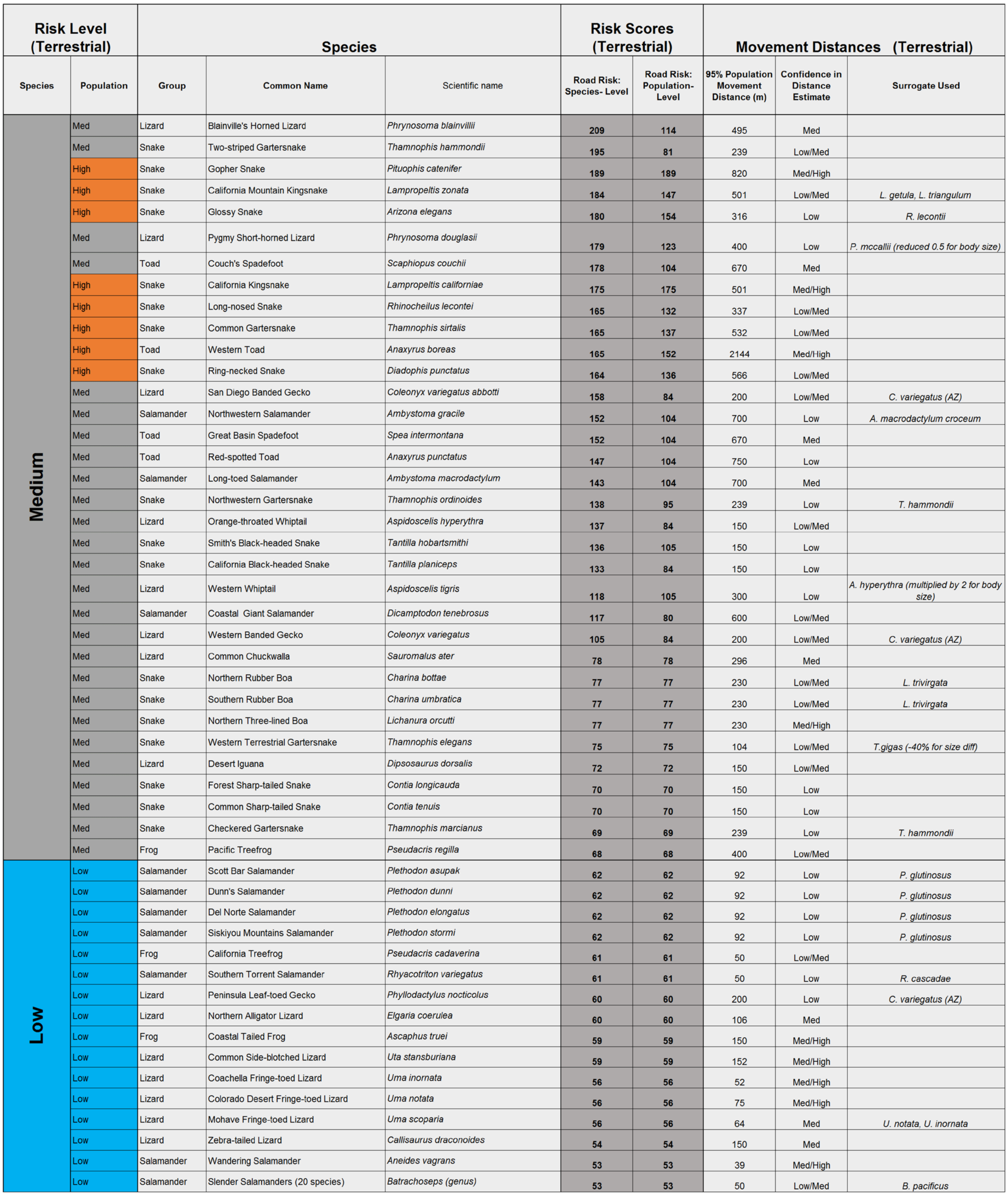
[e] 4 Batrachoseps species with conservation status

Table 9 Terrestrial risk ranking and population buffer distances



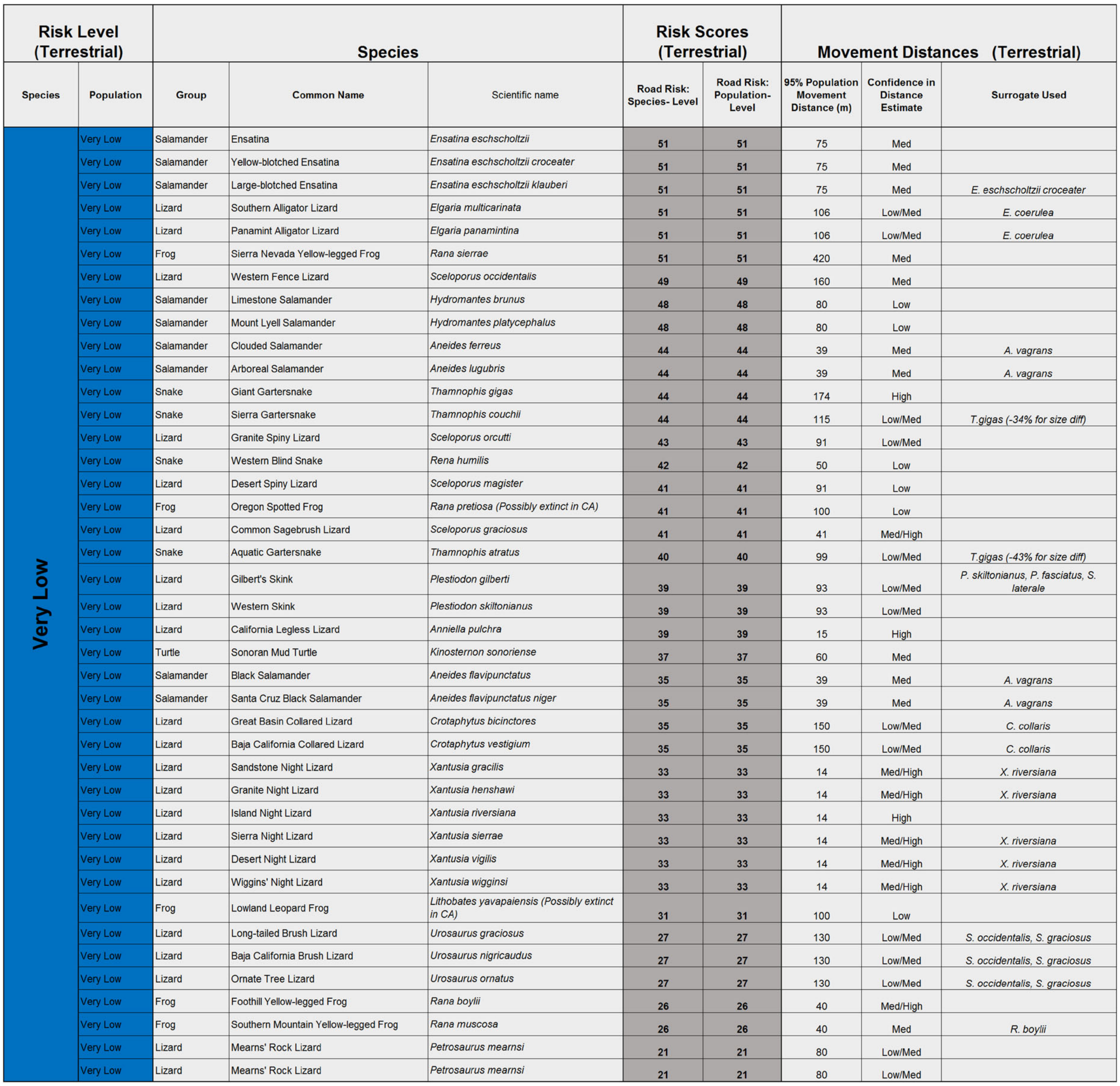
Risk Level (Terrestrial)		Species			Risk Scores (Terrestrial)		Movement Distances (Terrestrial)		
Species	**Population**	**Group**	**Common Name**	Scientific name	**Road Risk: Species- Level**	**Road Risk: Population-Level**	**95% Population Movement Distance (m)**	**Confidence in Distance Estimate**	**Surrogate Used**
Very High	Very High	Snake	San Joaquin Coachwhip	*Masticophis flagellum ruddocki*	**689**	**285**	1618	High	*M. fulginosus*
	Very High	Snake	Alameda Striped Racer	*Masticophis lateralis euryxanthus*	**652**	**221**	631	Med/High	
	Very High	Tortoise	Mohave Desert Tortoise	*Gopherus agassizii*	**580**	**240**	1155	High	
	Very High	Salamander	Red-bellied Newt	*Taricha rivularis*	**561**	**228**	1600	High	
	Very High	Snake	Baja California Coachwhip	*Masticophis fuliginosus*	**534**	**285**	1904	High	
	Very High	Snake	Coast Patch-nosed Snake	*Salvadora hexalepis virgultea*	**533**	**221**	631	Low	*M. lateralis*
	Very High	Salamander	California Newt	*Taricha torosa*	**532**	**228**	2500	Med/High	
	Very High	Lizard	Banded Gila Monster	*Heloderma suspectum cinctum*	**446**	**210**	1250	High	
	High	Salamander	California Tiger Salamander	*Ambystoma californiense*	**437**	**152**	1849	Med/High	
	Very High	Salamander	Sierra Newt	*Taricha sierrae*	**437**	**228**	2050	Med	*T. torosa, T. rivularis*
	Very High	Snake	Striped Whipsnake	*Masticophis taeniatus*	**425**	**300**	2380	Med	
	Very High	Lizard	Flat-tail Horned Lizard	*Phrynosoma mcallii*	**425**	**217**	788	Med/High	
	High	Lizard	Blunt-nosed Leopard Lizard	*Gambelia sila*	**393**	**133**	510	High	
	Very High	Snake	Baja California Ratsnake	*Bogertophis rosaliae*	**387**	**238**	780	Low	*Elaphe obsoleta*
	Very High	Snake	Panamint Rattlesnake	*Crotalus stephensi*	**387**	**238**	938	Med	*C. mitchelli*
	High	Frog	California Red-legged Frog	*Rana draytonii*	**380**	**152**	2360	High	
	High	Toad	Yosemite Toad	*Anaxyrus canorus*	**379**	**128**	1152	Med/High	
	High	Toad	Black Toad	*Anaxyrus exsul*	**379**	**128**	951	Low	*A. canorus, A. punctatus*
	High	Lizard	Cope's Leopard Lizard	*Gambelia copeii*	**372**	**175**	643	Low/Med	*G. wislenzii*
	High	Toad	Sonoran Desert Toad	*Incilius alvarius (Possibly extinct in CA)*	**361**	**152**	1400	Low/Med	*A. cognatus*
	Very High	Lizard	Desert Horned Lizard	*Phrynosoma platyrhinos*	**356**	**259**	1308	Med/High	
	High	Snake	California Glossy Snake	*Arizona elegans occidentalis*	**340**	**154**	316	Low	*R. lecontii*
	Very High	Snake	North American Racer	*Coluber constrictor*	**334**	**308**	1800	Med	
	Very High	Snake	Coachwhip	*Masticophis flagellum*	**333**	**285**	1618	High	*M. fulginosus*
	High	Toad	Arroyo Toad	*Anaxyrus californicus*	**331**	**128**	1082	Med/High	
	Very High	Snake	Striped Racer	*Masticophis lateralis*	**322**	**221**	631	Med	
High	High	Snake	Red Diamond Rattlesnake	*Crotalus ruber*	**321**	**175**	853	High	
	Very High	Snake	Speckled Rattlesnake	*Crotalus mitchellii*	**317**	**238**	938	High	
	Med	Salamander	Santa Cruz Long-toed Salamander	*Ambystoma macrodactylum croceum*	**308**	**104**	700	High	
	Very High	Salamander	Rough-skinned Newt	*Taricha granulosa*	**304**	**228**	2050	Med	*T. torosa, T. rivularis*
	High	Snake	Regal Ring-necked Snake	*Diadophis punctatus regalis*	**298**	**152**	566	Low/Med	
	Very High	Snake	California Lyresnake	*Trimorphodon lyrophanes*	**293**	**195**	800	Low	
	High	Frog	Northern Red-legged Frog	*Rana aurora*	**291**	**152**	2360	Med	*R. draytonii*
	High	Turtle	Southern Western Pond Turtle	*Actinemys pallida*	**283**	**128**	309	Med-High	
	High	Snake	Mojave Rattlesnake	*Crotalus scutulatus*	**276**	**189**	815	Med/High	
	Very High	Snake	Western Patch-nosed Snake	*Salvadora hexalepis*	**276**	**221**	631	Low	*M. lateralis*
	High	Snake	Sidewinder	*Crotalus cerastes*	**263**	**186**	767	High	
	Med	Salamander	California Giant Salamander	*Dicamptodon ensatus*	**260**	**120**	600	Low	*D. tenebrosus*
	Very High	Snake	Sonoran Lyresnake	*Trimorphodon lambda*	**260**	**195**	800	Low	
	Very High	Snake	Western Rattlesnake	*Crotalus oreganus*	**250**	**231**	1096	Med/High	
	High	Snake	Desert Nightsnake	*Hypsiglena chlorophaea*	**241**	**175**	566	Low	*D. punctatus*
	Med	Snake	San Francisco Gartersnake	*Thamnophis sirtalis tetrataenia*	**238**	**81**	300	Med	
	Med	Lizard	Switak's Banded Gecko	*Coleonyx switaki*	**236**	**90**	200	Low	*C. variegatus (AZ)*
	Med	Toad	Western Spadefoot	*Spea hammondii*	**234**	**104**	670	Med	
	High	Snake	Coast Nightsnake	*Hypsiglena ochrorhyncha*	**233**	**175**	566	Low	*D. punctatus*
	High	Lizard	Long-nosed Leopard Lizard	*Gambelia wislizenii*	**226**	**175**	643	Med/High	
	High	Toad	Great Plains Toad	*Anaxyrus cognatus*	**222**	**152**	1400	Med/High	
	High	Toad	Woodhouse's Toad	*Anaxyrus woodhousii*	**222**	**152**	1400	Low	*A. cognatus*
	Med	Lizard	Coastal Whiptail	*Aspidoscelis tigris stejnegeri*	**219**	**105**	300	Low	*A. hyperythra (multiplied by 2 for body size)*
	High	Turtle	Northern Western Pond Turtle	*Actinemys marmorata*	**219**	**128**	448	Med	
	High	Snake	Western Shovel-nosed Snake	*Chionactis occipitalis*	**218**	**154**	400	Low	
	High	Snake	Spotted Leaf-nosed Snake	*Phyllorhynchus decurtatus*	**218**	**154**	400	Low	*C. occipitalis, M. taeniatus*
	Med	Salamander	Southern Long-toed Salamander	*Ambystoma macrodactylum sigillatum*	**217**	**104**	700	Med	
	Med	Frog	Cascades Frog	*Rana cascadae*	**217**	**104**	759	High	
	High	Snake	Western Diamond-backed Rattlesnake	*Crotalus atrox*	**214**	**147**	484	Med	
	High	Snake	Western Groundsnake	*Sonora semiannulata*	**212**	**154**	400	Low	*C. occipitalis*
	Med	Snake	California Red-sided Gartersnake	*Thamnophis sirtalis infernalis*	**211**	**81**	300	Low/Med	*T.s. tetrataenia*

Table 9 continued



Risk Level (Terrestrial)		Species			Risk Scores (Terrestrial)		Movement Distances (Terrestrial)		
Species	**Population**	**Group**	**Common Name**	Scientific name	**Road Risk: Species- Level**	**Road Risk: Population-Level**	**95% Population Movement Distance (m)**	**Confidence in Distance Estimate**	**Surrogate Used**
Medium	Med	Lizard	Blainville's Horned Lizard	*Phrynosoma blainvillii*	**209**	**114**	495	Med	
	Med	Snake	Two-striped Gartersnake	*Thamnophis hammondii*	**195**	**81**	239	Low/Med	
	High	Snake	Gopher Snake	*Pituophis catenifer*	**189**	**189**	820	Med/High	
	High	Snake	California Mountain Kingsnake	*Lampropeltis zonata*	**184**	**147**	501	Low/Med	*L. getula, L. triangulum*
	High	Snake	Glossy Snake	*Arizona elegans*	**180**	**154**	316	Low	*R. lecontii*
	Med	Lizard	Pygmy Short-horned Lizard	*Phrynosoma douglasii*	**179**	**123**	400	Low	*P. mccallii (reduced 0.5 for body size)*
	Med	Toad	Couch's Spadefoot	*Scaphiopus couchii*	**178**	**104**	670	Med	
	High	Snake	California Kingsnake	*Lampropeltis californiae*	**175**	**175**	501	Med/High	
	High	Snake	Long-nosed Snake	*Rhinocheilus lecontei*	**165**	**132**	337	Low/Med	
	High	Snake	Common Gartersnake	*Thamnophis sirtalis*	**165**	**137**	532	Low/Med	
	High	Toad	Western Toad	*Anaxyrus boreas*	**165**	**152**	2144	Med/High	
	High	Snake	Ring-necked Snake	*Diadophis punctatus*	**164**	**136**	566	Low/Med	
	Med	Lizard	San Diego Banded Gecko	*Coleonyx variegatus abbotti*	**158**	**84**	200	Low/Med	*C. variegatus (AZ)*
	Med	Salamander	Northwestern Salamander	*Ambystoma gracile*	**152**	**104**	700	Low	*A. macrodactylum croceum*
	Med	Toad	Great Basin Spadefoot	*Spea intermontana*	**152**	**104**	670	Med	
	Med	Toad	Red-spotted Toad	*Anaxyrus punctatus*	**147**	**104**	750	Low	
	Med	Salamander	Long-toed Salamander	*Ambystoma macrodactylum*	**143**	**104**	700	Med	
	Med	Snake	Northwestern Gartersnake	*Thamnophis ordinoides*	**138**	**95**	239	Low	*T. hammondii*
	Med	Lizard	Orange-throated Whiptail	*Aspidoscelis hyperythra*	**137**	**84**	150	Low/Med	
	Med	Snake	Smith's Black-headed Snake	*Tantilla hobartsmithi*	**136**	**105**	150	Low	
	Med	Snake	California Black-headed Snake	*Tantilla planiceps*	**133**	**84**	150	Low	
	Med	Lizard	Western Whiptail	*Aspidoscelis tigris*	**118**	**105**	300	Low	*A. hyperythra (multiplied by 2 for body size)*
	Med	Salamander	Coastal Giant Salamander	*Dicamptodon tenebrosus*	**117**	**80**	600	Low/Med	
	Med	Lizard	Western Banded Gecko	*Coleonyx variegatus*	**105**	**84**	200	Low/Med	*C. variegatus (AZ)*
	Med	Lizard	Common Chuckwalla	*Sauromalus ater*	**78**	**78**	296	Med	
	Med	Snake	Northern Rubber Boa	*Charina bottae*	**77**	**77**	230	Low/Med	*L. trivirgata*
	Med	Snake	Southern Rubber Boa	*Charina umbratica*	**77**	**77**	230	Low/Med	*L. trivirgata*
	Med	Snake	Northern Three-lined Boa	*Lichanura orcutti*	**77**	**77**	230	Med/High	
	Med	Snake	Western Terrestrial Gartersnake	*Thamnophis elegans*	**75**	**75**	104	Low/Med	*T.gigas (-40% for size diff)*
	Med	Lizard	Desert Iguana	*Dipsosaurus dorsalis*	**72**	**72**	150	Low/Med	
	Med	Snake	Forest Sharp-tailed Snake	*Contia longicauda*	**70**	**70**	150	Low	
	Med	Snake	Common Sharp-tailed Snake	*Contia tenuis*	**70**	**70**	150	Low	
	Med	Snake	Checkered Gartersnake	*Thamnophis marcianus*	**69**	**69**	239	Low	*T. hammondii*
	Med	Frog	Pacific Treefrog	*Pseudacris regilla*	**68**	**68**	400	Low/Med	
Low	Low	Salamander	Scott Bar Salamander	*Plethodon asupak*	**62**	**62**	92	Low	*P. glutinosus*
	Low	Salamander	Dunn's Salamander	*Plethodon dunni*	**62**	**62**	92	Low	*P. glutinosus*
	Low	Salamander	Del Norte Salamander	*Plethodon elongatus*	**62**	**62**	92	Low	*P. glutinosus*
	Low	Salamander	Siskiyou Mountains Salamander	*Plethodon stormi*	**62**	**62**	92	Low	*P. glutinosus*
	Low	Frog	California Treefrog	*Pseudacris cadaverina*	**61**	**61**	50	Low/Med	
	Low	Salamander	Southern Torrent Salamander	*Rhyacotriton variegatus*	**61**	**61**	50	Low	*R. cascadae*
	Low	Lizard	Peninsula Leaf-toed Gecko	*Phyllodactylus nocticolus*	**60**	**60**	200	Low	*C. variegatus (AZ)*
	Low	Lizard	Northern Alligator Lizard	*Elgaria coerulea*	**60**	**60**	106	Med	
	Low	Frog	Coastal Tailed Frog	*Ascaphus truei*	**59**	**59**	150	Med/High	
	Low	Lizard	Common Side-blotched Lizard	*Uta stansburiana*	**59**	**59**	152	Med/High	
	Low	Lizard	Coachella Fringe-toed Lizard	*Uma inornata*	**56**	**56**	52	Med/High	
	Low	Lizard	Colorado Desert Fringe-toed Lizard	*Uma notata*	**56**	**56**	75	Med/High	
	Low	Lizard	Mohave Fringe-toed Lizard	*Uma scoparia*	**56**	**56**	64	Med	*U. notata, U. inornata*
	Low	Lizard	Zebra-tailed Lizard	*Callisaurus draconoides*	**54**	**54**	150	Med	
	Low	Salamander	Wandering Salamander	*Aneides vagrans*	**53**	**53**	39	Med/High	
	Low	Salamander	Slender Salamanders (20 species)	*Batrachoseps (genus)*	**53**	**53**	50	Low/Med	*B. pacificus*

Table 9 continued



Risk Level (Terrestrial)		Species			Risk Scores (Terrestrial)		Movement Distances (Terrestrial)		
Species	Population	Group	Common Name	Scientific name	Road Risk: Species- Level	Road Risk: Population-Level	95% Population Movement Distance (m)	Confidence in Distance Estimate	Surrogate Used
Very Low	Very Low	Salamander	Ensatina	*Ensatina eschscholtzii*	51	51	75	Med	
	Very Low	Salamander	Yellow-blotched Ensatina	*Ensatina eschscholtzii croceater*	51	51	75	Med	
	Very Low	Salamander	Large-blotched Ensatina	*Ensatina eschscholtzii klauberi*	51	51	75	Med	*E. eschscholtzii croceater*
	Very Low	Lizard	Southern Alligator Lizard	*Elgaria multicarinata*	51	51	106	Low/Med	*E. coerulea*
	Very Low	Lizard	Panamint Alligator Lizard	*Elgaria panamintina*	51	51	106	Low/Med	*E. coerulea*
	Very Low	Frog	Sierra Nevada Yellow-legged Frog	*Rana sierrae*	51	51	420	Med	
	Very Low	Lizard	Western Fence Lizard	*Sceloporus occidentalis*	49	49	160	Med	
	Very Low	Salamander	Limestone Salamander	*Hydromantes brunus*	48	48	80	Low	
	Very Low	Salamander	Mount Lyell Salamander	*Hydromantes platycephalus*	48	48	80	Low	
	Very Low	Salamander	Clouded Salamander	*Aneides ferreus*	44	44	39	Med	*A. vagrans*
	Very Low	Salamander	Arboreal Salamander	*Aneides lugubris*	44	44	39	Med	*A. vagrans*
	Very Low	Snake	Giant Gartersnake	*Thamnophis gigas*	44	44	174	High	
	Very Low	Snake	Sierra Gartersnake	*Thamnophis couchii*	44	44	115	Low/Med	*T.gigas (-34% for size diff)*
	Very Low	Lizard	Granite Spiny Lizard	*Sceloporus orcutti*	43	43	91	Low/Med	
	Very Low	Snake	Western Blind Snake	*Rena humilis*	42	42	50	Low	
	Very Low	Lizard	Desert Spiny Lizard	*Sceloporus magister*	41	41	91	Low	
	Very Low	Frog	Oregon Spotted Frog	*Rana pretiosa (Possibly extinct in CA)*	41	41	100	Low	
	Very Low	Lizard	Common Sagebrush Lizard	*Sceloporus graciosus*	41	41	41	Med/High	
	Very Low	Snake	Aquatic Gartersnake	*Thamnophis atratus*	40	40	99	Low/Med	*T.gigas (-43% for size diff)*
	Very Low	Lizard	Gilbert's Skink	*Plestiodon gilberti*	39	39	93	Low/Med	*P. skiltonianus, P. fasciatus, S. laterale*
	Very Low	Lizard	Western Skink	*Plestiodon skiltonianus*	39	39	93	Low/Med	
	Very Low	Lizard	California Legless Lizard	*Anniella pulchra*	39	39	15	High	
	Very Low	Turtle	Sonoran Mud Turtle	*Kinosternon sonoriense*	37	37	60	Med	
	Very Low	Salamander	Black Salamander	*Aneides flavipunctatus*	35	35	39	Med	*A. vagrans*
	Very Low	Salamander	Santa Cruz Black Salamander	*Aneides flavipunctatus niger*	35	35	39	Med	*A. vagrans*
	Very Low	Lizard	Great Basin Collared Lizard	*Crotaphytus bicinctores*	35	35	150	Low/Med	*C. collaris*
	Very Low	Lizard	Baja California Collared Lizard	*Crotaphytus vestigium*	35	35	150	Low/Med	*C. collaris*
	Very Low	Lizard	Sandstone Night Lizard	*Xantusia gracilis*	33	33	14	Med/High	*X. riversiana*
	Very Low	Lizard	Granite Night Lizard	*Xantusia henshawi*	33	33	14	Med/High	*X. riversiana*
	Very Low	Lizard	Island Night Lizard	*Xantusia riversiana*	33	33	14	High	
	Very Low	Lizard	Sierra Night Lizard	*Xantusia sierrae*	33	33	14	Med/High	*X. riversiana*
	Very Low	Lizard	Desert Night Lizard	*Xantusia vigilis*	33	33	14	Med/High	*X. riversiana*
	Very Low	Lizard	Wiggins' Night Lizard	*Xantusia wigginsi*	33	33	14	Med/High	*X. riversiana*
	Very Low	Frog	Lowland Leopard Frog	*Lithobates yavapaiensis (Possibly extinct in CA)*	31	31	100	Low	
	Very Low	Lizard	Long-tailed Brush Lizard	*Urosaurus graciosus*	27	27	130	Low/Med	*S. occidentalis, S. graciosus*
	Very Low	Lizard	Baja California Brush Lizard	*Urosaurus nigricaudus*	27	27	130	Low/Med	*S. occidentalis, S. graciosus*
	Very Low	Lizard	Ornate Tree Lizard	*Urosaurus ornatus*	27	27	130	Low/Med	*S. occidentalis, S. graciosus*
	Very Low	Frog	Foothill Yellow-legged Frog	*Rana boylii*	26	26	40	Med/High	
	Very Low	Frog	Southern Mountain Yellow-legged Frog	*Rana muscosa*	26	26	40	Med	*R. boylii*
	Very Low	Lizard	Mearns' Rock Lizard	*Petrosaurus mearnsi*	21	21	80	Low/Med	
	Very Low	Lizard	Mearns' Rock Lizard	*Petrosaurus mearnsi*	21	21	80	Low/Med	

over the surface during high flow events. These may be used as road crossings by species traveling along ephemeral stream corridors with or without water flow. Given these potential vulnerabilities, we believe that road impacts to aquatic connectivity of herpetofauna deserve greater consideration.

Across broad taxonomic groups, chelonids (tortoises/turtles) and snakes had the greatest percentages of species at 'high' or 'very high' risk from roads. They are similar in that many move long distances (home range and/or migratory), tend not to avoid roads (or are attracted to them for thermoregulation), are long lived, and have relatively low fecundity in comparison to other herpetofaunal groups. Because of these traits, chelonids and snakes have been identified elsewhere as being particularly susceptible to negative population effects from roads (Gibbs and Shriver 2002; Andrews et al. 2015b; Jackson et al. 2015).

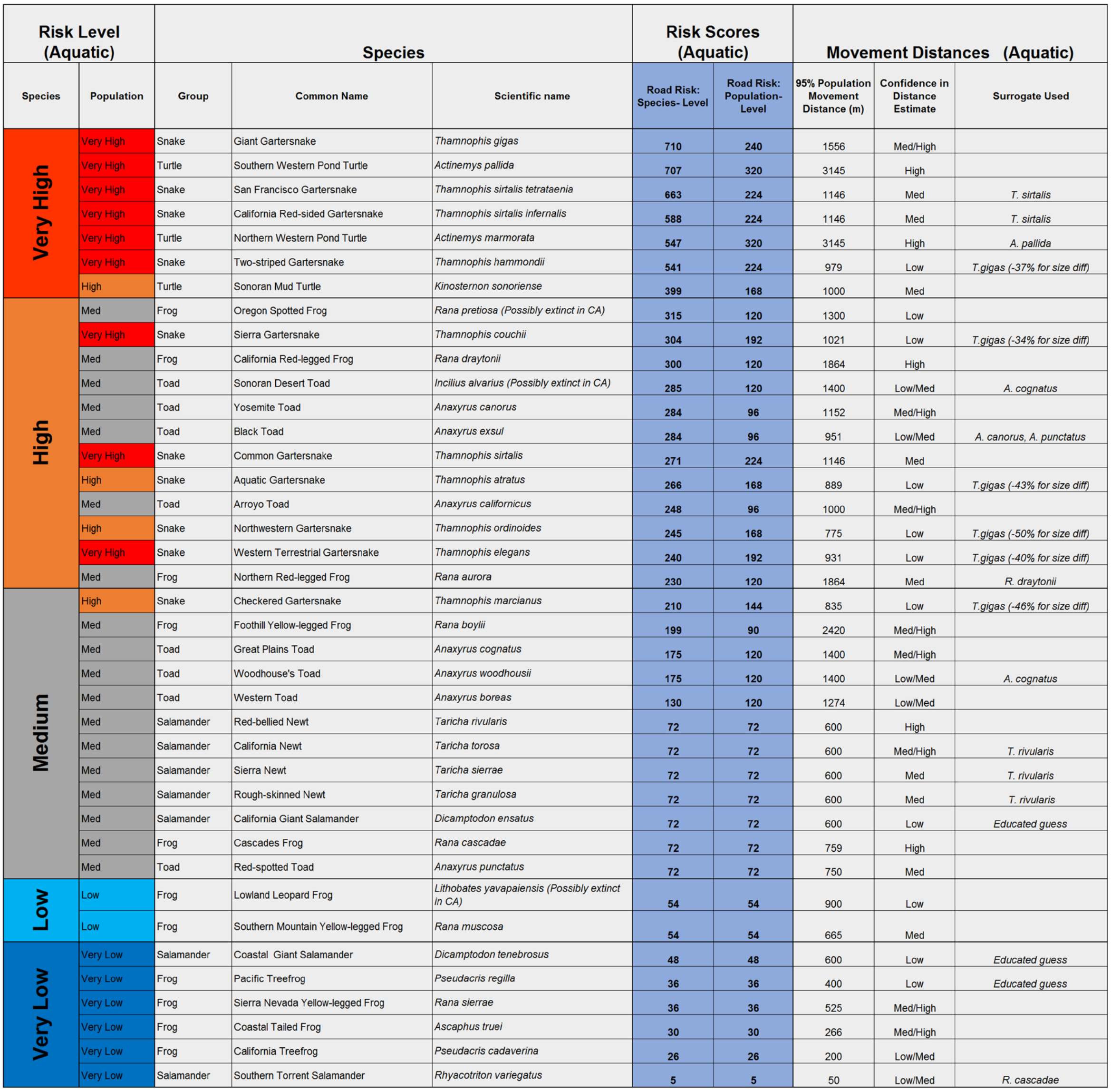
There are only four species of chelonids in California, (desert tortoise (*Gopherus agazzii*), Northwestern pond turtle (*Actinemys marmorata*), Southwestern pond turtle (*Actinemys pallida*), and the Sonoran mud turtle (*Kinosternon sonoriense*)). There has been a high level of attention to road impacts on the desert tortoise (*Gopherus agazzii*) as numerous studies have documented not only high road mortality, but measurable road effect zones, and mostly positive responses to barriers and underpasses (e.g., Boarman and Sazaki 1996, 2006; Peaden et al. 2016; but see Peadon et al. 2017). Although not listed as a primary threat to pond turtle populations in California (Thomson et al. 2016), road mortality is a major concern for western pond turtle populations in Oregon (Rosenberg et al. 2009). Pond turtles travel kilometers within perennial waters and from pool to pool in intermittent aquatic habitats to forage and find mates (Goodman and Stewart 2000). In addition, females nest and lay eggs in terrestrial habitats up to 0.5 km away from water which make roads that parallel aquatic habitat a threat to both females and hatchlings (Reese and Welsh 1997; Rathbun et al. 2002; Pilliod et al. 2013). In fact, road mortality of females has been identified as a cause for male-biased sex ratios in some populations of pond turtles and other freshwater turtle species (Steen et al. 2006; Rosenberg et al. 2009; Reid and Peery 2014). Therefore, this species requires consideration of both aquatic and terrestrial connectivity to satisfy their annual resource requirements. Sonoran mud turtles also travel long distances within intermittent streams and thus may be at risk of roads that transect their aquatic habitat (Hensley et al. 2010).

Larger colubrid snakes (Family Colubridae; many genera) and rattlesnakes (genus *Crotalus*) were ranked among the highest risk from negative road effects. In addition to being attracted to paved road surfaces for thermoregulation, many large snakes have wide home-ranges or may move large distances between winter hibernacula and summer foraging areas. In contrast to smaller species, larger snakes are also less likely to avoid roads (Rosen and Lowe 1994; Andrews and Gibbons 2005; Andrews et al. 2008; Siers et al. 2016). High road mortality (e.g., Klauber 1931; Rosen and Lowe 1994; Jones et al. 2011), reduced abundance near roads (Rudolph et al. 1999; Jones et al. 2011), increased extinction risk (Row et al. 2007), and decreased genetic diversity (Clark et al. 2010; Hermann et al. 2017) have been documented for numerous snake species; as have positive responses to barriers and underpasses (Dodd et al. 2004; Colley et al. 2017). In our statewide risk analysis, coachwhips (genus *Masticophis/Coluber*) were amongst the highest risk groups at both the population and species-levels. These are particularly wide-ranging and very active foragers in comparison to other snake genera (Stebbins and McGinnis 2012). The coachwhip (*Masticophis flagellum)* was found to be ninefold more likely to be extirpated from habitats that were fragmented by roads and urbanization, contributing to their decline throughout California (Case and Fisher 2001; Mitrovich 2006). Similarly, habitat fragmentation from roads and urbanization were identified as primary threats to the Alameda whipsnake (*Masticophis lateralis euryxanthus* USFWS 2011). Although road use and mortality have been documented for many other terrestrial California snake species on road-riding surveys (e.g., Klauber 1931; Jones et al. 2011; Shilling and Waetjen 2017), there is a paucity of studies examining population-level effects of roads on California snake species. We could find only one such study, where presence of a highway was shown to reduce gene flow in the Western diamond-backed rattlesnake (*Crotalus atrox)* in the Sonoran Desert, AZ (Hermann et al. 2017).

Long foraging movements within aquatic habitats also contributed to the majority of garter snakes (genus: *Thamnophis*) falling within the highest road risk categories. Maintaining aquatic and wetland connectivity is of primary concern for these species. Garter snakes also use terrestrial habitats for overwintering, reproduction, and for moving among wetland or aquatic patches. Some migrate long distances to winter hibernacula, making them also susceptible to roads within adjacent terrestrial habitats (Roe et al. 2006; Jackson et al. 2015). The highly aquatic giant garter snake (*Thamnophis gigas*) had the highest aquatic road risk score. Because it moves only short distances on land (Halstead et al. 2015), mitigation may best focus on functional aquatic passages with lengths of adjacent road barriers based upon their terrestrial movement distances.

Toads were the third highest ranking group with 64% ranked in the highest risk categories. In particular, Bufonid toads (family Bufonidae) may move large distances (> 1 km) in both aquatic and terrestrial habitats to satisfy their annual resource requirements; thus 5 of 7 bufonid species ranked high or very high risk from roads. Consistent with our risk assessment

Table 10 Aquatic risk ranking and population buffer distances



Risk Level (Aquatic)		Species			Risk Scores (Aquatic)		Movement Distances (Aquatic)		
Species	Population	Group	Common Name	Scientific name	Road Risk: Species- Level	Road Risk: Population-Level	95% Population Movement Distance (m)	Confidence in Distance Estimate	Surrogate Used
Very High	Very High	Snake	Giant Gartersnake	*Thamnophis gigas*	710	240	1556	Med/High	
	Very High	Turtle	Southern Western Pond Turtle	*Actinemys pallida*	707	320	3145	High	
	Very High	Snake	San Francisco Gartersnake	*Thamnophis sirtalis tetrataenia*	663	224	1146	Med	*T. sirtalis*
	Very High	Snake	California Red-sided Gartersnake	*Thamnophis sirtalis infernalis*	588	224	1146	Med	*T. sirtalis*
	Very High	Turtle	Northern Western Pond Turtle	*Actinemys marmorata*	547	320	3145	High	*A. pallida*
	Very High	Snake	Two-striped Gartersnake	*Thamnophis hammondii*	541	224	979	Low	*T.gigas (-37% for size diff)*
	High	Turtle	Sonoran Mud Turtle	*Kinosternon sonoriense*	399	168	1000	Med	
High	Med	Frog	Oregon Spotted Frog	*Rana pretiosa (Possibly extinct in CA)*	315	120	1300	Low	
	Very High	Snake	Sierra Gartersnake	*Thamnophis couchii*	304	192	1021	Low	*T.gigas (-34% for size diff)*
	Med	Frog	California Red-legged Frog	*Rana draytonii*	300	120	1864	High	
	Med	Toad	Sonoran Desert Toad	*Incilius alvarius (Possibly extinct in CA)*	285	120	1400	Low/Med	*A. cognatus*
	Med	Toad	Yosemite Toad	*Anaxyrus canorus*	284	96	1152	Med/High	
	Med	Toad	Black Toad	*Anaxyrus exsul*	284	96	951	Low/Med	*A. canorus, A. punctatus*
	Very High	Snake	Common Gartersnake	*Thamnophis sirtalis*	271	224	1146	Med	
	High	Snake	Aquatic Gartersnake	*Thamnophis atratus*	266	168	889	Low	*T.gigas (-43% for size diff)*
	Med	Toad	Arroyo Toad	*Anaxyrus californicus*	248	96	1000	Med/High	
	High	Snake	Northwestern Gartersnake	*Thamnophis ordinoides*	245	168	775	Low	*T.gigas (-50% for size diff)*
	Very High	Snake	Western Terrestrial Gartersnake	*Thamnophis elegans*	240	192	931	Low	*T.gigas (-40% for size diff)*
	Med	Frog	Northern Red-legged Frog	*Rana aurora*	230	120	1864	Med	*R. draytonii*
Medium	High	Snake	Checkered Gartersnake	*Thamnophis marcianus*	210	144	835	Low	*T.gigas (-46% for size diff)*
	Med	Frog	Foothill Yellow-legged Frog	*Rana boylii*	199	90	2420	Med/High	
	Med	Toad	Great Plains Toad	*Anaxyrus cognatus*	175	120	1400	Med/High	
	Med	Toad	Woodhouse's Toad	*Anaxyrus woodhousii*	175	120	1400	Low/Med	*A. cognatus*
	Med	Toad	Western Toad	*Anaxyrus boreas*	130	120	1274	Low/Med	
	Med	Salamander	Red-bellied Newt	*Taricha rivularis*	72	72	600	High	
	Med	Salamander	California Newt	*Taricha torosa*	72	72	600	Med/High	*T. rivularis*
	Med	Salamander	Sierra Newt	*Taricha sierrae*	72	72	600	Med	*T. rivularis*
	Med	Salamander	Rough-skinned Newt	*Taricha granulosa*	72	72	600	Med	*T. rivularis*
	Med	Salamander	California Giant Salamander	*Dicamptodon ensatus*	72	72	600	Low	*Educated guess*
	Med	Frog	Cascades Frog	*Rana cascadae*	72	72	759	High	
	Med	Toad	Red-spotted Toad	*Anaxyrus punctatus*	72	72	750	Med	
Low	Low	Frog	Lowland Leopard Frog	*Lithobates yavapaiensis (Possibly extinct in CA)*	54	54	900	Low	
	Low	Frog	Southern Mountain Yellow-legged Frog	*Rana muscosa*	54	54	665	Med	
Very Low	Very Low	Salamander	Coastal Giant Salamander	*Dicamptodon tenebrosus*	48	48	600	Low	*Educated guess*
	Very Low	Frog	Pacific Treefrog	*Pseudacris regilla*	36	36	400	Low	*Educated guess*
	Very Low	Frog	Sierra Nevada Yellow-legged Frog	*Rana sierrae*	36	36	525	Med/High	
	Very Low	Frog	Coastal Tailed Frog	*Ascaphus truei*	30	30	266	Med/High	
	Very Low	Frog	California Treefrog	*Pseudacris cadaverina*	26	26	200	Low/Med	
	Very Low	Salamander	Southern Torrent Salamander	*Rhyacotriton variegatus*	5	5	50	Low/Med	*R. cascadae*

results, there is evidence that bufonid toads are particularly susceptible to negative impacts from roads elsewhere (Trenham et al. 2003; Orłowski 2007; Eigenbrod et al. 2008).

Roads and traffic have been associated with reduced abundance and species richness of frog populations (e.g., Fahrig et al. 1995; Houlahan and Findlay 2003). However, approximately half of California species are small, primarily aquatic, highly fecund, with relatively limited movements and thus ranked low for road impacts. Four of 11 species ranked within the highest risk groupings; California red-legged frog (*Rana draytonii*), Oregon spotted frog (*R. pretiosa*), Northern red-legged frog (*R. aurora*), and Cascades frog (*R. cascadae*). The Oregon spotted frog (*R. pretiosa*) is known to move large distances within aquatic habitats (Bourque 2008; USFWS 2009). Construction of a highway that bisected the

Yellowstone population of Oregon spotted frogs was one important factor that reduced the population dramatically in the 1950s (see discussion in Watson et al. 2003). Although portions of the populations show high site fidelity, California red-legged frog and Northern red-legged frog migrants can move large distances (> 1 km) across both aquatic and terrestrial habitats (Bulger et al. 2003; Fellers and Kleeman 2007; Hayes et al. 2007). Road mortality or habitat fragmentation from roads and urbanization were listed as primary threats to these species elsewhere (USFWS 2002; COSEWIC 2015).

Lizards had relatively low percentages of species in the high risk groupings. Many lizard species are small, non-migratory, territorial, have small home ranges and are thus at low risk of negative road effects. Similar to snakes, lizards can also be attracted to road surfaces for thermoregulation. A few wide ranging species scored in the highest risk categories including the Gila monster (*Heloderma suspectum*), leopard lizards (genus *Gambelia*) and two horned lizard species (genus *Phrynosoma*). The Gila monster has been negatively associated with urbanization, where larger home ranges and greater movement rates result in higher mortality for males (Kwiatkowski et al. 2008). Sensitive to habitat fragmentation, the blunt-nosed leopard lizard (*Gambelia sila*) was found to be largely absent from habitat patches less than 250 ha (Bailey and Germano 2015). Flat-tailed horned lizards (*Phrynosoma mccallii*) are also susceptible to habitat fragmentation with very large home ranges for their size, particularly in wet years (Young and Young 2000). In fact, road mortality is a well-known threat for this species (see review by CDFW 2016b). Horned lizards are also particularly vulnerable to being killed on roads due to their tendency to flatten and remain motionless while being approached (Young and Young 2000).

Salamanders also had relatively low percentages of species in the high risk grouping. Over 75% (35/46) of the California salamanders are lungless salamanders (Plethodontidae) and Torrent salamanders (Rhyacotritonidae). These species are mostly small, sedentary, non-migratory, closed habitat specialists with limited movement distances and these traits have resulted in a high level of speciation. This is exemplified by there being at least 20 species of slender salamanders (genus *Batrachoseps*) in California alone (Martinez-Solano et al. 2007; Vences and Wake 2007). However, within the salamander group, newts and several other migratory salamander species were ranked within the highest risk categories from negative road effects. There is substantial evidence that habitat fragmentation and mortality due to roads negatively affect many of these species. For instance, newts regularly migrate long distances over land from and to breeding ponds, and to terrestrial foraging habitats (> 2 km; Trenham 1998). Large numbers are found dead on roads during dispersal periods and newt species are often the first to disappear in fragmented landscapes (Gibbs 1998; Trenham 1998, Shields pers. comm.). Similarly, road mortality and habitat fragmentation are primary threats to the California tiger salamander and other Ambystomid salamanders because terrestrial habitat is used for interpond migration and overwintering (Semlitsch 1998; Trenham et al. 2001; Bolster 2010).

Because this assessment covers a wide array of species and habitats, the risk to particular species populations must be re-assessed on a local level. This includes consideration of the locations, types, and densities of roads in relation to population and species ranges along with goals for functional, meta-population, and genetic connectivity (e.g., Marsh and Jaeger 2015). Due to very low road densities in their limited ranges, some species and populations may be at lower risk. For instance the Gila monster, Oregon spotted frog, Sonoran mud turtle, Sonoran desert toad (*Incilius alvarius*) and Yosemite toad (*Anaxyrus canorus*) scored high due to life history and space-use characteristics, however their limited ranges are largely in protected or low road density areas in the state. Thus roads may not be a significant threat to these species in California. In contrast, high road densities may increase the risk for species within coastal regions such as remaining populations of Santa Cruz long-toed salamander (*Ambystoma macrodactylum croceum*), Alameda striped racer (*Masticophis lateralis euryxanthus*), and San Francisco garter snake (*Thamnophis sirtalis tetrataenia*). However, most species consist of numerous populations with a myriad of differing road-related threat levels. Although detailed species ranges and occupancy within ranges are well known for some species with very limited ranges, for most species range-wide surveys have not been conducted. Therefore, only general range boundaries are available that encompass large portions of the state and availability of species distribution models of habitat suitability and occupancy within their ranges is rare. This lack of detailed spatial information on species distribution further limits the potential to incorporate road locations, types, and densities in a state and species-wide assessment.

We also note that relative risk to negative road impacts is provided for both populations and species. Risk was elevated for species with small and isolated ranges and that are facing a myriad of other threats. Because of this, a few common widespread species scored high at the population-level but not at the species-level. This included gopher snakes (*Pituophis catenifer*) and western toads (*Anaxyrus boreas*) where road mortality has been identified as a threat to the persistence of local populations (e.g., COSEWIC 2012; Jochimsen et al. 2014).

To potentially aid in local assessments, we have provided distance estimates or "buffer zones" that contain estimates for 95% of population-level movements for all species (e.g., Semlitsch and Bodie 2003). We provide all references evaluated for distance estimates in Appendix 2. Meta-population movements can be very important to the stability of pond-breeding amphibians (e.g., Semlitsch 2008; Jackson et al. 2015) and are included in many of the buffer zone calculations. However, we note that buffer zones may not include meta-population-level movements if the rate of these dispersal movements was less than 5% in the studies we used for our analyses.

This should be considered an initial assessment of susceptibility to negative road impacts in a hierarchical framework (e.g., see Level 2; Hobday et al. 2011). Therefore, as previously stated it will be important to re-assess the risk of specific populations to roads within their habitat and to evaluate and compare alternatives at the local scale (e.g., Suter 2016). This may include more detailed information on specific road attributes (e.g., density, type, location), as well as species behavior (Jaeger et al. 2005; Rouse et al. 2011; Rytwinski and Fahrig 2013; Jacobson et al. 2016). Age structured and spatially explicit population viability models are valuable tools to predict long-term population responses to roads and to compare outcomes of multiple mitigation scenarios (e.g., Gibbs and Shriver 2005; Borda-de-Água et al. 2014; Polak et al. 2014; Crawford 2015). Need and placement of mitigation structures can be guided by local population or meta-population dynamics, landscape attributes, movement routes, and road mortality hot spots (e.g., Bissonette and Adair 2008; Langen et al. 2009, 2015b; D'Amico et al. 2016; Loraamm and Downs 2016).

The quantity and quality of life history information, particularly movement data, are highly variable among species (see confidence levels; Tables 9 and 10). Therefore it is important to re-assess risk as new information becomes available. Finally, this is a structured assessment of comparative risk across a range of target species; therefore specific values for high risk have not been established. The ranking or assessment methodology should be adaptive and updated with advancements of road ecology science (e.g., Linkov et al. 2006).

Conclusion

Although roads are a significant cause of mortality and habitat fragmentation for many wildlife populations, road-related risk rankings have been based largely on expert opinion due to a scarcity of literature on road effects for most species. Therefore, we developed an objective and scientifically-based comparative risk approach to assess the potential threat from negative road impacts using species life history and movement data. After applying it to over 160 herpetofaunal species (and subspecies) in the state of California, the results are consistent with road ecology literature in identifying known high risk species, and call attention to some species not previously identified. Overall, we found that snakes and chelonids had the largest proportion of species at high risk for negative road impacts due to longer movement distances (home range and/or migratory), lack of road avoidance, and relatively low fecundity in comparison to other herpetofaunal groups. Results also indicated that consideration of aquatic connectivity appears to be under-represented for semi-aquatic herpetofauna that use both terrestrial and stream, riverine, or wetland habitats.

In addition to informing transportation planning and mitigation considerations for California herpetofauna, we believe this approach may be useful for comparing the risk of road-related fragmentation and mortality for species elsewhere and for other taxonomic groups. The results can help to inform multi-criteria threat assessments for special status species or those in consideration for listing. Finally, this serves to highlight species that may deserve further study and consideration for aquatic and terrestrial road mitigation to reduce mortality and to maintain population-level connectivity.

This risk assessment approach compares the susceptibility of species to negative road impacts. Commonly, there are numerous populations within a species range that occupy areas with greatly differing road pressures. Therefore, the actual risk to specific species populations will depend upon local road densities, road-types, traffic, and road locations in relation to species habitat and movement corridors.

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References

Andrews KM, Gibbons JW (2005) How do highways influence snake movement? Behavioral responses to roads and vehicles. Copeia 4:772–782

Andrews KM, Gibbons JW, Jochimsen D, Mitchell J (2008) Ecological effects of roads on amphibians and reptiles: a literature review. In: Mitchell JC, Jung Brown RE, Bartholomew B (eds) Urban Herpetology, Herpetological Conservation 3. Society for the Study of Reptiles and Amphibians, Salt-Lake City, UT, pp 121–143

Andrews KM, Nanjappa P, Riley SP (eds) (2015a) Roads and ecological infrastructure: concepts and applications for small animals. JHU Press, Baltimore, MD

Andrews KM, Langen TA, Struijk RPJH (2015b) Reptiles: Overlooked but often at risk from roads. Handbook of Road Ecology. Wiley, New York, pp 271–280

Bailey CV, Germano DJ (2015) Probability of occupancy of blunt-nosed leopard lizards on habitat patches of various sizes in the San Joaquin Desert of California. W Wild 2:23–28

Bissonette JA, Adair W (2008) Restoring habitat permeability to roaded landscapes with isometrically-scaled wildlife crossings. Biol Conserv 141(2):482–488

Boarman WI, Sazaki M (1996) Highway mortality in desert tortoises and small vertebrates: success of barrier fences and culverts (No. FHWA-PD-96-041)

Boarman WI, Sazaki M (2006) A highway's road-effect zone for desert tortoises (*Gopherus agassizii*). J Arid Environ 65(1):94–101

Bolster BC (2010) A status review of the California tiger salamander (*Ambystoma californiense).* Report to the Fish and Game Commission, State of California. Nongame Wildlife Program Report 2010–4

Bonnet X, Naulleau G, Shine R (1999) The dangers of leaving home: dispersal and mortality in snakes. Biol Conserv 89(1):39–50

Borda-de-Água L, Grilo C, Pereira HM (2014) Modeling the impact of road mortality on barn owl (*Tyto alba*) populations using age-structured models. Ecol Model 276:29–37

Bourque R (2008) [North Coast] spatial ecology of an inland population of the foothill yellow-legged frog (*Rana boylii*) in Tehama County, California. Masters Thesis, California State University, Humboldt, pp 107

Brehme CS, Tracey JA, McClenaghan LR, Fisher RN (2013) Permeability of roads to movement of scrubland lizards and small mammals. Conserv Biol 27(4):710–720

Bulger JB, Scott NJ, Seymour RB (2003) Terrestrial activity and conservation of adult California red-legged frogs *Rana aurora draytonii* in coastal forests and grasslands. Biol Conserv 110(1):85–95

California Department of Fish and Wildlife (CDFW) (2016a) Threatened and endangered species. http://www.dfg.ca.gov/wildlife/nongame/t_e_spp/ (accessed August 2016)

California Department of Fish and Wildlife (CDFW) (2016b) A status review of the flat-tailed horned lizard (*Phrynosoma mcallii*) in California. Report to the Fish and Game Commission

Carr LW, Fahrig L (2001) Effect of road traffic on two amphibian species of differing vagility. Conserv Biol 15(4):1071–1078

Case TJ, Fisher RN (2001) Measuring and predicting species presence: coastal sage scrub case study. In: Hunsaker CT, Goodchild MF, Friedl MA, Case TJ (eds) Spatial uncertainty in ecology. Springer-Verlag, New York, pp 47–71

Clark RW, Brown WS, Stechert R, Zamudio KR (2010) Roads, interrupted dispersal, and genetic diversity in timber rattlesnakes. Conserv Biol 24(4):1059–1069

Clarkin K, Conner A, Furniss MJ, Gibernick B, Love M, Moynan K, Wilson S (2005) National inventory and assessment procedure for identifying barriers to aquatic organism passage at road-stream crossings. US Dep Agric for Serv. http://www.stream.fs.fed.us/publications/PDFs/NIAP.pdf

Colino-Rabanal VJ, Lizana M (2012) Herpetofauna and roads: a review. Basic Appl Herpetol 26:5–31

Colley M, Lougheed SC, Otterbein K, Litzgus JD (2017) Mitigation reduces road mortality of a threatened rattlesnake. Wildlife Res. https://doi.org/10.1071/WR16130

Congress US (1973) Endangered species act. US Code 16:1534–1544

COSEWIC (Committee on the Status of Endangered Wildlife in Canada) (2012) COSEWIC assessment and status report on the Western Toad *Anaxyrus boreas* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xiv + 71 pp. (www.registrelep-sararegistry.gc.ca/default_e.cfm)

COSEWIC (Committee on the Status of Endangered Wildlife in Canada) (2015) COSEWIC assessment and status report on the Northern Red-legged Frog *Rana aurora* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xii + 69 pp. (www.registrelep-sararegistry.gc.ca/default_e.cfm)

Crawford BA (2015) Lessons from terrapin mortality and management on the Jekyll Island Causeway, Georgia, USA. In: Andrews KM, Nanjappa P, Riley SPD (eds) Roads and ecological infrastructure. Concepts and applications for small animals. Johns Hopkins University Press, Baltimore, pp 21–41

D'Amico M, Román J, De los Reyes L, Revilla E (2015) Vertebrate road-kill patterns in Mediterranean habitats: who, when and where. Biol Conserv 191:234–242

D'Amico M, Périquet S, Román J, Revilla E (2016) Road avoidance responses determine the impact of heterogeneous road networks at a regional scale. J Appl Ecol 53(1):181–190

Dodd CK, Barichivich WJ, Smith LL (2004) Effectiveness of a barrier wall and culverts in reducing wildlife mortality on a heavily traveled highway in Florida. Biol Conserv 118(5):619–631

Eigenbrod F, Hecnar SJ, Fahrig L (2008) The relative effects of road traffic and forest cover on anuran populations. Biol Conserv 141(1):35–46

Evelyn CJ, Sweet SS (2012) Conservation status of amphibians and reptiles on USDA National Forests, Pacific Southwest Region, 2012. Prepared for: USDA National Forest Service, Region 5, Pacific Southwest Region

Fahrig L, Rytwinski T (2009) Effects of roads on animal abundance: an empirical review and synthesis. Ecol Soc 14. http://www.ecologyandsociety.org/vol14/iss11/art21

Fahrig L, Pedlar JH, Pope SE, Taylor PD, Wegner JF (1995) Effect of road traffic on amphibian density. Biol Conserv 73(3):177–182

Fellers GM, Kleeman PM (2007) California red-legged frog (*Rana draytonii*) movement and habitat use: implications for conservation. J Herpetol 41(2):276–286

Forman RT, Sperling D, Bissonette JA, Clevenger AP, Cutshall CD, Dale VH, Fahrig L, France R, Goldman CR, Heanue K, Jones JA (2003) Road ecology. Science and Solutions. Island Press, Washington

Furniss MJ, Roelofs TD, Yee CS (1991) Road construction and maintenance. Am Fish Soc Special Publ 19:297–323

Gibbs JP (1998) Amphibian movements in response to forest edges, roads, and streambeds in southern New England. J Wildl Manage 62:584–589

Gibbs JP, Shriver WG (2002) Estimating the effects of road mortality on turtle populations. Conserv Biol 16(6):1647–1652

Gibbs JP, Shriver WG (2005) Can road mortality limit populations of pool-breeding amphibians? Wetl Ecol Manag 13:281–289

Glista DJ, DeVault TL, DeWoody JA (2008) Vertebrate road mortality predominantly impacts amphibians. Herpetol Conserv Biol 3(1):77–87

Goodman RH, Stewart GR (2000) Aquatic home ranges of female Western Pond Turtles, *Clemmys marmorata*, at two sites in Southern California. Chelonian Conserv Biol 3(4):743–744

Gregory PT (1984) Communal denning in snakes. In: Seigel RA, Hunt LE, Knight JL, Maralet LA, Zuschlag NL (eds) Contributions to vertebrate ecology and systematics: a tribute to Henry S. Fitch. University of Kansas Museum of Natural History Special Publication 10:57–75

Halstead BJ, Skalos SM, Wylie GD, Casazza ML (2015) Terrestrial ecology of semi-aquatic giant gartersnakes (*Thamnophis gigas*). Herpetol Conserv Bio 10(2):633–644

Hayes MP, Rombough CJ, Hayes CB (2007) Natural History: *Rana aurora* (Northern red-legged frog) movement. Herpetol Rev 38:192–193

Hensley FR, Jones TR, Maxwell MS, Adams LJ, Nedella NS (2010) Demography, terrestrial behavior, and growth of Sonora mud turtles (*Kinosternon sonoriense*) in an extreme habitat. Herpetol Monogr 24:174–193

Hermann HW, Pozarowski KM, Ochoa A, Schuett GW (2017) An interstate highway affects gene flow in a top reptilian predator (*Crotalus atrox*) of the Sonoran Desert. Conserv Genet 18:911–924

Hickman JC (ed) (1993) The Jepson manual of higher plants of California. University of California Press, Berkeley

Hobday AJ, Smith ADM, Stobutzki IC, Bulman C, Daley R, Dambacher JM, Deng RA, Dowdney J, Fuller M, Furlani D, Griffiths SP (2011) Ecological risk assessment for the effects of fishing. Fish Res 108(2):372–384

Houlahan JE, Findlay CS (2003) The effects of adjacent land use on wetland amphibian species richness and community composition. Can J Fish Aquat Sci 60:1078–1094

Hozo SP, Djulbegovic B, Hozo I (2005) Estimating the mean and variance from the median, range, and the size of a sample. BMC Med Res Methodol 5(1):1

IUCN (2017) The IUCN Red List of Threatened Species. Version 2017-1. http://www.iucnredlist.org

Jackson ND, Fahrig L (2011) Relative effects of road mortality and decreased connectivity on population genetic diversity. Biol Conserv 144(12):3143–3148

Jackson SD, Langen TA, Marsh DM, Andrews KM (2015) Natural history and physiological characteristics of small animals in relation to roads. In: Andrews KM, Nanjappa P, Riley SPD (eds) Roads and ecological infrastructure. Concepts and applications for small animals. Johns Hopkins University Press, Baltimore, pp 21–41

Jacobson SL, Bliss-Ketchum LL, Rivera CE, Smith WP (2016) A behavior-based framework for assessing barrier effects to wildlife from vehicle traffic volume. Ecosphere 7(4):e01345

Jaeger JA (2000) Landscape division, splitting index, and effective mesh size: new measures of landscape fragmentation. Land Ecol 15(2):115–130

Jaeger JA, Bowman J, Brennan J, Fahrig L, Bert D, Bouchard J, Charbonneau N, Frank K, Gruber B, von Toschanowitz KT (2005) Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. Ecol Model 185(2):329–348

Januchowski-Hartley SR, McIntyre PB, Diebel M, Doran PJ, Infante DM, Joseph C, Allan JD (2013) Restoring aquatic ecosystem connectivity requires expanding inventories of both dams and road crossings. Front Ecol Environ 11(4):211–217

Jochimsen DM, Peterson CR, Andrews KM, Gibbons JW, Drawer E (2004) A literature review of the effects of roads on amphibians and reptiles and the measures used to minimize those effects. USDA Forest Service, Idaho Fish and Game Department, Washington, DC

Jochimsen DM, Peterson CR, Harmon LJ (2014) Influence of ecology and landscape on snake road mortality in a sagebrush-steppe ecosystem. Anim Conserv 17(6):583–592

Jones TR, Babb RD, Hensley FR, LiWanPo C, Sullivan BK (2011) Sonoran Desert snake communities at two sites: concordance and effects of increased road traffic. Herpetol Conserv Biol 6(1):61–71

Kemp PS, O'hanley JR (2010) Procedures for evaluating and prioritising the removal of fish passage barriers: a synthesis. Fish Manag Ecol 17(4):297–322

Klauber LM (1931) A statistical survey of the snakes of the southern border of California. Bull Zool Soc San Diego 8:1–93

Kwiatkowski MA, Schuett GW, Repp RA, Nowak EM, Sullivan BK (2008) Does urbanization influence the spatial ecology of Gila monsters in the Sonoran Desert? J Zool 276(4):350–357

Langen TA, Ogden KM, Schwarting LL (2009) Predicting hot spots of herpetofauna road mortality along highway networks. J Wildl Manag 73(1):104–114

Langen TA, Andrews KM, Brady SP, Karraker NE, Smith DJ (2015a) Road effects on habitat quality for small animals. In: Andrews KM, Nanjappa P, Riley SPD (eds) Roads and ecological infrastructure. Concepts and applications for small animals. Johns Hopkins University Press, Baltimore, pp 21–41

Langen TA, Gunson KE, Jackson SD, Smith DJ, Ruediger W (2015b) Planning and designing mitigation of road effects on small animals. In: Andrews KM, Nanjappa P, Riley SPD (eds) Roads and ecological infrastructure. Concepts and applications for small animals. Johns Hopkins University Press, Baltimore, pp 146–177

Langton TES (2015) A history of small animal road ecology. Roads and ecological infrastructure. Concepts and applications for small animals. Johns Hopkins University Press, Baltimore, pp 21–41

Lannoo MJ (2005) Amphibian declines: the conservation status of United States species. University of California Press, Berkeley

Levine KK (2013) California amphibian and reptile crossing preliminary investigation. Report to Caltrans Division of Environmental Planning

Linkov I, Satterstrom FK, Kiker G, Batchelor C, Bridges T, Ferguson E (2006) From comparative risk assessment to multi-criteria decision analysis and adaptive management: recent developments and applications. Environ Int 32(8):1072–1093

Litvaitis JA, Tash JP (2008) An approach toward understanding wildlife-vehicle collisions. Environ Manag 42(4):688–697

Loraamm RW, Downs JA (2016) A wildlife movement approach to optimally locate wildlife crossing structures. Int J Geogr Inf Sci 30(1):74–88

Mace GM, Collar NJ, Gaston KJ, Hilton-Taylor C, Akçakaya HR, Leader-Williams N, Milner-Gulland EJ, Stuart SN (2008) Quantification of extinction risk: IUCN's system for classifying threatened species. Conserv Biol 22(6):1424–1442

Marsh DM, Jaeger JAG (2015) Direct effects of roads on small animal populations. Roads and ecological infrastructure. Concepts and applications for small animals. Johns Hopkins University Press, Baltimore, pp 21–41

Martinez-Solano I, Jockusch EL, Wake DB (2007) Extreme population subdivision throughout a continuous range: phylogeography of *Batrachoseps attenuatus* (Caudata: Plethodontidae) in western North America. Mol Ecol 16(20):4335–4355

Mazerolle MJ, Huot M, Gravel M (2005) Behavior of amphibians on the road in response to car traffic. Herpetologica 61(4):380–388

Mccardle LD, Fontenot CL (2016) The influence of thermal biology on road mortality risk in snakes. J Thermal Biol 56:39–49

Mitrovich MJ (2006) A case study in conservation science: The spatial ecology and evolutionary history of the coachwhip snake (*Masticophis flagellum*) and striped racer (*M. lateralis*). Ph.D. dissertation. University of California, Davis, and San Diego State University. San Diego

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403(6772):853–858

NatureServe (2017) NatureServe explorer: An online encyclopedia of life [web application]. Version 7.1. NatureServe, Arlington, Virginia. http://explorer.natureserve.org. (Accessed: May 25, 2017)

Orłowski G (2007) Spatial distribution and seasonal pattern in road mortality of the common toad *Bufo bufo* in an agricultural landscape of south-western Poland. Amphibia-Reptilia 28(1):25–31

Peaden JM, Tuberville TD, Buhlmann KA, Nafus MG, Todd BD (2016) Delimiting road-effect zones for threatened species: implications for mitigation fencing. Wildl Res 42(8):650–659

Peaden JM, Nowakowski AJ, Tuberville TD, Buhlmann KA, Todd BD (2017) Effects of roads and roadside fencing on movements, space use, and carapace temperatures of a threatened tortoise. Biol Conserv 214:13–22

Pianka ER (1966) Convexity, desert lizards, and spatial heterogeneity. Ecology 47(6):1055–1059

Pilliod DS, Welty JL, Stafford R (2013) Terrestrial movement patterns of western pond turtles (*Actinemys marmorata*) in central California. Herpetol Conserv Bio 8(1):207–221

Polak T, Rhodes JR, Jones D, Possingham HP (2014) Optimal planning for mitigating the impacts of roads on wildlife. J Appl Ecol 51(3):726–734

Rathbun GB, Scott NJ Jr, Murphey TG (2002) Terrestrial habitat use by Pacific pond turtles in a Mediterranean climate. Southwest Nat 47(2):225–235

Reese DA, Welsh HH (1997) Use of terrestrial habitat by western pond turtles, *Clemmys marmorata*: implications for management. In Proceedings: Conservation, restoration, and management of tortoises and turtles–an international conference. State University of New York, Purchase, New York, pp 352–357)

Reid BN, Peery MZ (2014) Land use patterns skew sex ratios, decrease genetic diversity and trump the effects of recent climate change in an endangered turtle. Divers Distrib 20(12):1425–1437

Roe JH, Gibson J, Kingsbury BA (2006) Beyond the wetland border: estimating the impact of roads for two species of water snakes. Biol Conserv 130(2):161–168

Rosen PC, Lowe CH (1994) Highway mortality of snakes in the Sonoran Desert of southern Arizona. Biol Conserv 68(2):143–148

Rosenberg D, Gervais J, Vesely D, Barnes S, Holts L, Horn R, Swift R, Todd L, Yee C (2009) Conservation assessment of the Western pond turtle in Oregon (*Actinemys marmorata*). USDI Bureau of Land Management and Fish and Wildlife Service, USDA Forest Service Region 6, Oregon

Rouse JD, Willson RJ, Black R, Brooks RJ (2011) Movement and spatial dispersion of *Sistrurus catenatus* and *Heterodon platirhinos*: implications for interactions with roads. Copeia 3:443–456

Row JR, Blouin-Demers G, Weatherhead PJ (2007) Demographic effects of road mortality in black ratsnakes (*Elaphe obsoleta*). Biol Conserv 137(1):117–124

Rudolph DC, Burgdorf SJ, Conner RN, Schaefer RR (1999) Preliminary evaluation of the impact of roads and associated vehicular traffic on snake populations in eastern Texas. In: Proceedings of the Third International Conference on Wildlife Ecology and Transportation. FL-ER-73-99. Evink GL, Garrett P, Zeigler D (eds) Florida Department of Transportation, Tallahassee, Florida, pp 129–136

Rytwinski T, Fahrig L (2012) Do species life history traits explain population responses to roads? A meta-analysis. Biol Conserv 147(1):87–98

Rytwinski T, Fahrig L (2013) Why are some animal populations unaffected or positively affected by roads? Oecologia 173(3):1143–1156

Rytwinski T, Fahrig L (2015) The impacts of roads and traffic on terrestrial animal populations. Handbook of Road Ecology. Wiley, New York, pp 237–246

Semlitsch RD (1998) Biological delineation of terrestrial buffer zones for pond-breeding salamanders. Conserv Biol 12(5):1113–1119

Semlitsch RD (2008) Differentiating migration and dispersal processes for pond-breeding amphibians. J Wildl Manag 72(1):260–267

Semlitsch RD, Bodie JR (2003) Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conserv Biol 17(5):1219–1228

Shilling F, Waetjen D (2017) California Roadkill Observation System. UC Davis Road Ecology Center. http://wildlifecrossing.net/california(accessed April 2017)

Siers SR, Reed RN, Savidge JA (2016) To cross or not to cross: modeling wildlife road crossings as a binary response variable with contextual predictors. Ecosphere 7(5):19

Stebbins RC, McGinnis SM (2012) Field guide to amphibians and reptiles of California, vol 103. University of California Press, Berkeley

Steen DA, Aresco MJ, Beilke SG, Compton BW, Condon EP, Dodd KC, Forrester H, Gibbons JW, Greene JL, Johnson G, Langen TA (2006) Relative vulnerability of female turtles to road mortality. Anim Conserv 9(3):269–273

Sullivan BK (2012) Road riding. In: McDiarmid RW (ed) Reptile biodiversity: standard methods for inventory and monitoring. University of California Press, Oakland, CA, pp 215–218

Suter GW II (2016) Ecological risk assessment. CRC Press, Boca Raton, FL

Thomson RC, Wright AN, Shaffer HB (2016) California amphibian and reptile species of special concern. University of California Press, Oakland, CA

Trenham PC (1998) Demography, migration, and metapopulation structure of pond-breeding salamanders. Ph.D. dissertation. University of California, Davis

Trenham PC, Koenig WD, Shaffer HB (2001) Spatially autocorrelated demography and interpond dispersal in the salamander *Ambystoma californiense*. Ecology 82(12):3519–3530

Trenham PC, Koenig WD, Mossman MJ, Stark SL, Jagger LA (2003) Regional dynamics of wetland-breeding frogs and toads: turnover and synchrony. Ecol Appl 13(6):1522–1532

US Fish and Wildlife (USFWS) (2016) United States species: Endangered and threatened wildlife (50 CFR 17.11). https://www.fws.gov/endangered/species/us-species.html (accessed August 2016)

US Fish and Wildlife Service (USFWS) (2002) Recovery plan for the California red-legged frog (*Rana aurora draytonii*). US Fish and Wildlife Service, Portland, Oregon, viii + 173 pp

US Fish and Wildlife Service (USFWS) (2009) *Rana pretiosa.* Species assessment and listing priority assignment form. USFWS Region 1, Portland

US Fish and Wildlife Service (USFWS) (2011) Alameda whipsnake (*Masticophis lateralis euryxanthus*) 5-year review summary and evaluation. US Fish and Wildlife Service, Sacramento, CA

van der Ree R, Smith DJ, Grilo C (2015) Handbook of road ecology. Wiley, New York

Vangel MG (2015) Tolerance interval. Statistics Reference Online. Wiley StatsRef, New York, pp 1–7

Vences M, Wake DB (2007) Speciation, species boundaries and phylogeography of amphibians. Amphib Biol 7:2613–2671

Watson JW, McAllister KR, Pierce DJ (2003) Home ranges, movements, and habitat selection of Oregon Spotted Frogs (*Rana pretiosa*). J Herp 37(2):292–300

Young KV, Young AT (2000) Final report: scientific study of the flat-tailed horned lizard, *Phrynosoma mcallii*. US Dept. of Navy Contracts N68711-95-LT-C0032, N68711-95-LT-C0035. 72 pp

Zimmermann Teixeira F, Kindel A, Hartz S, Mitchell S, Fahrig L (2017) When road-kill hotspots do not indicate the best sites for road-kill mitigation. J Appl Ecol 54(5):1544–1551

Research to Inform Caltrans Best Management Practices for Reptile and Amphibian Road Crossings

Research to Inform Caltrans Best Management Practices for Reptile and Amphibian Road Crossings

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Introduction

In October of 2014, the U.S. Geological Survey (USGS) began a 5-year project to conduct research to inform Best Management Practices (BMPs) for amphibian and reptile crossing and barrier systems in California. To inform future conservation and transportation planning, this project involved identification of species at highest risk of negative road impacts, creation of geodatabase and spatial mapping tools that crosswalk with California Essential Habitat Connectivity Planning, and field research to address information gaps in the efficacy of reptile and amphibian passage and barrier systems.

Per the agreement with California Department of Transportation (Caltrans; agreement 65A0553), this project was part of a broader collaborative effort between the Western Transportation Institute (WTI) of Montana State University and USGS Western Ecological Research Center (WERC). As part of this broader project, WTI conducted a worldwide literature review and gap analysis and produced a BMP manual for herpetofauna in California (Langton and Clevenger 2020). WTI and USGS were contracted separately although we worked closely together throughout this broader effort and each brought particular expertise to the project. WTI has expertise in highways, the attributes of the highway environment, and broad international experience with road ecology and herpetofauna connectivity systems worldwide. USGS WERC has expertise with California amphibian and reptile species and their ecology, study design and implementation, and landscape connectivity and road ecology.

Overall Program Objectives and Tasks

To meet the objectives in the contract, the project was composed of six major tasks:

1) Meet with Caltrans and other California herpetologists to establish collaborative networks with California herpetologists and inform them about the Caltrans amphibian and reptile highway crossing design project.

2) Perform a risk analysis based on an evaluation of California amphibian and reptile species ranges, life histories, population locations, habitat needs, and movement patterns to identify road sensitive species and/or confirm road sensitive species previously identified by Caltrans.

3) Create spatial data and maps to crosswalk with the California Essential Connectivity Map (Caltrans/California Department of Fish and Wildlife (CDFW) / U.S. Department of Transportation (DOT)) and Amphibian and Reptile Species of Special Concern Maps (CDFW) for species evaluated in Task 2 and identify primary roadways that transect habitats for these sensitive species. This was done in consultation with the WTI research team, Caltrans, wildlife agencies (U.S. Fish and Wildlife Service (USFWS) and CDFW) and species experts.

4) Assist WTI in the synthesis of the state of the practice in reptile and amphibian highway crossings by compiling and reviewing literature on amphibians and reptiles and mitigation measures to reduce road impacts, including identifying research gaps and future research needs.

5) Using expertise from within WERC and input on roadways and animal crossings from WTI, develop and design a plan for field research to evaluate key design and environmental attributes of functional passage structures for select amphibian and reptile species. Select sensitive amphibian and reptile species from the prioritized list developed in Task 2. Conduct field studies at existing (and new if possible) crossing structures to determine effective means for enhancing the ability of the selected species to cross highways. Give preference to multiple replicated sites that allow for simple experimental manipulations.

6) Provide expertise on California amphibians and reptiles to the WTI research team for the preparation of the Best Management Practices (BMPs) manual. Prepare report of Tasks 1-5 and a manuscript for presentation and/or publication.

Establishing Collaborative Networks (Task 1)

We began the first task by holding a special session at the California-Nevada Amphibian Populations Task Force (APTF) in Calabasas, CA on January 8-10, 2015. The session was entitled "Amphibian (and Amphibious Reptile) Road Ecology" and hosted by USGS with guest speakers Tony Clevenger (WTI), Tom Langton (Herpetofauna C I Ltd), Sally Brown (USFWS), Michael Westphal (U.S. Bureau of Land Management), Michael Hobbs (San Jose State University) and Chris Brown (USGS). We used this venue to highlight the project and to begin collaborative networking. Collaborations continued throughout the contract period through many meetings and communications with WTI, California scientists and herpetologists, Caltrans state and district biologists, USFWS, CDFW, U.S. Forest Service (USFS), and other scientists and herpetologists throughout the state. We also attended and presented at multiple conferences and meetings such as the Desert Tortoise Council Symposium (2016), annual APTF meetings (2015-16, 2018-2019), Western Section of the Wildlife Society (2019), USGS Amphibian Research Monitoring Initiative (ARMI 2015-2019), and the International Conference of Ecology and Transportation (2015, 2019).

Tasks 2 through 5 are individually summarized in the following subsections of Chapter 1 of this report along with summaries of findings, relevance of findings to informing the BMPs, and suggestions for future studies. Individual comprehensive reports for the risk analysis (task 2), geodatabase (task 3), and field research (task 5) are presented in subsequent Chapters.

Risk Assessment (Task 2)

Caltrans considers the need for barrier structures and safe wildlife road-crossings important to maintain the long-term viability of wildlife populations (Caltrans 2019). To prioritize these efforts for herpetofauna, we identified species that are most at risk of extirpation from road-related impacts. With over 160 California species and a lack of species-specific research data, we developed an objective risk assessment method based upon road ecology science. Risk scores were based upon a suite of life history, movement, and space-use characteristics associated with negative road effects that were applied in a hierarchical manner from individuals to species (Figure 1). Considerations included movement distances, movement frequency, speed, habitat preferences, movement behavior (territorial, non-territorial, vs. migratory), fecundity, range size and conservation status. All California herpetofauna species (and some subspecies) were ranked into five relative categories of road-related risk to both aquatic and terrestrial connectivity (very-high to very-low) based upon 20% increments of all species scores.

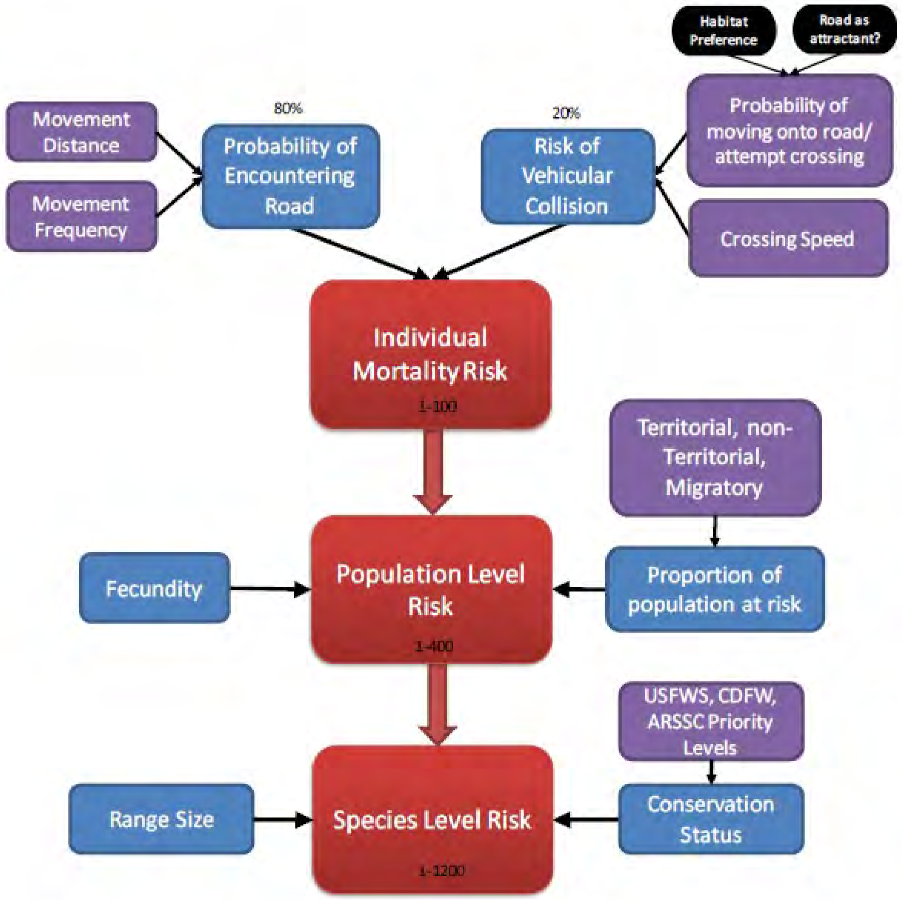

Figure 1. California Reptile and Amphibian Road Risk Assessment Conceptual Model.

All chelonids, 72% of snakes, 50% of anurans, 18% of lizards and 17% of salamander species in California were ranked at high or very-high risk from negative road impacts. Results were largely consistent with local and global scientific literature in identifying high risk species and groups.

Overall, snakes and chelonids had the largest proportion of species at high risk for negative road impacts due to longer movement distances (home range and/or migratory), lack of road avoidance, and relatively low fecundity in comparison to other herpetofaunal groups. This includes the desert tortoise, that has been shown to suffer from high road mortality negatively affecting population abundance in the Mojave Desert, and pond turtles, that travel kilometers within perennial waters and intermittent aquatic habitats to forage and find mates. In addition, female pond turtles migrate from their aquatic habitat to terrestrial habitats to nest and lay eggs, which make roads that parallel aquatic habitat a threat to both females and hatchlings.

Many large colubrid snakes and rattlesnakes ranked high. They are not only attracted to paved road surfaces for thermoregulation but have wide home ranges or move large distances between winter hibernacula and summer foraging areas. Long foraging movements within aquatic habitats also contributed to many garter snakes falling within the highest road risk categories.

Approximately half of California anuran species were ranked at high risk of negative road effects. These include Bufonid toads and red-legged frogs that may move large distances in both aquatic and terrestrial habitats to satisfy their annual resource requirements. Newts and several Ambystomid salamander species whose populations annually migrate between aquatic and upland habitats also ranked as high risk. Only a few wide-ranging lizard species scored in the highest risk categories including the Gila monster, leopard lizards, and two horned lizard species.

This risk assessment approach compared the susceptibility of species to negative road impacts. Commonly, there are numerous populations that occupy areas with greatly differing road pressures within a single species range. The actual risk to specific populations will depend upon local road densities, road types, traffic, and road locations in relation to species habitat and movement corridors. Therefore, it will be important to reassess the risk of roads to specific populations and to evaluate and compare alternatives at the local scale.

To help inform transportation planning and for evaluating the suitability of different best management practices, the risk of roads to both terrestrial and aquatic connectivity was assessed. Thus, semi-aquatic species have two risk scores. Some scored high in both habitats, while others scored high in only one. This is important when evaluating the need for underpasses and other terrestrial crossings versus bridges and fish passages. For example, underpasses, barriers and other structures may be suitable for species with high terrestrial risk scores; such as tortoises, colubrid snakes, rattlesnakes, and Ambystomid salamanders. Conversely, the use of fish passages and bridges could also be considered for species with high aquatic risk scores; such as the giant gartersnake, California red-sided gartersnake, two-striped gartersnake, and Sonoran mud turtle. Both terrestrial and aquatic passages may be needed for species groups that ranked high in both categories; such as pond turtles, Bufonid toads, newts and red-legged frogs. Along with this, buffer distances for terrestrial and aquatic habitats were calculated to encompass 95% of population level movements of all species. This provides information to agencies deciding whether a population is close enough to a road (within buffer distance) to warrant mitigation, the need for a barrier, and whether a goal should be to provide population-level connectivity or allow for occasional dispersal to provide long-term genetic connectivity.

A simplified list of high and very-high risk species is provided in Table 1. This work has been published (Brehme et al. 2018). The journal article with all California species rankings and buffer distances is included as Chapter 2 and is available at *https://link.springer.com/article/10.1007/s10980-018-0640-1*.

Table 1. California Amphibians and Reptiles Ranked at High and Very-high Risk of Negative Road-related Impacts.

GROUP	VERY-HIGH RISK	HIGH RISK
Terrestrial Snakes	Alameda Striped Racer Baja California Coachwhip Baja California Ratsnake California Glossy Snake Coachwhip Coast Patch-nosed Snake North American Racer Panamint Rattlesnake San Joaquin Coachwhip Striped Racer	California Lyresnake Desert Nightsnake Mojave Rattlesnake Nightsnake Red Diamond Rattlesnake Regal Ring-necked Snake Sidewinder Sonoran Lyresnake Speckled Rattlesnake Spotted Leaf-nosed Snake Western Groundsnake Western Diamond-backed Rattlesnake Western Patch-nosed Snake Western Shovel-nosed Snake Western Rattlesnake
Aquatic Snakes	California Red-sided Gartersnake Giant Gartersnake San Francisco Gartersnake Two-striped Gartersnake	Aquatic Gartersnake Common Gartersnake Northwestern Gartersnake Sierra Gartersnake Western Terrestrial Gartersnake
Freshwater Turtles	Northern Western Pond Turtle Southern Western Pond Turtle Sonora Mud Turtle	
Tortoises	Mohave Desert Tortoise	
Toads	Arroyo Toad Black Toad Sonoran Desert Toad Yosemite Toad	Great Plains Toad Western Spadefoot Woodhouse's Toad
Frogs	California Red-legged Frog	Cascades Frog Northern Red-legged Frog Oregon Spotted Frog
Lizards	Banded Gila Monster Blunt-nosed Leopard Lizard Cope's Leopard Lizard Desert Horned Lizard Flat-tailed Horned Lizard	Long-nosed Leopard Lizard San Diegan Tiger Whiptail Switak's Banded Gecko
Salamanders	California Newt Callifornia Tiger Salamander Red-bellied Newt Sierra Newt	California Giant Salamander Rough-skinned Newt Santa-Cruz Long-toed Salamander Southern Long-toed Salamander

Spatial Mapping (Task 3)

Caltrans and CDFW commissioned the California Essential Habitat Connectivity (CEHC) Project because they consider a functional network of connected wildlands essential to the continued support of California's diverse natural communities in the face of human development and climate change (Spencer et al. 2010). CEHC maps and spatial layers depict large, relatively natural habitat blocks greater than 809 ha (2000 acres) that support native biodiversity and areas deemed essential for regional scale animal and plant connectivity. These maps were intended to make transportation and land-use planning more efficient and less costly, while helping to reduce wildlife-vehicle collisions. They are available on the CDFW Biogeographic Information and Observation System (BIOS) website *https://wildlife.ca.gov/Data/BIOS*.

Essential Connectivity Areas (ECA), Natural Landscape Blocks (NLB), and Natural Areas_small (NA) from the Essential Connectivity Map geodatabase were provided by CDFW. Although habitat blocks greater than 809 ha are appropriate for planning connectivity for large mammals, small animals can persist on smaller size patches. Therefore, we merged ECA, NLB, and NA areas 10 ha or greater. The resulting layer was then dissolved into a single polygon feature class with a buffer of 100 meters added to it. This connected many of the smaller polygons and better represented natural areas large enough to support sensitive amphibian and reptile populations. We then prepared a spatial geodatabase that intersects the modified CEHC map, State Highways and high-risk species ranges from the California amphibian and reptile road risk assessment (Brehme et al. 2018). This geodatabase was designed to be a useful planning tool for Caltrans to quickly identify road segments which may warrant planning for increased connectivity of high-risk amphibian and reptile species.

The spatial geodatabase (CalTrans_SpeciesRoadRisk_Map.mpk) includes:

1) CEHC lands merged with smaller habitat blocks (>10 ha).
2) Ranges of high and very-high risk amphibian and reptile species.
3) California highway segments that intersect habitat ranges of high and very-high risk amphibian and reptile species.
3) California highway segments that intersect habitat ranges of high and very-high risk amphibian and reptile species and CEHC lands.
4) The total number of high and very-high risk species habitat ranges that intersect the highway segments and CEHC lands.

Here we show an example of a high-risk species density map for the state (Figure 2) and an individual species map (Figure 3), where the species habitat range intersects CEHC lands and state highway systems. Note that the accuracy of each species road risk map is dependent upon the accuracy of its most recent range map, which varies by species (see Chapter 3 for sources). Because many species are patchily distributed throughout their ranges, species may not be occupying habitat along all intersecting highway segments. Therefore, highlighted road segments indicate the possibility of species occupancy as well as known occupancy.

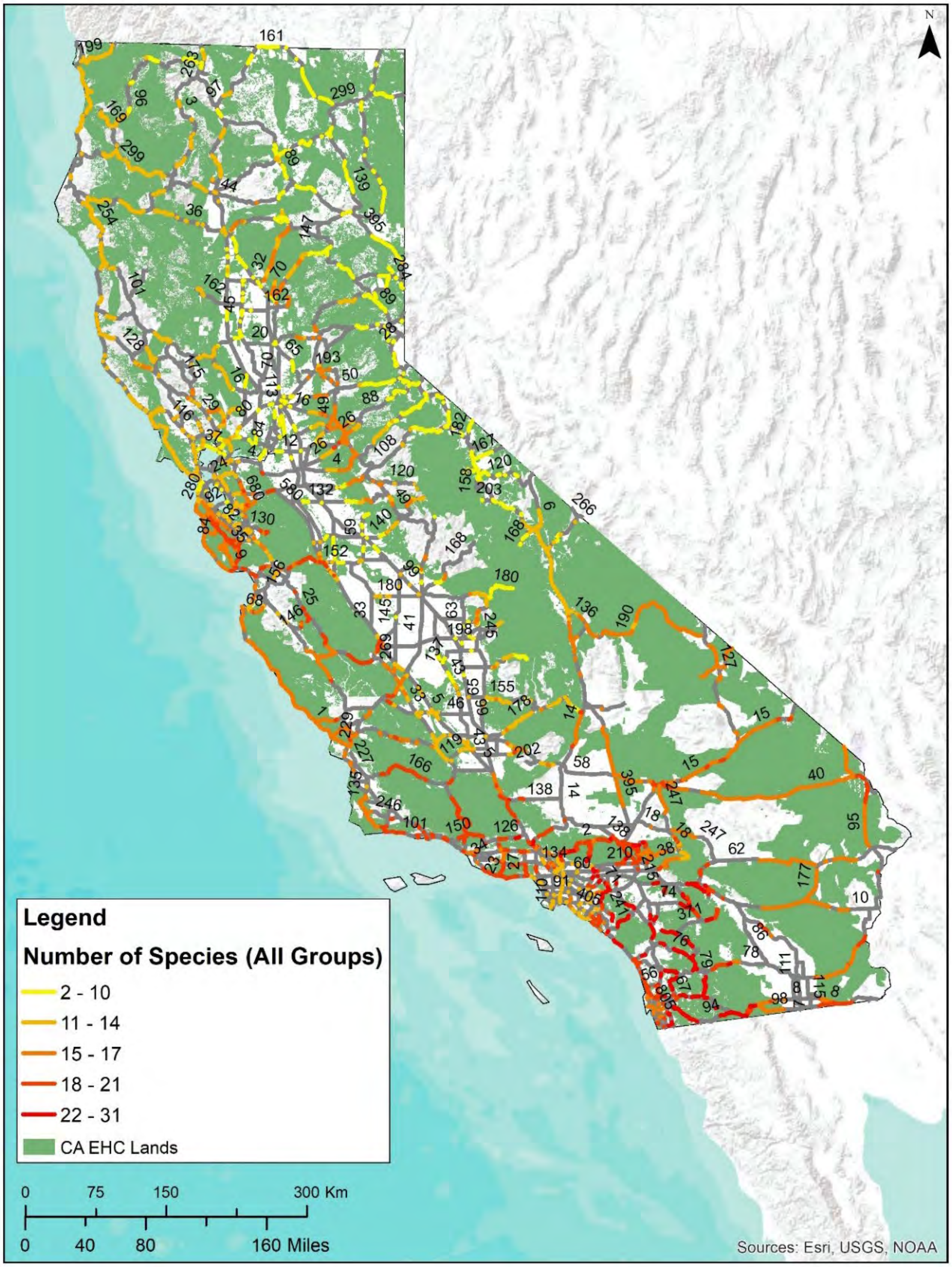

Figure 2. Density of High and Very-High Risk Reptile and Amphibian Species across the State Highway System (Elise Watson, USGS). Note: California Highway Numbers are in Black.

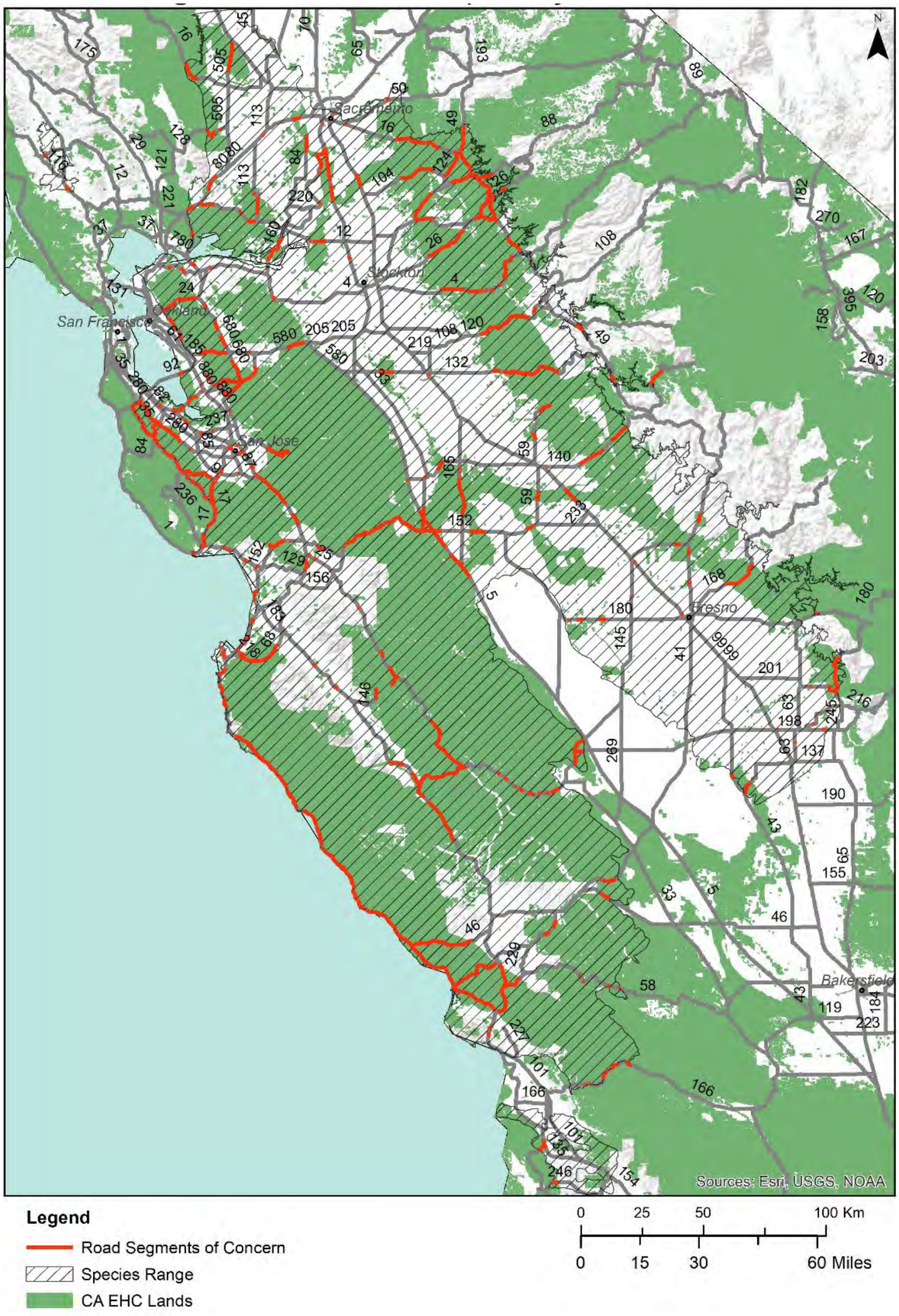

Figure 3. Overlay of Single Very-High Risk Species Range (*Ambystoma californiense*), CEHC Lands and the State Highway System (Elise Watson, USGS). Note: California Highway Numbers are in Black.

Literature Review and Gap Analysis (Task 4)

To synthesize what was currently known about reptile and amphibian crossing systems in California and throughout the world and to identify primary information gaps in scientific and practical knowledge to inform these crossing systems, WTI conducted a detailed literature review and synthesis with input from USGS (Langton and Clevenger 2017). The authors reviewed 52 studies on crossing systems with 125 individual taxa (75 reptile and 50 amphibian species or sub-species) throughout Europe, North America, South America and Australasia. Of these, 45% were for reptiles and 55% amphibians. Information from each paper was summarized into three study or 'knowledge area' categories: passage construction and use, passage environmental variables and barrier construction and use.

Langton and Clevenger (2017) concluded than in most cases road mitigation was installed primarily to reduce road mortality versus to maintain connectivity. However, large passages tended to be more permeable to amphibian and reptile crossings than smaller passages. They determined that the literature reflected a widely spread and low-inference scientific knowledge base regarding the efficacy of amphibian and reptile passages and barrier systems, although the body of literature has been growing in recent years with specific species and systems. They also found little information on the role of existing infrastructure and drainage culverts in helping to maintain genetic and population connectivity for herpetofauna.

Therefore, Langton and Clevenger (2017) concluded there was a need for more properly designed studies to evaluate the effectiveness of purpose-built (engineered) and non-engineered passages and barriers. Research studies (controlled experimental or field settings) were needed to directly measure, test and compare results among mitigation structures, their structural and environmental characteristics, and permeability to species and species groups. Information and knowledge gaps identified from this analysis included the following:

- Use of existing highway structures by herpetofauna.
- Relative permeability of most commonly built structures to different herpetofauna groups.
- Relationship between use and openness ratio and length and width of passage.
- Whether populations could benefit from addition of barrier fencing to existing structures.
- The most effective ways to simulate natural and artificial light, temperature and moisture within underpasses.
- The influence of fence material and opacity on barrier effectiveness and passage use.
- Effectiveness of turnarounds at fence ends.
- The best designs to extend barriers along road access points.

This review and synthesis, along with the risk assessment, was used to help guide field research and for developing California Best Management Practices (BMPs) for sensitive amphibian and reptile highway crossings (Langton and Clevenger 2020).

Research Questions and Field Studies (Task 5)

Based on the literature review and gap analysis, we devised a list of 9 research studies along with research objectives, target species/groups, general study designs, relative costs, and how each of these studies would inform Best Management Practices (BMPs) for Caltrans reptile and amphibian crossings. Representatives from Caltrans (Simon Bisrat, James Henke, Amy Golden, Amy Bailey), Western Transportation Institute (Tony Clevenger, Tom Langton), and USGS (Robert Fisher, Cheryl Brehme) met in September of 2017 to review the study options and select the studies that would be pursued as part of this project.

After reviewing and discussing each of the studies, the following studies were identified as being the most cost effective while providing valuable information for the BMPs. Below are the primary research questions, target species and locations chosen for these studies.

1. What is the maximum distance between passages to maintain permeability for migratory herpetofauna (pond breeding amphibians)?
    a. Target Species/Groups: California tiger salamander, Yosemite toad
    b. Locations: Stanford, Sierra National Forest.

2. How does fence material (transparency) influence species movement along barriers?
    a. Target Species/Groups: reptiles and amphibians, California tiger salamander, Yosemite toad
    b. Locations: San Diego, Stanford, Sierra National Forest

3. Fence ends: How effective are fence-end turnarounds?
    a. Target Species/Groups: reptiles and amphibians
    b. Location: San Diego, Stanford, Sierra National Forest

4. What designs of jump-outs are effective for herpetofauna and other small animals?
    a. Target Species/Groups: reptiles and amphibians
    b. Location: San Diego

Additionally, we included two extra questions in our studies as they developed.

5. What is the relative permeability of a special built passage system for California tiger salamanders (Type 5: Micro-underpass)?
    a. Target Species/Groups: California tiger salamander
    b. Location: Stanford

6. Is there an alternative to the tunnel passage system design for migratory amphibians and other high risk herpetofauna? Evaluation of a novel elevated road segment passage.
    a. Target Species/Groups: Yosemite toad
    b. Location: Sierra National Forest.

Individual reports of all field studies are provided in Chapters 4 through 7.

Summary of Research Findings and Relevance to Caltrans BMP's (Task 6)

The results of our field studies inform the Caltrans Best Management Practices for amphibian and reptile crossing systems regarding passage spacing for migratory amphibians, barrier fencing materials, and the effectiveness of turnarounds and jump-outs. We also evaluated the permeability of an existing amphibian tunnel system and a novel pilot elevated road segment passage.

Movement Distances along Barriers to Inform Passage Spacing for Migratory Amphibians *(Question 1 above)*

Our results from studies of California tiger salamanders (CTS) in Stanford, CA and Yosemite toads in the Sierra National Forest showed that many of these amphibians migrating between wetland and upland habitats were unlikely to reach the road passage systems if they encountered the barrier fencing away from the passage. CTS moved an average distance of 40 m and Yosemite toads moved an average distance of 52 m along barrier fencing before "giving up," and their probability of making it to a crossing decreased rapidly with increasing distance. In addition to distance moved, the direction the salamanders and toads turned when reaching the barrier fencing was a factor in whether they reached a passage. Individuals that reached the barrier fencing and then travelled in the wrong direction (away from the passage) were significantly less likely to reach the crossing than those that made the correct initial direction choice. The average distance moved by these amphibians indicates that approximately half of the individuals moved greater distances and half moved shorter distances before "giving up." We estimated a distance between passages of less than 12.5 m (CTS) and 20 m (Yosemite toads) would be needed along migratory pathways to maintain a high level of permeability.

Therefore, the likelihood by distance that animals reach a passage can inform the planning and spacing of crossing systems for migratory amphibians and other migratory species. Without considering this, amphibian road crossing systems composed of barrier fencing and underpasses have the potential to become a greater barrier to movement. This is particularly relevant when high connectivity is important for the sustainability of the population, such as for migratory amphibian species that must make population level movements between upland and breeding habitats. With non-migratory species, less frequent cross-road movements could be acceptable if roads do not transect seasonal habitats or vital resources. In these cases, occasional crossings to enable reproductive and genetic connectivity may be sufficient to maintain long term population persistence.

Barrier Fencing Materials *(Question 2 above)*

Three of our studies were relevant to herpetofaunal responses to fencing materials of various transparencies. One was the fence trial behavioral study of reptiles in Rancho Jamul, one was our CTS study at Stanford, and the third was our Yosemite toad study in the Sierra Nevada.

The results from our behavioral studies show that herpetofauna are more likely to interact with the transparent and semi-transparent fences by poking at them with their noses, pacing back and forth, and attempting to climb. The transparent (hardware cloth) and semi-transparent fencing (polymer matrix "mesh") used in our studies were not only see-through, but permeable to the movement of air in comparison to plastic solid fencing. Because sight and chemoreception senses are typically well developed in reptiles, it is not clear to what extent these different senses are driving fence interaction behaviors. However, it is clear from our observations that animals exhibiting these behaviors appeared to be trying to find a way through the fence to the other side.

Although fence interaction behaviors have been documented elsewhere in comparing hardware cloth and solid fencing (Ruby et al. 1994, Milburn-Rodríguez et al. 2016), our trial behavioral studies showed a clear gradation of response from solid to semi-transparent to transparent fencing in all taxa studied. In addition, our studies showed that these behavioral responses typically resulted in animals moving slower, or spending more time, along transparent/permeable fencing in comparison to solid fencing. This may not be a large concern when the purpose of the fence is primarily to exclude animals. However, it may be an important consideration when a dual objective is to lead species toward a road crossing structure, particularly when high permeability and population connectivity across the structure is desired.

In our migratory amphibian studies, the transparency of fencing (mesh vs. solid) did not significantly affect the movement distances of CTS or Yosemite toads or their probability of making it to the underpass system, although the estimated probabilities of reaching underpasses were slightly lower for the semi-transparent fencing. With preliminary data, the speed and time of travel for Yosemite toads were not significantly different by fence type. However, for CTS, the speed and time of travel varied significantly by fence type. CTS moving along solid fencing moved at almost twice the average speed and were 3 times less likely to turn around and repeatedly move back and forth. Therefore, CTS moving along fencing that they could see through resulted in them expending a higher amount of time and energy to make it to the crossing.

There are many reasons why different fencing types (hardware cloth, mesh, or solid) may be used in particular landscapes, habitats, and climates with considerations that include heat, rain and wind, permeability, durability, and aesthetics (see Langton and Clevenger 2020). Our behavioral study was the first to show that addition of a simple visual barrier (6 in./153 mm in our study) from the ground upwards, at the base of transparent and semi-transparent fencing, can reduce fence interaction behaviors and increase rates of movement. In fact, for most measures, herpetofauna responses to mesh and hardware cloth fencing with a visual barrier were not significantly different than to the solid barrier. This could allow for more flexibility in the decision-making and planning processes for barrier systems for herpetofauna.

Turnarounds *(Question 3 above)*

Three studies were relevant to the efficacy of turnarounds. One was done in Rancho Jamul, one was our CTS study at Stanford, and the third was our Yosemite toad study in the Sierra Nevada. A general graphic of the turn-around design used is depicted in Figure 4.

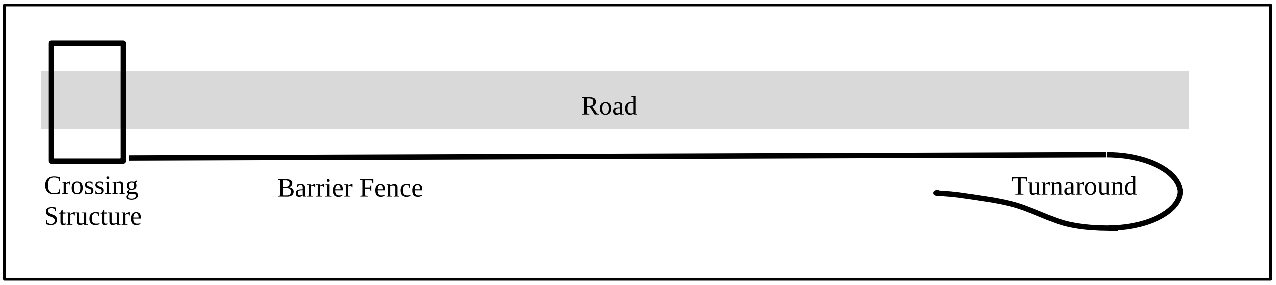

Figure 4. Diagram of Turn-around at Barrier Fence End

Our Rancho Jamul study was the first to show that small turnarounds at fence ends can be effective in changing the trajectory of movement for herpetofauna and small mammals. The turnarounds in our studies were approximately 1.5 m long and 1 m wide at the widest point with the turnaround ending approximately 0.4 m from the original fence line and extending another 0.4 m parallel to the fence. Turnarounds at fence ends were made of hardware cloth, mesh, or solid fencing (2 each). We documented that over 90% of herpetofauna (lizards, snakes and toads) and 69% of small mammals changed course after leaving a turnaround. Of those that changed their trajectory, 67% of herpetofauna and 43% of small mammals moved back along the original fence line while the remainder turned away from the fence line toward the habitat. We previously observed that animals spend more time interacting (e.g. poking, back and forth movements, climbing) with fencing that they can see and smell through (Question 2, Chapter 6). Animals also generally spent increased amounts of time in transparent/permeable and semi-transparent/permeable turnarounds than solid impermeable turnarounds.

Our results also suggest the use of transparent or semi-transparent fencing for turnarounds may increase their effectiveness for some species groups (Chapter 7). These results could be related to animals interacting with the fencing and spending more time in transparent turnarounds, so that they were less likely to remember and continue on their original trajectory. The results may also be related to the different types of spatial learning and memory used for navigation when animals are subjected to solid barriers (egocentric) in comparison to transparent barriers (allocentric) as has been shown in maze-food trials with rodents (Violle et al. 2009, Vorhees and Williams 2014). Validation of these findings in other locations and possibly more specific research studies addressing spatial learning and movement responses in reptiles, amphibians, and small mammals in their natural environments would be needed to further our understanding of these results.

We did not compare different sizes or shapes of turnarounds in our study; however, we hypothesize that having the end of the turnaround close to the original fence line may help to steer animals back along the original barrier in the direction of original origin. Longer or larger turnarounds encompassing smaller turnarounds have been proposed to increase the probability that animals do not go out onto the roadways if they turn away from the fence and into habitat on leaving the turn around (Langton and Clevenger 2020).

In this study, we only documented animal movement for up to 1 m (3.4 feet) after leaving the turnaround. It is entirely possible that animals changed course again after they left the field of view of the video camera. In our Stanford and Sierra movement studies (Chapters 3 and 4), two out of three CTS that presumably reached a turnaround at the fence end were subsequently documented on another camera 25-125 m away moving back along the fence line. Preliminary results suggest seven out of 10 Yosemite toads changed course at a turnaround, while three continued in the direction past the fence ends. Of the seven toads that changed course, four were subsequently documented on another camera 40-80 m away moving back along the fence line toward the passage. Further studies using more cameras and/or tracking methods are needed to better understand how turnarounds affect movement of animals over a longer distances and time frames. Higher mortality of herpetofauna has been well documented at fence ends even with turnarounds (Gunson et al. 2014, Langton and Clevenger 2017, Helldin and Petrovan 2019). However, the high proportion of herpetofauna that changed directions in our study supports the use of turnarounds in attempts to reduce the chances that small animals go out onto the roadway at fence ends and potentially to help ‘steer’ them back toward to a crossing structure.

Jump-outs *(Question 4 above)*

Animals can get trapped within the roadway if they get through an opening in the fencing or overshoot the end of the fencing. Jump-outs provide a way for animals that get trapped within a roadway surrounded by vertical barrier fencing to safely get back into the habitat on the other side of the fence. Although jump-outs are commonly built structures along wildlife fencing for large mammals, they have not been incorporated into transportation planning for reptile and amphibian barriers. However, short curved or sloped fencing has been designed for amphibians that angles toward the habitat to allow movement over the top in one direction.

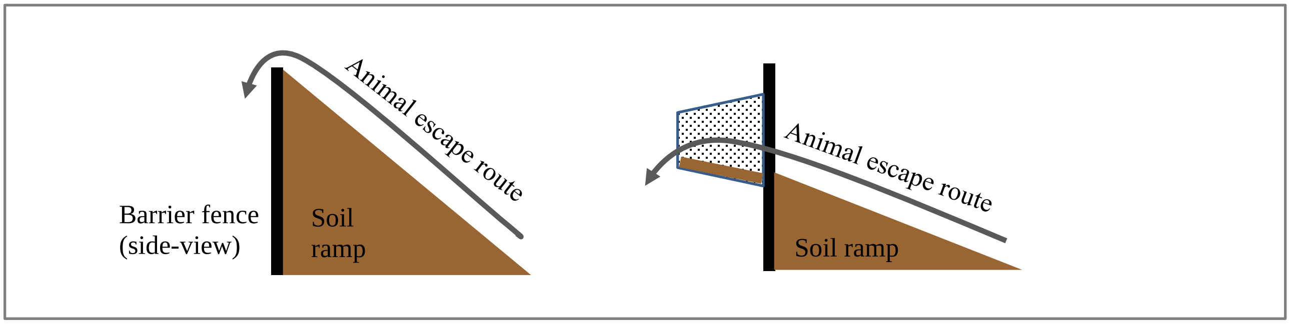

Figure 5. Diagram of Jump-out Configurations a) Over Fence and b) Through Fence.

Our experimental behavioral study showed that two jump-out configurations (Figure 5) were largely effective in allowing animals trapped on the 'wrong' side of a vertical fence to escape back into the habitat. One was simply a soil ramp to the top of the exclusion fencing (Figure 5a: 50 cm. in height) and the other was a polymer box funnel placed at a height of 25 cm above the ground within the exclusion fencing with a small soil ramp leading up to it (Figure 5b). A total of 75% of lizards, 95% of snakes, and 1 of 2 toads used a jump-out to escape the enclosure. There was little difference between the use of the high ramp and low funnel jump-outs by lizards or snakes. We observed that lizards often sat on top of the 50 cm high ramp for long periods of time before jumping to the ground, whereas there was little hesitation with the lower 25 cm jump-outs.

We suggest jump-outs be provided at regular intervals along vertical barriers in the form of a ramp leading to the top of the barrier or leading to a funnel type structure that opens to the habitat. It is also important that any jump-out design for herpetofauna consider the safety of other wildlife. This includes minimizing the size difference of the entrance and exit of box funnel designs so that larger animals do not get stuck in the funnel. Rectangular or cylindrical shapes with the same entry and exit size could be considered. For short barrier fencing, most other wildlife can simply step, climb, or jump over the barrier. For taller barrier fences, escape routes may include jump-outs of several sizes to accommodate a wider variety of species.

Effectiveness of Crossing Structures: Amphibian Tunnels and a Novel Elevated Road Segment *(Questions 5 and 6 above)*

Many small animals, especially amphibian populations that must migrate between aquatic and terrestrial habitats, are susceptible to negative impacts from roads within their habitat (e.g. Hamer et al. 2008, Semlitsch 2008, Brehme et al. 2018). In the winter breeding seasons of 2018 and 2019, we studied the movement of CTS across three existing micro-passage amphibian tunnels spaced approximately 5 m apart from one another along Junipero Serra Blvd in Stanford, CA. The road bisects a historic CTS breeding pond and upland CTS habitat. CTS that did reach the opening of the passage system had a very high probability (87%) of making a complete crossing to the other side. The passages are made of inert materials (polymer concrete) and incorporate a slotted ceiling at the road surface to allow natural light, moisture and rainfall to permeate the length of the passage. These passages have been shown to be permeable to amphibian movement in North America and Europe (Jackson and Tyning 1989, Pagnucco et al. 2012, Langton and Clevenger 2017). Although they have not been used for amphibian passage on the state highway system to date, these results are promising for possible use of these and/or similarly designed passages by Caltrans.

Although micro-passage tunnels are a standard mitigation solution to reduce amphibian road mortality, there is evidence that these systems may filter movements of populations that disperse over large areas, particularly if passages are placed too far apart from one another across the migratory pathways (e.g. Allaback and Laabs 2002, Pagnucco et al. 2012, Ottburg and van der Grift 2019). In 2018 we tested a new and novel passage elevated road segment (ERS) prototype, an eight-in. high elevated road segment using road mats designed for use by heavy equipment at construction sites. The ERS was installed on top of a USFS road along a Yosemite toad mortality "hotspot" with directional barrier fencing. The ERS provides a safe crossing nearly 100 ft wide while allowing both light and rain to pass through. We monitored Yosemite toad and other herpetofaunal activity along fencing and under the passage using specialized cameras. Initial results show that toads and other herpetofauna as well as small mammals used the passage and mortality was greatly reduced. Although the prototype was a 100-ft wide passage, theoretically they could be made to any length. This ERS prototype offers a new concept design to increase permeability of roads to migratory amphibians and other species. There is currently an effort underway by DOT and other transportation engineers to adapt this concept design to more permanent highway applications.

Considerations for Future Studies

To further inform the design of effective barrier and passage systems for herpetofauna, we suggest consideration of the following research:

1. Continue study of Yosemite toads in Sierra National Forest to increase sample size and confidence in model predictions on passage spacing, fence opacity, and the permeability of the ERS crossing system.

2. Include one or more new study locations and species to better predict underpass spacing needs for high-risk migratory amphibian species. This would address the question of whether movement distances along barrier fencing are predictable among species groups and size classes.

3. Continue California tiger salamander and Yosemite toad studies to explore modifications to increase effectiveness of passages. Address the following questions:
   a. Will affixing a visual barrier to transparent or semi-transparent fencing change CTS behavior so that it more closely resembles the reaction to solid fencing? This is useful because in some areas, mesh fencing may be preferred for water/wind permeability, etc.
   b. Would more turnarounds along the length of barrier fencing help to increase the probability of success for animals that start out moving away from tunnels?

4. Continue research to assess the effectiveness of fence end treatments by studying the effect of turnaround length, materials and configuration on amphibian and reptile turnaround rates. Monitor animal movements over longer distances after exiting turnaround.

5. Work with engineers familiar with Caltrans materials and specifications to design (and test if possible) new options to add to existing BMP elements for increasing effectiveness of road crossings for herpetofauna such as:
    a. Elevated road segment (ERS) concept designs for primary roadways.
    b. Artificial lighting in tunnels that best simulates natural lighting for diurnal species. This is mainly for long underpasses where grated skylights in the shoulders and median are not feasible or sufficient to illuminate a passage .
    c. Drip or other drainage systems that deposit a path of moisture in otherwise dry underpasses during rain events.
    d. Design modifications to decrease the temperature differential between tunnel interiors and the surrounding environment.
    e. Design modifications to incorporate cover and ledges for herpetofauna within larger passages.

6. Design and implement studies to better understand if herpetofauna use existing passages and culverts for movement across roads.
    a. If so, what is the relative permeability of the most commonly built structures to different herpetofauna groups?
    b. Is the probability of use related to size of passage? If so, for which species groups?
    c. How is use of passages related to length and openness ratio?
    d. Would barrier fencing increase the use of non-engineered structures (i.e. culverts)?

These proposed studies will allow Caltrans to better evaluate the effectiveness of existing barrier and road crossing systems, to increase the ‘toolbox’ of innovative solutions, to increase the effectiveness of crossing systems for reptiles and amphibians in California, and to make more informed decisions on underpass spacing for high-risk migratory species.

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References

Note: more extensive citations are included in individual study chapters

Allaback, ML and DM Laabs. 2002. Effectiveness of road tunnels for the Santa Cruz long-toed salamander. Transactions of the Western Section of the Wildlife Society 38: 5–8.

Brehme, CS, SA Hathaway, and RN Fisher. 2018. An objective road risk assessment method for multiple species: Ranking 166 reptiles and amphibians in California. Landscape Ecology 33(6): 911–935.

Caltrans. 2019. Securing Safe Passage for Wildlife. Accessed August 11, 2020. *https://dot.ca.gov/-/media/dot-media/programs/risk-strategic-management/documents/mile-marker/mm-2019-q2-wildlife-crossing-a11y.pdf.*

Gunson, KE, DC Seburn and D. Lesbarrères. 2014. Monitoring turtle movements on Highways 7 & 41; 2012 and 2013. Final report submitted to the Ministry of Transportation, Kingston, Ontario.

Hamer, AJ and MJ McDonnell. 2008. Amphibian ecology and conservation in the urbanising world: a review. Biological Conservation 141(10): 2432–2449.

Helldin, JO and SO Petrovan. 2019. Effectiveness of small road tunnels and fences in reducing amphibian roadkill and barrier effects at retrofitted roads in Sweden. PeerJ 7: p.e7518.

Langton, TES and AP Clevenger 2017. Amphibian and Reptile Highway Crossings: State of the practice, gap analysis and decision support tool. Report prepared for the State of California, Department of Transportation, Division of Research, Innovation and System Information, Office of Materials and Infrastructure Research, June 2017

Langton, TES and AP Clevenger. 2020. Measures to Reduce Road Impacts on Amphibians and Reptiles in California. Best Management Practices and Technical Guidance. Prepared by Western Transportation Institute for California Department of Transportation, Division of Research, Innovation and System Information.

Milburn-Rodríguez JC, J Hathaway, K Gunson, D Moffat, S Béga and D Swensson. 2016. Road mortality mitigation: The effectiveness of Animex fencing versus mesh fencing. *https://animexfencing.com/whyanimex/animex-vs-mesh*

Ottburg, FG and EA van der Grift. 2019. Effectiveness of road mitigation for common toads (*Bufo bufo*) in the Netherlands. Frontiers in Ecology and Evolution, 7, p.23.Hamer, A.J. and McDonnell, M.J., 2008. Amphibian ecology and conservation in the urbanising world: a review. Biological Conservation 141(10): 2432–2449.

Pagnucco KS, CA Paszkowski and GJ Scrimgeour. 2012. Characterizing movement patterns and spatio-temporal use of under-road tunnels by long-toed salamanders in Waterton Lakes National Park, Canada. Copeia 2012(2): 331–340 DOI 10.1643/CE-10-128.

Ruby, DE, JR Spotila, SK Martin and SJ Kemp. 1994. Behavioral responses to barriers by desert tortoises: implications for wildlife management. Herpetological Monographs 8: 144–160.

Semlitsch, RD. 2008. Differentiating migration and dispersal processes for pond-breeding amphibians. Journal of Wildlife Management 72(1): 260–267.

Spencer, WD, P Beier, K Penrod, K Winters, C Paulman, H Rustigian-Romsos, J Strittholt, M Parisi, and A Pettler. 2010. California Essential Habitat Connectivity Project: A Strategy for Conserving a Connected California. Prepared for California Department of Transportation, California Department of Fish and Game, and Federal Highways Administration.

Vorhees, C and MT Williams. 2014. Assessing spatial learning and memory in rodents. ILAR Journal, 55(2), pp. 310–332.

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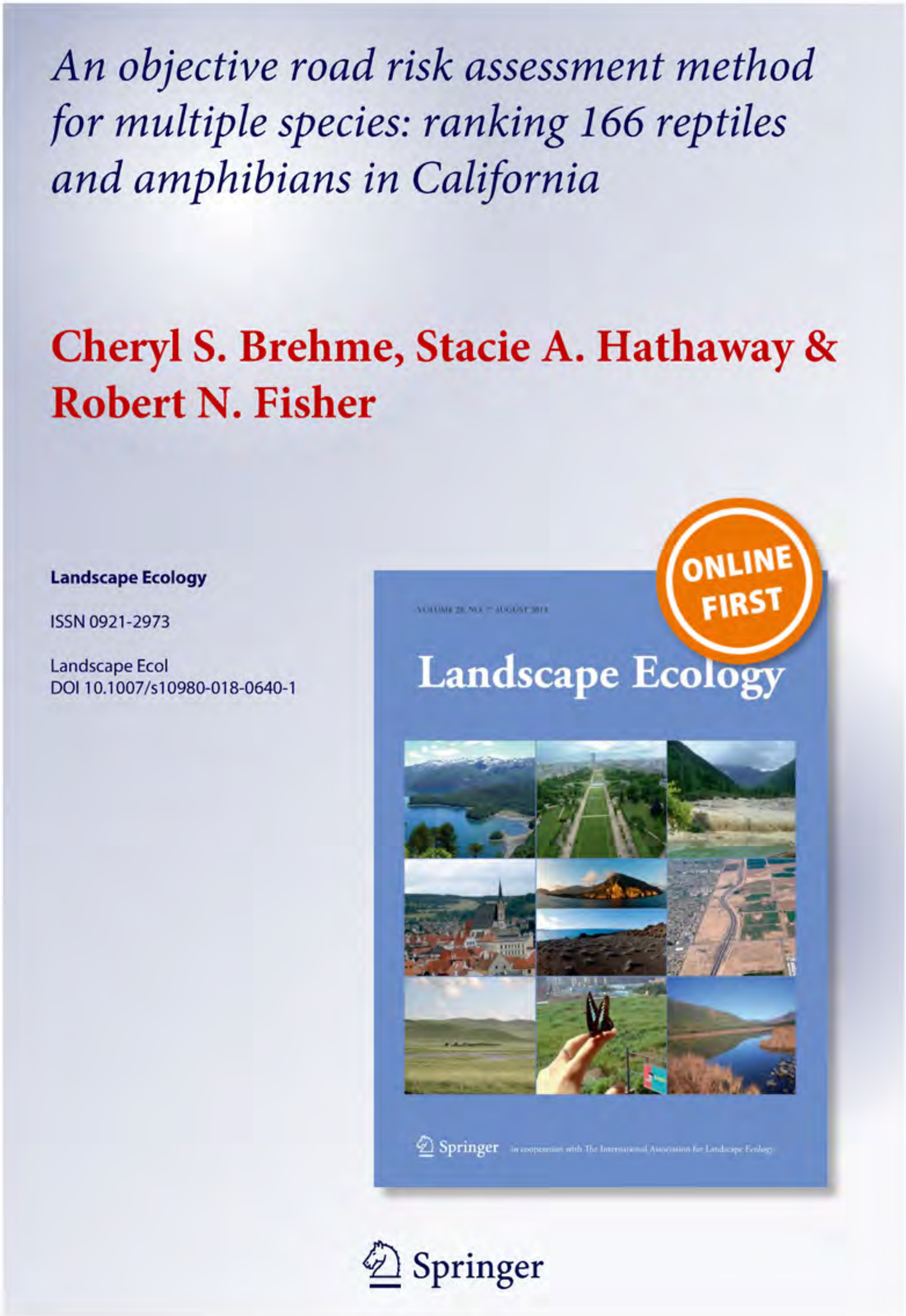

An objective road risk assessment method for multiple species: ranking 166 reptiles and amphibians in California

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RESEARCH ARTICLE

An objective road risk assessment method for multiple species: ranking 166 reptiles and amphibians in California

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Abstract

Context Transportation and wildlife agencies may consider the need for barrier structures and safe wildlife road-crossings to maintain the long-term viability of wildlife populations. In order to prioritize these efforts, it is important to identify species that are most at risk of extirpation from road-related impacts.

Purpose Our goal was to identify reptiles and amphibians in California most susceptible to road mortality and fragmentation. With over 160 species and a lack of species-specific research data, we developed an objective risk assessment method based upon road ecology science.

Methods Risk scoring was based upon a suite of life history and space-use characteristics associated with negative road effects applied in a hierarchical manner from individuals to species. We evaluated risk to both aquatic and terrestrial connectivity and calculated buffer distances to encompass 95% of population-level movements. We ranked species into five relative categories of road-related risk (very-high to very-low) based upon 20% increments of all species scores.

Results All chelonids, 72% of snakes, 50% of anurans, 18% of lizards and 17% of salamander species in California were ranked at high or very-high risk from negative road impacts. Results were largely consistent with local and global scientific literature in identifying high risk species and groups.

Conclusions This comparative risk assessment method provides a science-based framework to identify species most susceptible to negative road impacts. The results can inform regional-scale road mitigation planning and prioritization efforts and threat assessments for special-status species. We believe this approach is applicable to numerous landscapes and taxonomic groups.

Keywords Reptile · Amphibian · Road mortality · Habitat fragmentation · Road ecology · Risk assessment · Road

Introduction

There have been many attempts to better characterize and quantify threat criteria in order to classify species at higher risk of extinction at state, national, and global levels (Congress 1973 (U.S. Endangered Species Act); Mace et al. 2008; Hobday et al. 2011; Thomson et al. 2016; IUCN 2017). Roads are a significant threat to wildlife populations (e.g., Forman et al. 2003;

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Andrews et al. 2015a; van der Ree et al. 2015), causing both barrier (habitat fragmentation) and depletion (road mortality) effects. Barrier effects occur when animals avoid crossing roads, in which case roads essentially fragment species habitat. Barrier effects include reduced size and quality of available habitat, reduced effective population size, reduced ability to find mates and resources, increased genetic structuring, and increased probability of local extirpation (e.g., Forman et al. 2003; Fahrig and Rytwinski 2009; D'Amico et al. 2016). Depletion effects occur when animals attempt to cross roads and are killed by vehicles. Depletion effects include all of the risks from barrier effects as well as reduced survivorship, making high road mortality an even greater concern (Jackson and Fahrig 2011). Among other stressors, such as habitat loss and fragmentation, invasive species, pesticide use, changing climate, and disease, the negative impacts from roads may independently or cumulatively threaten the persistence of populations and even species.

Amphibians and reptiles have been identified as being particularly susceptible to the negative effects of roads within their habitat (e.g., Klauber 1931; Forman et al. 2003; Rytwinski and Fahrig 2012; Andrews et al. 2015a, b; D'Amico et al. 2015). Many are slow moving, do not avoid roads, and are simply too small for drivers to see and avoid. During rains many amphibians make long linear terrestrial movements regardless of the presence of intersecting roadways (Glista et al. 2008), and because paved roads typically absorb and retain more heat than the surrounding habitat, snakes and lizards are often attracted to roads for thermoregulation (Case and Fisher 2001; Jochimsen et al. 2004). In fact, road surveys are one of the most common methods for surveying these reptiles (e.g., Sullivan 2012). Many herpetofauna species utilize both aquatic and terrestrial habitat for breeding, development, foraging, and overwintering and therefore require connectivity within and between both aquatic and terrestrial habitats to support basic life history requirements.

The primary goal of this study was to provide information to transportation and other planning agencies in California to assist them in prioritizing road mitigation efforts for amphibian and reptile species. Although there is still a lot to learn about the effectiveness of different designs of road mitigation systems, the use of barrier systems, underpasses, and overpasses can reduce road mortality and help to maintain connectivity and safe passage across roads for herpetofauna and other wildlife (Jochimsen et al. 2004; Colino-Rabanal and Lizana 2012; Langton 2015; Langen et al. 2015b). Because it is currently unrealistic and cost prohibitive to mitigate all roadways for all species, it is vital to identify species most susceptible to road-related impacts. Within species ranges, risks to populations and need for mitigation can then be evaluated based upon local road densities and matrix, road-types, traffic, and road locations in relation to species habitat and movement corridors (e.g., Jaeger 2000; Litvaitis and Tash 2008; Langen et al. 2015b; Zimmermann Teixeira et al. 2017).

Here we describe a road risk assessment methodology applied to native amphibian and reptile species in California, a global biodiversity hotspot (Myers et al. 2000). We also included analysis of subspecies if they had special federal or state protection status. This includes 166 species and subspecies of frogs, toads, salamanders, snakes, lizards, turtles, and tortoise. Rankings and prioritizations such as these can be very subjective. In order to avoid including low risk species that may be favored by the assessors or to unintentionally overlook species that are at high risk, it was important for this be done in an objective manner informed by current road ecology literature.

Very few quantitative data are available on the impact of roads on population persistence. Jaeger et al. (2005) were the first to develop a relative ranking system to compare the impact of roads on wildlife populations. Their ranking system was largely based upon behavioral responses of animal species to the road surface, road size, traffic noise, and vehicles with varying road sizes and traffic volumes. However, knowledge of these detailed behavioral responses to ranges in road and traffic characteristics is rarely found in literature and the link between individual behavior and population-level effects has not been clearly established (Rytwinski and Fahrig 2012, 2013).

Rytwinski and Fahrig (2012) performed a meta-analysis of wildlife groups to test whether certain life history characteristics were related to negative responses to roads. High reproductive rate (fecundity) was negatively associated with the magnitude of population-level effects for amphibians. No associations were significant in reptiles, although there were few studies to inform this analysis. However, a strong link was shown between body size, greater mobility, lower reproductive rates and the magnitude of negative road effects in mammals, the most studied wildlife group. Conversely, simulations predicted populations of species with small home ranges and high reproductive rates were the least likely to be affected by roads (Rytwinski and Fahrig 2013).

We used these findings as a basis for creating a multi-tiered system to rank and identify reptile and amphibian species that may be most susceptible to road impacts. We based our ranking upon a suite of species life history and space-use characteristics associated with negative road effects, as well as including species distribution and conservation status. We evaluated risk to both aquatic and terrestrial connectivity and include buffer distances that were calculated to encompass 95% of population movements. Relative confidence in these distances is given for each species based upon the amount of support from scientific studies. We solely focused on the direct effects of roads as barriers and sources of road mortality and not impacts from road construction and maintenance or indirect effects from increased human use of the landscape once a road is in place (see review by Langen et al. 2015a).

Because we based the risk assessment solely upon space-use and life history characteristics, this represents a species relative susceptibility to road impacts. It is understood that circumstances associated with particular populations (e.g., local road types, locations, densities) may elevate or reduce the risk for certain populations and species.

Methods

Road risk assessment (overview)

We assessed the relative risk of California herpetofauna species to negative road-related impacts at three scales in a hierarchical fashion. We first assessed risk at the scale of an individual animal and then expanded the risk to the population and then to species (Fig. 1).

At the individual-level, we based road risk primarily upon the likelihood that an individual would encounter one or more roads. We considered this a product of movement distance (home range, seasonal migrations) and movement frequency (e.g., active foragers, seasonal migrants, sit-and-wait predators vs. sedentary species) (e.g., Bonnet et al. 1999; Carr and Fahrig 2001). Because many species are semi-aquatic, movement distance and frequency were scored separately for both aquatic and terrestrial habitats.

There is a theorized higher risk associated with depletion effects (i.e., road mortality) in comparison to barrier effects (Fahrig and Rytwinski 2009; Jackson and Fahrig 2011). Therefore, we gave additional weight to those species more likely to go out onto a road surface and be killed by vehicular traffic. For this we considered factors of habitat preference (e.g., open vs. closed), roads as potential attractants (e.g., for basking), and movement speed (e.g., slow vs. fast). However, individuals within and among species may respond differently to roads (attraction vs. avoidance) based upon local landscape features, road width, traffic volume, and perceived danger (Forman et al. 2003; Andrews 2005; Brehme et al. 2013; Jacobson et al. 2016). Because a state-wide analysis encompasses extreme variation in landscape and road characteristics, the extent to which roads act as barriers or sources of direct mortality within a species range is unknown. The risk disparity between depletion and barrier effects could also be highly variable. Therefore, we limited the additional weight for potential depletion effects to twenty percent of the individual risk score.

We assessed population-level road risk by multiplying individual risk with scores representing: (1) the relative proportion of the population at risk; and (2) the species ability to sustain higher rates of mortality. For instance, the proportion of the population at risk was expected to be higher for migratory species than for territorial species. Highly fecund species were expected to better withstand (or more quickly recover from) higher mortality in comparison to those with few annual offspring.

Finally, we assessed species-level road risk by multiplying population road risk with scores for range size (both within and outside of California) and conservation status according to the U.S. Fish and Wildlife Service (USFWS 2016) and the California Department of Fish and Wildlife (CDFW 2016a; Thomson et al. 2016). Species with smaller ranges typically have fewer populations and are thus less resilient to population-level stressors. Endangered, threatened, and special concern species have already been designated at risk of extirpation, often due to

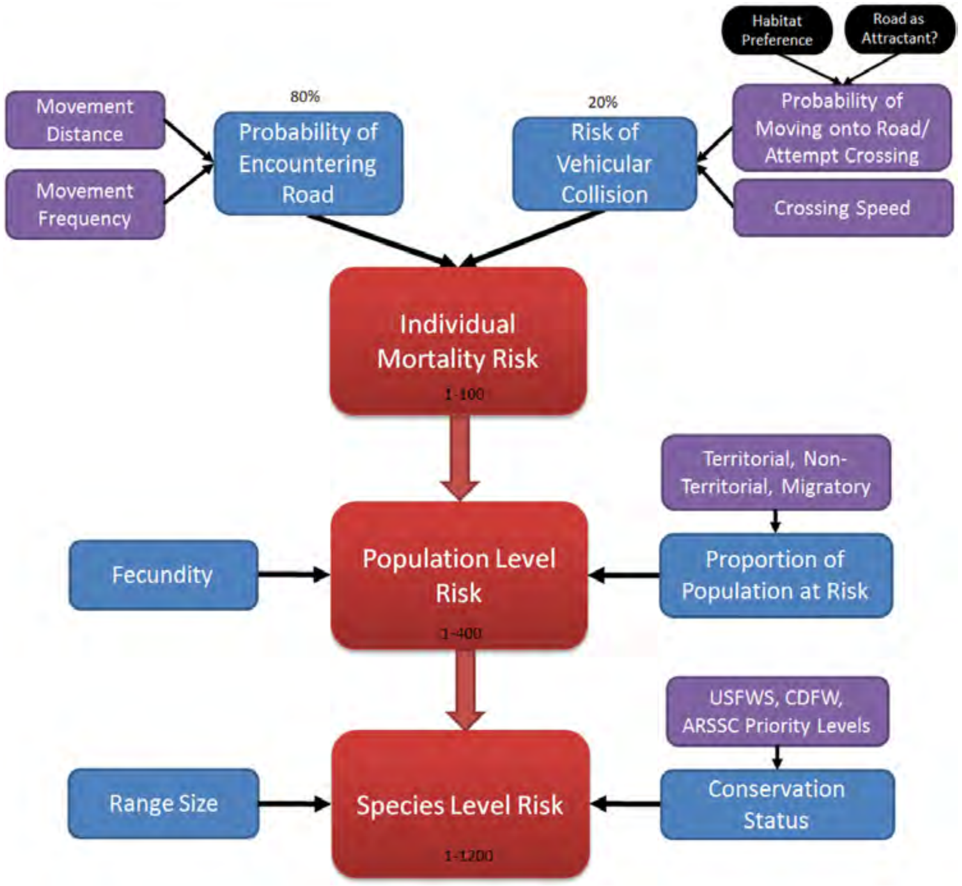


Fig. 1 California reptile and amphibian road risk assessment conceptual model (*ARSSC* Amphibian and Reptile Species of Special Concern (Thomson et al. 2016))

multiple stressors, and are thus thought to be less likely to be resilient to additional road impacts.

Although we present both aquatic and terrestrial risk scores for semi-aquatic species, we used the higher of the two scores for the overall risk ranking.

Literature review

Species life history data were primarily taken from and cross-checked among the following species account review sources;

1. U.S. Fish and Wildlife Service (USFWS) Recovery Plans and 5-year Reviews https://www.fws.gov/endangered/.
2. California Amphibian and Reptile Species of Special Concern (ARSSC; Thomson et al. 2016).
3. A Field Guide to Amphibians and Reptiles of California (Stebbins and McGinnis 2012)
4. Amphibian declines: the conservation status of United States species (Lannoo 2005).
5. Conservation Status of Amphibians and Reptiles on USDA National Forests, Pacific Southwest Region, 2012 (Evelyn and Sweet 2012).
6. Natureserve Explorer (natureserve.org): Species Accounts largely authored by G. Hammerson (2003–2016).

When these reviews were lacking life history information needed for the road risk assessment, we then searched for supplementary peer-reviewed literature using the Google Scholar search engine. Because movement distances (terrestrial, aquatic, home range, migratory) were so important for the risk assessment, we acquired referenced articles from the species accounts and independently searched the literature to acquire these data. Search terms included the species common name, scientific name, or genus and terms such as “movement”, “home-range”, “spatial”, and “telemetry”. We also reviewed articles for citations of other studies to find more recent information on movement. This literature included published articles, book chapters, M.S. Theses, Ph.D. dissertations, agency reports, and consultant reports. In the case that specific life history or movement information was not found for a species, we chose a surrogate species based upon phylogeny, habitat, and body size. We first looked for the closest related species within the genus or family and chose a closely related surrogate based upon similar habitat and body size. If surrogates were used, these are clearly reported.

Road risk metrics

The following section describes in detail the rank scoring used for Individual-level Road Risk, Population-level Road Risk, and Species-level Road Risk. All rank values are meant to represent the relative contribution of each attribute to either additive or multiplicative road risk.

Individual-level risk (100 points possible)

Out of a total of 100 points for individual road mortality risk, we attributed up to 80 points (80%) to the risk of encountering a road and up to 20 points (20%) for the risk of an individual moving onto a road and being killed by a motor vehicle.

The risk of encountering a road was based on a combination of movement distance and general movement frequency. Movement distance was ranked 1–40 based upon home range movement distances (diameter) for non-migrants or migration distances for seasonal migrants that spanned from 0 to > 1200 m (Table 1). The scores are linearly correlated with increasing movement distance.

For species that use both terrestrial and wetland/stream/riverine habitats, such as frogs, toads, aquatic snakes and turtles, we scored aquatic and terrestrial movement distances and frequencies separately. This was necessary as some species move much larger distances and at different frequencies in one habitat versus the other. This also informs the type(s) of mitigation structures that may be warranted based upon habitat type, buffer distances and risk scores for each species. Aquatic movement distances were not calculated for pond-breeding amphibians. Ponds are typically small ephemeral bodies of water and terrestrial movements of amphibians to and among ponds account for the majority of movement for these species.

Table 1 Individual-level Road Risk (IRR): Score criteria for risk of individuals encountering a road

Risk of individuals encountering a road = Movement distance × frequency

Movement distance (m)	Score	Frequency	Score
> 1200	40	Active throughout home range	2
901–1200	32	Migratory (2–4 × per year)/ non-migratory sit and wait foragers	1.5
601–900	24	Sedentary, confined to specialized habitat	1
451–600	16		
301–450	12		
201–300	8		
101–200	5		
51–100	3		
0–50	1		

The calculations and rankings for movement distances were well considered and deserve further explanation. Our original thinking was that maximum distances should reflect relative movement distances across species and these data were commonly reported in species accounts. However, it became increasingly difficult to determine whether maximum distances reported were seasonal migration movements, home range movements or rarer dispersal events. We believed this assessment should reflect annual movement distances and not rare dispersal events. We considered using average/median movement distances; however, these often underestimate the movement of seasonal migrants because in many cases a sizeable portion of the population may remain close to a breeding site, while another sizable portion make longer distance migrations causing an average or median to be uninformative. Therefore, we decided to use a buffer distance that incorporates the movement distances of 95% of the population studied. A 95% population movement distance is commonly accepted for the delineation of terrestrial buffer zones for amphibians (i.e., Semlitsch 1998; Semlitsch and Bodie 2003) and we believe it was the most biologically meaningful and useful measure for this study. This measure, which we will refer to as Maximum Population Movement Distance (MPMD), should include almost all population movements, such as seasonal migration distances and annual home ranges (diameter), but not rare dispersal events. The MPMD should also be useful for local risk assessments as these distances can be used to aide in mapping and mitigation decisions.

The calculation we used for MPMD is commonly known as the 95% upper tolerance interval (Vangel 2015). A tolerance interval is an interval that is meant to contain a specified percentage of individual population measurements. This should not be confused with a confidence interval, which is an interval that is meant to contain the population mean. We chose a 50% confidence level for the upper 95% confidence limit of movement distances which is equal to the 95% prediction interval for future observations and is the mean + 1.645 × standard deviation. In cases where a standard deviation was not reported, we back calculated standard deviation from the standard error and sample size, calculated it from the individual data, or estimated it based on the methods recommended by Hozo et al. (2005). Although non-parametric tolerance intervals would be more appropriate for non-normally distributed movement data, the data required to calculate these is rarely reported in the published literature. In the case of non-normally distributed data where medians, sample sizes and ranges are reported, Hozo et al. (2005) methods allow for approximation of means and standard deviations with no assumption of the underlying data distribution. We found the resulting MPMDs to be reasonable in excluding large outliers but including multiple long distance movements below the maximum movement distance.

We recognize that for any species there can be substantial variability in movement distances that depend upon varying local, landscape, and climatic factors. This was often reflected in studies with sometimes widely varying estimates of home range and migration distances. We attempted to be conservative by using the study data for calculation of MPMD in which the largest population movement distances were observed. For studies where movement distance significantly varied between females and males, we used the information from the wider ranging sex. For migratory distances, we did not use distances from extreme environments, such as Canada, where suitable overwintering sites are typically much farther away from breeding and summer activity areas than in milder California climates (e.g., Gregory 1984). We did use study data from adjacent states or lower estimates of migration distances from those reported in Midwestern states. In some cases where little information was available, we made an educated guess based upon limited study data and/or closely related species and noted these in the tables. For all MPMDs, we report a relative confidence level based upon the number and quality of studies, sample sizes, and locations in or adjacent to California. It is intended that the scores be adjusted as new information becomes available.

To compute the risk of encountering a road, the MPMD was multiplied by a relative index of the expected frequency of longer distance movements (1–2 points; Table 1). We defined three frequency categories largely based upon annual migratory movements or foraging strategies for non-migratory species. The highest category included actively foraging predators which are characterized by frequent wandering movements throughout their home range (Pianka 1966). Less frequent movers included seasonal migrants traveling among breeding, summer foraging, and/or overwintering sites and non-migratory 'sit-and-wait' predators that remain still for long periods of time to ambush prey (Pianka 1966). Finally, low frequency included highly sedentary species with high site fidelity, particularly specialized rock, crevice, soil, or tree dwellers that may rarely traverse terrestrial or aquatic habitats.

The risk of an individual moving onto a road and being killed by a moving vehicle was ranked by attributes of habitat preference, road use, and movement speed (Table 2). Habitat preference represents the degree to which an individual is expected to go out onto or avoid an open road as predicted from their habitat and microhabitat preferences. Open habitat specialists and generalists were expected to more readily move onto a road than species that prefer cover (e.g., Forman et al. 2003; Brehme et al. 2013). Although many amphibians are closed habitat specialists, most readily move through open habitats during rain events, when most overland migratory movements tend to occur (Glista et al. 2008). Therefore, amphibians were considered open habitat specialists for this ranking. An additional factor that may increase road use is for thermoregulation for lizards

Table 2 Individual-level Road Risk (IRR): Score criteria for risk of road mortality

Risk of road mortality = Habitat preference + road use + movement speed

Habitat preference	Score	Road use	Score	Movement speed	Score
Open habitat specialist/amphibians	10	Thermoregulation (snakes/lizards)	4	Slow (< 0.6 m/s)	6
Generalist	8	Other	0	Medium (0.6–2.0 m/s)	3
Edge specialist	4			Fast (> 2.0 m/s)	0
Closed habitat or aquatic specialist	0				

Table 3 Population-level Road Risk (PRR): Score criteria for population level road risk

PRR = IRR × (Fecundity + Proportion of population at risk)

Fecundity	Ave. potential offspring/year	Score	Proportion of population at risk	Score
Low	0–10	2	Seasonal migrants (Migratory)	2
Med	11–25	1.5	Wandering	1.5
High	26–100	1	Territorial	1
Very high	> 100	0		

and snakes, as roads often retain more heat than the surrounding environment (Colino-Rabanal and Lizana 2012; Mccardle and Fontenot 2016). Finally, there is an increased risk of road mortality for slow versus fast moving species (see Andrews and Gibbons 2005; Mazerolle et al. 2005; Andrews et al. 2015b).

Population-level Road Risk (400 points possible)

To assess the risk of negative road impacts on the persistence of a population we incorporated scores for population-level movement behavior and fecundity (Table 3). For the proportion of a population expected to encounter a road, we scored the greatest risk to species that seasonally migrate to overwintering and breeding areas (Jackson et al. 2015). For those that do not migrate, we expected higher proportions of non-territorial or loosely territorial species (“wandering”) to encounter roads than species that defend distinct territories.

Species with low fecundity are less resilient to road mortality impacts than highly fecund species (Rytwinski and Fahrig 2013). Relative fecundity was simply calculated from the average number of potential offspring per year whether the animals were oviparous or live-bearing. For egg-laying species, the number of potential offspring was calculated by multiplying the average clutch size by the average number of clutches per year.

Individual mortality risk (1–100 points) was multiplied by the sum of these population-level factors (1–4 points) to calculate population-level road risk.

Species-level road risk (1200 points possible)

In comparison to population-level risk, we considered the overall risk of roads to species to be negatively associated with species range and conservation status. Although some populations may be at high risk, species with a wide distribution and many populations should be more resilient to localized declines and extirpations. Therefore, we assigned a range isolation score ranging from 0 to 1 that considered species distributions range-wide (North America) and within California (CA) (Table 4). Range-wide distribution varied from “CA only” to “widespread” (> 4 states). If the species range extended into Mexico and/or Canada, these countries were counted as another state for calculation of the index. California-wide distribution was calculated based upon the number of CA geographic regions occupied out of twelve regions defined by Hickman (1993) and used in Stebbins and

Table 4 Species-level Road Risk (SRR): Score criteria for species-level road risk

SRR[a] = PRR × ((Range isolation score + Conservation status score)/2)

(a) Range isolation score = (North America range + CA range)/2

North America range	Rank/score
CA only	1.00
2 states (very restricted distribution)	1.00
2 states (restricted)	0.67
2–3 states	0.33
Widespread (4 + states)	0.00

California range (No. of geographic regions occupied)	Rank/score
1	0.92
2	0.83
3	0.75
4	0.67
5	0.58
6	0.50
7	0.42
8	0.33
9	0.25
10	0.17
11	0.08
12	0.00

(b) Conservation status score

Conservation status	Rank/score[a]
CA or federal threatened/endangered	1.00
SSC priority 1	0.75
SSC priority 2	0.50
SSC priority 3	0.25
None	0.00

[a] Population-level risk > 80 only

McGinnis (2012). These two scores (Range-wide isolation, CA isolation) were summed and divided by two in order to normalize the overall range isolation score to a 0 to 1 scale.

At the species-level, we also incorporated conservation status (Table 4). Some species are declining and are at higher risk of extinction often due to multiple stressors. Federal and State Threatened and Endangered Species were given the highest score (1.0). In California, forty-five species are designated “Species of Special Concern (SSC)” with a ranking of 1, 2, or 3 based upon severity and immediacy of threats affecting each taxon (Thomson et al. 2016). SSC species were given a conservation status score ranging from 0.25 to 0.75 based upon their SSC ranking. Population-level Road Risk (score range 1–400) was multiplied by (1 + Range Isolation Score + Conservation Status Score; score range 1–3) to calculate the final Species-level Road Risk.

Range and conservation status were only used as a multiplier for species-level road risk if the population-level road risk was greater than 80 (20% of possible population score). This helped to prevent false inflation of the road risk metrics for low road susceptible species.

Because all members of the genus *Batrachoseps* (slender salamanders) are similar in body size, range size and general life history characteristics, we scored

Table 5 Species-level frequency distributions and road risk rankings

Percentile	Scores	Relative ranks
81–100	322–710	Very high
61–80	213–321	High
41–60	63–212	Medium
21–40	53–62	Low
1–20	0–52	Very Low

the genus as whole with the most conservative estimates and conservation status but included all 20 species in the final count and calculations.

Once all 166 species (including subspecies with conservation status) were scored for species-level road risk within both terrestrial and aquatic habitats, we took the maximum score for each species and sorted them from the highest to lowest scores. We grouped species into categories of risk (Very high, high, medium, low, and very low) based upon ranges of values that represented frequency distributions in 20% increments of all species scores (Table 5, Fig. 2).

As a way to support the results of our ranking model with species literature, we focused on special status species. We reviewed recovery plans and 5-year reviews for federally listed species and state species accounts for California listed species and species of special concern (collectively referred to as special status species). For each rank group (i.e., "very low" to "very high"), we calculated the percentage of special status species where roads were specifically listed as a threat. Similarly, we tallied the number of species identified in a recent California preliminary road risk assessment (Levine 2013, Amy Golden pers. comm.) and compared the number of species that fell within each of our road risk categories.

Results

All chelonids, 72% of snakes, 50% of anurans, 18% of lizards and 17% of salamander species were ranked as high or very high risk from negative road impacts. (Table 6, Fig. 3).

Review of species accounts, recovery plans, and 5-year reviews for all special status species showed

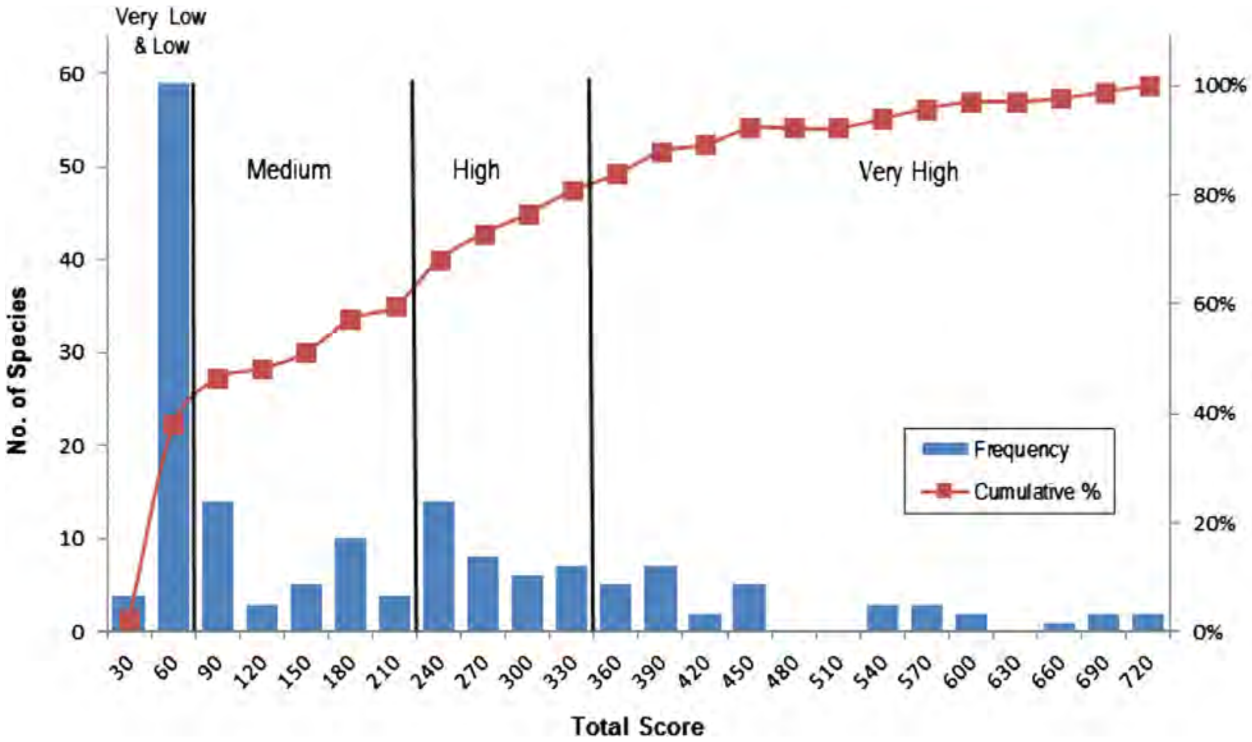


Fig. 2 Histogram of species-level scores and approximate 20 percentile road risk categories

Table 6 Numbers of species by taxa within each risk category

Species group	Species-level rankings				
	Very high	High	Med	Low	Very low
Salamander	4	4	3	26	9
Lizard	5	3	8	7	21
Anuran	5	6	6	4	1
Snake	15	21	13	0	1
Tortoise	1	0	0	0	0
Turtle	3	0	0	0	0

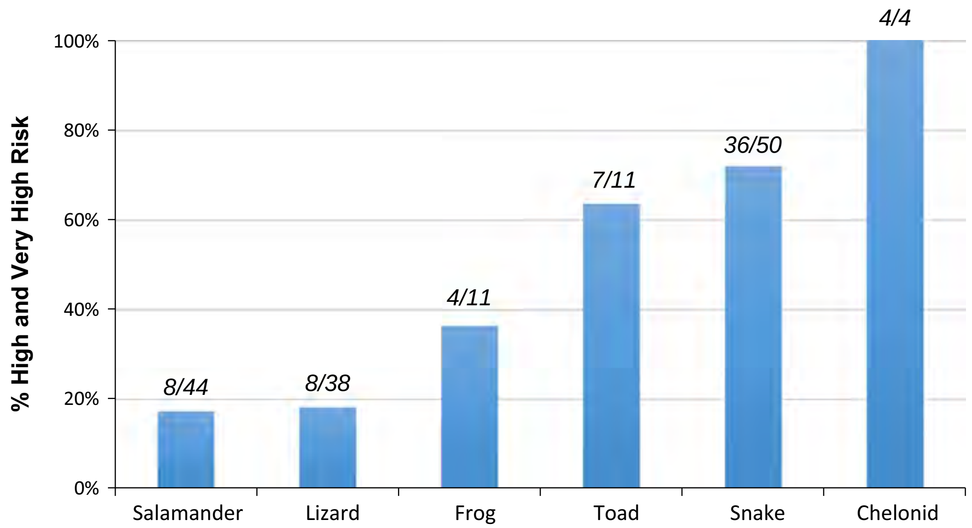


Fig. 3 Percentages of species by taxa in high and very high road risk categories

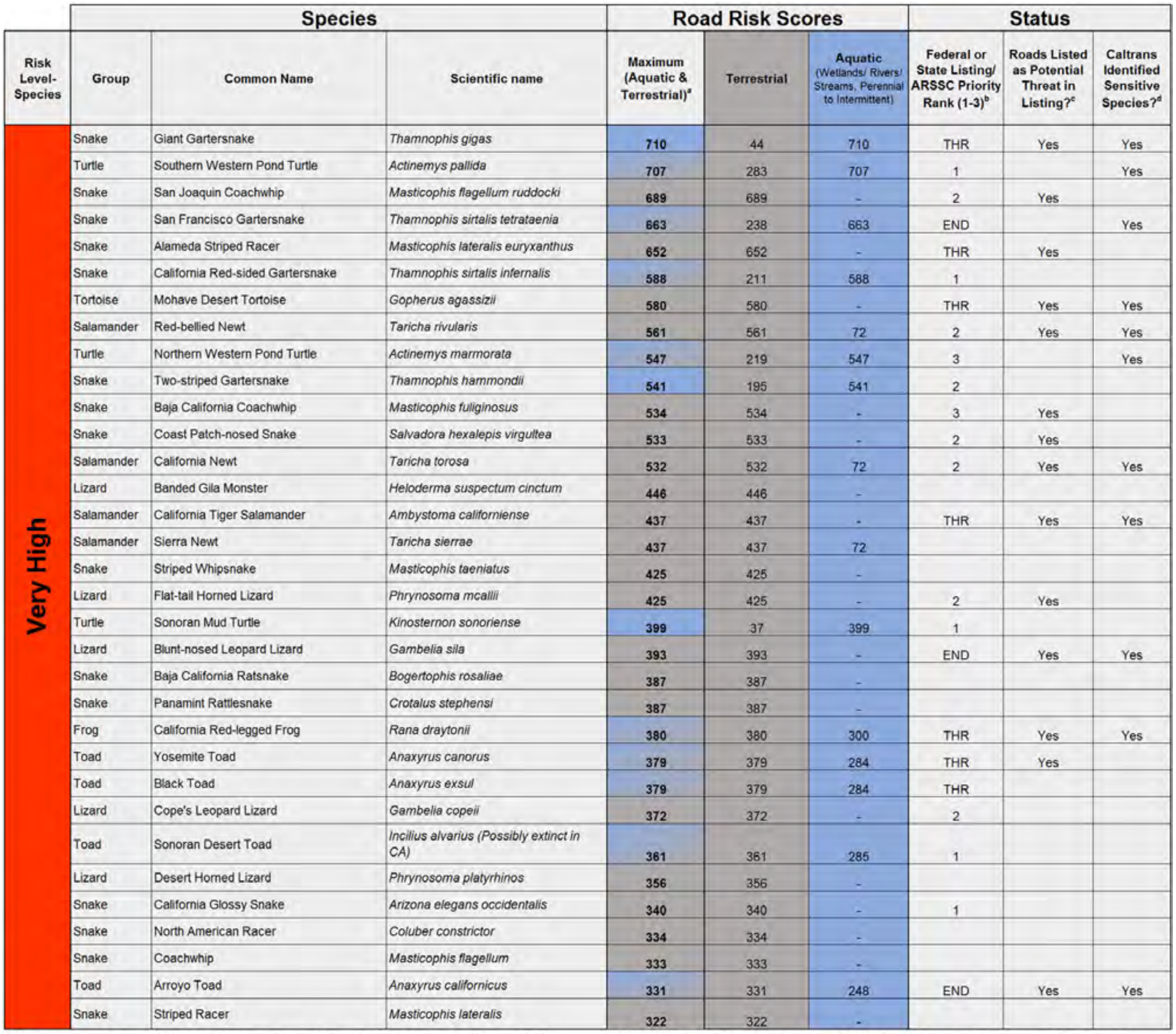
that 94% (17/18) of species accounts that referenced roads as a threat to the species were ranked as “high” or “very high” in our risk assessment (Table 7). Of the special status species that ranked ‘high’ and ‘very high’, close to fifty percent (17/35) had road-related threats referenced in their listing literature. In comparison, only 4% (1/27) of ‘medium’ to ‘very low’ risk special status species accounts mentioned roads as a potential threat. In addition, 79% (15/19) of species of concern recommended in a recent Caltrans preliminary road risk assessment scored as ‘high’ or ‘very high’ risk in our analysis (Levine 2013, Amy Golden pers. comm.).

Table 7 Comparison of road risk results and number of special status species with roads listed as threat

Road risk level	Special status species			Caltrans PI[a]
	No. species in road risk level	No. species with roads listed as threat	% of Total	No. Spp in road risk level
Very high	25	14	56	11
High	11	3	27	4
Medium	5	1	20	3
Low	10	0	0	1
Very low	7	0	0	0

[a] Caltrans PI are Caltrans identified sensitive species

Table 8 Amphibian and reptile road risk assessment: very high risk species (80–100% percentile), high risk species (60–80% percentile), medium risk species (40–60% percentile range), low risk species (20–40% percentile) and very low risk species (0–20% percentile)



	Species			Road Risk Scores			Status		
Risk Level-Species	Group	Common Name	Scientific name	Maximum (Aquatic & Terrestrial)[a]	Terrestrial	Aquatic (Wetlands/ Rivers/ Streams, Perennial to Intermittent)	Federal or State Listing/ ARSSC Priority Rank (1-3)[b]	Roads Listed as Potential Threat in Listing?[c]	Caltrans Identified Sensitive Species?[d]
Very High	Snake	Giant Gartersnake	*Thamnophis gigas*	**710**	44	710	THR	Yes	Yes
	Turtle	Southern Western Pond Turtle	*Actinemys pallida*	**707**	283	707	1		Yes
	Snake	San Joaquin Coachwhip	*Masticophis flagellum ruddocki*	**689**	689	-	2	Yes	
	Snake	San Francisco Gartersnake	*Thamnophis sirtalis tetrataenia*	**663**	238	663	END		Yes
	Snake	Alameda Striped Racer	*Masticophis lateralis euryxanthus*	**652**	652	-	THR	Yes	
	Snake	California Red-sided Gartersnake	*Thamnophis sirtalis infernalis*	**588**	211	588	1		
	Tortoise	Mohave Desert Tortoise	*Gopherus agassizii*	**580**	580	-	THR	Yes	Yes
	Salamander	Red-bellied Newt	*Taricha rivularis*	**561**	561	72	2	Yes	Yes
	Turtle	Northern Western Pond Turtle	*Actinemys marmorata*	**547**	219	547	3		Yes
	Snake	Two-striped Gartersnake	*Thamnophis hammondii*	**541**	195	541	2		
	Snake	Baja California Coachwhip	*Masticophis fuliginosus*	**534**	534	-	3	Yes	
	Snake	Coast Patch-nosed Snake	*Salvadora hexalepis virgultea*	**533**	533	-	2	Yes	
	Salamander	California Newt	*Taricha torosa*	**532**	532	72	2	Yes	Yes
	Lizard	Banded Gila Monster	*Heloderma suspectum cinctum*	**446**	446	-			
	Salamander	California Tiger Salamander	*Ambystoma californiense*	**437**	437	-	THR	Yes	Yes
	Salamander	Sierra Newt	*Taricha sierrae*	**437**	437	72			
	Snake	Striped Whipsnake	*Masticophis taeniatus*	**425**	425	-			
	Lizard	Flat-tail Horned Lizard	*Phrynosoma mcallii*	**425**	425	-	2	Yes	
	Turtle	Sonoran Mud Turtle	*Kinosternon sonoriense*	**399**	37	399	1		
	Lizard	Blunt-nosed Leopard Lizard	*Gambelia sila*	**393**	393	-	END	Yes	Yes
	Snake	Baja California Ratsnake	*Bogertophis rosaliae*	**387**	387	-			
	Snake	Panamint Rattlesnake	*Crotalus stephensi*	**387**	387	-			
	Frog	California Red-legged Frog	*Rana draytonii*	**380**	380	300	THR	Yes	Yes
	Toad	Yosemite Toad	*Anaxyrus canorus*	**379**	379	284	THR	Yes	
	Toad	Black Toad	*Anaxyrus exsul*	**379**	379	284	THR		
	Lizard	Cope's Leopard Lizard	*Gambelia copeii*	**372**	372	-	2		
	Toad	Sonoran Desert Toad	*Incilius alvarius (Possibly extinct in CA)*	**361**	361	285	1		
	Lizard	Desert Horned Lizard	*Phrynosoma platyrhinos*	**356**	356	-			
	Snake	California Glossy Snake	*Arizona elegans occidentalis*	**340**	340	-	1		
	Snake	North American Racer	*Coluber constrictor*	**334**	334	-			
	Snake	Coachwhip	*Masticophis flagellum*	**333**	333	-			
	Toad	Arroyo Toad	*Anaxyrus californicus*	**331**	331	248	END	Yes	Yes
	Snake	Striped Racer	*Masticophis lateralis*	**322**	322	-			

[a] Maximum scores color-coded for toad risk type; terrestrial (gray), aquatic (blue), or both (gray/blue)

[b] END=Endangered, THR= Threatened, 1-3= ARSSC Priority Ranking

[c] Federal Recovery plans, 5-year reviews, California species accounts for special status species

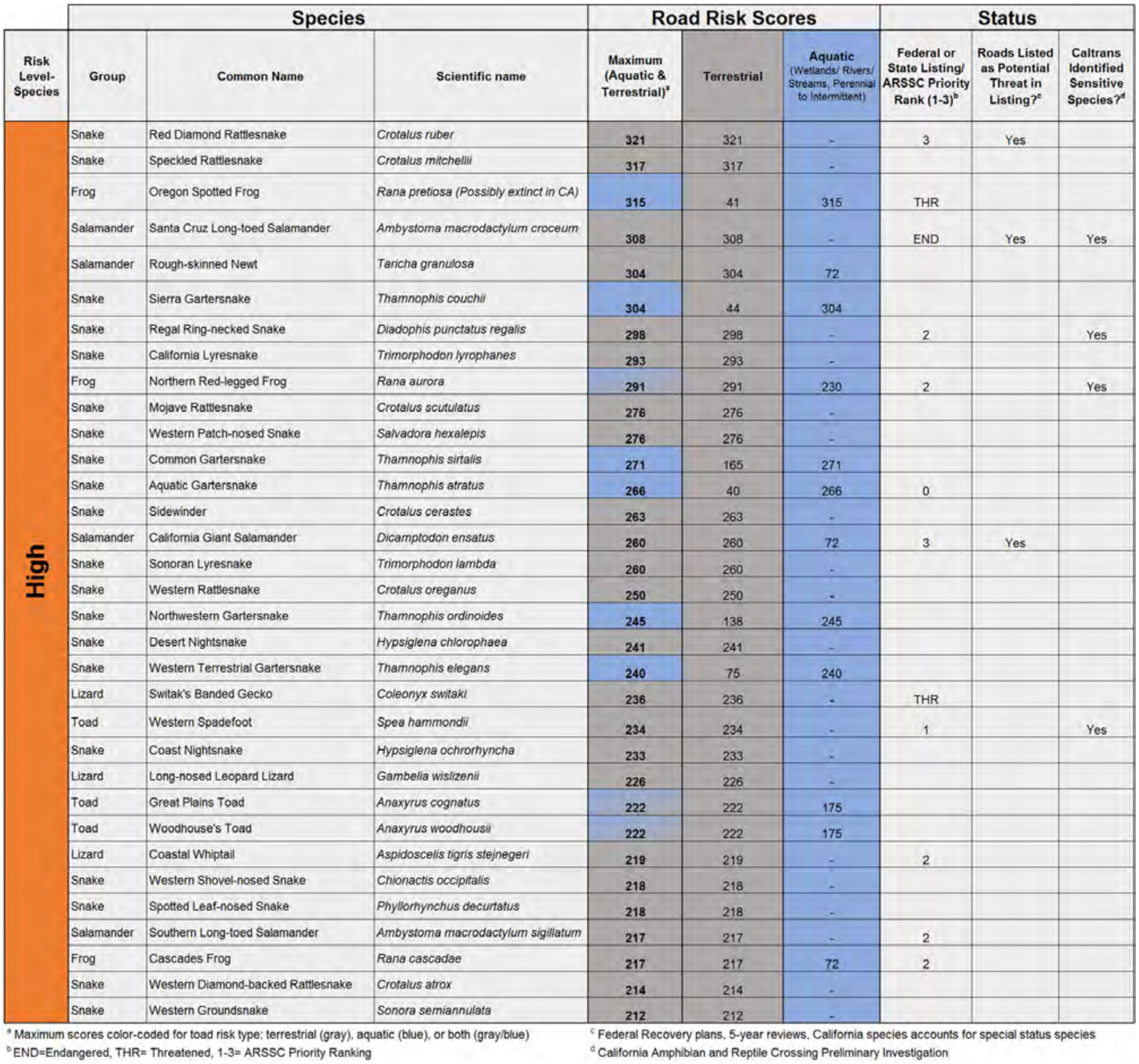
[d] California Amphibian and Reptile Crossing Preliminary Investigation

Risk scores and relative rankings for California reptile and amphibian species in both terrestrial and aquatic habitats are presented in Tables 8. Terrestrial and Aquatic rankings are provided separately in Tables 9 and 10 and also include population-level risk scores, 95% population buffer distances, confidence levels, and identification of any surrogate species used for the distance calculations. Species scores for all ranking criteria and life history and movement references are provided in Appendices 1 and 2.

Discussion

To our knowledge, this is the first attempt to objectively assess the relative risk of roads at a species level using a logical and scientifically based framework and apply it across a large array of species and habitats. We believe this approach could be useful for assessing and comparing susceptibility of species to negative road impacts within and among all taxonomic groups. To date, such risk assessments have been based largely upon expert opinion, limited information available on

Table 8 continued



	Species			Road Risk Scores			Status		
Risk Level-Species	Group	Common Name	Scientific name	Maximum (Aquatic & Terrestrial)[a]	Terrestrial	Aquatic (Wetlands/ Rivers/ Streams, Perennial to Intermittent)	Federal or State Listing/ ARSSC Priority Rank (1-3)[b]	Roads Listed as Potential Threat in Listing?[c]	Caltrans Identified Sensitive Species?[d]
High	Snake	Red Diamond Rattlesnake	*Crotalus ruber*	**321**	321	-	3	Yes	
	Snake	Speckled Rattlesnake	*Crotalus mitchellii*	**317**	317	-			
	Frog	Oregon Spotted Frog	*Rana pretiosa (Possibly extinct in CA)*	**315**	41	315	THR		
	Salamander	Santa Cruz Long-toed Salamander	*Ambystoma macrodactylum croceum*	**308**	308	-	END	Yes	Yes
	Salamander	Rough-skinned Newt	*Taricha granulosa*	**304**	304	72			
	Snake	Sierra Gartersnake	*Thamnophis couchii*	**304**	44	304			
	Snake	Regal Ring-necked Snake	*Diadophis punctatus regalis*	**298**	298	-	2		Yes
	Snake	California Lyresnake	*Trimorphodon lyrophanes*	**293**	293	-			
	Frog	Northern Red-legged Frog	*Rana aurora*	**291**	291	230	2		Yes
	Snake	Mojave Rattlesnake	*Crotalus scutulatus*	**276**	276	-			
	Snake	Western Patch-nosed Snake	*Salvadora hexalepis*	**276**	276	-			
	Snake	Common Gartersnake	*Thamnophis sirtalis*	**271**	165	271			
	Snake	Aquatic Gartersnake	*Thamnophis atratus*	**266**	40	266	0		
	Snake	Sidewinder	*Crotalus cerastes*	**263**	263	-			
	Salamander	California Giant Salamander	*Dicamptodon ensatus*	**260**	260	72	3	Yes	
	Snake	Sonoran Lyresnake	*Trimorphodon lambda*	**260**	260	-			
	Snake	Western Rattlesnake	*Crotalus oreganus*	**250**	250	-			
	Snake	Northwestern Gartersnake	*Thamnophis ordinoides*	**245**	138	245			
	Snake	Desert Nightsnake	*Hypsiglena chlorophaea*	**241**	241	-			
	Snake	Western Terrestrial Gartersnake	*Thamnophis elegans*	**240**	75	240			
	Lizard	Switak's Banded Gecko	*Coleonyx switaki*	**236**	236	-	THR		
	Toad	Western Spadefoot	*Spea hammondii*	**234**	234	-	1		Yes
	Snake	Coast Nightsnake	*Hypsiglena ochrorhyncha*	**233**	233	-			
	Lizard	Long-nosed Leopard Lizard	*Gambelia wislizenii*	**226**	226	-			
	Toad	Great Plains Toad	*Anaxyrus cognatus*	**222**	222	175			
	Toad	Woodhouse's Toad	*Anaxyrus woodhousii*	**222**	222	175			
	Lizard	Coastal Whiptail	*Aspidoscelis tigris stejnegeri*	**219**	219	-	2		
	Snake	Western Shovel-nosed Snake	*Chionactis occipitalis*	**218**	218	-			
	Snake	Spotted Leaf-nosed Snake	*Phyllorhynchus decurtatus*	**218**	218	-			
	Salamander	Southern Long-toed Salamander	*Ambystoma macrodactylum sigillatum*	**217**	217	-	2		
	Frog	Cascades Frog	*Rana cascadae*	**217**	217	72	2		
	Snake	Western Diamond-backed Rattlesnake	*Crotalus atrox*	**214**	214	-			
	Snake	Western Groundsnake	*Sonora semiannulata*	**212**	212	-			

[a] Maximum scores color-coded for toad risk type: terrestrial (gray), aquatic (blue), or both (gray/blue)

[b] END=Endangered, THR= Threatened, 1-3= ARSSC Priority Ranking

[c] Federal Recovery plans, 5-year reviews, California species accounts for special status species

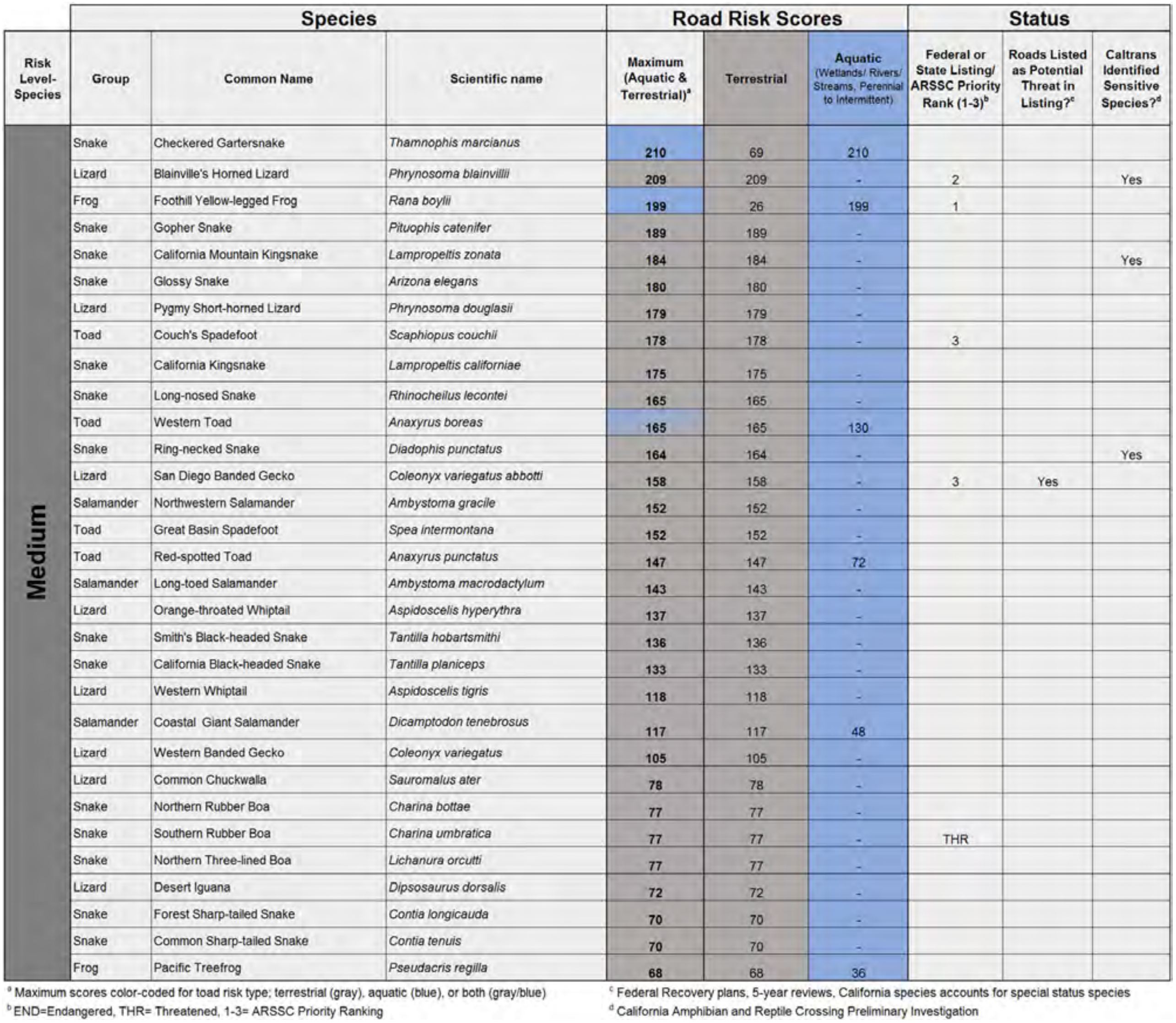
[d] California Amphibian and Reptile Crossing Preliminary Investigation

road mortality, and even less information available on population or species-level road effects (Levine 2013; Rytwinski and Fahrig 2015).

Overall, this is meant to be a first step in highlighting reptile and amphibian species that may be at highest risk from roads transecting their habitat. These species may deserve consideration for further study and for implementing mitigation solutions to reduce mortality and to maintain or enhance connectivity. The risk assessment was done for both terrestrial and aquatic habitats to further inform mitigation. Some aquatic species may greatly benefit from fish passages while others may better benefit from terrestrial barriers and wildlife crossings or both.

Although data are currently lacking to validate completely the scoring and results of the risk assessment, our review of species accounts, recovery plans, 5-year reviews for federal and state-listed species and California species of special concern show a strong association between elevated road risk from our

Table 8 continued



	Species			Road Risk Scores			Status		
Risk Level-Species	Group	Common Name	Scientific name	Maximum (Aquatic & Terrestrial)[a]	Terrestrial	Aquatic (Wetlands/ Rivers/ Streams, Perennial to Intermittent)	Federal or State Listing/ ARSSC Priority Rank (1-3)[b]	Roads Listed as Potential Threat in Listing?[c]	Caltrans Identified Sensitive Species?[d]
Medium	Snake	Checkered Gartersnake	*Thamnophis marcianus*	**210**	69	210			
	Lizard	Blainville's Horned Lizard	*Phrynosoma blainvillii*	**209**	209	-	2		Yes
	Frog	Foothill Yellow-legged Frog	*Rana boylii*	**199**	26	199	1		
	Snake	Gopher Snake	*Pituophis catenifer*	**189**	189	-			
	Snake	California Mountain Kingsnake	*Lampropeltis zonata*	**184**	184	-			Yes
	Snake	Glossy Snake	*Arizona elegans*	**180**	180	-			
	Lizard	Pygmy Short-horned Lizard	*Phrynosoma douglasii*	**179**	179	-			
	Toad	Couch's Spadefoot	*Scaphiopus couchii*	**178**	178	-	3		
	Snake	California Kingsnake	*Lampropeltis californiae*	**175**	175	-			
	Snake	Long-nosed Snake	*Rhinocheilus lecontei*	**165**	165	-			
	Toad	Western Toad	*Anaxyrus boreas*	**165**	165	130			
	Snake	Ring-necked Snake	*Diadophis punctatus*	**164**	164	-			Yes
	Lizard	San Diego Banded Gecko	*Coleonyx variegatus abbotti*	**158**	158	-	3	Yes	
	Salamander	Northwestern Salamander	*Ambystoma gracile*	**152**	152	-			
	Toad	Great Basin Spadefoot	*Spea intermontana*	**152**	152	-			
	Toad	Red-spotted Toad	*Anaxyrus punctatus*	**147**	147	72			
	Salamander	Long-toed Salamander	*Ambystoma macrodactylum*	**143**	143	-			
	Lizard	Orange-throated Whiptail	*Aspidoscelis hyperythra*	**137**	137	-			
	Snake	Smith's Black-headed Snake	*Tantilla hobartsmithi*	**136**	136	-			
	Snake	California Black-headed Snake	*Tantilla planiceps*	**133**	133	-			
	Lizard	Western Whiptail	*Aspidoscelis tigris*	**118**	118	-			
	Salamander	Coastal Giant Salamander	*Dicamptodon tenebrosus*	**117**	117	48			
	Lizard	Western Banded Gecko	*Coleonyx variegatus*	**105**	105	-			
	Lizard	Common Chuckwalla	*Sauromalus ater*	**78**	78	-			
	Snake	Northern Rubber Boa	*Charina bottae*	**77**	77	-			
	Snake	Southern Rubber Boa	*Charina umbratica*	**77**	77	-	THR		
	Snake	Northern Three-lined Boa	*Lichanura orcutti*	**77**	77	-			
	Lizard	Desert Iguana	*Dipsosaurus dorsalis*	**72**	72	-			
	Snake	Forest Sharp-tailed Snake	*Contia longicauda*	**70**	70	-			
	Snake	Common Sharp-tailed Snake	*Contia tenuis*	**70**	70	-			
	Frog	Pacific Treefrog	*Pseudacris regilla*	**68**	68	36			

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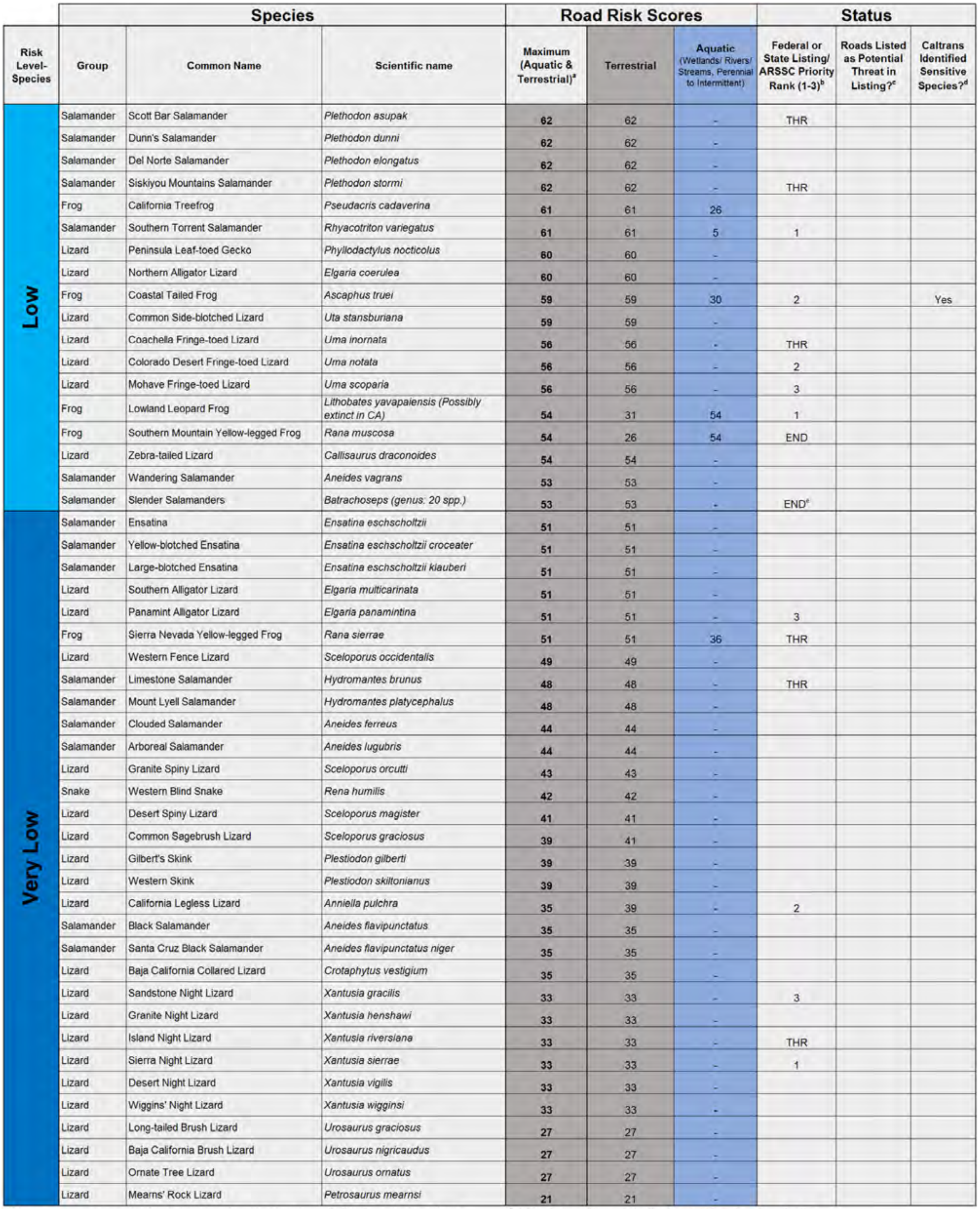
[d] California Amphibian and Reptile Crossing Preliminary Investigation

objective analysis and the probability that roads are listed as a potential threat to the species in the species listing literature.

Although more than 40% of special status species are semi-aquatic, roads were rarely considered a threat to aquatic connectivity in the species literature. This may be accurate if bridges or large culverts currently exist for water flow that also provide permeability to aquatic movement. Bridges are generally considered to be completely passable by all aquatic species. Bridges are more likely to be constructed adjacent to or over large water bodies and rivers, presumably resulting in less risk to aquatic movement of populations that inhabit lake and river systems. However, culverts that are more commonly constructed under roads in streams and wetlands vary in passability depending on factors such as diameter, length, slope, outlet configuration, and other characteristics (Furniss et al. 1991; Clarkin et al. 2005; Kemp and O'Hanley 2010). In fact, Januchowski-Hartley et al. (2013) found that only 36% of road crossings were fully passable to fish in the Great Lakes basin. In addition, many low water crossings in arid regions of the state are simply a dip in the road that allows water to flow

Table 8 continued



	Species			Road Risk Scores			Status		
Risk Level-Species	Group	Common Name	Scientific name	Maximum (Aquatic & Terrestrial)[a]	Terrestrial	Aquatic (Wetlands/ Rivers/ Streams, Perennial to Intermittent)	Federal or State Listing/ ARSSC Priority Rank (1-3)[b]	Roads Listed as Potential Threat in Listing?[c]	Caltrans Identified Sensitive Species?[d]
Low	Salamander	Scott Bar Salamander	*Plethodon asupak*	**62**	62	-	THR		
	Salamander	Dunn's Salamander	*Plethodon dunni*	**62**	62	-			
	Salamander	Del Norte Salamander	*Plethodon elongatus*	**62**	62	-			
	Salamander	Siskiyou Mountains Salamander	*Plethodon stormi*	**62**	62	-	THR		
	Frog	California Treefrog	*Pseudacris cadaverina*	**61**	61	26			
	Salamander	Southern Torrent Salamander	*Rhyacotriton variegatus*	**61**	61	5	1		
	Lizard	Peninsula Leaf-toed Gecko	*Phyllodactylus nocticolus*	**60**	60	-			
	Lizard	Northern Alligator Lizard	*Elgaria coerulea*	**60**	60	-			
	Frog	Coastal Tailed Frog	*Ascaphus truei*	**59**	59	30	2		Yes
	Lizard	Common Side-blotched Lizard	*Uta stansburiana*	**59**	59	-			
	Lizard	Coachella Fringe-toed Lizard	*Uma inornata*	**56**	56	-	THR		
	Lizard	Colorado Desert Fringe-toed Lizard	*Uma notata*	**56**	56	-	2		
	Lizard	Mohave Fringe-toed Lizard	*Uma scoparia*	**56**	56	-	3		
	Frog	Lowland Leopard Frog	*Lithobates yavapaiensis (Possibly extinct in CA)*	**54**	31	54	1		
	Frog	Southern Mountain Yellow-legged Frog	*Rana muscosa*	**54**	26	54	END		
	Lizard	Zebra-tailed Lizard	*Callisaurus draconoides*	**54**	54	-			
	Salamander	Wandering Salamander	*Aneides vagrans*	**53**	53	-			
	Salamander	Slender Salamanders	*Batrachoseps (genus: 20 spp.)*	**53**	53	-	END[e]		
Very Low	Salamander	Ensatina	*Ensatina eschscholtzii*	**51**	51	-			
	Salamander	Yellow-blotched Ensatina	*Ensatina eschscholtzii croceater*	**51**	51	-			
	Salamander	Large-blotched Ensatina	*Ensatina eschscholtzii klauberi*	**51**	51	-			
	Lizard	Southern Alligator Lizard	*Elgaria multicarinata*	**51**	51	-			
	Lizard	Panamint Alligator Lizard	*Elgaria panamintina*	**51**	51	-	3		
	Frog	Sierra Nevada Yellow-legged Frog	*Rana sierrae*	**51**	51	36	THR		
	Lizard	Western Fence Lizard	*Sceloporus occidentalis*	**49**	49	-			
	Salamander	Limestone Salamander	*Hydromantes brunus*	**48**	48	-	THR		
	Salamander	Mount Lyell Salamander	*Hydromantes platycephalus*	**48**	48	-			
	Salamander	Clouded Salamander	*Aneides ferreus*	**44**	44	-			
	Salamander	Arboreal Salamander	*Aneides lugubris*	**44**	44	-			
	Lizard	Granite Spiny Lizard	*Sceloporus orcutti*	**43**	43	-			
	Snake	Western Blind Snake	*Rena humilis*	**42**	42	-			
	Lizard	Desert Spiny Lizard	*Sceloporus magister*	**41**	41	-			
	Lizard	Common Sagebrush Lizard	*Sceloporus graciosus*	**39**	41	-			
	Lizard	Gilbert's Skink	*Plestiodon gilberti*	**39**	39	-			
	Lizard	Western Skink	*Plestiodon skiltonianus*	**39**	39	-			
	Lizard	California Legless Lizard	*Anniella pulchra*	**35**	39	-	2		
	Salamander	Black Salamander	*Aneides flavipunctatus*	**35**	35	-			
	Salamander	Santa Cruz Black Salamander	*Aneides flavipunctatus niger*	**35**	35	-			
	Lizard	Baja California Collared Lizard	*Crotaphytus vestigium*	**35**	35	-			
	Lizard	Sandstone Night Lizard	*Xantusia gracilis*	**33**	33	-	3		
	Lizard	Granite Night Lizard	*Xantusia henshawi*	**33**	33	-			
	Lizard	Island Night Lizard	*Xantusia riversiana*	**33**	33	-	THR		
	Lizard	Sierra Night Lizard	*Xantusia sierrae*	**33**	33	-	1		
	Lizard	Desert Night Lizard	*Xantusia vigilis*	**33**	33	-			
	Lizard	Wiggins' Night Lizard	*Xantusia wigginsi*	**33**	33	-			
	Lizard	Long-tailed Brush Lizard	*Urosaurus graciosus*	**27**	27	-			
	Lizard	Baja California Brush Lizard	*Urosaurus nigricaudus*	**27**	27	-			
	Lizard	Ornate Tree Lizard	*Urosaurus ornatus*	**27**	27	-			
	Lizard	Mearns' Rock Lizard	*Petrosaurus mearnsi*	**21**	21	-			

[a] Maximum scores color-coded for toad risk type; terrestrial (gray), aquatic (blue), or both (gray/blue)

[b] END=Endangered, THR= Threatened, 1-3= ARSSC Priority Ranking

[c] Federal Recovery plans, 5-year reviews, California species accounts for special status species

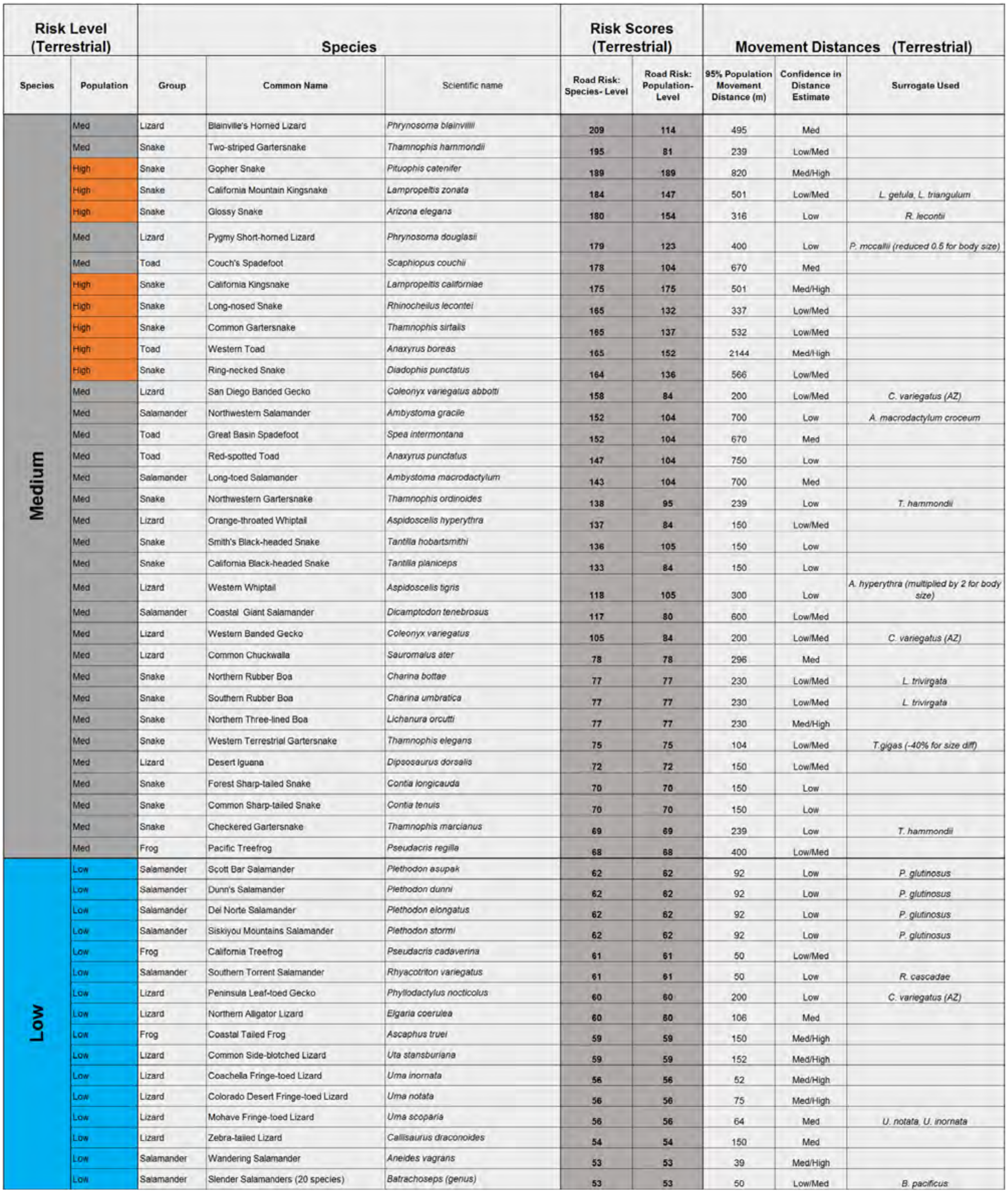
[d] California Amphibian and Reptile Crossing Preliminary Investigation

[e] 4 Batrachoseps species with conservation status

Table 9 Terrestrial risk ranking and population buffer distances

Risk Level (Terrestrial)		Species			Risk Scores (Terrestrial)		Movement Distances (Terrestrial)		
Species	Population	Group	Common Name	Scientific name	Road Risk: Species- Level	Road Risk: Population-Level	95% Population Movement Distance (m)	Confidence in Distance Estimate	Surrogate Used
Very High	Very High	Snake	San Joaquin Coachwhip	*Masticophis flagellum ruddocki*	689	285	1618	High	*M. fuliginosus*
	Very High	Snake	Alameda Striped Racer	*Masticophis lateralis euryxanthus*	652	221	631	Med/High	
	Very High	Tortoise	Mohave Desert Tortoise	*Gopherus agassizii*	580	240	1155	High	
	Very High	Salamander	Red-bellied Newt	*Taricha rivularis*	561	228	1600	High	
	Very High	Snake	Baja California Coachwhip	*Masticophis fuliginosus*	534	285	1904	High	
	Very High	Snake	Coast Patch-nosed Snake	*Salvadora hexalepis virgultea*	533	221	631	Low	*M. lateralis*
	Very High	Salamander	California Newt	*Taricha torosa*	532	228	2500	Med/High	
	Very High	Lizard	Banded Gila Monster	*Heloderma suspectum cinctum*	446	210	1250	High	
	High	Salamander	California Tiger Salamander	*Ambystoma californiense*	437	152	1849	Med/High	
	Very High	Salamander	Sierra Newt	*Taricha sierrae*	437	228	2050	Med	*T. torosa, T. rivularis*
	Very High	Snake	Striped Whipsnake	*Masticophis taeniatus*	425	300	2380	Med	
	Very High	Lizard	Flat-tail Horned Lizard	*Phrynosoma mcallii*	425	217	788	Med/High	
	High	Lizard	Blunt-nosed Leopard Lizard	*Gambelia sila*	393	133	510	High	
	Very High	Snake	Baja California Ratsnake	*Bogertophis rosaliae*	387	238	780	Low	*Elaphe obsoleta*
	Very High	Snake	Panamint Rattlesnake	*Crotalus stephensi*	387	238	938	Med	*C. mitchelli*
	High	Frog	California Red-legged Frog	*Rana draytonii*	380	152	2360	High	
	High	Toad	Yosemite Toad	*Anaxyrus canorus*	379	128	1152	Med/High	
	High	Toad	Black Toad	*Anaxyrus exsul*	379	128	951	Low	*A. canorus, A. punctatus*
	High	Lizard	Cope's Leopard Lizard	*Gambelia copeii*	372	175	643	Low/Med	*G. wislenzii*
	High	Toad	Sonoran Desert Toad	*Incilius alvarius (Possibly extinct in CA)*	361	152	1400	Low/Med	*A. cognatus*
	Very High	Lizard	Desert Horned Lizard	*Phrynosoma platyrhinos*	356	259	1308	Med/High	
	High	Snake	California Glossy Snake	*Arizona elegans occidentalis*	340	154	316	Low	*R. lecontii*
	Very High	Snake	North American Racer	*Coluber constrictor*	334	308	1800	Med	
	Very High	Snake	Coachwhip	*Masticophis flagellum*	333	285	1618	High	*M. fuliginosus*
	High	Toad	Arroyo Toad	*Anaxyrus californicus*	331	128	1082	Med/High	
	Very High	Snake	Striped Racer	*Masticophis lateralis*	322	221	631	Med	
High	High	Snake	Red Diamond Rattlesnake	*Crotalus ruber*	321	175	853	High	
	Very High	Snake	Speckled Rattlesnake	*Crotalus mitchellii*	317	238	938	High	
	Med	Salamander	Santa Cruz Long-toed Salamander	*Ambystoma macrodactylum croceum*	308	104	700	High	
	Very High	Salamander	Rough-skinned Newt	*Taricha granulosa*	304	228	2050	Med	*T. torosa, T. rivularis*
	High	Snake	Regal Ring-necked Snake	*Diadophis punctatus regalis*	298	152	566	Low/Med	
	Very High	Snake	California Lyresnake	*Trimorphodon lyrophanes*	293	195	800	Low	
	High	Frog	Northern Red-legged Frog	*Rana aurora*	291	152	2360	Med	*R. draytonii*
	High	Turtle	Southern Western Pond Turtle	*Actinemys pallida*	283	128	309	Med-High	
	High	Snake	Mojave Rattlesnake	*Crotalus scutulatus*	276	189	815	Med/High	
	Very High	Snake	Western Patch-nosed Snake	*Salvadora hexalepis*	276	221	631	Low	*M. lateralis*
	High	Snake	Sidewinder	*Crotalus cerastes*	263	186	767	High	
	Med	Salamander	California Giant Salamander	*Dicamptodon ensatus*	260	120	600	Low	*D. tenebrosus*
	Very High	Snake	Sonoran Lyresnake	*Trimorphodon lambda*	260	195	800	Low	
	Very High	Snake	Western Rattlesnake	*Crotalus oreganus*	250	231	1096	Med/High	
	High	Snake	Desert Nightsnake	*Hypsiglena chlorophaea*	241	175	566	Low	*D. punctatus*
	Med	Snake	San Francisco Gartersnake	*Thamnophis sirtalis tetrataenia*	238	81	300	Med	
	Med	Lizard	Switak's Banded Gecko	*Coleonyx switaki*	236	90	200	Low	*C. variegatus (AZ)*
	Med	Toad	Western Spadefoot	*Spea hammondii*	234	104	670	Med	
	High	Snake	Coast Nightsnake	*Hypsiglena ochrorhyncha*	233	175	566	Low	*D. punctatus*
	High	Lizard	Long-nosed Leopard Lizard	*Gambelia wislizenii*	226	175	643	Med/High	
	High	Toad	Great Plains Toad	*Anaxyrus cognatus*	222	152	1400	Med/High	
	High	Toad	Woodhouse's Toad	*Anaxyrus woodhousii*	222	152	1400	Low	*A. cognatus*
	Med	Lizard	Coastal Whiptail	*Aspidoscelis tigris stejnegeri*	219	105	300	Low	*A. hyperythra (multiplied by 2 for body size)*
	High	Turtle	Northern Western Pond Turtle	*Actinemys marmorata*	219	128	448	Med	
	High	Snake	Western Shovel-nosed Snake	*Chionactis occipitalis*	218	154	400	Low	
	High	Snake	Spotted Leaf-nosed Snake	*Phyllorhynchus decurtatus*	218	154	400	Low	*C. occipitalis, M. taeniatus*
	Med	Salamander	Southern Long-toed Salamander	*Ambystoma macrodactylum sigillatum*	217	104	700	Med	
	Med	Frog	Cascades Frog	*Rana cascadae*	217	104	759	High	
	High	Snake	Western Diamond-backed Rattlesnake	*Crotalus atrox*	214	147	484	Med	
	High	Snake	Western Groundsnake	*Sonora semiannulata*	212	154	400	Low	*C. occipitalis*
	Med	Snake	California Red-sided Gartersnake	*Thamnophis sirtalis infernalis*	211	81	300	Low/Med	*T.s. tetrataenia*

Table 9 continued



Risk Level (Terrestrial)		Species			Risk Scores (Terrestrial)		Movement Distances (Terrestrial)		
Species	Population	Group	Common Name	Scientific name	Road Risk: Species- Level	Road Risk: Population- Level	95% Population Movement Distance (m)	Confidence in Distance Estimate	Surrogate Used
Medium	Med	Lizard	Blainville's Horned Lizard	*Phrynosoma blainvillii*	209	114	495	Med	
	Med	Snake	Two-striped Gartersnake	*Thamnophis hammondii*	195	81	239	Low/Med	
	High	Snake	Gopher Snake	*Pituophis catenifer*	189	189	820	Med/High	
	High	Snake	California Mountain Kingsnake	*Lampropeltis zonata*	184	147	501	Low/Med	*L. getula, L. triangulum*
	High	Snake	Glossy Snake	*Arizona elegans*	180	154	316	Low	*R. lecontii*
	Med	Lizard	Pygmy Short-horned Lizard	*Phrynosoma douglasii*	179	123	400	Low	*P. mccallii (reduced 0.5 for body size)*
	Med	Toad	Couch's Spadefoot	*Scaphiopus couchii*	178	104	670	Med	
	High	Snake	California Kingsnake	*Lampropeltis californiae*	175	175	501	Med/High	
	High	Snake	Long-nosed Snake	*Rhinocheilus lecontei*	165	132	337	Low/Med	
	High	Snake	Common Gartersnake	*Thamnophis sirtalis*	165	137	532	Low/Med	
	High	Toad	Western Toad	*Anaxyrus boreas*	165	152	2144	Med/High	
	High	Snake	Ring-necked Snake	*Diadophis punctatus*	164	136	566	Low/Med	
	Med	Lizard	San Diego Banded Gecko	*Coleonyx variegatus abbotti*	158	84	200	Low/Med	*C. variegatus (AZ)*
	Med	Salamander	Northwestern Salamander	*Ambystoma gracile*	152	104	700	Low	*A. macrodactylum croceum*
	Med	Toad	Great Basin Spadefoot	*Spea intermontana*	152	104	670	Med	
	Med	Toad	Red-spotted Toad	*Anaxyrus punctatus*	147	104	750	Low	
	Med	Salamander	Long-toed Salamander	*Ambystoma macrodactylum*	143	104	700	Med	
	Med	Snake	Northwestern Gartersnake	*Thamnophis ordinoides*	138	95	239	Low	*T. hammondii*
	Med	Lizard	Orange-throated Whiptail	*Aspidoscelis hyperythra*	137	84	150	Low/Med	
	Med	Snake	Smith's Black-headed Snake	*Tantilla hobartsmithi*	136	105	150	Low	
	Med	Snake	California Black-headed Snake	*Tantilla planiceps*	133	84	150	Low	
	Med	Lizard	Western Whiptail	*Aspidoscelis tigris*	118	105	300	Low	*A. hyperythra (multiplied by 2 for body size)*
	Med	Salamander	Coastal Giant Salamander	*Dicamptodon tenebrosus*	117	80	600	Low/Med	
	Med	Lizard	Western Banded Gecko	*Coleonyx variegatus*	105	84	200	Low/Med	*C. variegatus (AZ)*
	Med	Lizard	Common Chuckwalla	*Sauromalus ater*	78	78	296	Med	
	Med	Snake	Northern Rubber Boa	*Charina bottae*	77	77	230	Low/Med	*L. trivirgata*
	Med	Snake	Southern Rubber Boa	*Charina umbratica*	77	77	230	Low/Med	*L. trivirgata*
	Med	Snake	Northern Three-lined Boa	*Lichanura orcutti*	77	77	230	Med/High	
	Med	Snake	Western Terrestrial Gartersnake	*Thamnophis elegans*	75	75	104	Low/Med	*T.gigas (-40% for size diff)*
	Med	Lizard	Desert Iguana	*Dipsosaurus dorsalis*	72	72	150	Low/Med	
	Med	Snake	Forest Sharp-tailed Snake	*Contia longicauda*	70	70	150	Low	
	Med	Snake	Common Sharp-tailed Snake	*Contia tenuis*	70	70	150	Low	
	Med	Snake	Checkered Gartersnake	*Thamnophis marcianus*	69	69	239	Low	*T. hammondii*
	Med	Frog	Pacific Treefrog	*Pseudacris regilla*	68	68	400	Low/Med	
Low	Low	Salamander	Scott Bar Salamander	*Plethodon asupak*	62	62	92	Low	*P. glutinosus*
	Low	Salamander	Dunn's Salamander	*Plethodon dunni*	62	62	92	Low	*P. glutinosus*
	Low	Salamander	Del Norte Salamander	*Plethodon elongatus*	62	62	92	Low	*P. glutinosus*
	Low	Salamander	Siskiyou Mountains Salamander	*Plethodon stormi*	62	62	92	Low	*P. glutinosus*
	Low	Frog	California Treefrog	*Pseudacris cadaverina*	61	61	50	Low/Med	
	Low	Salamander	Southern Torrent Salamander	*Rhyacotriton variegatus*	61	61	50	Low	*R. cascadae*
	Low	Lizard	Peninsula Leaf-toed Gecko	*Phyllodactylus nocticolus*	60	60	200	Low	*C. variegatus (AZ)*
	Low	Lizard	Northern Alligator Lizard	*Elgaria coerulea*	60	80	106	Med	
	Low	Frog	Coastal Tailed Frog	*Ascaphus truei*	59	59	150	Med/High	
	Low	Lizard	Common Side-blotched Lizard	*Uta stansburiana*	59	59	152	Med/High	
	Low	Lizard	Coachella Fringe-toed Lizard	*Uma inornata*	56	56	52	Med/High	
	Low	Lizard	Colorado Desert Fringe-toed Lizard	*Uma notata*	56	56	75	Med/High	
	Low	Lizard	Mohave Fringe-toed Lizard	*Uma scoparia*	56	56	64	Med	*U. notata, U. inornata*
	Low	Lizard	Zebra-tailed Lizard	*Callisaurus draconoides*	54	54	150	Med	
	Low	Salamander	Wandering Salamander	*Aneides vagrans*	53	53	39	Med/High	
	Low	Salamander	Slender Salamanders (20 species)	*Batrachoseps (genus)*	53	53	50	Low/Med	*B. pacificus*

Table 9 continued

Risk Level (Terrestrial)		Species			Risk Scores (Terrestrial)		Movement Distances (Terrestrial)		
Species	Population	Group	Common Name	Scientific name	Road Risk: Species- Level	Road Risk: Population-Level	95% Population Movement Distance (m)	Confidence in Distance Estimate	Surrogate Used
Very Low	Very Low	Salamander	Ensatina	*Ensatina eschscholtzii*	51	51	75	Med	
	Very Low	Salamander	Yellow-blotched Ensatina	*Ensatina eschscholtzii croceater*	51	51	75	Med	
	Very Low	Salamander	Large-blotched Ensatina	*Ensatina eschscholtzii klauberi*	51	51	75	Med	*E. eschscholtzii croceater*
	Very Low	Lizard	Southern Alligator Lizard	*Elgaria multicarinata*	51	51	106	Low/Med	*E. coerulea*
	Very Low	Lizard	Panamint Alligator Lizard	*Elgaria panamintina*	51	51	106	Low/Med	*E. coerulea*
	Very Low	Frog	Sierra Nevada Yellow-legged Frog	*Rana sierrae*	51	51	420	Med	
	Very Low	Lizard	Western Fence Lizard	*Sceloporus occidentalis*	49	49	160	Med	
	Very Low	Salamander	Limestone Salamander	*Hydromantes brunus*	48	48	80	Low	
	Very Low	Salamander	Mount Lyell Salamander	*Hydromantes platycephalus*	48	48	80	Low	
	Very Low	Salamander	Clouded Salamander	*Aneides ferreus*	44	44	39	Med	*A. vagrans*
	Very Low	Salamander	Arboreal Salamander	*Aneides lugubris*	44	44	39	Med	*A. vagrans*
	Very Low	Snake	Giant Gartersnake	*Thamnophis gigas*	44	44	174	High	
	Very Low	Snake	Sierra Gartersnake	*Thamnophis couchii*	44	44	115	Low/Med	*T.gigas (-34% for size diff)*
	Very Low	Lizard	Granite Spiny Lizard	*Sceloporus orcutti*	43	43	91	Low/Med	
	Very Low	Snake	Western Blind Snake	*Rena humilis*	42	42	50	Low	
	Very Low	Lizard	Desert Spiny Lizard	*Sceloporus magister*	41	41	91	Low	
	Very Low	Frog	Oregon Spotted Frog	*Rana pretiosa (Possibly extinct in CA)*	41	41	100	Low	
	Very Low	Lizard	Common Sagebrush Lizard	*Sceloporus graciosus*	41	41	41	Med/High	
	Very Low	Snake	Aquatic Gartersnake	*Thamnophis atratus*	40	40	99	Low/Med	*T.gigas (-43% for size diff)*
	Very Low	Lizard	Gilbert's Skink	*Plestiodon gilberti*	39	39	93	Low/Med	*P. skiltonianus, P. fasciatus, S. laterale*
	Very Low	Lizard	Western Skink	*Plestiodon skiltonianus*	39	39	93	Low/Med	
	Very Low	Lizard	California Legless Lizard	*Anniella pulchra*	39	39	15	High	
	Very Low	Turtle	Sonoran Mud Turtle	*Kinosternon sonoriense*	37	37	60	Med	
	Very Low	Salamander	Black Salamander	*Aneides flavipunctatus*	35	35	39	Med	*A. vagrans*
	Very Low	Salamander	Santa Cruz Black Salamander	*Aneides flavipunctatus niger*	35	35	39	Med	*A. vagrans*
	Very Low	Lizard	Great Basin Collared Lizard	*Crotaphytus bicinctores*	35	35	150	Low/Med	*C. collaris*
	Very Low	Lizard	Baja California Collared Lizard	*Crotaphytus vestigium*	35	35	150	Low/Med	*C. collaris*
	Very Low	Lizard	Sandstone Night Lizard	*Xantusia gracilis*	33	33	14	Med/High	*X. riversiana*
	Very Low	Lizard	Granite Night Lizard	*Xantusia henshawi*	33	33	14	Med/High	*X. riversiana*
	Very Low	Lizard	Island Night Lizard	*Xantusia riversiana*	33	33	14	High	
	Very Low	Lizard	Sierra Night Lizard	*Xantusia sierrae*	33	33	14	Med/High	*X. riversiana*
	Very Low	Lizard	Desert Night Lizard	*Xantusia vigilis*	33	33	14	Med/High	*X. riversiana*
	Very Low	Lizard	Wiggins' Night Lizard	*Xantusia wigginsi*	33	33	14	Med/High	*X. riversiana*
	Very Low	Frog	Lowland Leopard Frog	*Lithobates yavapaiensis (Possibly extinct in CA)*	31	31	100	Low	
	Very Low	Lizard	Long-tailed Brush Lizard	*Urosaurus graciosus*	27	27	130	Low/Med	*S. occidentalis, S. graciosus*
	Very Low	Lizard	Baja California Brush Lizard	*Urosaurus nigricaudus*	27	27	130	Low/Med	*S. occidentalis, S. graciosus*
	Very Low	Lizard	Ornate Tree Lizard	*Urosaurus ornatus*	27	27	130	Low/Med	*S. occidentalis, S. graciosus*
	Very Low	Frog	Foothill Yellow-legged Frog	*Rana boylii*	26	26	40	Med/High	
	Very Low	Frog	Southern Mountain Yellow-legged Frog	*Rana muscosa*	26	26	40	Med	*R. boylii*
	Very Low	Lizard	Mearns' Rock Lizard	*Petrosaurus mearnsi*	21	21	80	Low/Med	
	Very Low	Lizard	Mearns' Rock Lizard	*Petrosaurus mearnsi*	21	21	80	Low/Med	

over the surface during high flow events. These may be used as road crossings by species traveling along ephemeral stream corridors with or without water flow. Given these potential vulnerabilities, we believe that road impacts to aquatic connectivity of herpetofauna deserve greater consideration.

Across broad taxonomic groups, chelonids (tortoises/turtles) and snakes had the greatest percentages of species at 'high' or 'very high' risk from roads. They are similar in that many move long distances (home range and/or migratory), tend not to avoid roads (or are attracted to them for thermoregulation), are long lived, and have relatively low fecundity in comparison to other herpetofaunal groups. Because of these traits, chelonids and snakes have been identified elsewhere as being particularly susceptible to negative population effects from roads (Gibbs and Shriver 2002; Andrews et al. 2015b; Jackson et al. 2015).

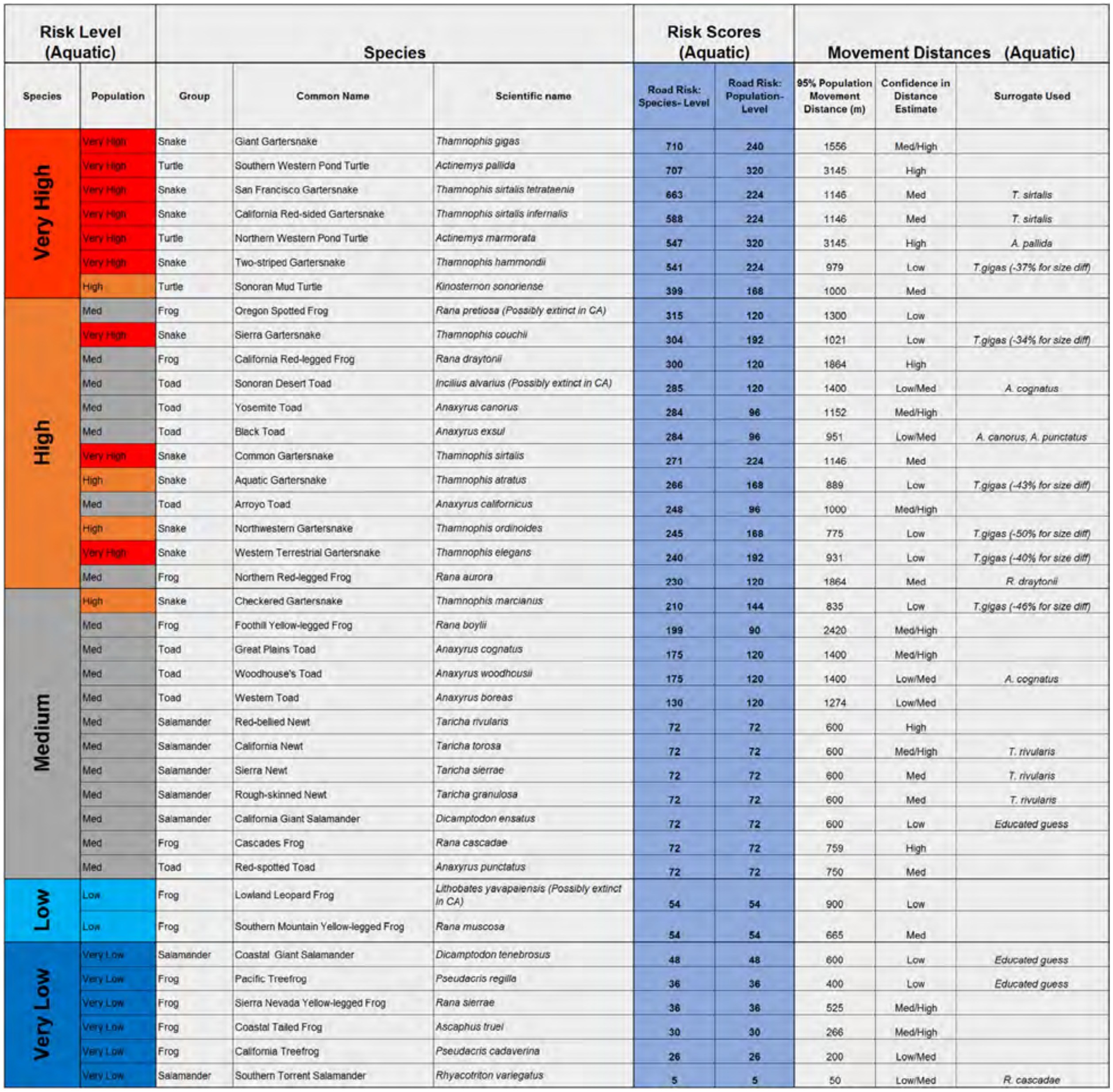
There are only four species of chelonids in California, (desert tortoise (*Gopherus agazzii*), Northwestern pond turtle (*Actinemys marmorata*), Southwestern pond turtle (*Actinemys pallida*), and the Sonoran mud turtle (*Kinosternon sonoriense*)). There has been a high level of attention to road impacts on the desert tortoise (*Gopherus agazzii*) as numerous studies have documented not only high road mortality, but measurable road effect zones, and mostly positive responses to barriers and underpasses (e.g., Boarman and Sazaki 1996, 2006; Peaden et al. 2016; but see Peadon et al. 2017). Although not listed as a primary threat to pond turtle populations in California (Thomson et al. 2016), road mortality is a major concern for western pond turtle populations in Oregon (Rosenberg et al. 2009). Pond turtles travel kilometers within perennial waters and from pool to pool in intermittent aquatic habitats to forage and find mates (Goodman and Stewart 2000). In addition, females nest and lay eggs in terrestrial habitats up to 0.5 km away from water which make roads that parallel aquatic habitat a threat to both females and hatchlings (Reese and Welsh 1997; Rathbun et al. 2002; Pilliod et al. 2013). In fact, road mortality of females has been identified as a cause for male-biased sex ratios in some populations of pond turtles and other freshwater turtle species (Steen et al. 2006; Rosenberg et al. 2009; Reid and Peery 2014). Therefore, this species requires consideration of both aquatic and terrestrial connectivity to satisfy their annual resource requirements. Sonoran mud turtles also travel long distances within intermittent streams and thus may be at risk of roads that transect their aquatic habitat (Hensley et al. 2010).

Larger colubrid snakes (Family Colubridae; many genera) and rattlesnakes (genus *Crotalus*) were ranked among the highest risk from negative road effects. In addition to being attracted to paved road surfaces for thermoregulation, many large snakes have wide home-ranges or may move large distances between winter hibernacula and summer foraging areas. In contrast to smaller species, larger snakes are also less likely to avoid roads (Rosen and Lowe 1994; Andrews and Gibbons 2005; Andrews et al. 2008; Siers et al. 2016). High road mortality (e.g., Klauber 1931; Rosen and Lowe 1994; Jones et al. 2011), reduced abundance near roads (Rudolph et al. 1999; Jones et al. 2011), increased extinction risk (Row et al. 2007), and decreased genetic diversity (Clark et al. 2010; Hermann et al. 2017) have been documented for numerous snake species; as have positive responses to barriers and underpasses (Dodd et al. 2004; Colley et al. 2017). In our statewide risk analysis, coachwhips (genus *Masticophis/Coluber*) were amongst the highest risk groups at both the population and species-levels. These are particularly wide-ranging and very active foragers in comparison to other snake genera (Stebbins and McGinnis 2012). The coachwhip (*Masticophis flagellum)* was found to be ninefold more likely to be extirpated from habitats that were fragmented by roads and urbanization, contributing to their decline throughout California (Case and Fisher 2001; Mitrovich 2006). Similarly, habitat fragmentation from roads and urbanization were identified as primary threats to the Alameda whipsnake (*Masticophis lateralis euryxanthus* USFWS 2011). Although road use and mortality have been documented for many other terrestrial California snake species on road-riding surveys (e.g., Klauber 1931; Jones et al. 2011; Shilling and Waetjen 2017), there is a paucity of studies examining population-level effects of roads on California snake species. We could find only one such study, where presence of a highway was shown to reduce gene flow in the Western diamond-backed rattlesnake (*Crotalus atrox)* in the Sonoran Desert, AZ (Hermann et al. 2017).

Long foraging movements within aquatic habitats also contributed to the majority of garter snakes (genus: *Thamnophis*) falling within the highest road risk categories. Maintaining aquatic and wetland connectivity is of primary concern for these species. Garter snakes also use terrestrial habitats for overwintering, reproduction, and for moving among wetland or aquatic patches. Some migrate long distances to winter hibernacula, making them also susceptible to roads within adjacent terrestrial habitats (Roe et al. 2006; Jackson et al. 2015). The highly aquatic giant garter snake (*Thamnophis gigas*) had the highest aquatic road risk score. Because it moves only short distances on land (Halstead et al. 2015), mitigation may best focus on functional aquatic passages with lengths of adjacent road barriers based upon their terrestrial movement distances.

Toads were the third highest ranking group with 64% ranked in the highest risk categories. In particular, Bufonid toads (family Bufonidae) may move large distances (> 1 km) in both aquatic and terrestrial habitats to satisfy their annual resource requirements; thus 5 of 7 bufonid species ranked high or very high risk from roads. Consistent with our risk assessment

Table 10 Aquatic risk ranking and population buffer distances



Risk Level (Aquatic)		Species			Risk Scores (Aquatic)		Movement Distances (Aquatic)		
Species	Population	Group	Common Name	Scientific name	Road Risk: Species- Level	Road Risk: Population- Level	95% Population Movement Distance (m)	Confidence in Distance Estimate	Surrogate Used
Very High	Very High	Snake	Giant Gartersnake	*Thamnophis gigas*	710	240	1556	Med/High	
	Very High	Turtle	Southern Western Pond Turtle	*Actinemys pallida*	707	320	3145	High	
	Very High	Snake	San Francisco Gartersnake	*Thamnophis sirtalis tetrataenia*	663	224	1146	Med	*T. sirtalis*
	Very High	Snake	California Red-sided Gartersnake	*Thamnophis sirtalis infernalis*	588	224	1146	Med	*T. sirtalis*
	Very High	Turtle	Northern Western Pond Turtle	*Actinemys marmorata*	547	320	3145	High	*A. pallida*
	Very High	Snake	Two-striped Gartersnake	*Thamnophis hammondii*	541	224	979	Low	*T.gigas (-37% for size diff)*
	High	Turtle	Sonoran Mud Turtle	*Kinosternon sonoriense*	399	168	1000	Med	
High	Med	Frog	Oregon Spotted Frog	*Rana pretiosa (Possibly extinct in CA)*	315	120	1300	Low	
	Very High	Snake	Sierra Gartersnake	*Thamnophis couchii*	304	192	1021	Low	*T.gigas (-34% for size diff)*
	Med	Frog	California Red-legged Frog	*Rana draytonii*	300	120	1864	High	
	Med	Toad	Sonoran Desert Toad	*Incilius alvarius (Possibly extinct in CA)*	285	120	1400	Low/Med	*A. cognatus*
	Med	Toad	Yosemite Toad	*Anaxyrus canorus*	284	96	1152	Med/High	
	Med	Toad	Black Toad	*Anaxyrus exsul*	284	96	951	Low/Med	*A. canorus, A. punctatus*
	Very High	Snake	Common Gartersnake	*Thamnophis sirtalis*	271	224	1146	Med	
	High	Snake	Aquatic Gartersnake	*Thamnophis atratus*	266	168	889	Low	*T.gigas (-43% for size diff)*
	Med	Toad	Arroyo Toad	*Anaxyrus californicus*	248	96	1000	Med/High	
	High	Snake	Northwestern Gartersnake	*Thamnophis ordinoides*	245	168	775	Low	*T.gigas (-50% for size diff)*
	Very High	Snake	Western Terrestrial Gartersnake	*Thamnophis elegans*	240	192	931	Low	*T.gigas (-40% for size diff)*
	Med	Frog	Northern Red-legged Frog	*Rana aurora*	230	120	1864	Med	*R. draytonii*
Medium	High	Snake	Checkered Gartersnake	*Thamnophis marcianus*	210	144	835	Low	*T.gigas (-46% for size diff)*
	Med	Frog	Foothill Yellow-legged Frog	*Rana boylii*	199	90	2420	Med/High	
	Med	Toad	Great Plains Toad	*Anaxyrus cognatus*	175	120	1400	Med/High	
	Med	Toad	Woodhouse's Toad	*Anaxyrus woodhousii*	175	120	1400	Low/Med	*A. cognatus*
	Med	Toad	Western Toad	*Anaxyrus boreas*	130	120	1274	Low/Med	
	Med	Salamander	Red-bellied Newt	*Taricha rivularis*	72	72	600	High	
	Med	Salamander	California Newt	*Taricha torosa*	72	72	600	Med/High	*T. rivularis*
	Med	Salamander	Sierra Newt	*Taricha sierrae*	72	72	600	Med	*T. rivularis*
	Med	Salamander	Rough-skinned Newt	*Taricha granulosa*	72	72	600	Med	*T. rivularis*
	Med	Salamander	California Giant Salamander	*Dicamptodon ensatus*	72	72	600	Low	*Educated guess*
	Med	Frog	Cascades Frog	*Rana cascadae*	72	72	759	High	
	Med	Toad	Red-spotted Toad	*Anaxyrus punctatus*	72	72	750	Med	
Low	Low	Frog	Lowland Leopard Frog	*Lithobates yavapaiensis (Possibly extinct in CA)*	54	54	900	Low	
	Low	Frog	Southern Mountain Yellow-legged Frog	*Rana muscosa*	54	54	665	Med	
Very Low	Very Low	Salamander	Coastal Giant Salamander	*Dicamptodon tenebrosus*	48	48	600	Low	*Educated guess*
	Very Low	Frog	Pacific Treefrog	*Pseudacris regilla*	36	36	400	Low	*Educated guess*
	Very Low	Frog	Sierra Nevada Yellow-legged Frog	*Rana sierrae*	36	36	525	Med/High	
	Very Low	Frog	Coastal Tailed Frog	*Ascaphus truei*	30	30	266	Med/High	
	Very Low	Frog	California Treefrog	*Pseudacris cadaverina*	26	26	200	Low/Med	
	Very Low	Salamander	Southern Torrent Salamander	*Rhyacotriton variegatus*	5	5	50	Low/Med	*R. cascadae*

results, there is evidence that bufonid toads are particularly susceptible to negative impacts from roads elsewhere (Trenham et al. 2003; Orłowski 2007; Eigenbrod et al. 2008).

Roads and traffic have been associated with reduced abundance and species richness of frog populations (e.g., Fahrig et al. 1995; Houlahan and Findlay 2003). However, approximately half of California species are small, primarily aquatic, highly fecund, with relatively limited movements and thus ranked low for road impacts. Four of 11 species ranked within the highest risk groupings; California red-legged frog (*Rana draytonii*), Oregon spotted frog (*R. pretiosa*), Northern red-legged frog (*R. aurora*), and Cascades frog (*R. cascadae*). The Oregon spotted frog (*R. pretiosa*) is known to move large distances within aquatic habitats (Bourque 2008; USFWS 2009). Construction of a highway that bisected the

Yellowstone population of Oregon spotted frogs was one important factor that reduced the population dramatically in the 1950s (see discussion in Watson et al. 2003). Although portions of the populations show high site fidelity, California red-legged frog and Northern red-legged frog migrants can move large distances (> 1 km) across both aquatic and terrestrial habitats (Bulger et al. 2003; Fellers and Kleeman 2007; Hayes et al. 2007). Road mortality or habitat fragmentation from roads and urbanization were listed as primary threats to these species elsewhere (USFWS 2002; COSEWIC 2015).

Lizards had relatively low percentages of species in the high risk groupings. Many lizard species are small, non-migratory, territorial, have small home ranges and are thus at low risk of negative road effects. Similar to snakes, lizards can also be attracted to road surfaces for thermoregulation. A few wide ranging species scored in the highest risk categories including the Gila monster (*Heloderma suspectum*), leopard lizards (genus *Gambelia*) and two horned lizard species (genus *Phrynosoma*). The Gila monster has been negatively associated with urbanization, where larger home ranges and greater movement rates result in higher mortality for males (Kwiatkowski et al. 2008). Sensitive to habitat fragmentation, the blunt-nosed leopard lizard (*Gambelia sila*) was found to be largely absent from habitat patches less than 250 ha (Bailey and Germano 2015). Flat-tailed horned lizards (*Phrynosoma mccallii*) are also susceptible to habitat fragmentation with very large home ranges for their size, particularly in wet years (Young and Young 2000). In fact, road mortality is a well-known threat for this species (see review by CDFW 2016b). Horned lizards are also particularly vulnerable to being killed on roads due to their tendency to flatten and remain motionless while being approached (Young and Young 2000).

Salamanders also had relatively low percentages of species in the high risk grouping. Over 75% (35/46) of the California salamanders are lungless salamanders (Plethodontidae) and Torrent salamanders (Rhyacotritonidae). These species are mostly small, sedentary, non-migratory, closed habitat specialists with limited movement distances and these traits have resulted in a high level of speciation. This is exemplified by there being at least 20 species of slender salamanders (genus *Batrachoseps*) in California alone (Martinez-Solano et al. 2007; Vences and Wake 2007). However, within the salamander group, newts and several other migratory salamander species were ranked within the highest risk categories from negative road effects. There is substantial evidence that habitat fragmentation and mortality due to roads negatively affect many of these species. For instance, newts regularly migrate long distances over land from and to breeding ponds, and to terrestrial foraging habitats (> 2 km; Trenham 1998). Large numbers are found dead on roads during dispersal periods and newt species are often the first to disappear in fragmented landscapes (Gibbs 1998; Trenham 1998, Shields pers. comm.). Similarly, road mortality and habitat fragmentation are primary threats to the California tiger salamander and other Ambystomid salamanders because terrestrial habitat is used for interpond migration and overwintering (Semlitsch 1998; Trenham et al. 2001; Bolster 2010).

Because this assessment covers a wide array of species and habitats, the risk to particular species populations must be re-assessed on a local level. This includes consideration of the locations, types, and densities of roads in relation to population and species ranges along with goals for functional, meta-population, and genetic connectivity (e.g., Marsh and Jaeger 2015). Due to very low road densities in their limited ranges, some species and populations may be at lower risk. For instance the Gila monster, Oregon spotted frog, Sonoran mud turtle, Sonoran desert toad (*Incilius alvarius*) and Yosemite toad (*Anaxyrus canorus*) scored high due to life history and space-use characteristics, however their limited ranges are largely in protected or low road density areas in the state. Thus roads may not be a significant threat to these species in California. In contrast, high road densities may increase the risk for species within coastal regions such as remaining populations of Santa Cruz long-toed salamander (*Ambystoma macrodactylum croceum*), Alameda striped racer (*Masticophis lateralis euryxanthus*), and San Francisco garter snake (*Thamnophis sirtalis tetrataenia*). However, most species consist of numerous populations with a myriad of differing road-related threat levels. Although detailed species ranges and occupancy within ranges are well known for some species with very limited ranges, for most species range-wide surveys have not been conducted. Therefore, only general range boundaries are available that encompass large portions of the state and availability of species distribution models of habitat suitability and occupancy within their ranges is rare. This lack of detailed spatial information on species distribution further limits the potential to incorporate road locations, types, and densities in a state and species-wide assessment.

We also note that relative risk to negative road impacts is provided for both populations and species. Risk was elevated for species with small and isolated ranges and that are facing a myriad of other threats. Because of this, a few common widespread species scored high at the population-level but not at the species-level. This included gopher snakes (*Pituophis catenifer*) and western toads (*Anaxyrus boreas*) where road mortality has been identified as a threat to the persistence of local populations (e.g., COSEWIC 2012; Jochimsen et al. 2014).

To potentially aid in local assessments, we have provided distance estimates or "buffer zones" that contain estimates for 95% of population-level movements for all species (e.g., Semlitsch and Bodie 2003). We provide all references evaluated for distance estimates in Appendix 2. Meta-population movements can be very important to the stability of pond-breeding amphibians (e.g., Semlitsch 2008; Jackson et al. 2015) and are included in many of the buffer zone calculations. However, we note that buffer zones may not include meta-population-level movements if the rate of these dispersal movements was less than 5% in the studies we used for our analyses.

This should be considered an initial assessment of susceptibility to negative road impacts in a hierarchical framework (e.g., see Level 2; Hobday et al. 2011). Therefore, as previously stated it will be important to re-assess the risk of specific populations to roads within their habitat and to evaluate and compare alternatives at the local scale (e.g., Suter 2016). This may include more detailed information on specific road attributes (e.g., density, type, location), as well as species behavior (Jaeger et al. 2005; Rouse et al. 2011; Rytwinski and Fahrig 2013; Jacobson et al. 2016). Age structured and spatially explicit population viability models are valuable tools to predict long-term population responses to roads and to compare outcomes of multiple mitigation scenarios (e.g., Gibbs and Shriver 2005; Borda-de-Água et al. 2014; Polak et al. 2014; Crawford 2015). Need and placement of mitigation structures can be guided by local population or meta-population dynamics, landscape attributes, movement routes, and road mortality hot spots (e.g., Bissonette and Adair 2008; Langen et al. 2009, 2015b; D'Amico et al. 2016; Loraamm and Downs 2016).

The quantity and quality of life history information, particularly movement data, are highly variable among species (see confidence levels; Tables 9 and 10). Therefore it is important to re-assess risk as new information becomes available. Finally, this is a structured assessment of comparative risk across a range of target species; therefore specific values for high risk have not been established. The ranking or assessment methodology should be adaptive and updated with advancements of road ecology science (e.g., Linkov et al. 2006).

Conclusion

Although roads are a significant cause of mortality and habitat fragmentation for many wildlife populations, road-related risk rankings have been based largely on expert opinion due to a scarcity of literature on road effects for most species. Therefore, we developed an objective and scientifically-based comparative risk approach to assess the potential threat from negative road impacts using species life history and movement data. After applying it to over 160 herpetofaunal species (and subspecies) in the state of California, the results are consistent with road ecology literature in identifying known high risk species, and call attention to some species not previously identified. Overall, we found that snakes and chelonids had the largest proportion of species at high risk for negative road impacts due to longer movement distances (home range and/or migratory), lack of road avoidance, and relatively low fecundity in comparison to other herpetofaunal groups. Results also indicated that consideration of aquatic connectivity appears to be under-represented for semi-aquatic herpetofauna that use both terrestrial and stream, riverine, or wetland habitats.

In addition to informing transportation planning and mitigation considerations for California herpetofauna, we believe this approach may be useful for comparing the risk of road-related fragmentation and mortality for species elsewhere and for other taxonomic groups. The results can help to inform multi-criteria threat assessments for special status species or those in consideration for listing. Finally, this serves to highlight species that may deserve further study and consideration for aquatic and terrestrial road mitigation to reduce mortality and to maintain population-level connectivity.

This risk assessment approach compares the susceptibility of species to negative road impacts. Commonly, there are numerous populations within a species range that occupy areas with greatly differing road pressures. Therefore, the actual risk to specific species populations will depend upon local road densities, road-types, traffic, and road locations in relation to species habitat and movement corridors.

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References

Andrews KM, Gibbons JW (2005) How do highways influence snake movement? Behavioral responses to roads and vehicles. Copeia 4:772–782

Andrews KM, Gibbons JW, Jochimsen D, Mitchell J (2008) Ecological effects of roads on amphibians and reptiles: a literature review. In: Mitchell JC, Jung Brown RE, Bartholomew B (eds) Urban Herpetology, Herpetological Conservation 3. Society for the Study of Reptiles and Amphibians, Salt-Lake City, UT, pp 121–143

Andrews KM, Nanjappa P, Riley SP (eds) (2015a) Roads and ecological infrastructure: concepts and applications for small animals. JHU Press, Baltimore, MD

Andrews KM, Langen TA, Struijk RPJH (2015b) Reptiles: Overlooked but often at risk from roads. Handbook of Road Ecology. Wiley, New York, pp 271–280

Bailey CV, Germano DJ (2015) Probability of occupancy of blunt-nosed leopard lizards on habitat patches of various sizes in the San Joaquin Desert of California. W Wild 2:23–28

Bissonette JA, Adair W (2008) Restoring habitat permeability to roaded landscapes with isometrically-scaled wildlife crossings. Biol Conserv 141(2):482–488

Boarman WI, Sazaki M (1996) Highway mortality in desert tortoises and small vertebrates: success of barrier fences and culverts (No. FHWA-PD-96-041)

Boarman WI, Sazaki M (2006) A highway's road-effect zone for desert tortoises (*Gopherus agassizii*). J Arid Environ 65(1):94–101

Bolster BC (2010) A status review of the California tiger salamander (*Ambystoma californiense).* Report to the Fish and Game Commission, State of California. Nongame Wildlife Program Report 2010–4

Bonnet X, Naulleau G, Shine R (1999) The dangers of leaving home: dispersal and mortality in snakes. Biol Conserv 89(1):39–50

Borda-de-Água L, Grilo C, Pereira HM (2014) Modeling the impact of road mortality on barn owl (*Tyto alba*) populations using age-structured models. Ecol Model 276:29–37

Bourque R (2008) [North Coast] spatial ecology of an inland population of the foothill yellow-legged frog (*Rana boylii*) in Tehama County, California. Masters Thesis, California State University, Humboldt, pp 107

Brehme CS, Tracey JA, McClenaghan LR, Fisher RN (2013) Permeability of roads to movement of scrubland lizards and small mammals. Conserv Biol 27(4):710–720

Bulger JB, Scott NJ, Seymour RB (2003) Terrestrial activity and conservation of adult California red-legged frogs *Rana aurora draytonii* in coastal forests and grasslands. Biol Conserv 110(1):85–95

California Department of Fish and Wildlife (CDFW) (2016a) Threatened and endangered species. http://www.dfg.ca.gov/wildlife/nongame/t_e_spp/ (accessed August 2016)

California Department of Fish and Wildlife (CDFW) (2016b) A status review of the flat-tailed horned lizard (*Phrynosoma mcallii*) in California. Report to the Fish and Game Commission

Carr LW, Fahrig L (2001) Effect of road traffic on two amphibian species of differing vagility. Conserv Biol 15(4):1071–1078

Case TJ, Fisher RN (2001) Measuring and predicting species presence: coastal sage scrub case study. In: Hunsaker CT, Goodchild MF, Friedl MA, Case TJ (eds) Spatial uncertainty in ecology. Springer-Verlag, New York, pp 47–71

Clark RW, Brown WS, Stechert R, Zamudio KR (2010) Roads, interrupted dispersal, and genetic diversity in timber rattlesnakes. Conserv Biol 24(4):1059–1069

Clarkin K, Conner A, Furniss MJ, Gibernick B, Love M, Moynan K, Wilson S (2005) National inventory and assessment procedure for identifying barriers to aquatic organism passage at road-stream crossings. US Dep Agric for Serv. http://www.stream.fs.fed.us/publications/PDFs/NIAP.pdf

Colino-Rabanal VJ, Lizana M (2012) Herpetofauna and roads: a review. Basic Appl Herpetol 26:5–31

Colley M, Lougheed SC, Otterbein K, Litzgus JD (2017) Mitigation reduces road mortality of a threatened rattlesnake. Wildlife Res. https://doi.org/10.1071/WR16130

Congress US (1973) Endangered species act. US Code 16:1534–1544

COSEWIC (Committee on the Status of Endangered Wildlife in Canada) (2012) COSEWIC assessment and status report on the Western Toad *Anaxyrus boreas* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xiv + 71 pp. (www.registrelep-sararegistry.gc.ca/default_e.cfm)

COSEWIC (Committee on the Status of Endangered Wildlife in Canada) (2015) COSEWIC assessment and status report on the Northern Red-legged Frog *Rana aurora* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. xii + 69 pp. (www.registrelep-sararegistry.gc.ca/default_e.cfm)

Crawford BA (2015) Lessons from terrapin mortality and management on the Jekyll Island Causeway, Georgia, USA. In: Andrews KM, Nanjappa P, Riley SPD (eds) Roads and ecological infrastructure. Concepts and applications for small animals. Johns Hopkins University Press, Baltimore, pp 21–41

D'Amico M, Román J, De los Reyes L, Revilla E (2015) Vertebrate road-kill patterns in Mediterranean habitats: who, when and where. Biol Conserv 191:234–242

D'Amico M, Périquet S, Román J, Revilla E (2016) Road avoidance responses determine the impact of heterogeneous road networks at a regional scale. J Appl Ecol 53(1):181–190

Dodd CK, Barichivich WJ, Smith LL (2004) Effectiveness of a barrier wall and culverts in reducing wildlife mortality on a heavily traveled highway in Florida. Biol Conserv 118(5):619–631

Eigenbrod F, Hecnar SJ, Fahrig L (2008) The relative effects of road traffic and forest cover on anuran populations. Biol Conserv 141(1):35–46

Evelyn CJ, Sweet SS (2012) Conservation status of amphibians and reptiles on USDA National Forests, Pacific Southwest Region, 2012. Prepared for: USDA National Forest Service, Region 5, Pacific Southwest Region

Fahrig L, Rytwinski T (2009) Effects of roads on animal abundance: an empirical review and synthesis. Ecol Soc 14. http://www.ecologyandsociety.org/vol14/iss11/art21

Fahrig L, Pedlar JH, Pope SE, Taylor PD, Wegner JF (1995) Effect of road traffic on amphibian density. Biol Conserv 73(3):177–182

Fellers GM, Kleeman PM (2007) California red-legged frog (*Rana draytonii*) movement and habitat use: implications for conservation. J Herpetol 41(2):276–286

Forman RT, Sperling D, Bissonette JA, Clevenger AP, Cutshall CD, Dale VH, Fahrig L, France R, Goldman CR, Heanue K, Jones JA (2003) Road ecology. Science and Solutions. Island Press, Washington

Furniss MJ, Roelofs TD, Yee CS (1991) Road construction and maintenance. Am Fish Soc Special Publ 19:297–323

Gibbs JP (1998) Amphibian movements in response to forest edges, roads, and streambeds in southern New England. J Wildl Manage 62:584–589

Gibbs JP, Shriver WG (2002) Estimating the effects of road mortality on turtle populations. Conserv Biol 16(6):1647–1652

Gibbs JP, Shriver WG (2005) Can road mortality limit populations of pool-breeding amphibians? Wetl Ecol Manag 13:281–289

Glista DJ, DeVault TL, DeWoody JA (2008) Vertebrate road mortality predominantly impacts amphibians. Herpetol Conserv Biol 3(1):77–87

Goodman RH, Stewart GR (2000) Aquatic home ranges of female Western Pond Turtles, *Clemmys marmorata*, at two sites in Southern California. Chelonian Conserv Biol 3(4):743–744

Gregory PT (1984) Communal denning in snakes. In: Seigel RA, Hunt LE, Knight JL, Maralet LA, Zuschlag NL (eds) Contributions to vertebrate ecology and systematics: a tribute to Henry S. Fitch. University of Kansas Museum of Natural History Special Publication 10:57–75

Halstead BJ, Skalos SM, Wylie GD, Casazza ML (2015) Terrestrial ecology of semi-aquatic giant gartersnakes (*Thamnophis gigas*). Herpetol Conserv Bio 10(2):633–644

Hayes MP, Rombough CJ, Hayes CB (2007) Natural History: *Rana aurora* (Northern red-legged frog) movement. Herpetol Rev 38:192–193

Hensley FR, Jones TR, Maxwell MS, Adams LJ, Nedella NS (2010) Demography, terrestrial behavior, and growth of Sonora mud turtles (*Kinosternon sonoriense*) in an extreme habitat. Herpetol Monogr 24:174–193

Hermann HW, Pozarowski KM, Ochoa A, Schuett GW (2017) An interstate highway affects gene flow in a top reptilian predator (*Crotalus atrox*) of the Sonoran Desert. Conserv Genet 18:911–924

Hickman JC (ed) (1993) The Jepson manual of higher plants of California. University of California Press, Berkeley

Hobday AJ, Smith ADM, Stobutzki IC, Bulman C, Daley R, Dambacher JM, Deng RA, Dowdney J, Fuller M, Furlani D, Griffiths SP (2011) Ecological risk assessment for the effects of fishing. Fish Res 108(2):372–384

Houlahan JE, Findlay CS (2003) The effects of adjacent land use on wetland amphibian species richness and community composition. Can J Fish Aquat Sci 60:1078–1094

Hozo SP, Djulbegovic B, Hozo I (2005) Estimating the mean and variance from the median, range, and the size of a sample. BMC Med Res Methodol 5(1):1

IUCN (2017) The IUCN Red List of Threatened Species. Version 2017-1. http://www.iucnredlist.org

Jackson ND, Fahrig L (2011) Relative effects of road mortality and decreased connectivity on population genetic diversity. Biol Conserv 144(12):3143–3148

Jackson SD, Langen TA, Marsh DM, Andrews KM (2015) Natural history and physiological characteristics of small animals in relation to roads. In: Andrews KM, Nanjappa P, Riley SPD (eds) Roads and ecological infrastructure. Concepts and applications for small animals. Johns Hopkins University Press, Baltimore, pp 21–41

Jacobson SL, Bliss-Ketchum LL, Rivera CE, Smith WP (2016) A behavior-based framework for assessing barrier effects to wildlife from vehicle traffic volume. Ecosphere 7(4):e01345

Jaeger JA (2000) Landscape division, splitting index, and effective mesh size: new measures of landscape fragmentation. Land Ecol 15(2):115–130

Jaeger JA, Bowman J, Brennan J, Fahrig L, Bert D, Bouchard J, Charbonneau N, Frank K, Gruber B, von Toschanowitz KT (2005) Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. Ecol Model 185(2):329–348

Januchowski-Hartley SR, McIntyre PB, Diebel M, Doran PJ, Infante DM, Joseph C, Allan JD (2013) Restoring aquatic ecosystem connectivity requires expanding inventories of both dams and road crossings. Front Ecol Environ 11(4):211–217

Jochimsen DM, Peterson CR, Andrews KM, Gibbons JW, Drawer E (2004) A literature review of the effects of roads on amphibians and reptiles and the measures used to minimize those effects. USDA Forest Service, Idaho Fish and Game Department, Washington, DC

Jochimsen DM, Peterson CR, Harmon LJ (2014) Influence of ecology and landscape on snake road mortality in a sagebrush-steppe ecosystem. Anim Conserv 17(6):583–592

Jones TR, Babb RD, Hensley FR, LiWanPo C, Sullivan BK (2011) Sonoran Desert snake communities at two sites: concordance and effects of increased road traffic. Herpetol Conserv Biol 6(1):61–71

Kemp PS, O'hanley JR (2010) Procedures for evaluating and prioritising the removal of fish passage barriers: a synthesis. Fish Manag Ecol 17(4):297–322

Klauber LM (1931) A statistical survey of the snakes of the southern border of California. Bull Zool Soc San Diego 8:1–93

Kwiatkowski MA, Schuett GW, Repp RA, Nowak EM, Sullivan BK (2008) Does urbanization influence the spatial ecology of Gila monsters in the Sonoran Desert? J Zool 276(4):350–357

Langen TA, Ogden KM, Schwarting LL (2009) Predicting hot spots of herpetofauna road mortality along highway networks. J Wildl Manag 73(1):104–114

Langen TA, Andrews KM, Brady SP, Karraker NE, Smith DJ (2015a) Road effects on habitat quality for small animals. In: Andrews KM, Nanjappa P, Riley SPD (eds) Roads and ecological infrastructure. Concepts and applications for small animals. Johns Hopkins University Press, Baltimore, pp 21–41

Langen TA, Gunson KE, Jackson SD, Smith DJ, Ruediger W (2015b) Planning and designing mitigation of road effects on small animals. In: Andrews KM, Nanjappa P, Riley SPD (eds) Roads and ecological infrastructure. Concepts and applications for small animals. Johns Hopkins University Press, Baltimore, pp 146–177

Langton TES (2015) A history of small animal road ecology. Roads and ecological infrastructure. Concepts and applications for small animals. Johns Hopkins University Press, Baltimore, pp 21–41

Lannoo MJ (2005) Amphibian declines: the conservation status of United States species. University of California Press, Berkeley

Levine KK (2013) California amphibian and reptile crossing preliminary investigation. Report to Caltrans Division of Environmental Planning

Linkov I, Satterstrom FK, Kiker G, Batchelor C, Bridges T, Ferguson E (2006) From comparative risk assessment to multi-criteria decision analysis and adaptive management: recent developments and applications. Environ Int 32(8):1072–1093

Litvaitis JA, Tash JP (2008) An approach toward understanding wildlife-vehicle collisions. Environ Manag 42(4):688–697

Loraamm RW, Downs JA (2016) A wildlife movement approach to optimally locate wildlife crossing structures. Int J Geogr Inf Sci 30(1):74–88

Mace GM, Collar NJ, Gaston KJ, Hilton-Taylor C, Akçakaya HR, Leader-Williams N, Milner-Gulland EJ, Stuart SN (2008) Quantification of extinction risk: IUCN's system for classifying threatened species. Conserv Biol 22(6):1424–1442

Marsh DM, Jaeger JAG (2015) Direct effects of roads on small animal populations. Roads and ecological infrastructure. Concepts and applications for small animals. Johns Hopkins University Press, Baltimore, pp 21–41

Martinez-Solano I, Jockusch EL, Wake DB (2007) Extreme population subdivision throughout a continuous range: phylogeography of *Batrachoseps attenuatus* (Caudata: Plethodontidae) in western North America. Mol Ecol 16(20):4335–4355

Mazerolle MJ, Huot M, Gravel M (2005) Behavior of amphibians on the road in response to car traffic. Herpetologica 61(4):380–388

Mccardle LD, Fontenot CL (2016) The influence of thermal biology on road mortality risk in snakes. J Thermal Biol 56:39–49

Mitrovich MJ (2006) A case study in conservation science: The spatial ecology and evolutionary history of the coachwhip snake (*Masticophis flagellum*) and striped racer (*M. lateralis*). Ph.D. dissertation. University of California, Davis, and San Diego State University. San Diego

Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403(6772):853–858

NatureServe (2017) NatureServe explorer: An online encyclopedia of life [web application]. Version 7.1. NatureServe, Arlington, Virginia. http://explorer.natureserve.org. (Accessed: May 25, 2017)

Orłowski G (2007) Spatial distribution and seasonal pattern in road mortality of the common toad *Bufo bufo* in an agricultural landscape of south-western Poland. Amphibia-Reptilia 28(1):25–31

Peaden JM, Tuberville TD, Buhlmann KA, Nafus MG, Todd BD (2016) Delimiting road-effect zones for threatened species: implications for mitigation fencing. Wildl Res 42(8):650–659

Peaden JM, Nowakowski AJ, Tuberville TD, Buhlmann KA, Todd BD (2017) Effects of roads and roadside fencing on movements, space use, and carapace temperatures of a threatened tortoise. Biol Conserv 214:13–22

Pianka ER (1966) Convexity, desert lizards, and spatial heterogeneity. Ecology 47(6):1055–1059

Pilliod DS, Welty JL, Stafford R (2013) Terrestrial movement patterns of western pond turtles (*Actinemys marmorata*) in central California. Herpetol Conserv Bio 8(1):207–221

Polak T, Rhodes JR, Jones D, Possingham HP (2014) Optimal planning for mitigating the impacts of roads on wildlife. J Appl Ecol 51(3):726–734

Rathbun GB, Scott NJ Jr, Murphey TG (2002) Terrestrial habitat use by Pacific pond turtles in a Mediterranean climate. Southwest Nat 47(2):225–235

Reese DA, Welsh HH (1997) Use of terrestrial habitat by western pond turtles, *Clemmys marmorata*: implications for management. In Proceedings: Conservation, restoration, and management of tortoises and turtles–an international conference. State University of New York, Purchase, New York, pp 352–357)

Reid BN, Peery MZ (2014) Land use patterns skew sex ratios, decrease genetic diversity and trump the effects of recent climate change in an endangered turtle. Divers Distrib 20(12):1425–1437

Roe JH, Gibson J, Kingsbury BA (2006) Beyond the wetland border: estimating the impact of roads for two species of water snakes. Biol Conserv 130(2):161–168

Rosen PC, Lowe CH (1994) Highway mortality of snakes in the Sonoran Desert of southern Arizona. Biol Conserv 68(2):143–148

Rosenberg D, Gervais J, Vesely D, Barnes S, Holts L, Horn R, Swift R, Todd L, Yee C (2009) Conservation assessment of the Western pond turtle in Oregon (*Actinemys marmorata*). USDI Bureau of Land Management and Fish and Wildlife Service, USDA Forest Service Region 6, Oregon

Rouse JD, Willson RJ, Black R, Brooks RJ (2011) Movement and spatial dispersion of *Sistrurus catenatus* and *Heterodon platirhinos*: implications for interactions with roads. Copeia 3:443–456

Row JR, Blouin-Demers G, Weatherhead PJ (2007) Demographic effects of road mortality in black ratsnakes (*Elaphe obsoleta*). Biol Conserv 137(1):117–124

Rudolph DC, Burgdorf SJ, Conner RN, Schaefer RR (1999) Preliminary evaluation of the impact of roads and associated vehicular traffic on snake populations in eastern Texas. In: Proceedings of the Third International Conference on Wildlife Ecology and Transportation. FL-ER-73-99. Evink GL, Garrett P, Zeigler D (eds) Florida Department of Transportation, Tallahassee, Florida, pp 129–136

Rytwinski T, Fahrig L (2012) Do species life history traits explain population responses to roads? A meta-analysis. Biol Conserv 147(1):87–98

Rytwinski T, Fahrig L (2013) Why are some animal populations unaffected or positively affected by roads? Oecologia 173(3):1143–1156

Rytwinski T, Fahrig L (2015) The impacts of roads and traffic on terrestrial animal populations. Handbook of Road Ecology. Wiley, New York, pp 237–246

Semlitsch RD (1998) Biological delineation of terrestrial buffer zones for pond-breeding salamanders. Conserv Biol 12(5):1113–1119

Semlitsch RD (2008) Differentiating migration and dispersal processes for pond-breeding amphibians. J Wildl Manag 72(1):260–267

Semlitsch RD, Bodie JR (2003) Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conserv Biol 17(5):1219–1228

Shilling F, Waetjen D (2017) California Roadkill Observation System. UC Davis Road Ecology Center. http://wildlifecrossing.net/california(accessed April 2017)

Siers SR, Reed RN, Savidge JA (2016) To cross or not to cross: modeling wildlife road crossings as a binary response variable with contextual predictors. Ecosphere 7(5):19

Stebbins RC, McGinnis SM (2012) Field guide to amphibians and reptiles of California, vol 103. University of California Press, Berkeley

Steen DA, Aresco MJ, Beilke SG, Compton BW, Condon EP, Dodd KC, Forrester H, Gibbons JW, Greene JL, Johnson G, Langen TA (2006) Relative vulnerability of female turtles to road mortality. Anim Conserv 9(3):269–273

Sullivan BK (2012) Road riding. In: McDiarmid RW (ed) Reptile biodiversity: standard methods for inventory and monitoring. University of California Press, Oakland, CA, pp 215–218

Suter GW II (2016) Ecological risk assessment. CRC Press, Boca Raton, FL

Thomson RC, Wright AN, Shaffer HB (2016) California amphibian and reptile species of special concern. University of California Press, Oakland, CA

Trenham PC (1998) Demography, migration, and metapopulation structure of pond-breeding salamanders. Ph.D. dissertation. University of California, Davis

Trenham PC, Koenig WD, Shaffer HB (2001) Spatially autocorrelated demography and interpond dispersal in the salamander *Ambystoma californiense*. Ecology 82(12):3519–3530

Trenham PC, Koenig WD, Mossman MJ, Stark SL, Jagger LA (2003) Regional dynamics of wetland-breeding frogs and toads: turnover and synchrony. Ecol Appl 13(6):1522–1532

US Fish and Wildlife (USFWS) (2016) United States species: Endangered and threatened wildlife (50 CFR 17.11). https://www.fws.gov/endangered/species/us-species.html (accessed August 2016)

US Fish and Wildlife Service (USFWS) (2002) Recovery plan for the California red-legged frog (*Rana aurora draytonii*). US Fish and Wildlife Service, Portland, Oregon, viii + 173 pp

US Fish and Wildlife Service (USFWS) (2009) *Rana pretiosa.* Species assessment and listing priority assignment form. USFWS Region 1, Portland

US Fish and Wildlife Service (USFWS) (2011) Alameda whipsnake (*Masticophis lateralis euryxanthus*) 5-year review summary and evaluation. US Fish and Wildlife Service, Sacramento, CA

van der Ree R, Smith DJ, Grilo C (2015) Handbook of road ecology. Wiley, New York

Vangel MG (2015) Tolerance interval. Statistics Reference Online. Wiley StatsRef, New York, pp 1–7

Vences M, Wake DB (2007) Speciation, species boundaries and phylogeography of amphibians. Amphib Biol 7:2613–2671

Watson JW, McAllister KR, Pierce DJ (2003) Home ranges, movements, and habitat selection of Oregon Spotted Frogs (*Rana pretiosa*). J Herp 37(2):292–300

Young KV, Young AT (2000) Final report: scientific study of the flat-tailed horned lizard, *Phrynosoma mcallii*. US Dept. of Navy Contracts N68711-95-LT-C0032, N68711-95-LT-C0035. 72 pp

Zimmermann Teixeira F, Kindel A, Hartz S, Mitchell S, Fahrig L (2017) When road-kill hotspots do not indicate the best sites for road-kill mitigation. J Appl Ecol 54(5):1544–1551

Chapter 3. Spatial Mapping - California Essential Habitat Connectivity Lands, Highways, and High-Risk Species

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Introduction

The California Department of Transportation (Caltrans) and California Department of Fish and Wildlife (CDFW) commissioned the California Essential Habitat Connectivity (CEHC) Project because a functional network of connected wildlands is essential to the continued support of California's diverse natural communities in the face of human development and climate change. This report is also intended to make transportation and land-use planning more efficient and less costly, while helping reduce dangerous wildlife-vehicle collisions (Spencer et al. 2010).

The statewide essential connectivity network consists of 850 relatively intact and well conserved Natural Landscape Blocks (ranging from 2,000 to about 3.7 million acres each) with over 1,000 potential connections among them. The 192 Essential Connectivity Areas represent principle connections between the Natural Landscape Blocks within which land conservation and management actions should be prioritized to maintain and enhance ecological connectivity (Spencer et al. 2010).

CEHC maps and spatial layers depict large, relatively natural habitat blocks that support native biodiversity and areas considered essential for regional large-scale connectivity. To better represent natural areas not included in the large-scale CEHC map but large enough to support sensitive amphibian and reptile populations in California, we also incorporated smaller natural areas between 25 to 2000 acres (10 to 809 ha) that were included in the CEHC map database for regional and local scale analyses. We then combined these into a spatial geodatabase to crosswalk the CEHC Map, State Highways, and the California amphibian and reptile road risk assessment (Brehme et al. 2018).

The spatial geodatabase includes:

1. CEHC natural habitat blocks greater than 10 ha (25 ac).
2. Range maps of high and very-high risk amphibian and reptile species.
3. California highway segments that intersect the ranges of high and very high-risk amphibian and reptile species.
4. California highway segments that intersect the ranges of high and very high-risk amphibian and reptile species and CEHC lands.
5. Postmile markers of all California highway segments that intersect the ranges of high and very high-risk amphibian and reptile species and CEHC lands.
6. The total number of high and very-high risk species ranges that intersect the highway segments and CEHC lands.

This geodatabase was designed to be a useful planning tool for Caltrans to quickly identify road segments that may warrant planning for increased connectivity of high-risk amphibian and reptile species.

Methods

The GIS analyses were conducted using ArcGIS 10.5.1 software. Species range and highway layers were obtained from Caltrans and CDFW.

Species Range Layers

Species ranges were obtained from the ARSSC_DFG_HerpRoadRiskRanges shapefile provided by Dr. Amber Wright (University of Hawaii), co-author of the California amphibian and reptile species of special concern (Thomson et al. 2016), and the California Wildlife Habitat Relationships (CWHR) GIS database (downloaded from the CDFW, *https://wildlife.ca.gov/Conservation/Planning/Data-and-Tools* on June 16, 2016). Updated range layers for 4 species were provided by email from CDFW in April 2020. All species range layers were merged into a single feature class, ARSSC_DFG_CWHR_SppRoadRiskRanges (CWHR). Table 1 lists the species that were included and the source of the GIS layers.

Table 1. List of High and Very-High Risk Species and GIS Source.

Scientific Name	**Common Name**	**Cons. Status**[a]	**Species Group**	**GIS Source**
Actinemys marmorata	Northern Western Pond Turtle	ARSSC 3	Turtle	ARSSC (2016)
Actinemys pallida	Southern Western Pond Turtle	ARSSC 1	Turtle	CWHR (2020)
Ambystoma californiense[1]	California Tiger Salamander	THR^{F,S}, END^{F}	Salamander	ARSSC (2016)
Ambystoma macrodactylum croceum	Santa Cruz Long-toed Salamander	END^{F,S}	Salamander	ARSSC (2016)
Ambystoma macrodactylum sigillatum	Southern Long-toed Salamander	ARSSC 2	Salamander	CWHR (2020)
Anaxyrus californicus	Arroyo Toad	END^{F},ARSSC 1	Toad	ARSSC (2016)
Anaxyrus canorus	Yosemite Toad	THR^{F},ARSSC 1	Toad	ARSSC (2016)
Anaxyrus cognatus	Great Plains Toad		Toad	ARSSC (2016)
Anaxyrus exsul	Black Toad	THR^{S}	Toad	ARSSC (2016)
Anaxyrus woodhousii	Woodhouse's Toad		Toad	CWHR (2016)
Arizona elegans occidentalis	California Glossy Snake	ARSSC 1	Snake-Terrestrial	ARSSC (2016)
Aspidoscelis tigris stejnegeri[2]	San Diegan Tiger Whiptail	ARSSC 2	Lizard	CWHR (2016)
Coleonyx switaki	Switak's Banded Gecko	THR^{S}	Lizard	CWHR (2016)
Coluber constrictor	North American racer		Snake-Terrestrial	ARSSC (2016)
Crotalus atrox	Western Diamond-backed Rattlesnake		Snake-Terrestrial	ARSSC (2016)
Crotalus cerastes	Sidewinder		Snake-Terrestrial	CWHR (2016)
Crotalus mitchellii	Speckled Rattlesnake		Snake-Terrestrial	ARSSC (2016)
Crotalus oreganus	Western Rattlesnake		Snake-Terrestrial	ARSSC (2016)
Crotalus ruber	Red Diamond Rattlesnake	ARSSC 3	Snake-Terrestrial	ARSSC (2016)
Crotalus scutulatus	Mojave Rattlesnake		Snake-Terrestrial	CWHR (2016)
Crotalus stephensi	Panamint Rattlesnake		Snake-Terrestrial	ARSSC (2016)
Diadophis punctatus regalis	Regal ring-necked Snake	ARSSC 2	Snake-Terrestrial	ARSSC (2016)
Dicamptodon ensatus	California Giant Salamander	ARSSC 3	Salamander	ARSSC (2016)
Gambelia copeii	Cope's Leopard Lizard	ARSSC	Lizard	ARSSC (2016)
Gambelia sila	Blunt-nosed Leopard Lizard	END^{F}	Lizard	ARSSC (2016)
Gambelia wislizenii	Long-nosed Leopard Lizard		Lizard	CWHR (2016)
Gopherus agassizii	Mohave Desert tortoise	THR^{F,S}	Tortoise	ARSSC (2016)

Scientific Name	**Common Name**	**Cons. Status**[a]	**Species Group**	**GIS Source**
Heloderma suspectum cinctum	Banded Gila Monster	ARSSC	Lizard	ARSSC (2016)
Hypsiglena chlorophaea	Desert Nightsnake		Snake-Terrestrial	CWHR (2016)
Hypsiglena ochrorhyncha	Nightsnake		Snake-Terrestrial	ARSSC (2016)
Incilius alvarius	Sonoran Desert Toad	ARSSC 1	Toad	ARSSC (2016)
Kinosternon sonoriense[3]	Sonora Mud turtle	ARSSC 1	Turtle	ARSSC (2016)
Phyllorhynchus decurtatus	Spotted Leaf-nosed Snake	ARSSC 2	Snake-Terrestrial	CWHR (2016)
Masticophis flagellum	Coachwhip		Snake-Terrestrial	ARSSC (2016)
Masticophis flagellum ruddocki	San Joaquin Coachwhip	ARSSC 2	Snake-Terrestrial	ARSSC (2016)
Masticophis fuliginosus	Baja California Coachwhip	ARSSC 3	Snake-Terrestrial	ARSSC (2016)
Masticophis lateralis	Striped Racer		Snake-Terrestrial	ARSSC (2016)
Masticophis lateralis euryxanthus	Alameda Striped Racer	THR^{F,S}	Snake-Terrestrial	CWHR (2020)
Masticophis taeniatus	Striped Whipsnake		Snake-Terrestrial	ARSSC (2016)
Phrynosoma mcallii	Flat-tailed Horned Lizard	THR^{F}, ARSSC 2	Lizard	ARSSC (2016)
Phrynosoma platyrhinos	Desert Horned Lizard		Lizard	ARSSC (2016)
Rana aurora	Northern Red-legged Frog	ARSSC 2	Frog	ARSSC (2016)
Rana cascadae	Cascades Frog	ARSSC 2	Frog	CWHR (2016)
Rana draytonii	California Red-legged Frog	THR^{F}, ARSSC 1	Frog	ARSSC (2016)
Rana pretiosa	Oregon Spotted Frog	THR^{F}, ARSSC 1	Frog	ARSSC (2016)
Salvadora hexalepis	Western Patch-nosed Snake		Snake-Terrestrial	ARSSC (2016)
Salvadora hexalepis virgultea	Coast Patch-nosed Snake	ARSSC 2	Snake-Terrestrial	ARSSC (2016)
Sonora occipitalis	Western Shovel-nosed Snake		Snake-Terrestrial	CWHR (2016)
Sonora semiannulata	Western Groundsnake		Snake-Terrestrial	CWHR (2016)
Spea hammondii	Western Spadefoot	ARSSC 1	Toad	ARSSC (2016)
Taricha granulosa	Rough-skinned Newt		Salamander	ARSSC (2016)
Taricha rivularis	Red-bellied Newt	ARSSC 2	Salamander	ARSSC (2016)
Taricha sierrae	Sierra Newt		Salamander	ARSSC (2016)
Taricha torosa	Coast Range Newt	ARSSC 2	Salamander	ARSSC (2016)
Thamnophis atratus	Aquatic Gartersnake		Snake-Aquatic	ARSSC (2016)
Thamnophis couchii	Sierra Gartersnake		Snake-Aquatic	ARSSC (2016)
Thamnophis elegans	Terrestrial Gartersnake		Snake-Aquatic	ARSSC (2016)
Thamnophis gigas	Giant Gartersnake	THR^{F,S}	Snake-Aquatic	ARSSC (2016)
Thamnophis hammondii	Two-striped Gartersnake	ARSSC 2	Snake-Aquatic	ARSSC (2016)
Thamnophis ordinoides	Northwestern Gartersnake		Snake-Aquatic	ARSSC (2016)
Thamnophis sirtalis infernalis[4]	California Red-sided Gartersnake	ARSSC 1	Snake-Aquatic	ARSSC (2016)
Thamnophis sirtalis tetrataenia	San Francisco Gartersnake	END^{F,S}	Snake-Aquatic	CWHR (2020)
Trimorphodon lambda	Sonoran Lyresnake		Snake-Terrestrial	ARSSC (2016)
Trimorphodon lyrophanes	California Lyresnake		Snake-Terrestrial	ARSSC (2016)

[a] Conservation Status: THR=Threatened, END= Endangered, Superscripts F and S are used to delineate State and Federal listing status, ARSSC= State Species of Special Concern with Priority Ranking 1-3.

[1] California tiger salamander Sonoma and Santa Barbara distinct population segments are federally endangered while central DPS is federally threatened.

[2] Species range layer for subspecies was not available so the species range for *Aspidoscelis tigris* was used.

[3] Species range does not contain any State highways

[4] Species range layer for subspecies was not available so the species range for *Thamnophis sirtalis spp*., and the South Coast Gartersnake, were used.

Connectivity Areas Layers

Essential Connectivity Areas (ECA), Natural Landscape Blocks (NLB), and Natural Areas_small (NA; Natural areas smaller than 2,000 acres that otherwise meet NLB criteria) from the Essential Connectivity Map geodatabase were provided by CDFW. The ECA and NLB were merged together with NA areas 10 hectares or greater. The resulting layer was then dissolved into a single polygon feature class with a buffer of 100 meters added to it. This connected many of the smaller polygons. This final layer was used to identify CEHC connectivity areas that overlapped with the target species ranges.

Roads Layers

Road features were obtained from the Caltrans 2012 State Highway Network (SHN) geodatabase provided by Caltrans. The roads layer was clipped to the merged Essential Habitat Connectivity layer (Merged NLB_ECA_NA areas) to create a layer of highway segments that occur in essential habitat connectivity areas. This layer was then clipped to select target species ranges (Table 1). The resulting SHN_Lines_SpeciesRanges feature class represents potential highway segments of concern where species ranges at high risk of negative road impacts intersect with both California highways and California Essential Habitat Connectivity lands. Potential highway segments of concern maps for high risk species with conservation status (threatened, endangered, and species of special concern) are presented in Figures 1–35. Potential highway segments of concern maps for high risk species with no conservation status are not presented in this report. Some species range maps are based on greater knowledge and survey efforts than others. Also, most species are patchily distributed across their known ranges. In this feature class, highway segments of concern are based upon the intersection of broad species range maps, CEHC lands, and State highways. Thus, the segments of concern likely over-represent locations of many species in relation to highways. This feature class is meant to represent potential presence of high risk herpetofauna species. Local knowledge or surveys may be needed to verify their presence or absence adjacent to specific highway segments.

Using the SHN_Lines_SpeciesRanges feature class, start and end point vertices were generated for each road segment of concern for each species (PostMileMarkers_SpeciesRanges). The nearest postmile marker along the same route was identified using the Near Analysis. Postmile marker features were identified using a State Highway Postmile shapefile obtained from Caltrans (shn204v3_TenthPM.shp). The distance from the road start/end point to the postmile the Odometer (distance in miles from start of highway to postmile), post mile marker interval, and route identifier of the marker were included in the feature class.

Species Density Layers

A hexagonal grid with an area of 15 km^2 per grid was generated for the entire state of California using the Generate Tessellation tool. This grid was then intersected with the species range layer (ARSSC_DFG_CWHR_SppRoadRiskRanges). The Summary Statistics tool was used to calculate the number of unique species whose ranges fell within each grid cell as well as number of species per group (frogs, toads, lizards, salamanders, terrestrial and aquatic snakes, turtles, and tortoise). This species density grid was intersected with the SHN lines feature class to create a species density overlay of the road network. These features overall and by group are included in a final map package provided to Caltrans. Densities of all high and very-high risk species across the state and associated highway segments are presented in Figures 36 and 37.

Results: Maps High and Very-High Risk Species

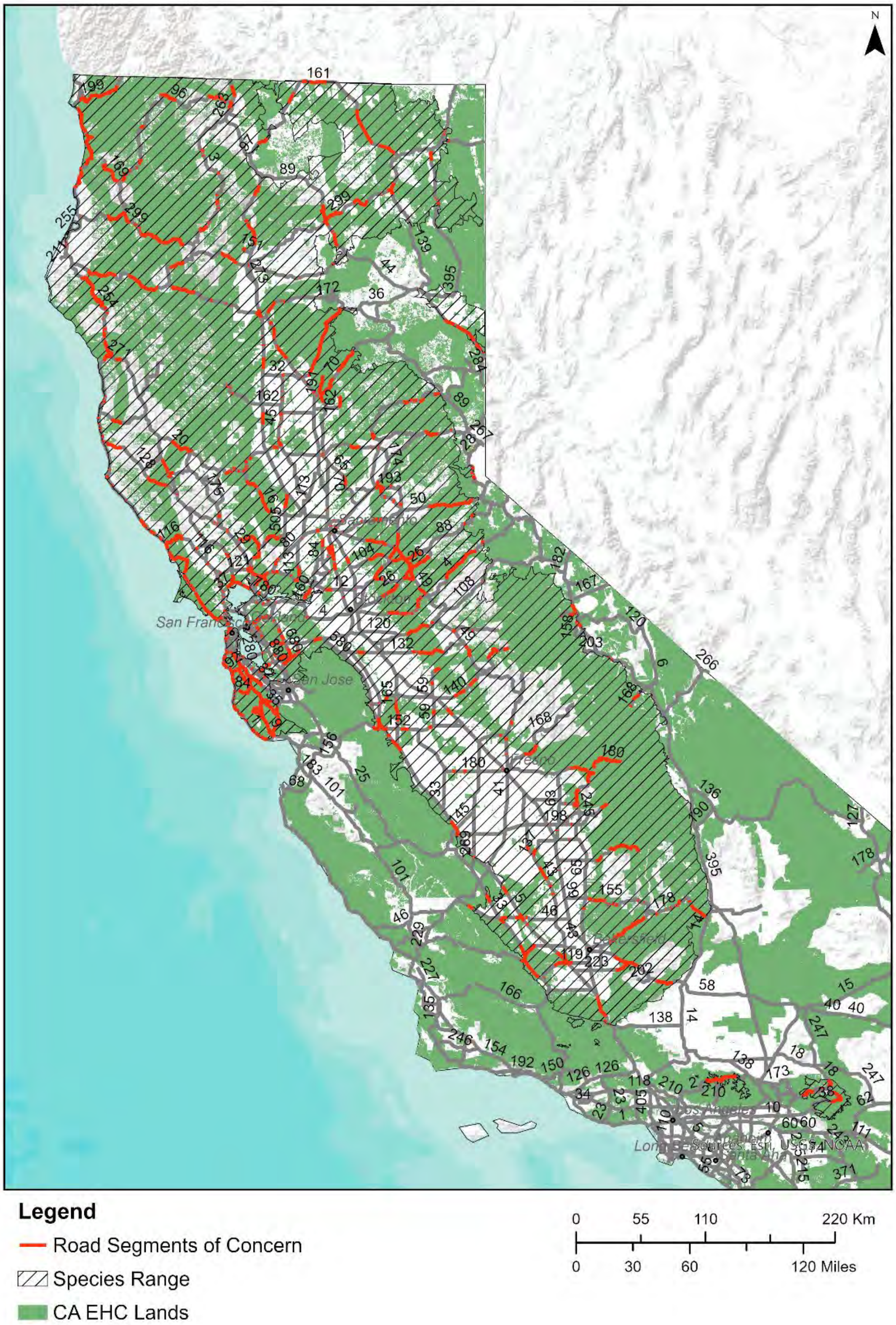


Figure 1. Highway Segments of Concern: Northern Western Pond Turtle (*Actinemys marmorata*)

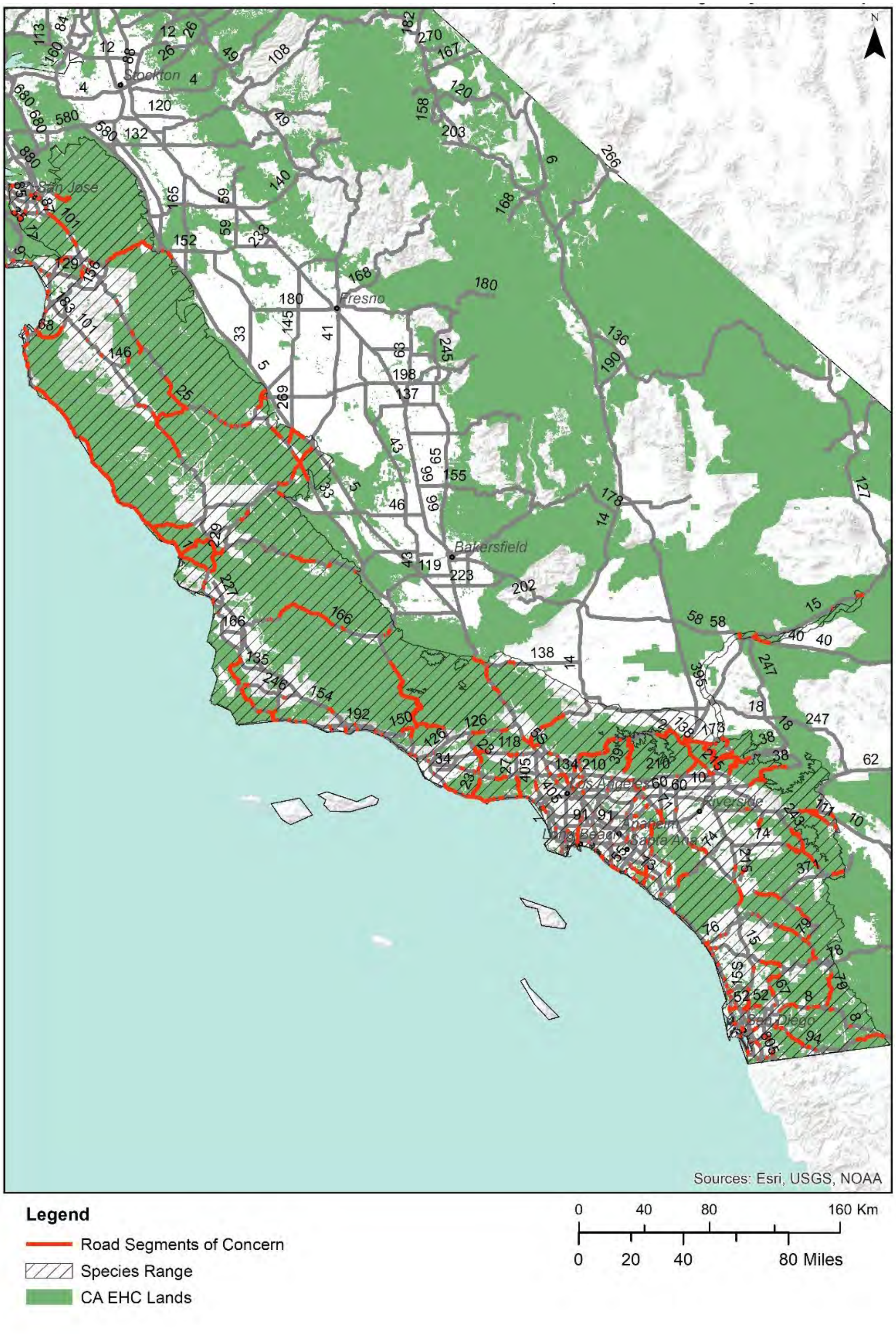


Figure 2. Highway Segments of Concern: Southern Western Pond Turtle (*Actinemys pallida*)

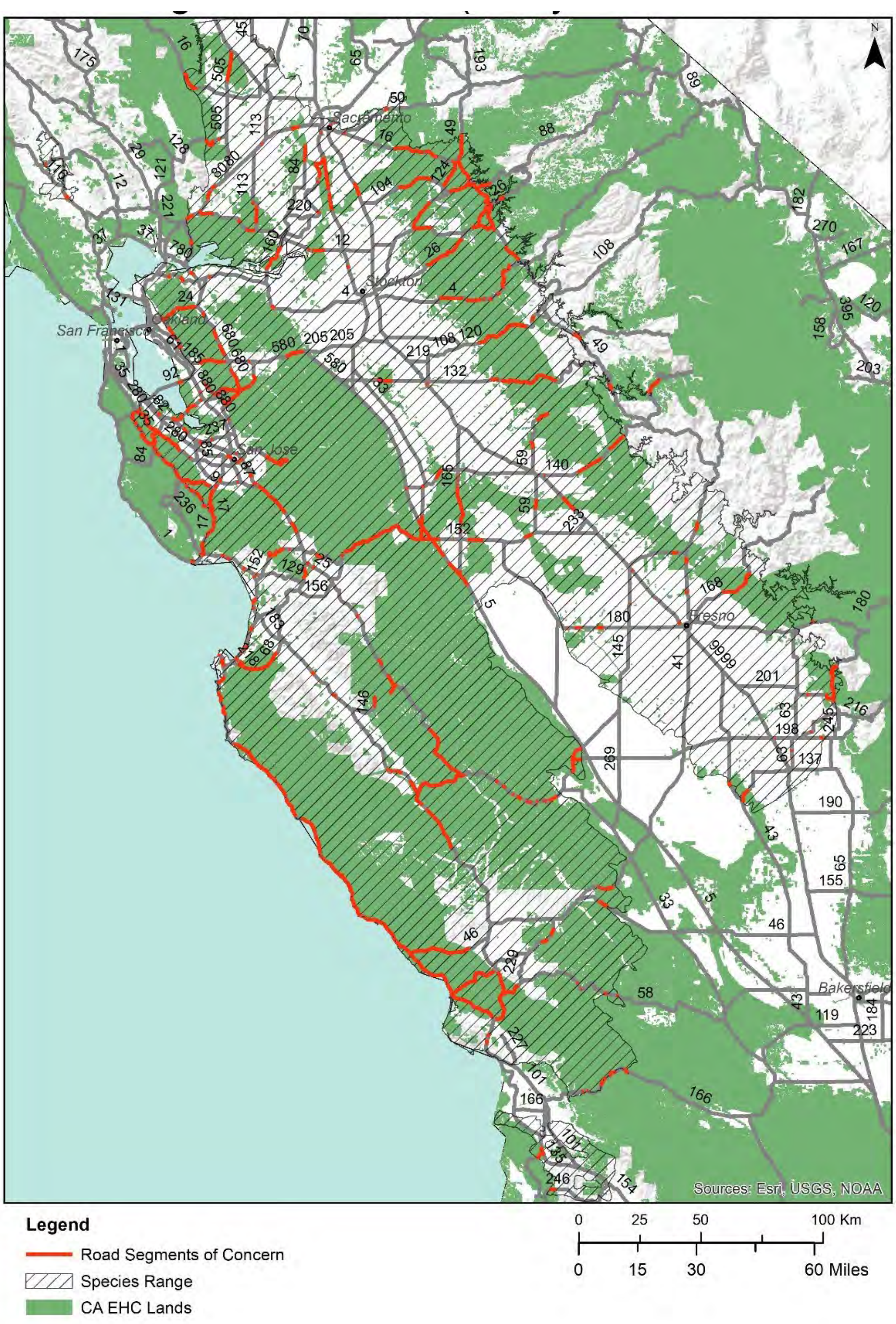


Figure 3. Highway Segments of Concern: California Tiger Salamander (*Ambystoma californiense*)

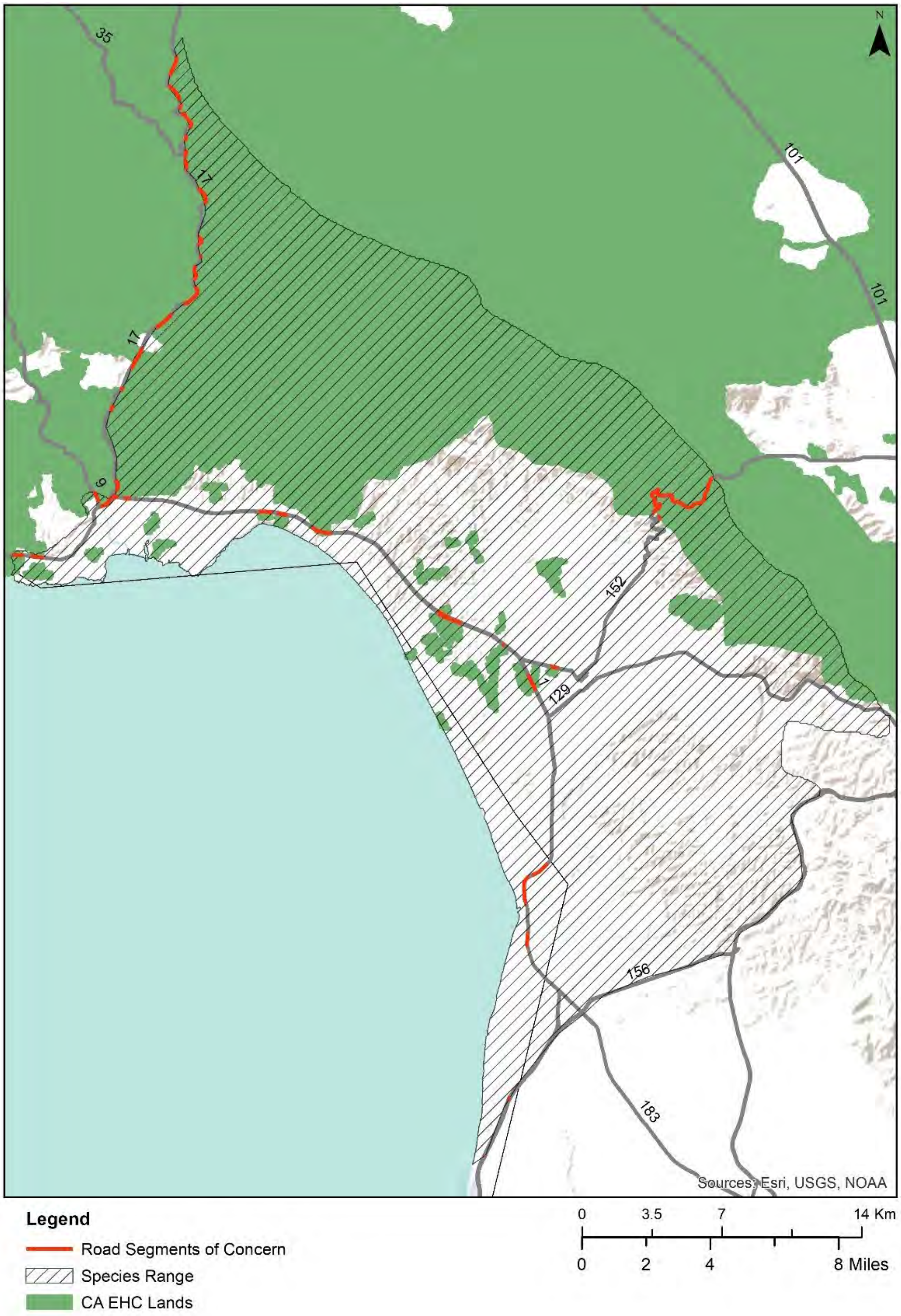


Figure 4. Highway Segments of Concern: Santa Cruz Long-toed Salamander (*Ambystoma macrodactylum croceum*)

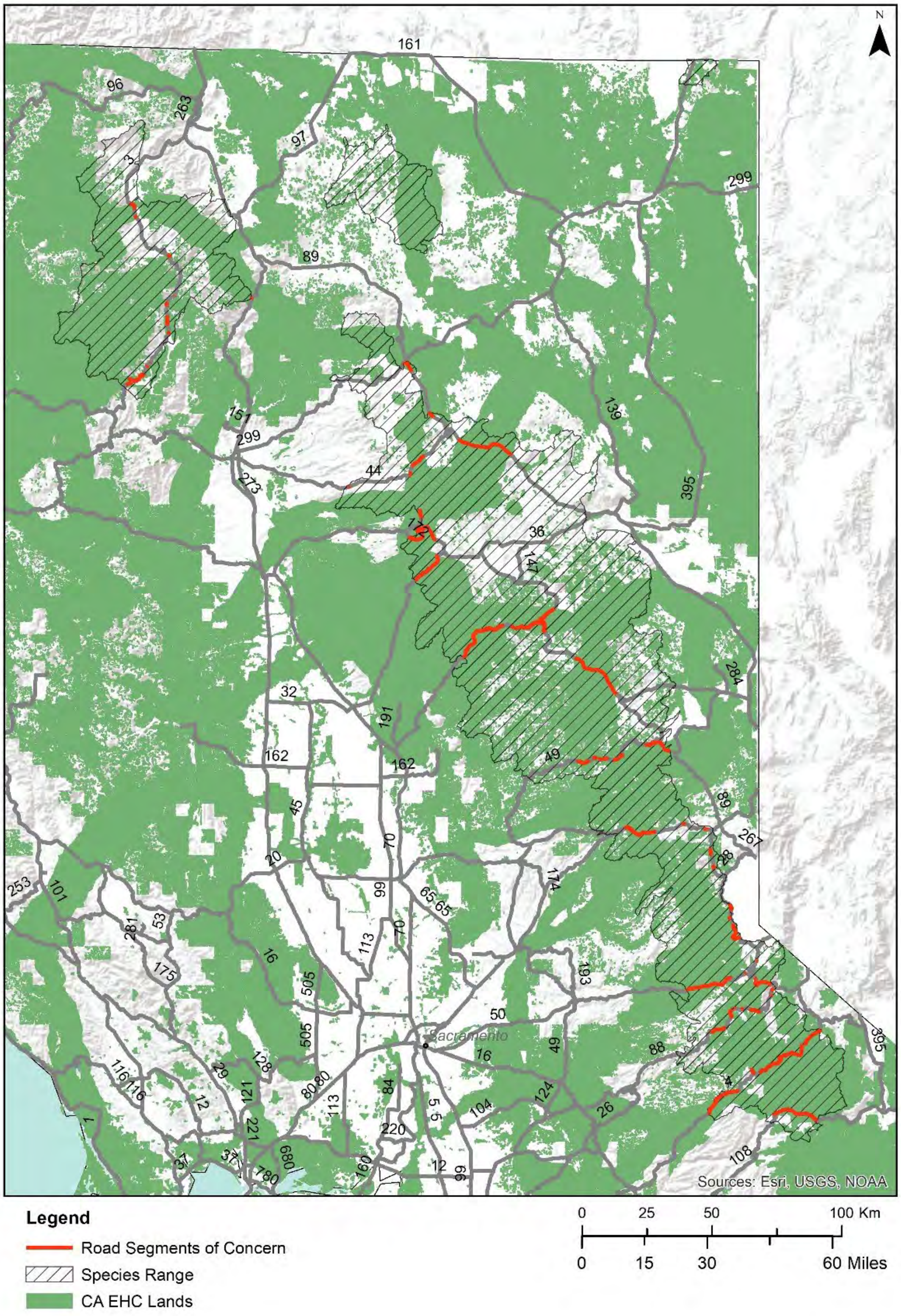


Figure 5. Highway Segments of Concern: Southern Long-toed Salamander (*Ambystoma macrodactylum sigillatum*)

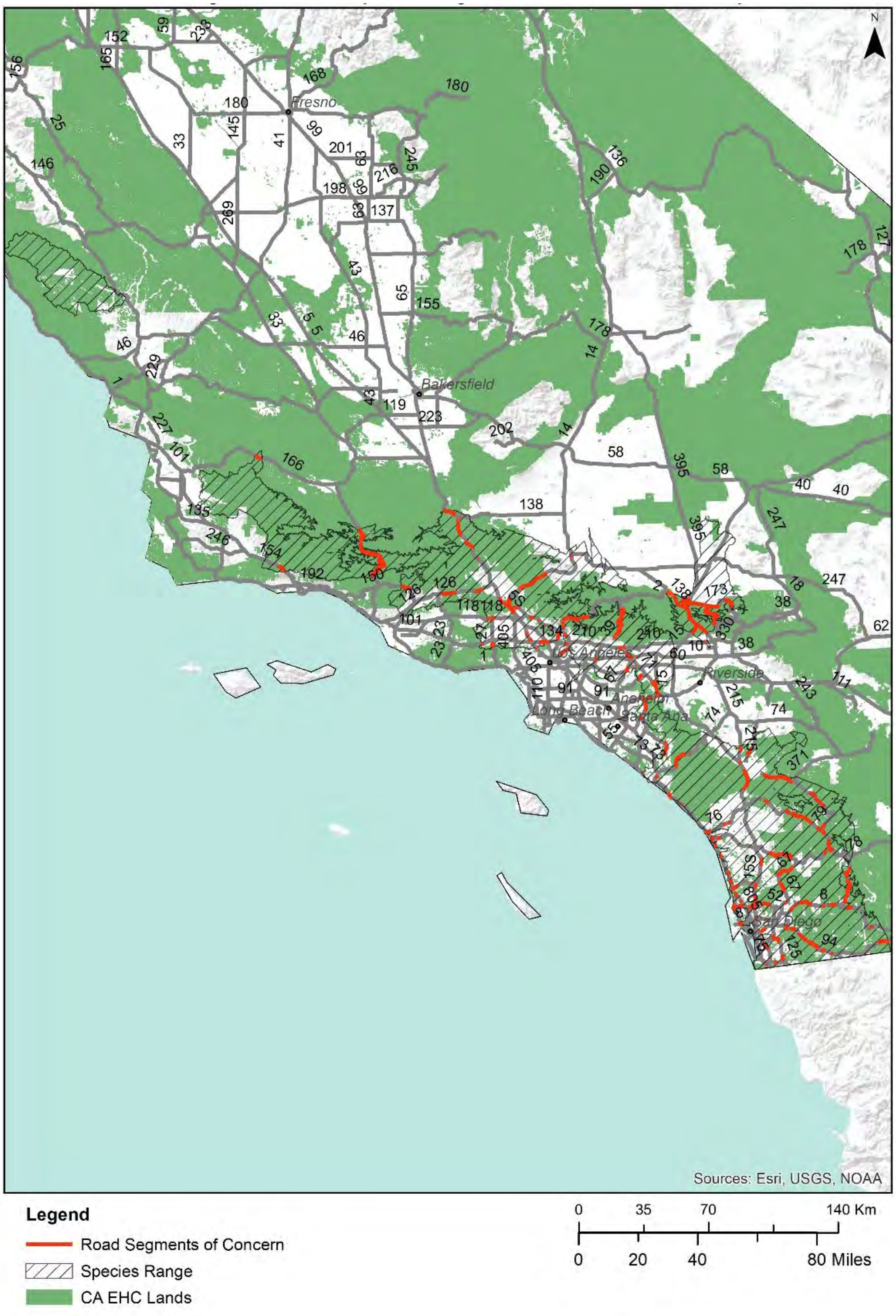


Figure 6. Highway Segments of Concern: Arroyo Toad (*Anaxyrus californicus*)

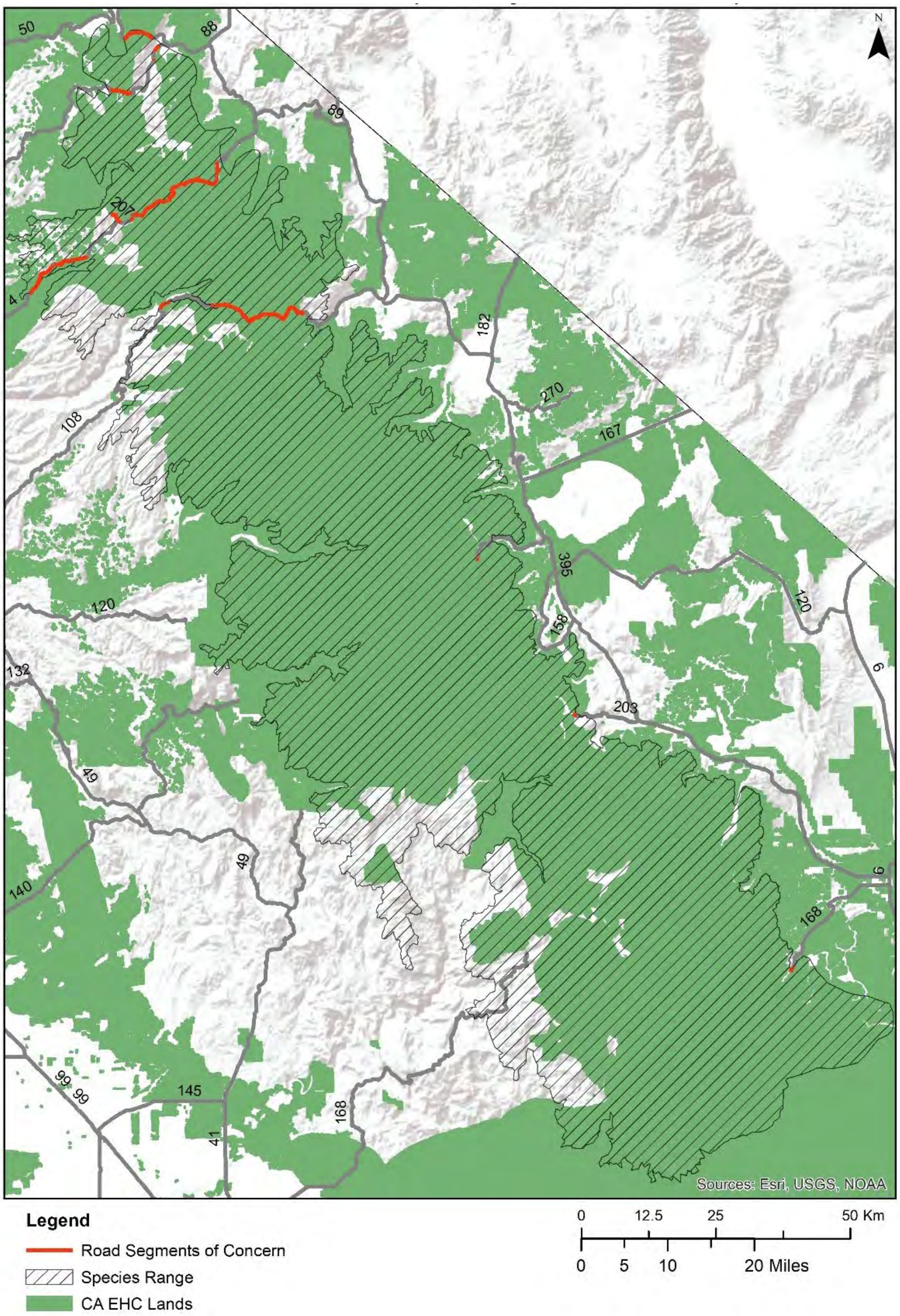


Figure 7. Highway Segments of Concern: Yosemite Toad (*Anaxyrus canorus*)

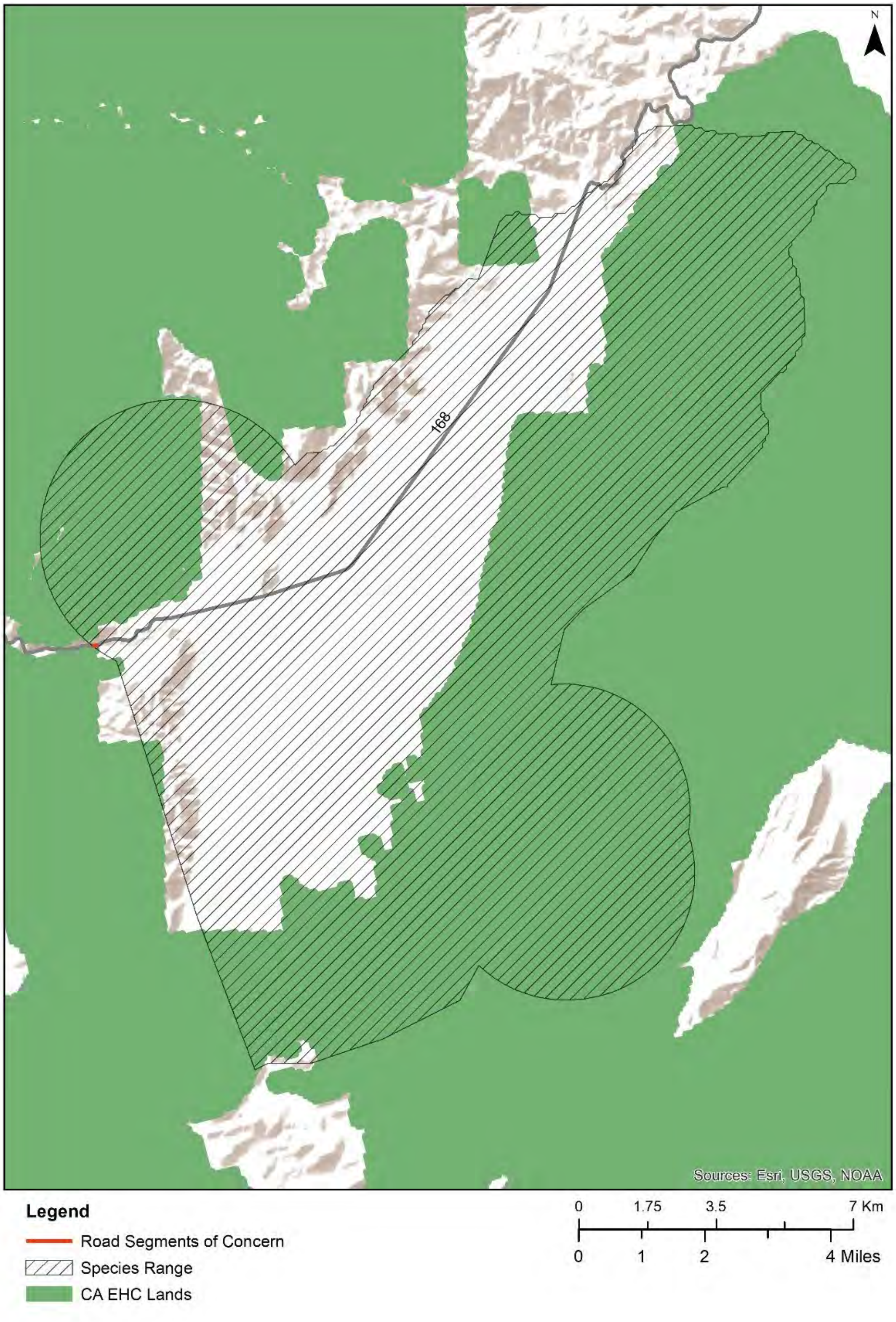


Figure 8. Highway Segments of Concern: Black Toad (*Anaxyrus exsul*)

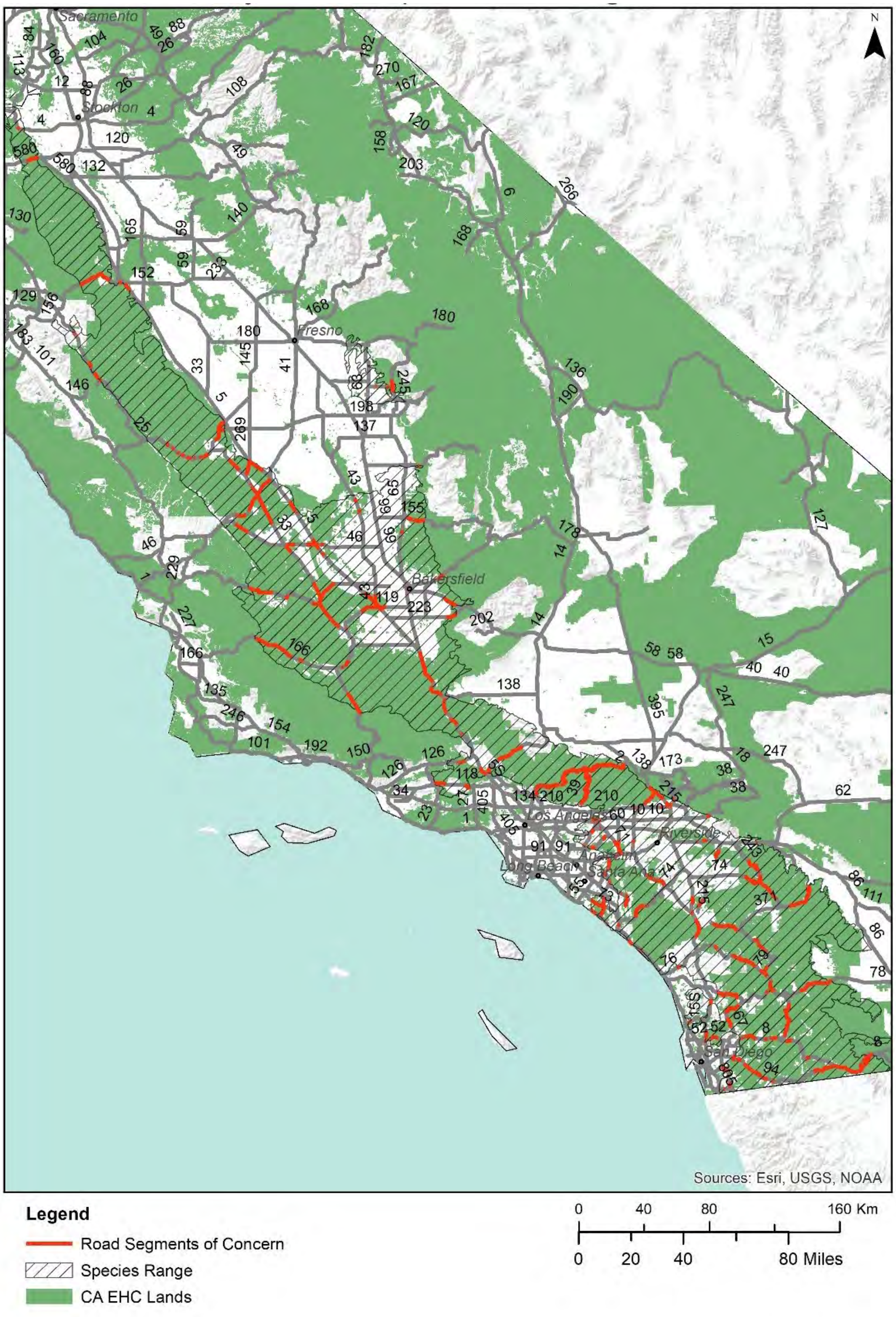


Figure 9. Highway Segments of Concern: California Glossy Snake (*Arizona elegans occidentalis*)

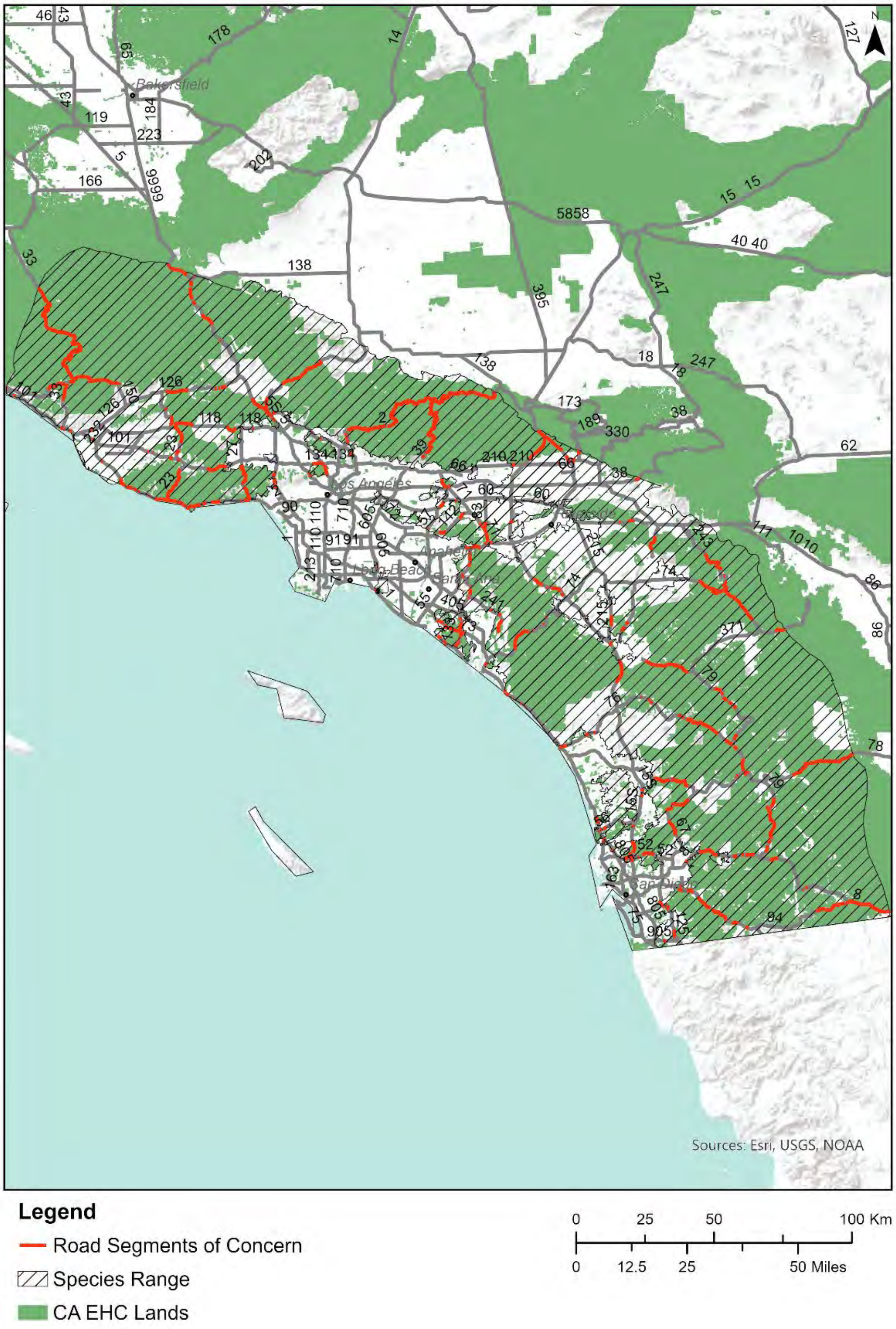


Figure 10. Highway Segments of Concern: San Diegan Tiger Whiptail (*Aspidoscelis tigris stejnegeri*)

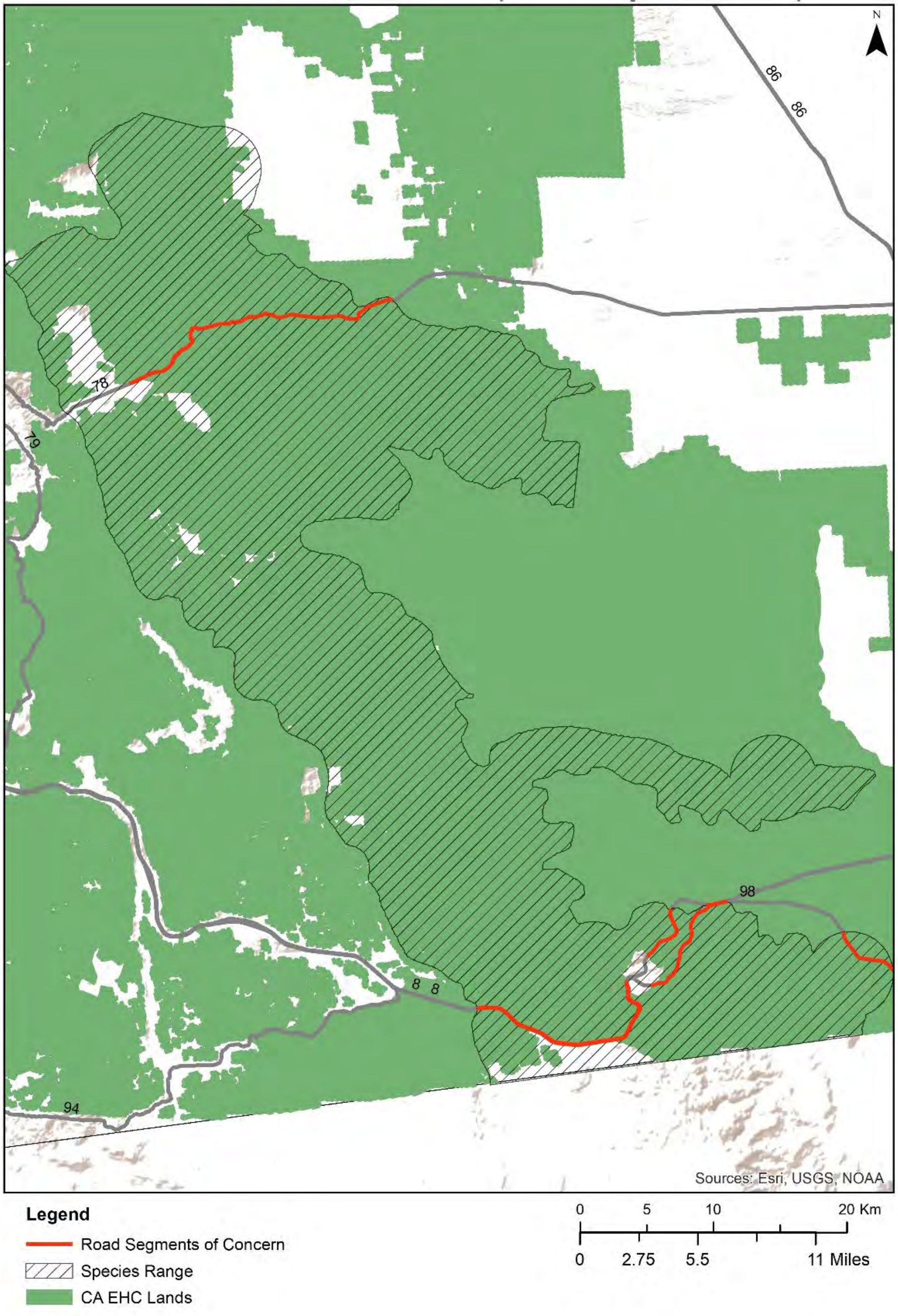


Figure 11. Highway Segments of Concern: Switak's Banded Gecko (*Coleonyx switaki*)

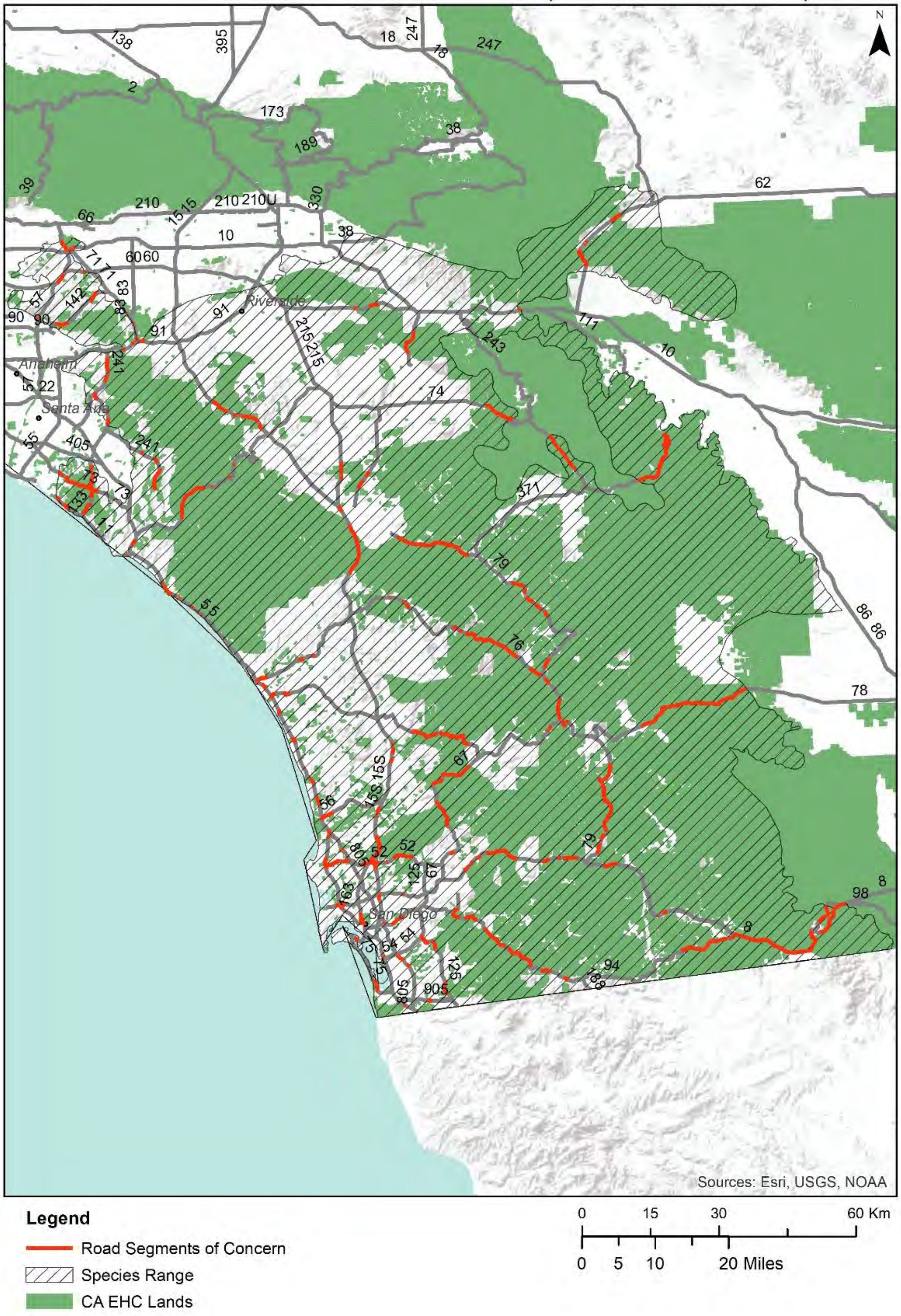


Figure 12. Highway Segments of Concern: Red Diamond Rattlesnake (*Crotalus ruber*)

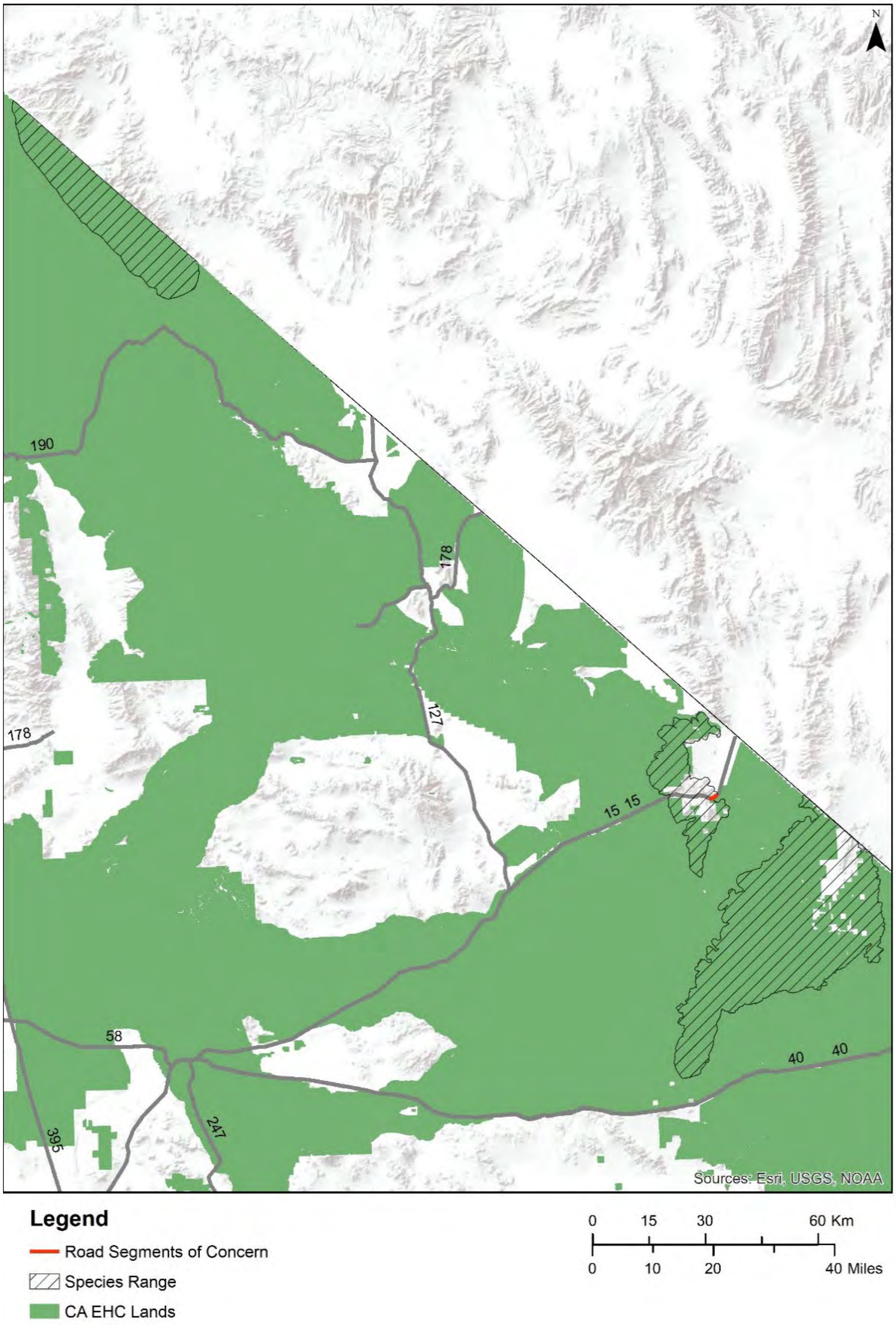


Figure 13. Highway Segments of Concern: Regal Ring-necked Snake (*Diadophis punctatus regalis*)

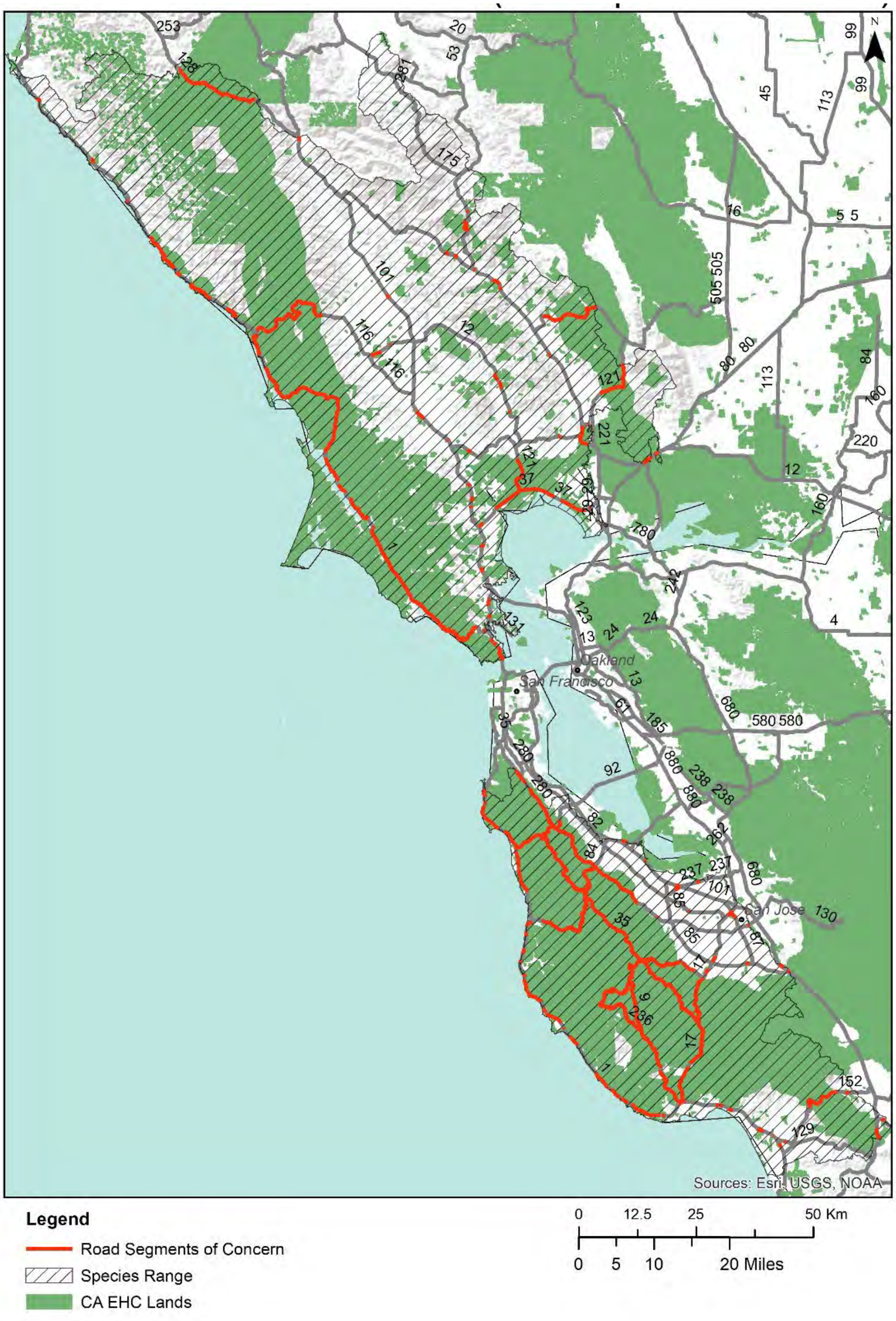


Figure 14. Highway Segments of Concern: California Giant Salamander (*Dicamptodon ensatus*)

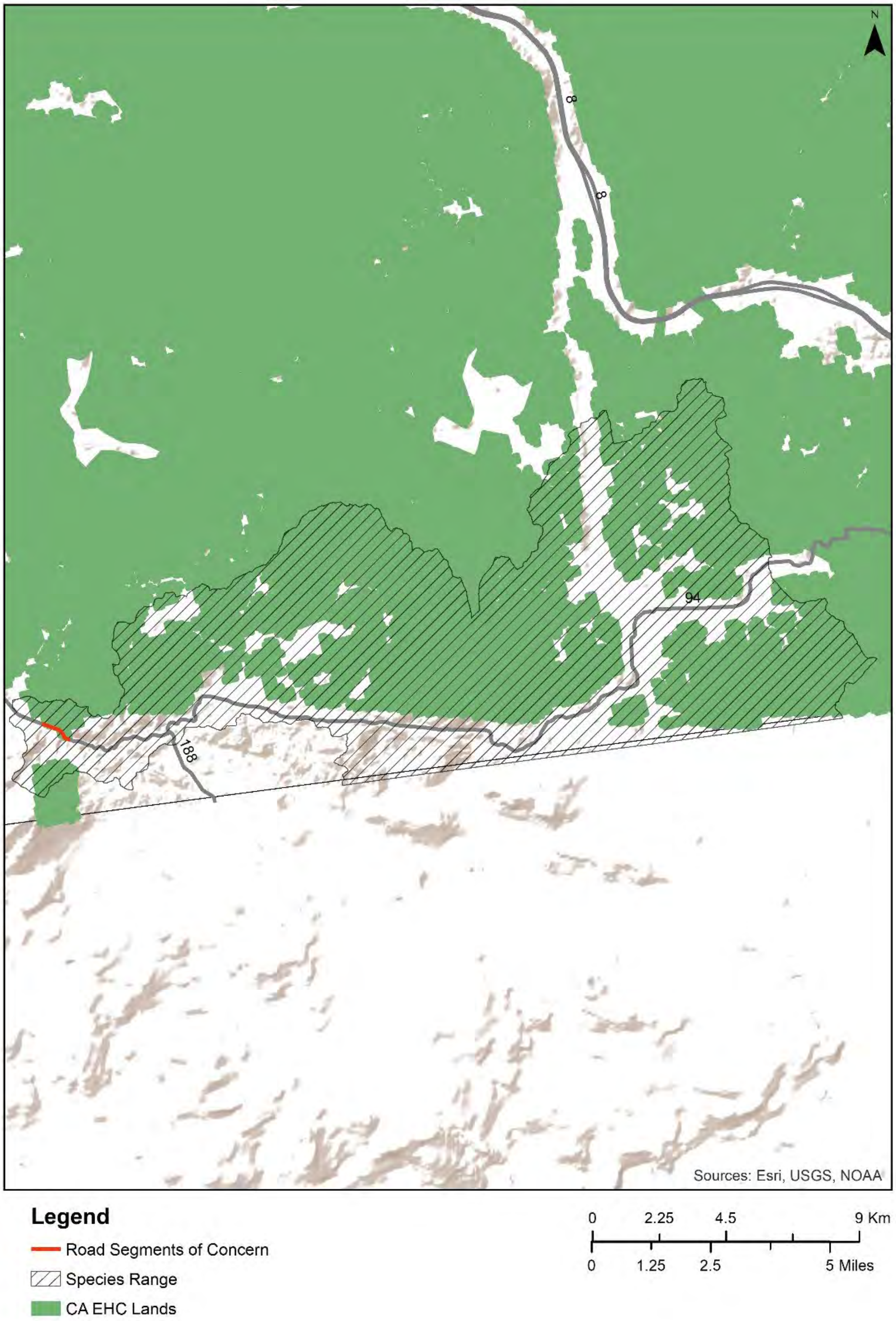


Figure 15. Highway Segments of Concern: Cope's Leopard Lizard (*Gambelia copeii*)

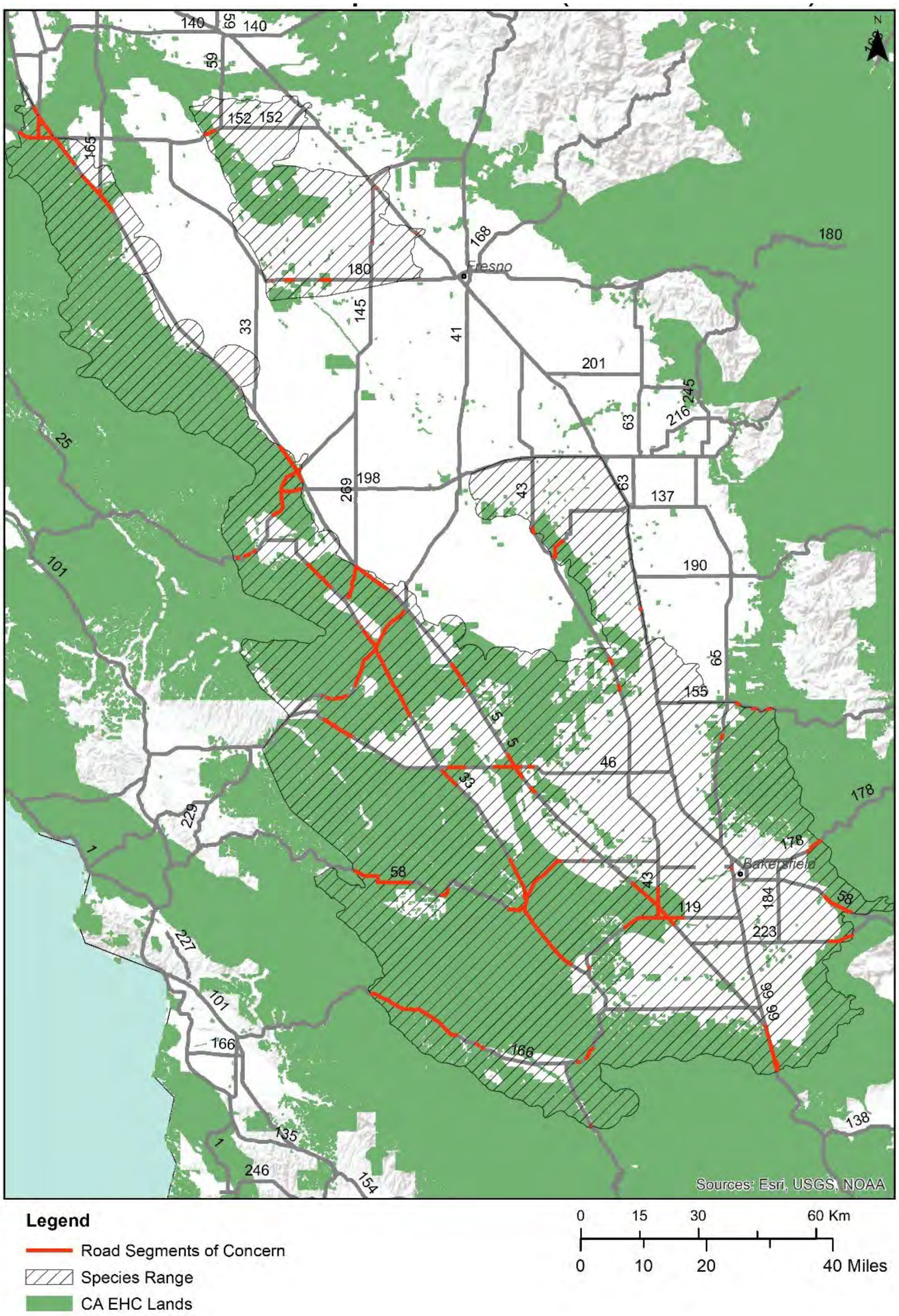


Figure 16. Highway Segments of Concern: Blunt-nosed Leopard Lizard (*Gambelia sila*)

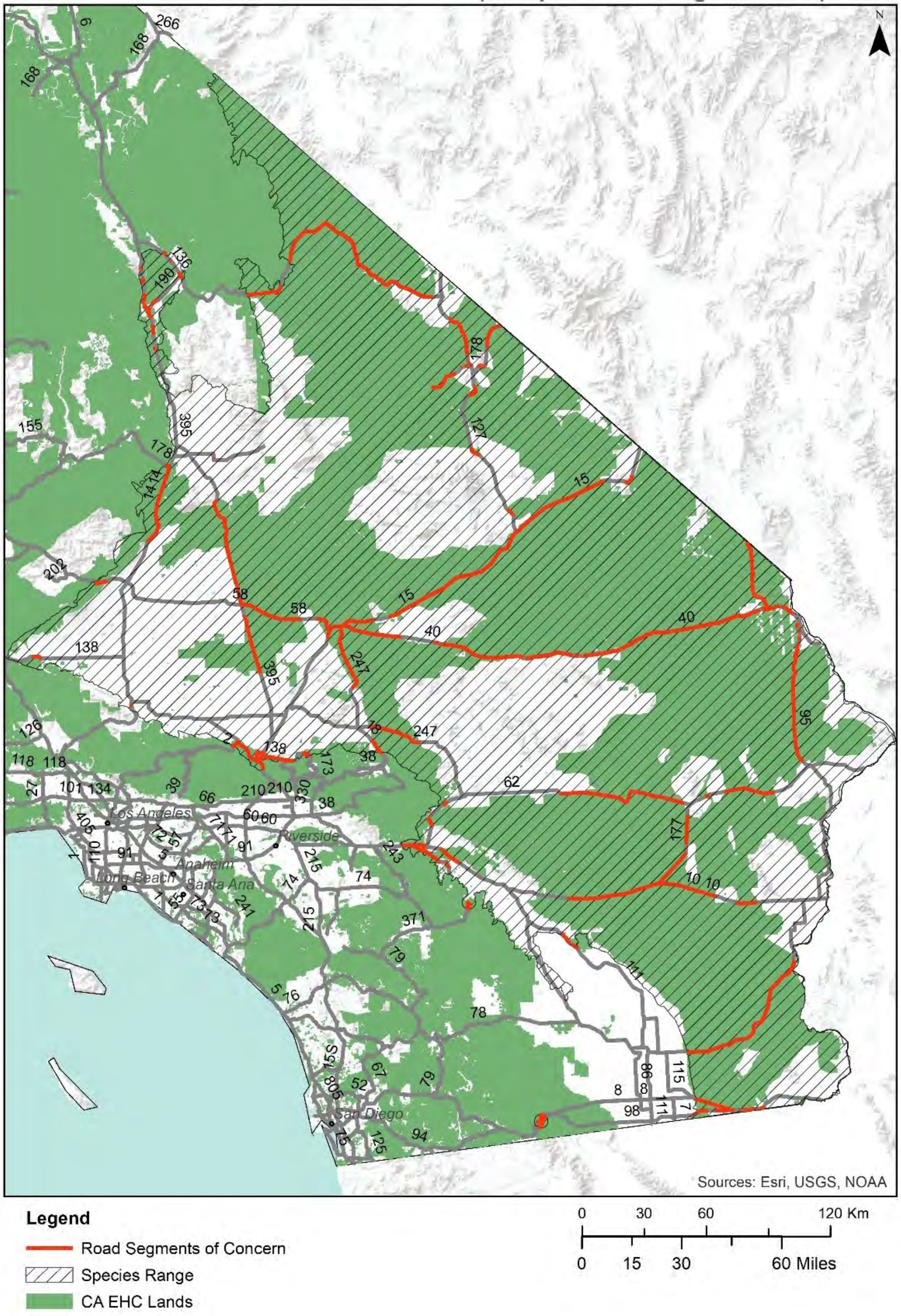


Figure 17. Highway Segments of Concern: Mohave Desert Tortoise (*Gopherus agassizii*)

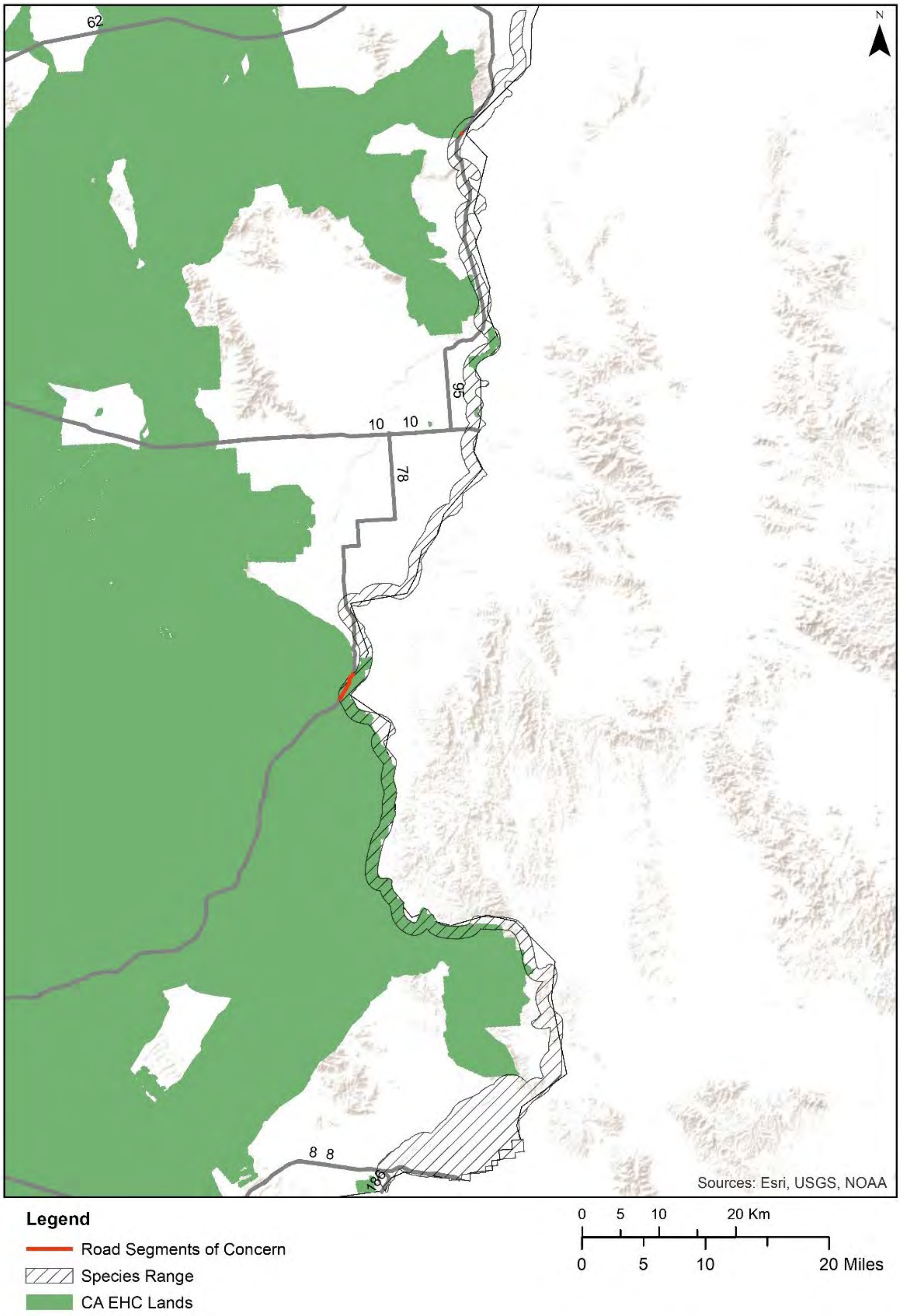


Figure 18. Highway Segments of Concern: Sonoran Desert Toad (*Incilius alvarius)*
Note: Possibly extinct in CA.

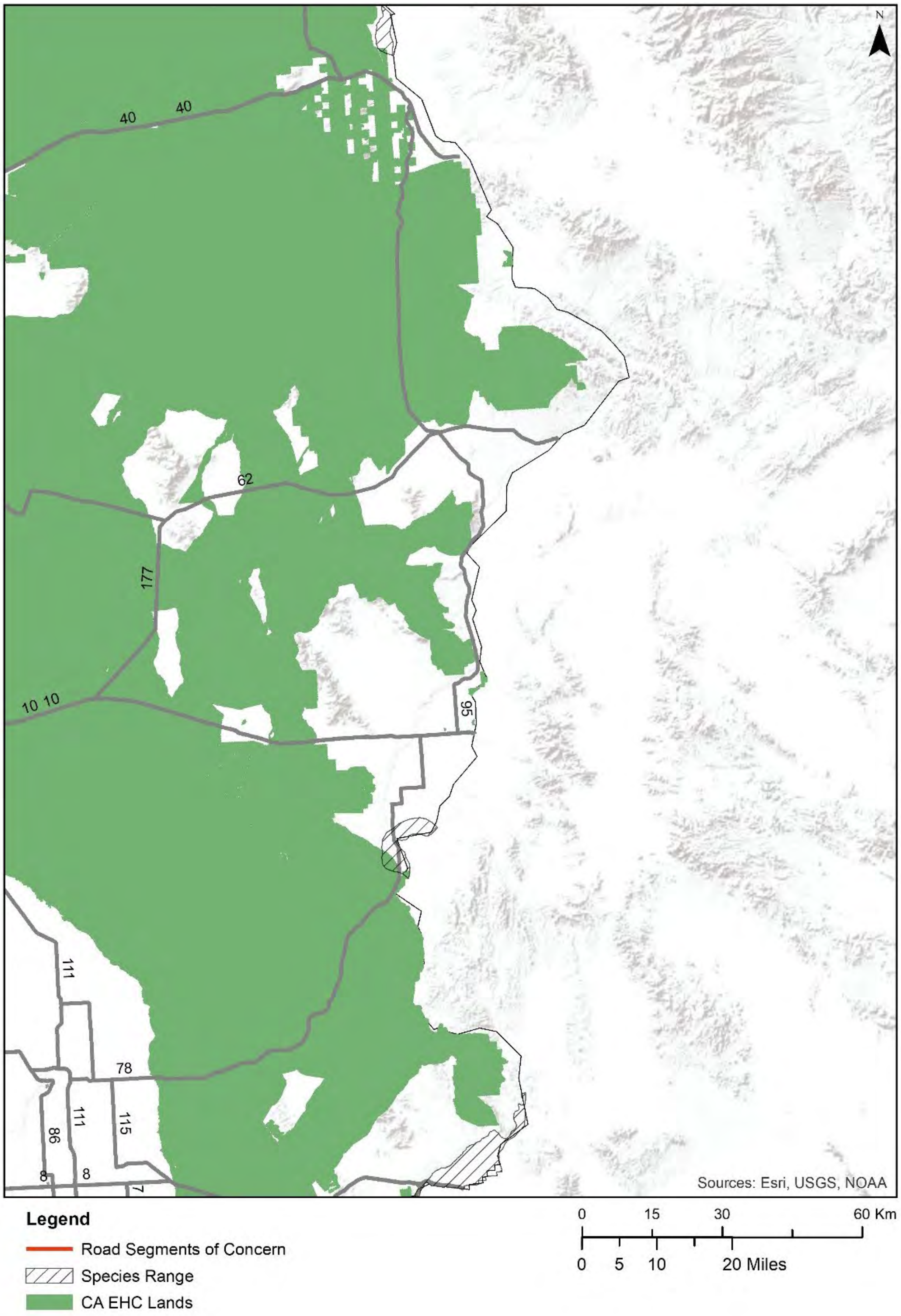


Figure 19. Highway Segments of Concern: Sonoran Mud Turtle (*Kinosternon sonoriense*)

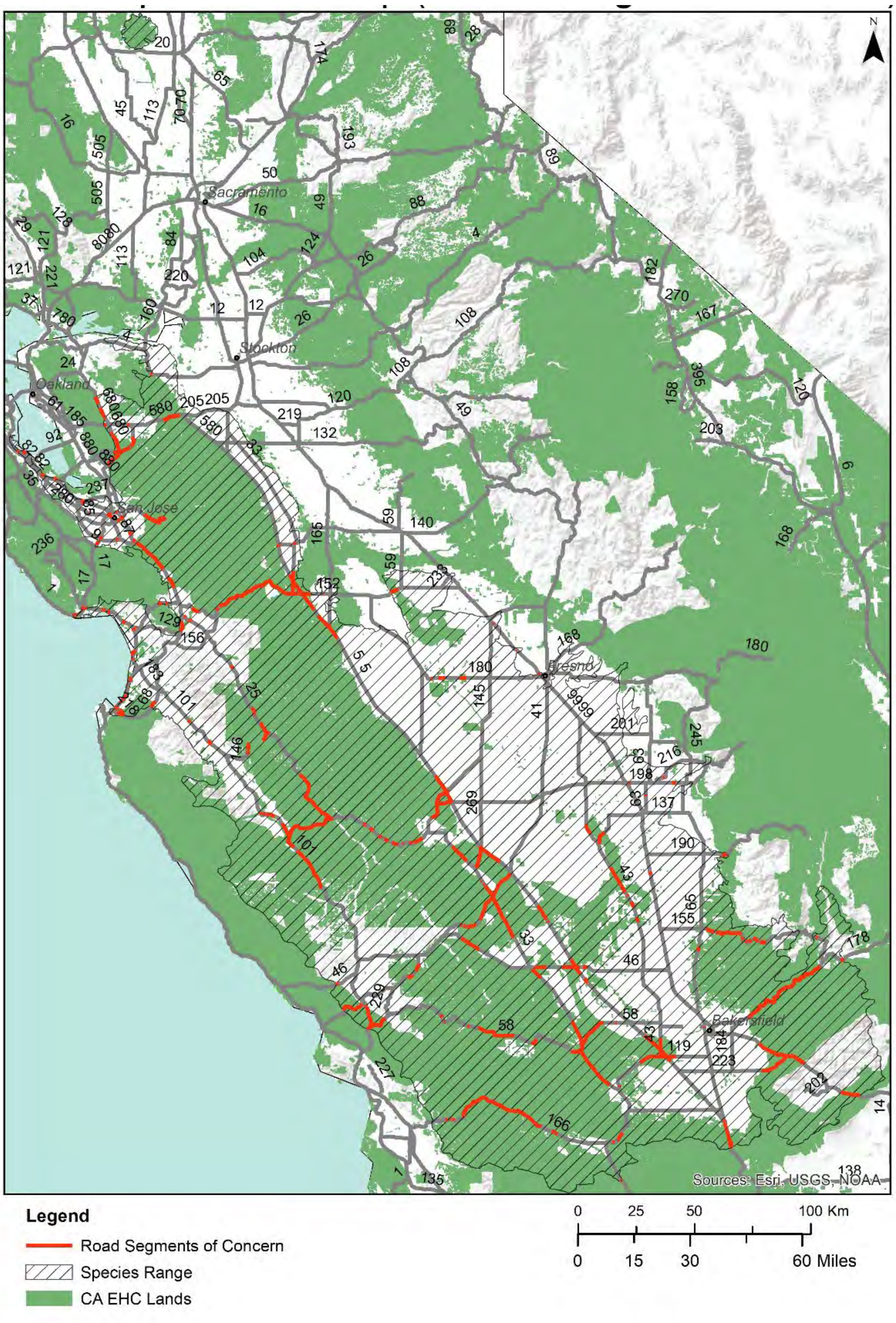


Figure 20. Highway Segments of Concern: San Joaquin Coachwhip (*Masticophis flagellum ruddocki*)

Figure 21. Highway Segments of Concern: Baja California Coachwhip (*Masticophis fuliginosus*)

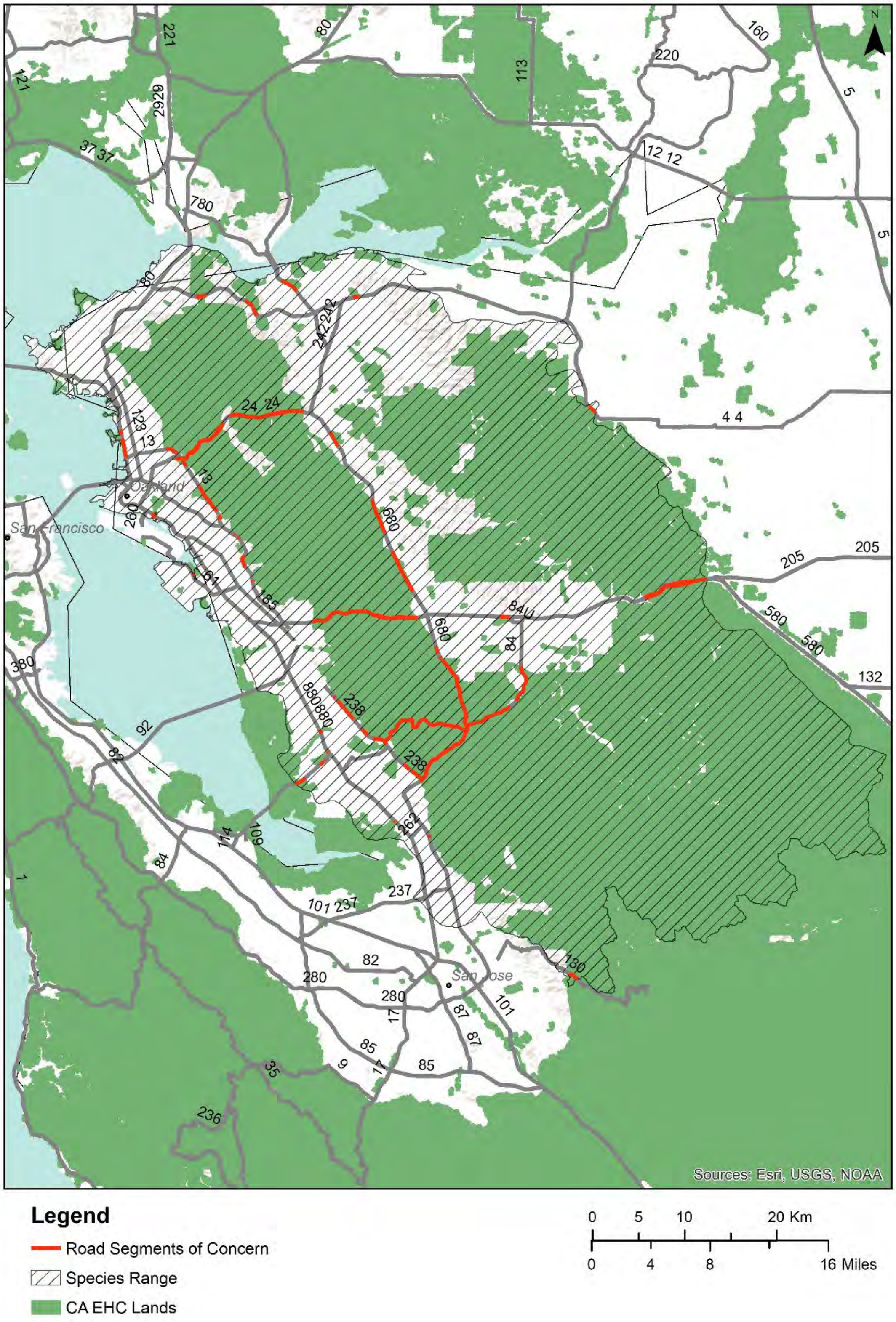
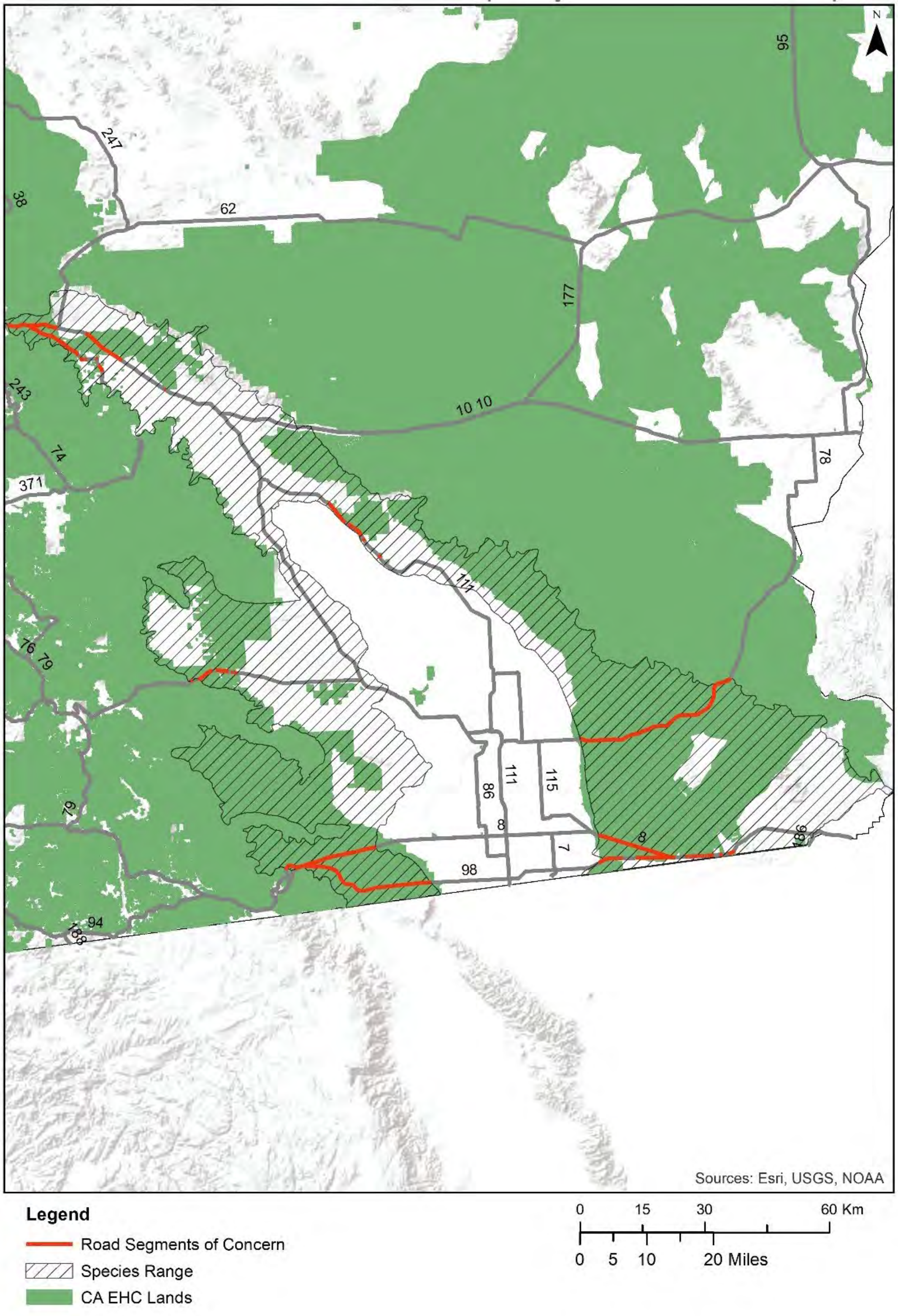


Figure 22. Highway Segments of Concern: Alameda Striped Racer (*Masticophis lateralis euryxanthus*)



Sources: Esri, USGS, NOAA

Figure 23. Highway Segments of Concern: Flat-tail Horned Lizard (*Phrynosoma mcallii*)

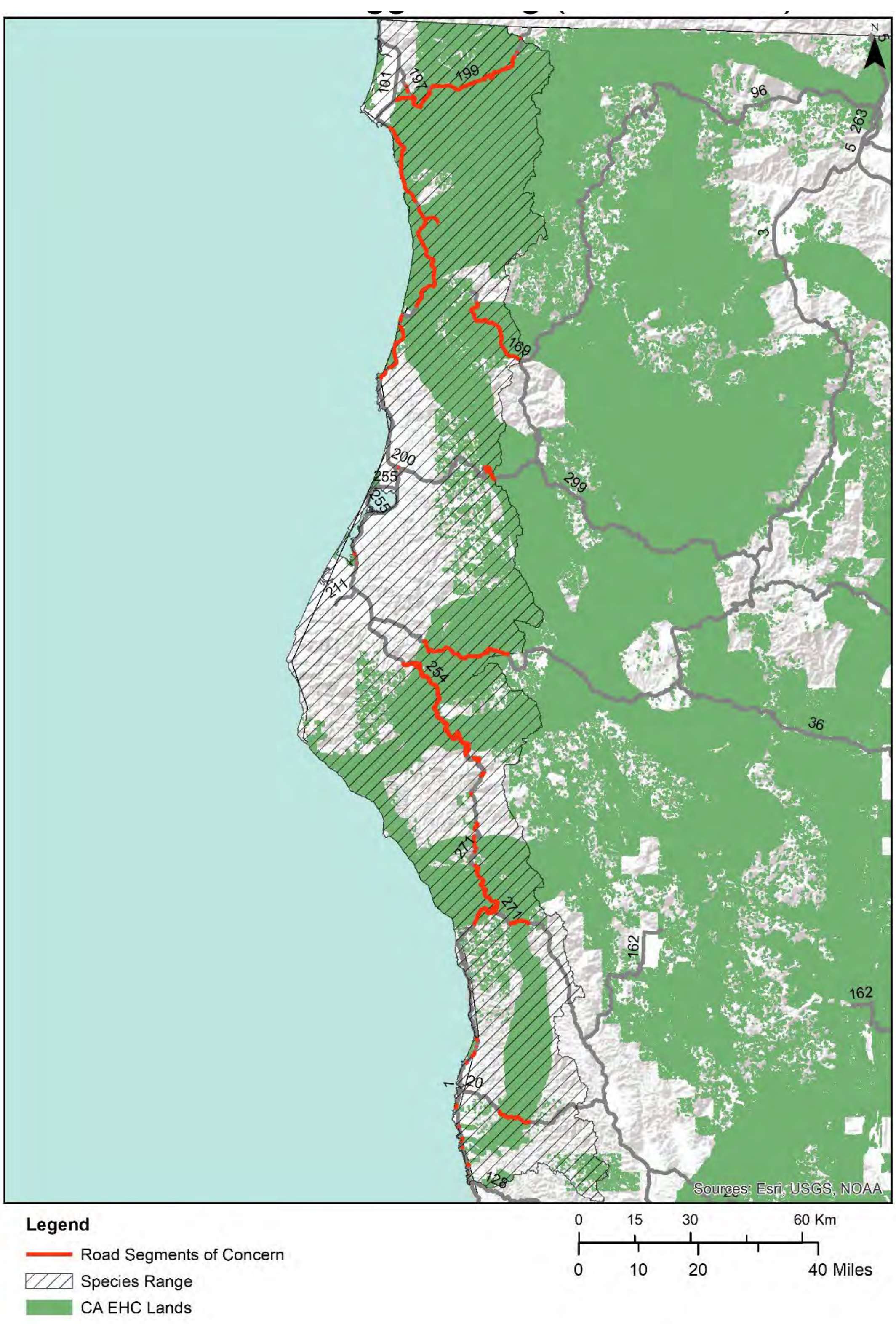


Figure 24. Highway Segments of Concern: Northern Red-legged Frog (*Rana aurora*)

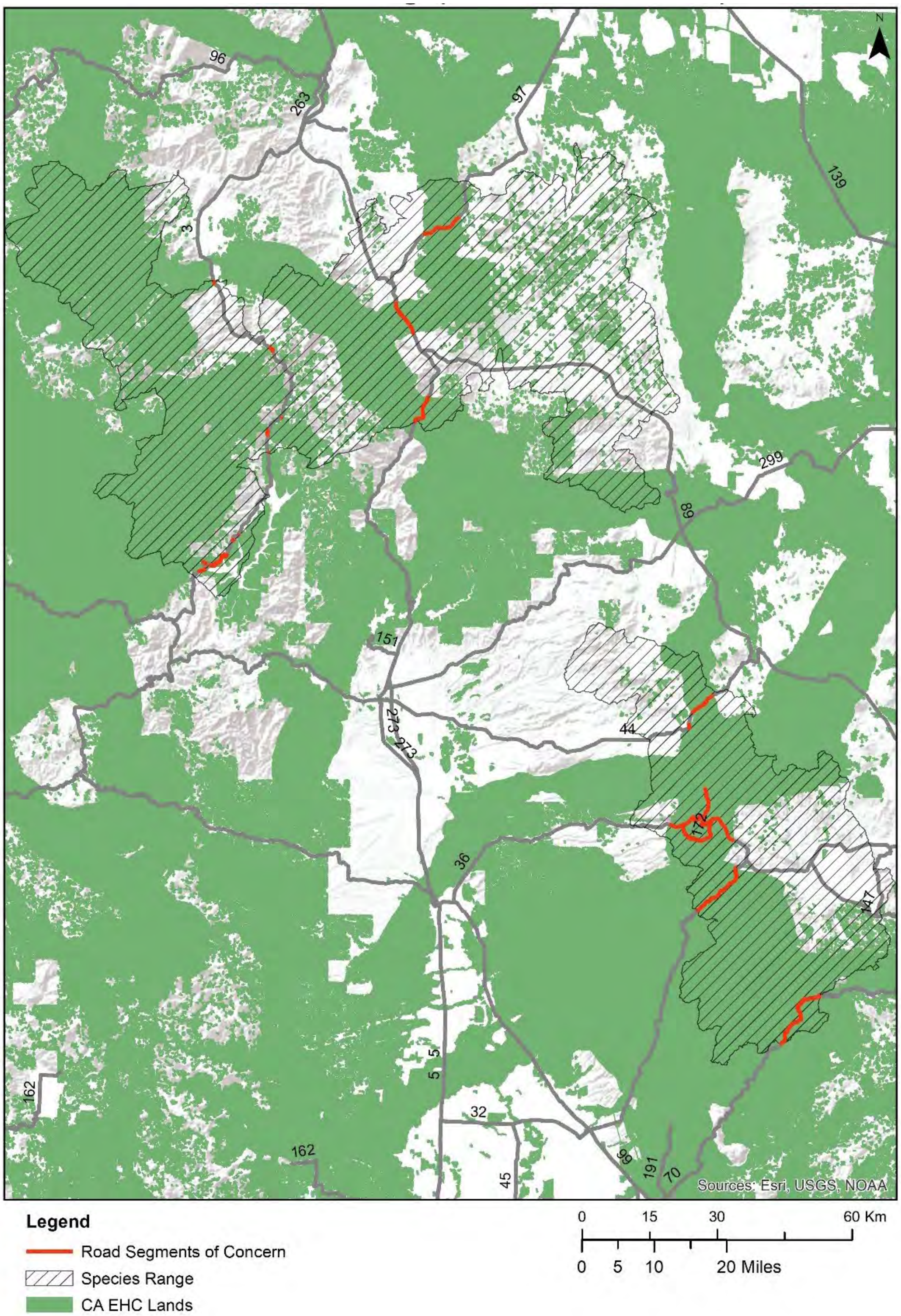


Figure 25. Highway Segments of Concern: Cascades Frog (*Rana cascadae*)

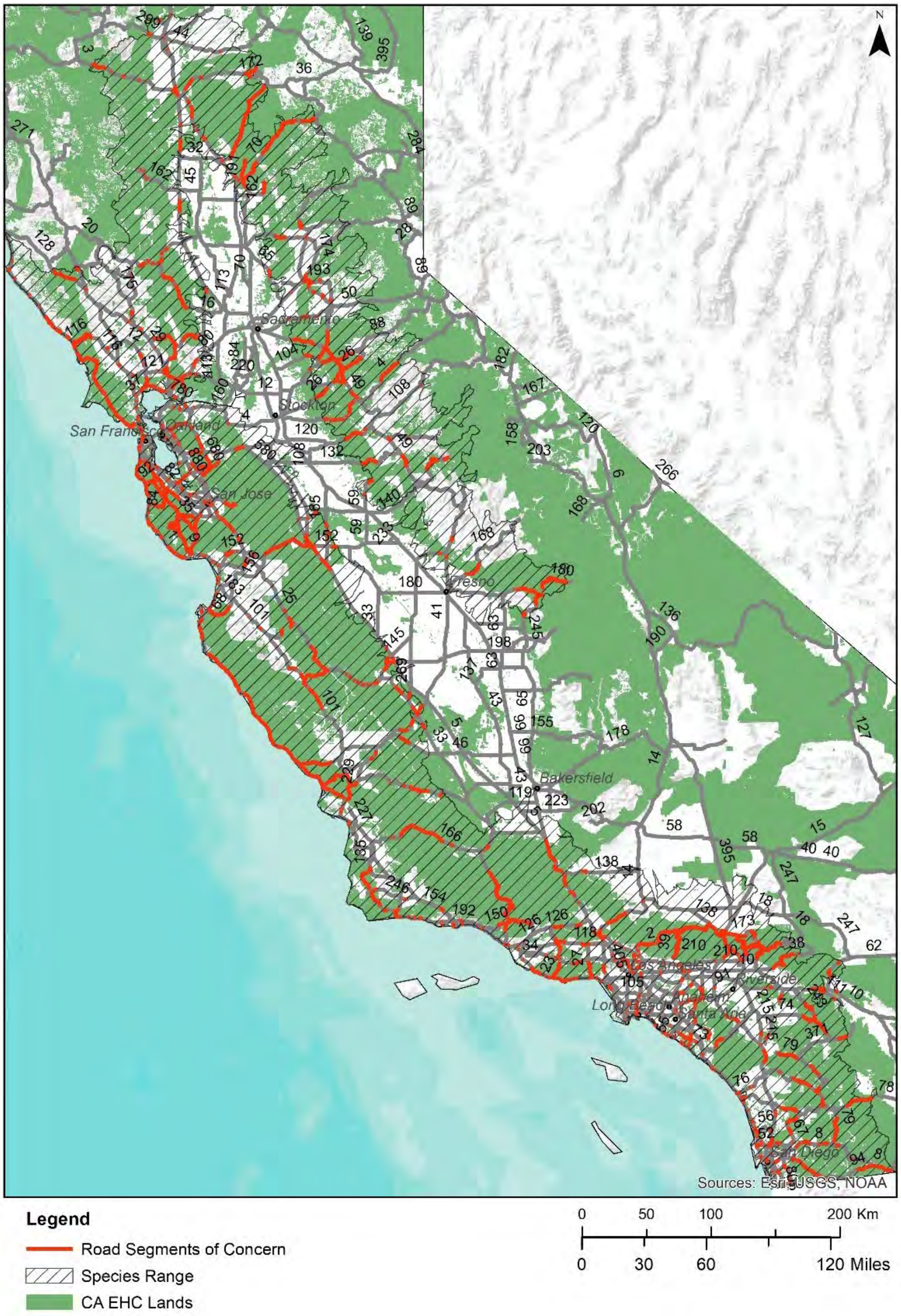
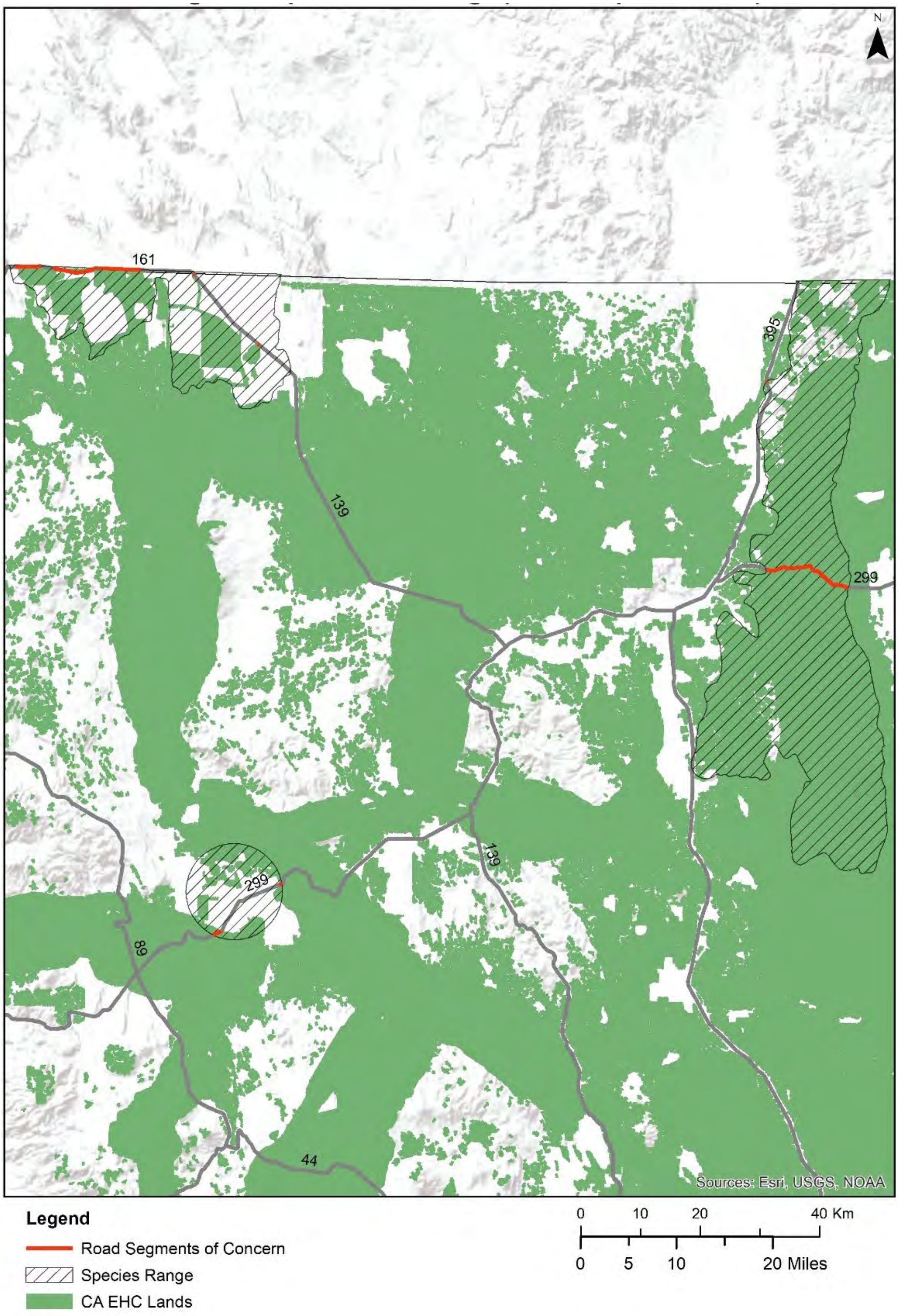


Figure 26. Highway Segments of Concern: California Red-legged Frog (*Rana draytonii*)



Sources: Esri, USGS, NOAA

Figure 27. Highway Segments of Concern: Oregon Spotted Frog (*Rana pretiosa*)
Note: Possibly extinct in CA.

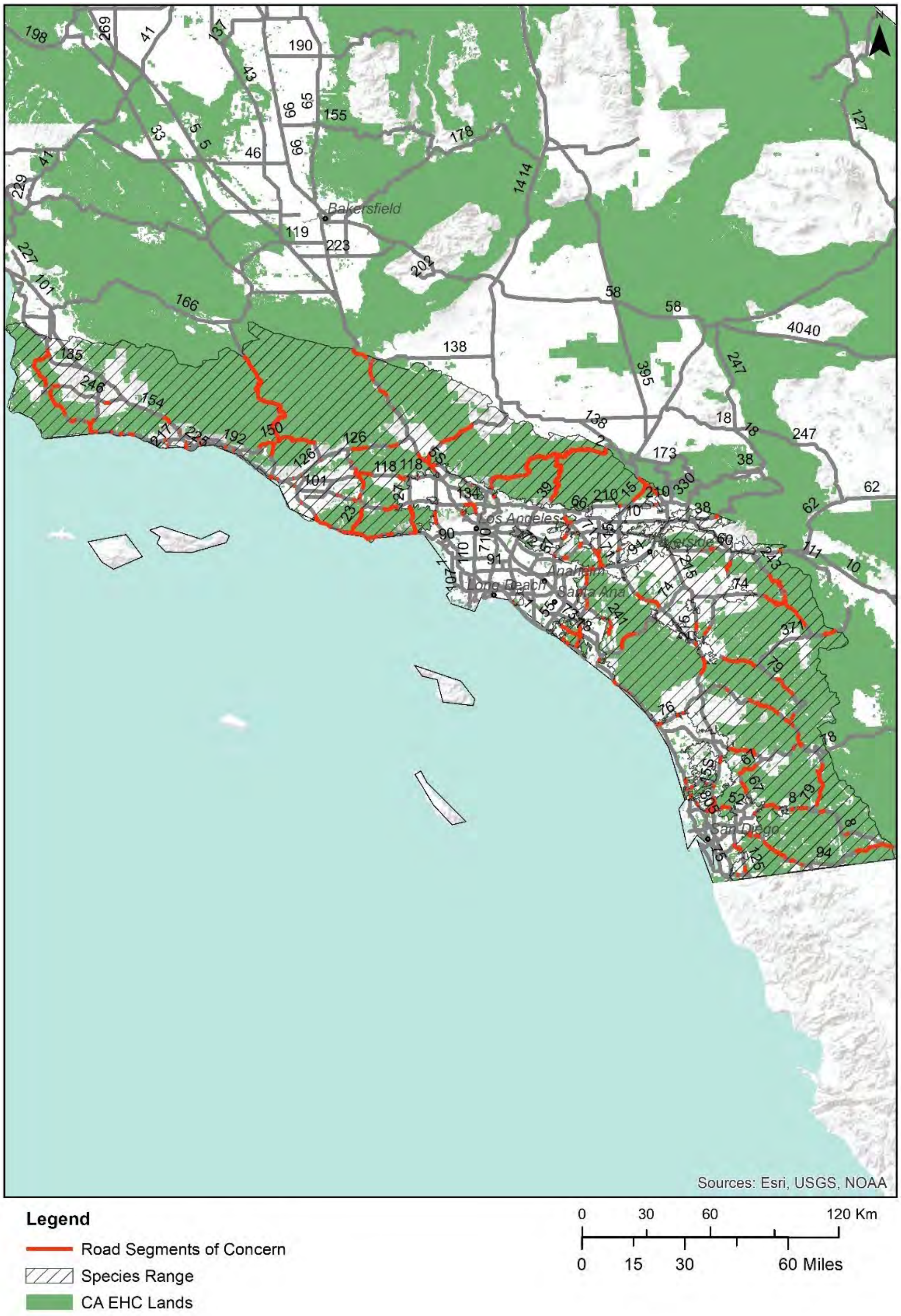


Figure 28. Highway Segments of Concern: Coast Patch-nosed Snake (*Salvadora hexalepis virgultea*)

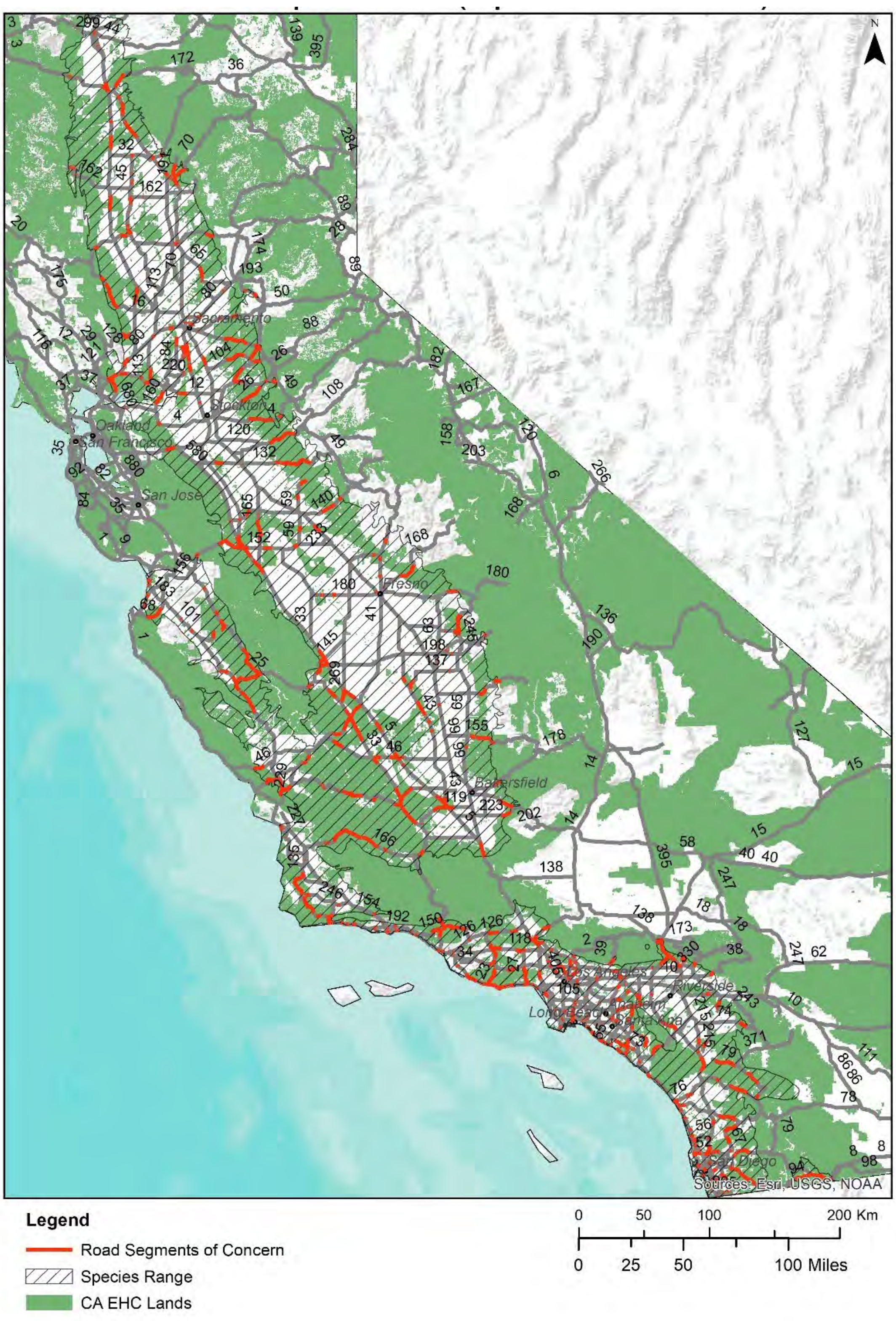


Figure 29. Highway Segments of Concern: Western Spadefoot (*Spea hammondii*)

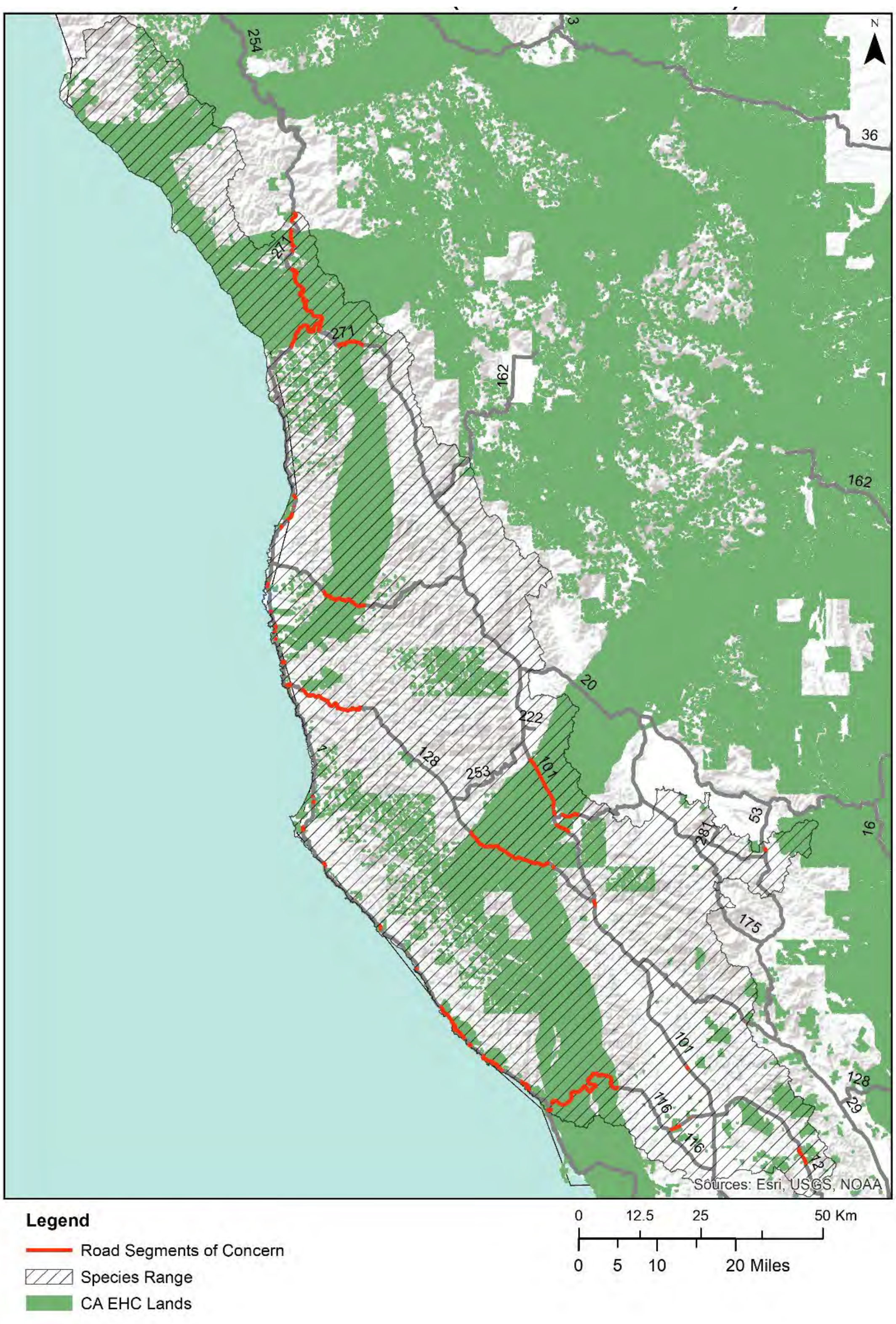


Figure 30. Highway Segments of Concern: Red-bellied Newt (*Taricha rivularis*)

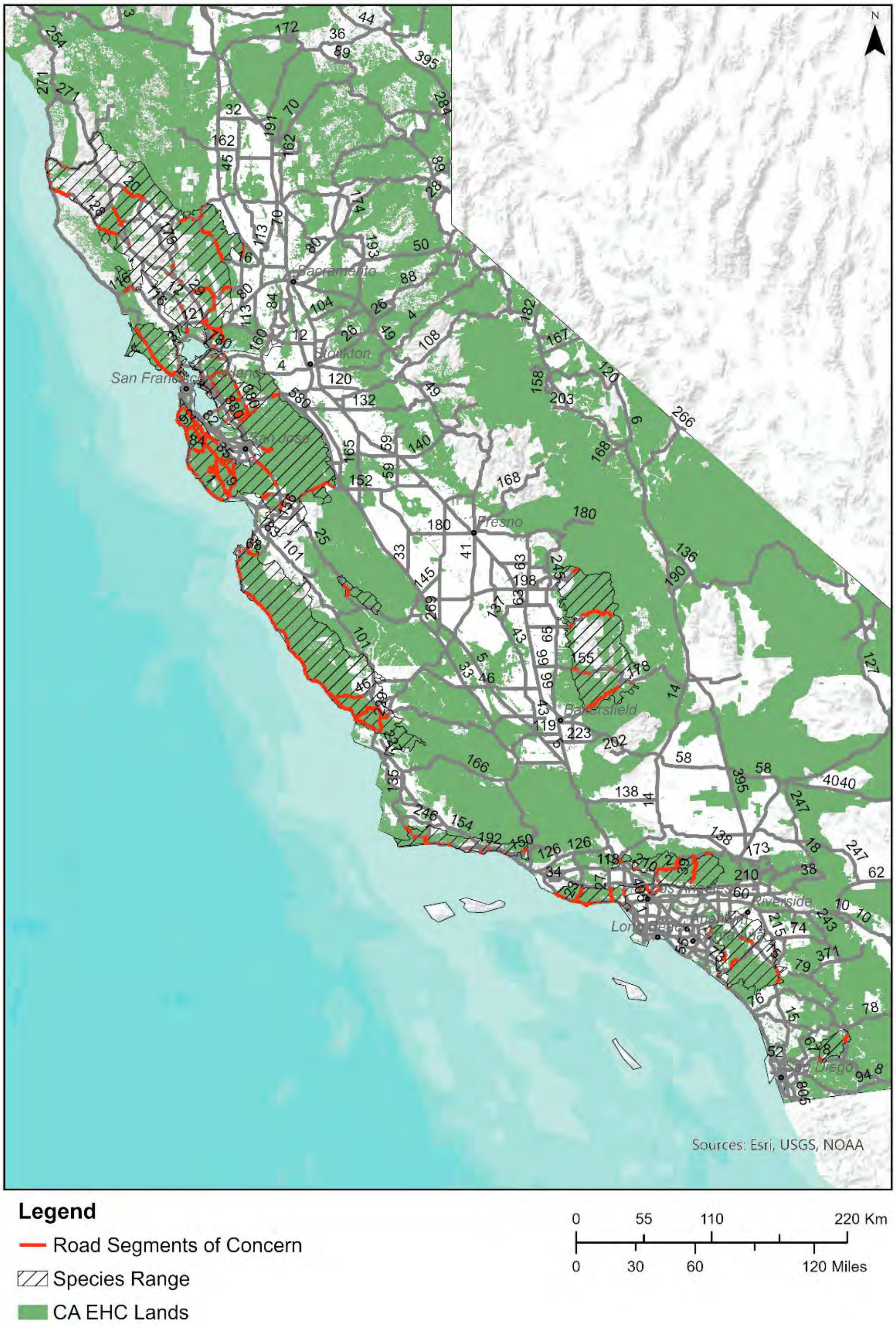


Figure 31. Highway Segments of Concern: Coast Range Newt (*Taricha torosa*)

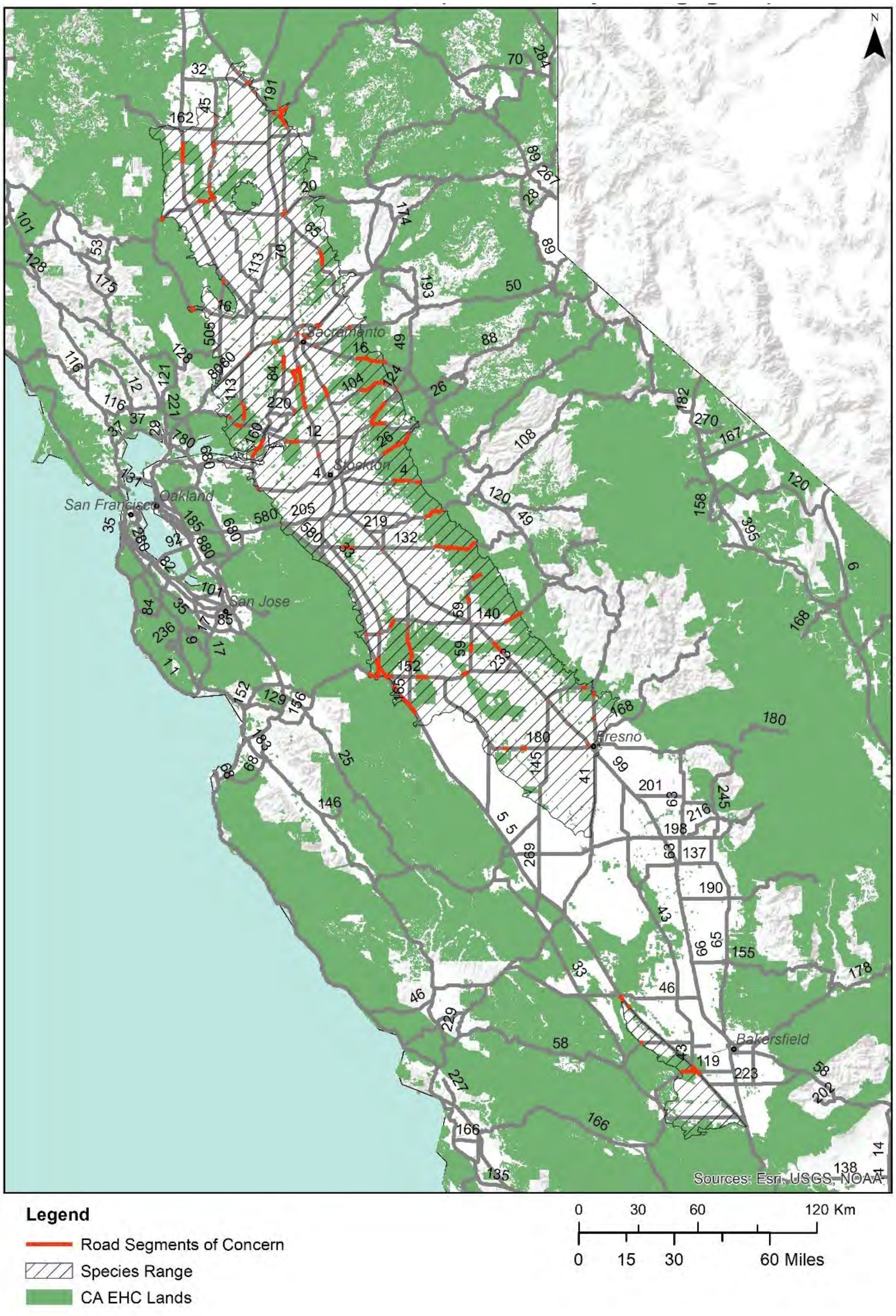


Figure 32. Highway Segments of Concern: Giant Gartersnake (*Thamnophis gigas*)

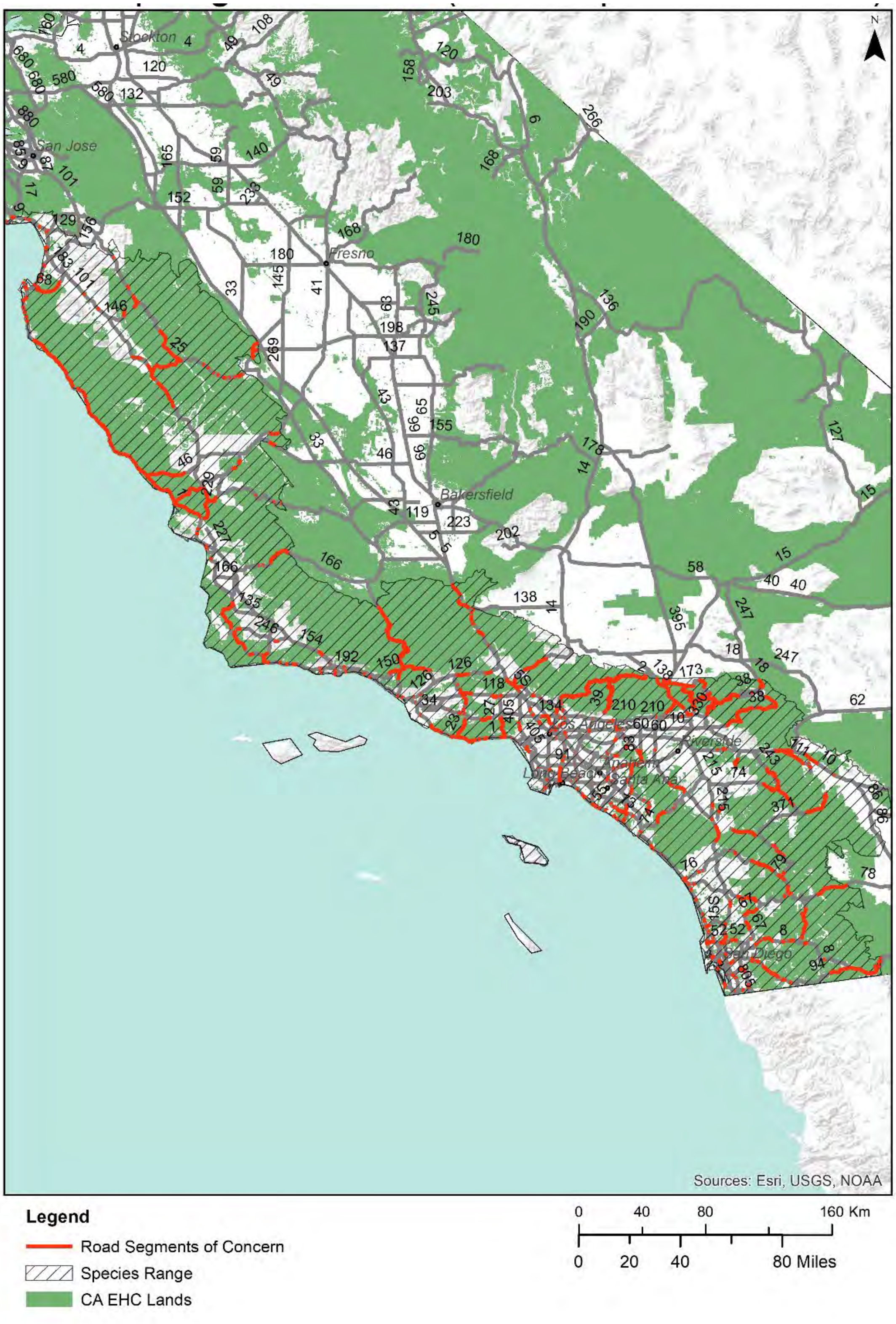


Figure 33. Highway Segments of Concern: Two-striped Gartersnake (*Thamnophis hammondii*)

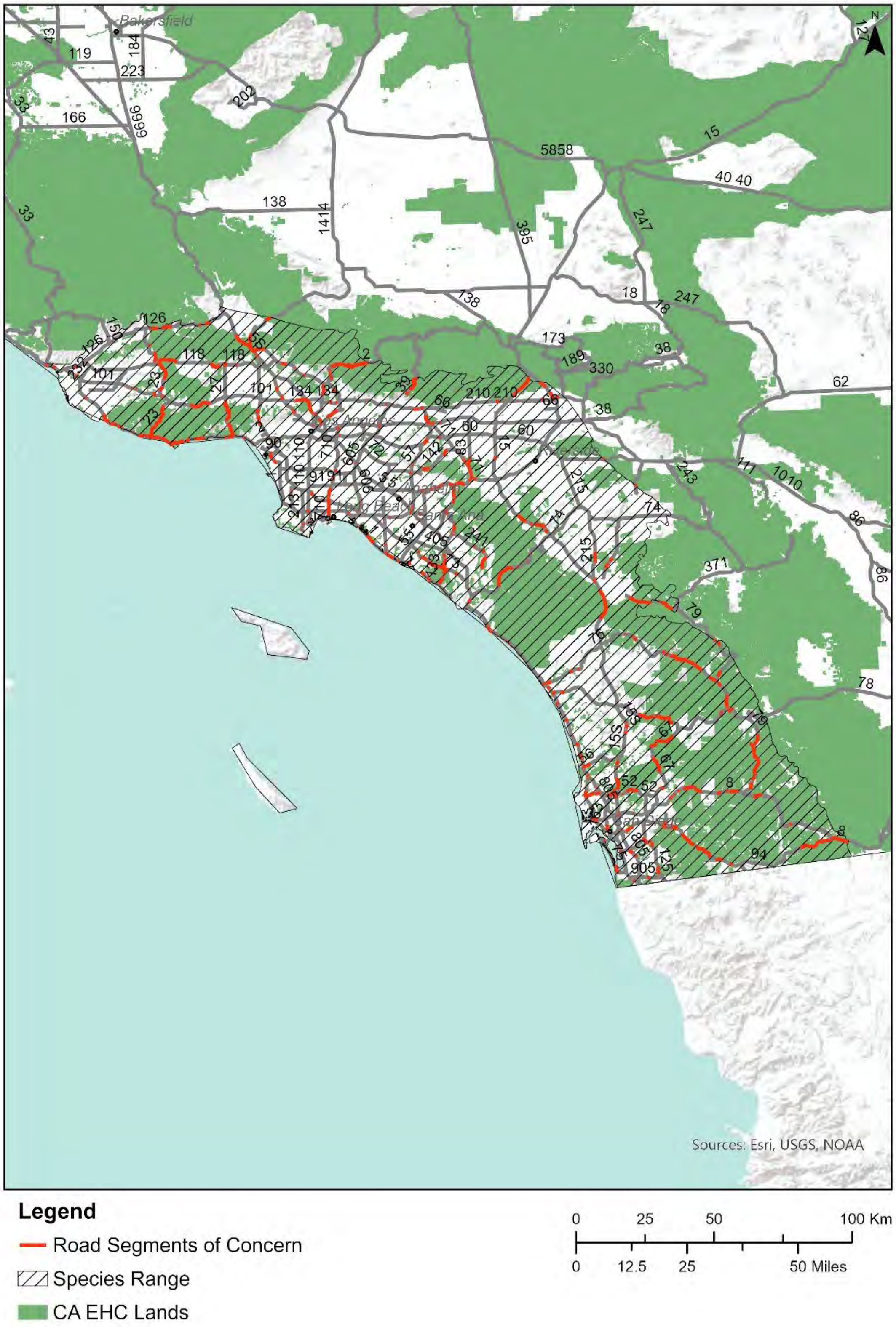


Figure 34. Highway Segments of Concern: California Red-sided Gartersnake (*Thamnophis sirtalis infernalis*)

Figure 35. Highway Segments of Concern: San Francisco Gartersnake (*Thamnophis sirtalis tetrataenia*)

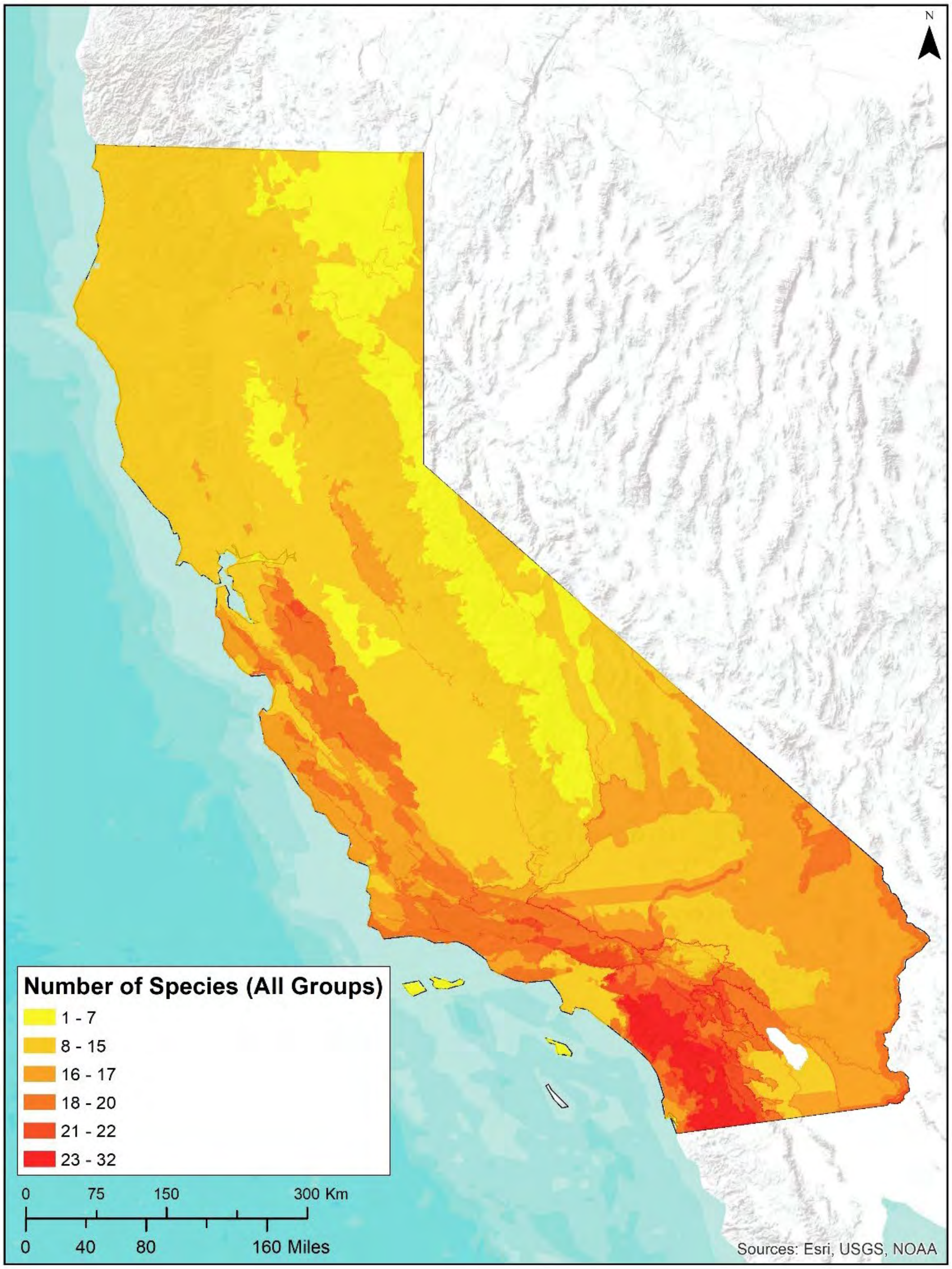


Figure 36. Range Density of Reptiles and Amphibians at High and Very-high Risk of Negative Road Impacts.

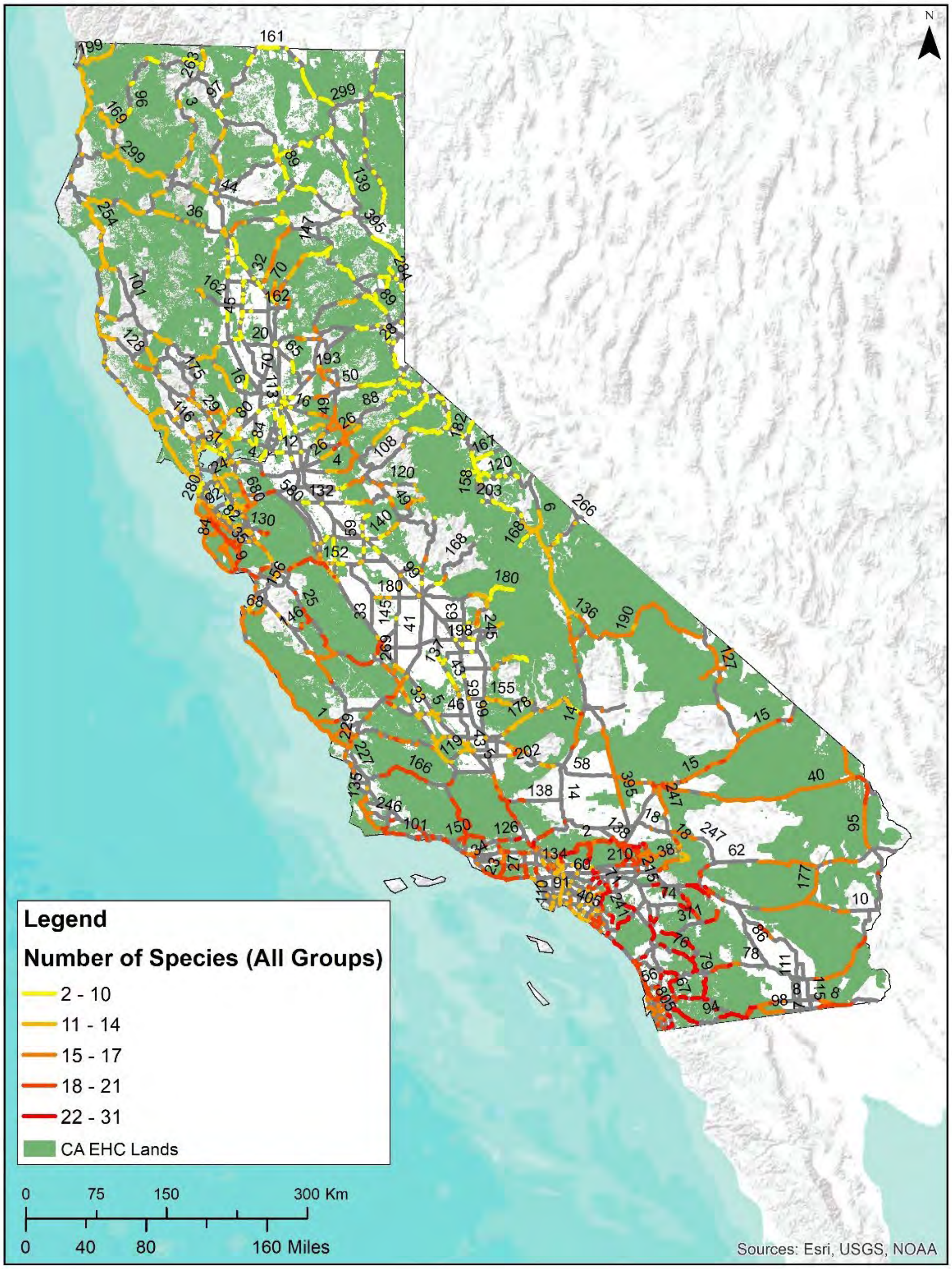


Figure 36. Range Density of Reptiles and Amphibians at High and Very-high Risk of Negative Road Impacts in Relation to California Highways

References

Spencer, WD, P Beier, K Penrod, K Winters, C Paulman, H Rustigian-Romsos, J Strittholt, M Parisi, and A Pettler. 2010. California Essential Habitat Connectivity Project: A Strategy for Conserving a Connected California. Prepared for California Department of Transportation, California Department of Fish and Game, and Federal Highways Administration.

Thomson, RC, AH Wright and NB Shaffer (2016) California amphibian and reptile species of special concern. Univ of California Press.

Chapter 4. Movement of California Tiger Salamanders Along Barrier Fencing and Underpasses in Stanford, CA

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Introduction

Many migratory amphibians make annual population level migrations among breeding wetlands and over-wintering and/or summer foraging upland terrestrial habitats. This requires high levels of connectivity among these habitats (Semlitch 2008, Hamer and McDonnell 2008, Hamer et al. 2015). Because roads often intersect these migratory pathways, all California migratory salamanders, toads and some frogs ranked in the highest risk categories for potential negative road effects, as analyzed by Brehme et al. (2018).

There is substantial evidence that habitat fragmentation and mortality due to roads negatively affect many of these amphibians. For instance, newts regularly migrate long distances over land between breeding ponds and terrestrial foraging habitats (2 km; Trenham 1998). Large numbers are found dead on roads during dispersal periods and newt species are often the first to disappear in fragmented landscapes (Gibbs 1998, Trenham 1998, Shields pers. comm.). Similarly, road mortality and habitat fragmentation are primary threats to the California tiger salamander and other Ambystomid salamanders because terrestrial habitat is used for interpond migration and overwintering (Semlitsch 1998, Trenham et al. 2001, Bolster 2010). There is also evidence that migrating bufonid toads are particularly susceptible to negative impacts from roads (Trenham et al. 2003, Orłowski 2007, Eigenbrod et al. 2008).

To reduce the negative impacts from road mortality on these vulnerable populations, it has been standard practice to build safe crossings in the form of small passages (e.g. culverts, tunnels, etc.) connected by barrier fencing as mitigation. There are a wide variety of small passages and barrier materials that have been constructed with varying degrees of success, although post mitigation monitoring is relatively rare (see review by Langton and Clevenger 2017). The permeability of tunnel systems to amphibian movement may be influenced by openness ratio ((height*width)/length), moisture and temperature conditions within the passage, noise and vibrations, and the correct placement of passages in the landscape (Jochimsen et al. 2004, Hamer et al. 2015, Langton and Clevenger 2017, Helldin and Petrovan 2019).

However, in addition to crossing success within the passage(s), the permeability of crossing systems to amphibian population movements is also dependent upon the proportion of migrating animals that even reach the passage opening. There is evidence that road mitigation systems with inadequate underpass spacing may filter movements of pond breeding amphibians (e.g. Langton 1989, Allaback and Laabs 2002, Pagnucco et al. 2012, Ottburg and van der Grift 2017, Matos et al. 2019). Individuals from a population of the common toad, *Bufo bufo,* in the Netherlands turned around or “gave-up” after an average of 50 m if they did not reach an underpass (Ottburg and van der Grift 2017). The authors considered this the main factor causing a steep population decline in the five years after the tunnel and barrier system was installed. The extent of this potential problem with other mitigation systems and species is largely unknown.

Currently, little science is available in California to inform decisions about the number of crossings and spacing between crossings. Therefore, we studied whether this “giving up” behavior is exhibited in pond breeding amphibians in California, and if so, at what distances different migratory species (and age classes of species) give-up when moving along barrier fencing? This information could inform best management practices for underpass spacing for these species.

There is also some evidence that animals may spend more time trying to climb or interact with transparent fencing compared to solid fencing (Ruby et al. 1994, Milburn-Rodriguez et al. 2016). Therefore, we were interested in whether fencing opacity affects the probability or speed at which CTS and other amphibians find wildlife crossings. Finally, we were also interested in whether ‘turnarounds’ at fence ends may be effective in altering the trajectory of CTS movement.

We studied a population of California tiger salamanders (CTS: *Ambystoma californiense*) in Stanford, CA to investigate these kinds of behaviors. In this location, a busy two-lane paved road (Juniper Serra Blvd: ave. 17,300 vehicles per day; (City of Menlo Park 2017)) transects upland habitat and Lagunita Lake, a historic CTS breeding site. Large rates of CTS road mortality spurred the construction of a three-tunnel system (5 m apart) in 2003 with approximately 5–10 m of barrier fencing on each side. For our study, we expanded the footprint of existing barrier fencing 150 m in each direction using solid fencing in one direction semi-transparent mesh fencing on the other side.

We addressed the following questions in this study:

1. What is the probability a salamander will reach an underpass based upon the distance from the underpass an animal first encounters the barrier wall?
2. How quickly do CTS travel along the barrier wall toward the underpass?
3. How does the opacity of fencing effect the questions above?
    a. Solid barrier (high-density polyethylene (HDPE-2); Animex®)
    b. Semi-transparent barrier (water- permeable rigid polymer matrix; ERTEC® E-Fence, referred to hereon as “mesh”)
4. Are fence end ‘turnarounds’ effective in redirecting the trajectory of CTS movement?
5. Once CTS reach the tunnels, what is the permeability of the road crossing tunnel system to CTS passage?

Methods

Field Study

We studied the movement of CTS adjacent to three existing underpasses along Junipero Serra Blvd. in Stanford, CA (Stanford University) in the winter breeding seasons of 2017/18 and 2018/19. The road bisects a historic CTS breeding pond (Lake Lagunita) and upland CTS habitat (Figure 1).

Figure 1. Map of Barrier and Tunnel Study System at Stanford University Between Upland and Breeding Habitat for CTS.

A total of 300 m of barrier fencing was installed along the south side of Juniper Serra Blvd. (150 m in each direction); the new fencing was connected to 5 m of existing barrier fencing adjacent to three salamander tunnels (ACO Wildlife ®). The tunnels, installed in 2003, are 14 m in length and spaced 5 m apart. One portion of the fencing installed was semi-transparent mesh (ERTEC ® rigid polymer matrix) and the other portion was solid (Animex ® high-density polyethylene (HDPE-2)). To minimize potential for vandalism, the fencing was placed within existing security fencing present on site. Jump-outs (ERTEC® cones and high berms) were installed a minimum of every 25 m along the fence to provide CTS and other small vertebrates a way to get back into the habitat if they ended up on the roadside of the barrier fencing. At outer fence ends, turnarounds were installed to redirect animals away from the road and back toward the upland habitat in a U-shaped fashion. The turnarounds were approximately 2 m long and 1 m in width. Fencing was installed with the bottom buried in the ground according to manufacturers' guidelines.

HALT ® camera systems (Hobbs and Brehme 2017) were placed every 25 m along the new fence lines from 0 to 125 m from the existing tunnel system (Figure 2). Each 0 m camera was approximately 5–8 m from the closest tunnel opening where our newly installed fencing intersected with the existing barrier fencing.

At fence end turnarounds, HALT camera systems were placed above the fence end at the turn-around to record video of animals' movement trajectory after coming out of the turn-around. Due to evidence of CTS turning around but not being recorded on video, in 2019, we narrowed the terminal end of the turnaround from 1 m to approximately 0.35 m from the main fence creating a tear drop shape. This allowed us to install the HALT trigger at the turnaround opening so that we could record animals entering and exiting the turnaround. In 2019, we also placed these camera systems within each tunnel opening and exit to record tunnel permeability. Cameras were set whenever rain was predicted and checked on a weekly basis during the winter adult migration season from the uplands toward the pond (Nov.–Feb.). Each time we set and checked the cameras, we took a photo of a battery powered atomic clock in order to calibrate exact minutes and seconds upon processing. All work was performed under Stanford University Habitat Conservation Plan (Federal incidental take permit # TE182827-0) and California State Consistency Determination (2080-2016-001-03)

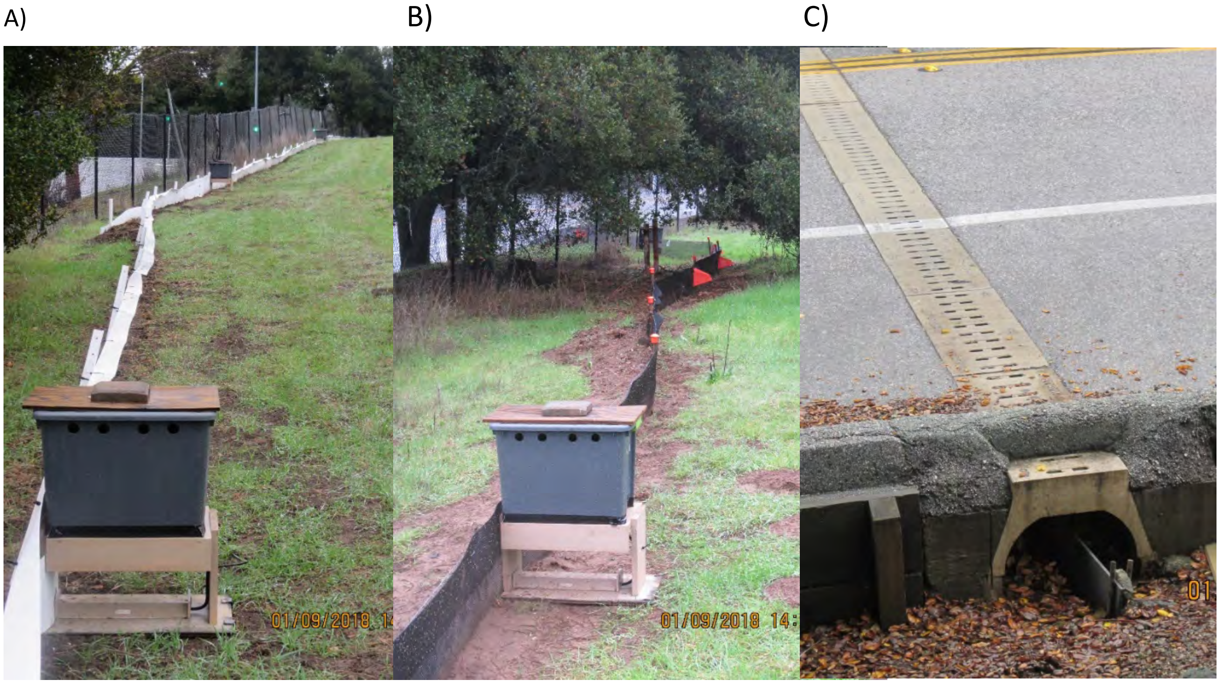

Figure2. Solid (A) and Mesh (B) Fence Lines with Cameras Within Wood Structures and Plastic Bins Facing Down Toward HALT Triggers. Fencing Leads to a Series of 3 Tunnels Under the Roadway (C).

Analysis

Photos of all CTS were analyzed using pattern recognition software to identify individuals by their unique spot patterns (I^3S Spot; Van Tienhoven et al. 2007; Figure 3). Camera location, time, and direction of movement were recorded for each individual. Snout to vent length was measured with Program ImageJ (Rasband 1997–2018) using the 1 cm grids from the HALT trigger for calibration.

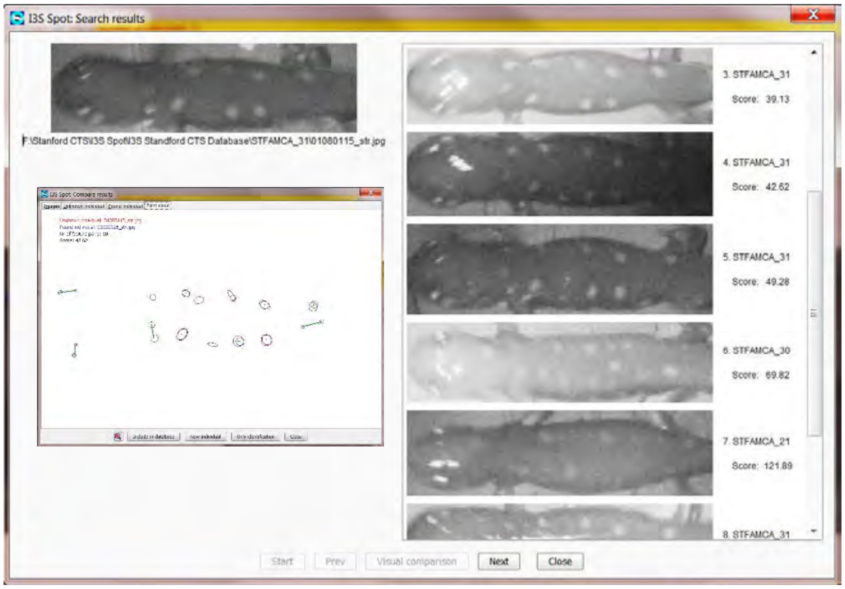

Figure 3. Example of CTS Identified to Individual Using I^3S Software to Distinguish Spot Patterns (top 3 on right are same individual)

For individual CTS, we then calculated movement distances along the fence lines, numbers of turn arounds, speed, and “success” at reaching 0 m cameras next to underpass system. Because cameras were placed 25 m apart, our margin of error for estimating fence movement distance ranged between 0 and 25 m. For instance, if an animal was only detected at a single camera between 25 m and 125m, then our average estimated distance was 25 m (12.5 m before reaching the camera and 12.5 m after exiting the camera). Similarly, if an individual was detected at multiple consecutive cameras moving in the same direction, our margin of error was typically 25 m. In the instances where individuals were detected at consecutive cameras, we also calculated the movement speed between segments. If such an individual then turned around and was re-detected at a camera while moving in the other direction, we were able to estimate the distance travelled along the fence before turning around by multiplying the time between detections by its average speed. Because of this, if individuals travelled back and forth several times, we were able to more accurately estimate the total distance of fence line traversed (fence movement distance). If an individual reached the 0 m camera (where the experimental fence lines attached to the short length of existing fence), this was considered a “success” at reaching the passage system with no added error for distance moved afterward.

We used Markov Chain Monte Carlo (MCMC) implemented in the R programming language and the runjags package (Denwood 2016) to interface with JAGS (Just Another Gibbs Sampler) to sample values of all unknown parameters from the joint posterior distribution. In each case, four chains were sampled to perform standard diagnostics for convergence. In all cases, non-informative prior distributions were used for all parameters.

Logistic Regression for Success in Reaching Underpass Opening

We modeled the probability of success of CTS in reaching the 0 m camera near the crossing opening. For this, we used a Bayesian approach to logistic regression modeling (Congdon 2006; Figure 4). The response was a Bernoulli random variable, where 0 indicates failure and 1 indicates success in being detected by the camera at the opening of the crossing (ReachedTunnel). The probability of success for the Bernoulli distribution is a logistic (i.e. p = exp(y)/(1 + exp(y)) function of the linear component of the model that consists of four predictors (FenceType, InitLoc, InitAway, InitLocAway) and five parameters that include an intercept and a regression coefficient corresponding to each of the predictors. FenceType is a binary variable where 0 indicates a mesh fence and 1 indicates a solid fence. InitLoc is the position along the fence where the animal was first detected in meters from the crossing opening (with error described in the previous paragraph), InitAway is a binary variable where 0 indicates that the animal was initially moving toward the crossing and 1 indicates it was initially moving away from the crossing, and InitLocAway is an interaction (product of) InitLoc and InitAway. All predictors were standardized (the mean subtracted from each value and then divided by the standard deviation) prior to modeling. The priors for the parameters were non-informative normal distributions with mean 0 and 0.001 precision (i.e. a variance of 1000). The parameters were sampled from their posterior distributions using MCMC (as described above) and described by mean, median, and quantiles of their marginal distributions. This allowed us to assess the effect of each predictor on the probability of success.

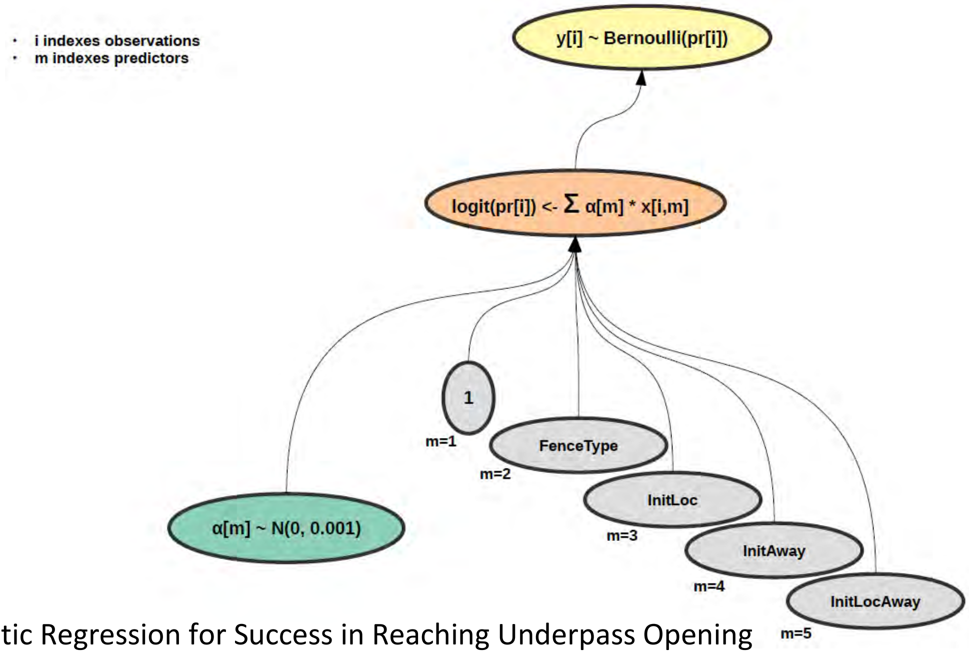

Figure 4. Logistic Regression for Success in Reaching Underpass Opening

Gamma Regression for Distance Moved Along Fence

We also modeled the distance that CTS moved along the fence. We used a Bayesian approach to regression modeling of the probability of successfully reaching the underpass opening (Figure 5). The response was assumed to be a gamma distributed random variable, which is a continuous positive variable representing the distance the animal moved along the fence as described. The gamma distribution has a shape parameter, which we assumed to be independent of any predictors, and a rate parameter that we model as an exponential (i.e. rate = exp(y)) function of the linear component of the model that consists of four predictors FenceType, InitLoc, InitAway, ReachedTunnel, InitLocAway and six parameters that include an intercept and a regression coefficient corresponding to each of the predictors. All predictors, except for ReachedTunnel, were standardized prior to modeling. The prior for the shape parameter was a non-informative exponential distribution with a rate of 0.00001. The priors for the regression parameters for the rate were normal distributions with mean 0 and 0.001 precision (i.e. a variance of 1000). The parameters were sampled from their posterior distributions using MCMC (as described above) and described by mean, median, and quantiles of their marginal distributions. This allowed us to assess the effect of each predictor on the distance moved along the fence.

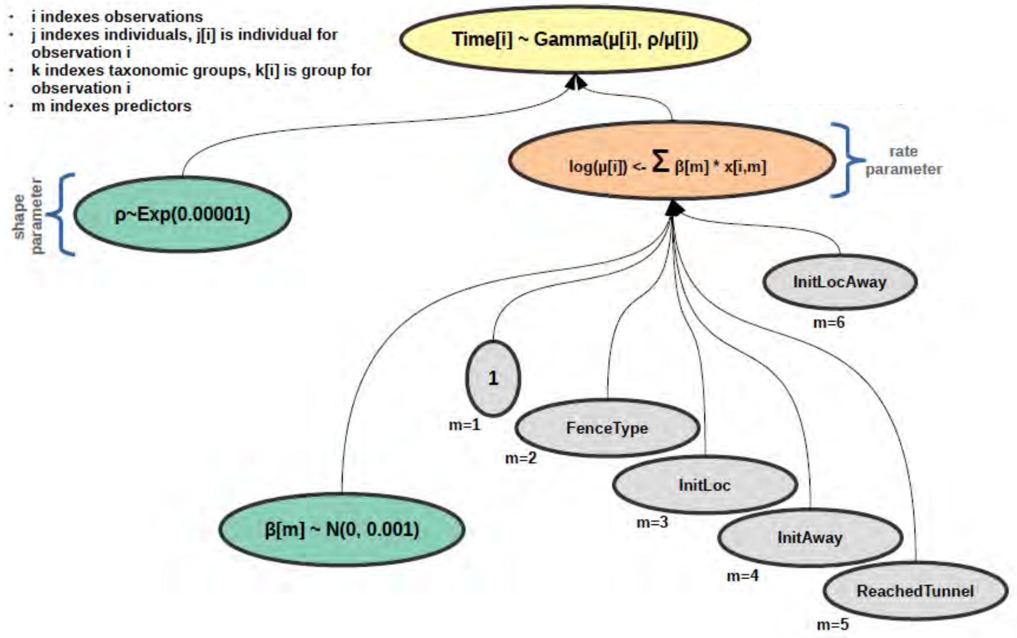

Figure 5. Gamma Regression for Distance Moved Along Fence

Tunnel System Permeability was calculated as the number of complete passes (individual detected at entrance and exit) divided by number of attempts. Other data, such as speed and turnaround rates, were also calculated.

Results

We documented 41 adult CTS over 4 nights in 2018 and 50 adults over 18 nights in 2019 moving along the fence-line. We did not compare individuals between years, and therefore, considered individual movements from 2018 and 2019 as independent in the analysis. Total precipitation during the winter months from November to March was 3.7 in. and 27.0 in. for 2018 and 2019, respectively (World Weather Online; Palo Alto). The average winter rainfall is 13 in. (Western Regional Climate Center Stn 046646-4). The Stanford University Conservation Program observed no recruitment in 2018 but confirmed high recruitment of CTS in 2019 (A. Launer and E. Adelsheim, pers. comm.).

Of the 91 CTS movements, 37 were along the solid fence line and 54 were along the mesh fence line. Fifty-six percent of CTS moved an estimated 25 m or less. Mean fence movement distances averaged approximately 40 m and did not differ by fence type. However, CTS movement speed was 43% slower and CTS changed direction an average of three times more frequently along the mesh fence than the solid fence (Table 1, Figure 6). Upon reaching the fence, 64% of CTS initially turned and moved in the direction of the passage system while 36% initially moved away from the passages. Two out of the three CTS that reached the fence ends 150 m from the passage system turned around and were subsequently documented on another camera 25-125 m away continuing to move back along the fence line.

Table 1. CTS Movement Metrics by Fence Type

		Fence Distance (m)		**Movement Speed (m/min)***		**Direction Changes (turnarounds/25m)**	
Fence Type	Sample Size	Mean	90% CI	Mean	90% CI	Mean	90% CI
Solid	37 (14*)	41.8	32.0- 47.8	2.1	1.7-2.5	0.13	0.04- 0.23
Mesh	54 (26*)	39.3	34.5- 42.2	1.2	1.0-1.4	0.41	0.15- 0.67

*individuals that passed more than one camera where movement speed was calculated

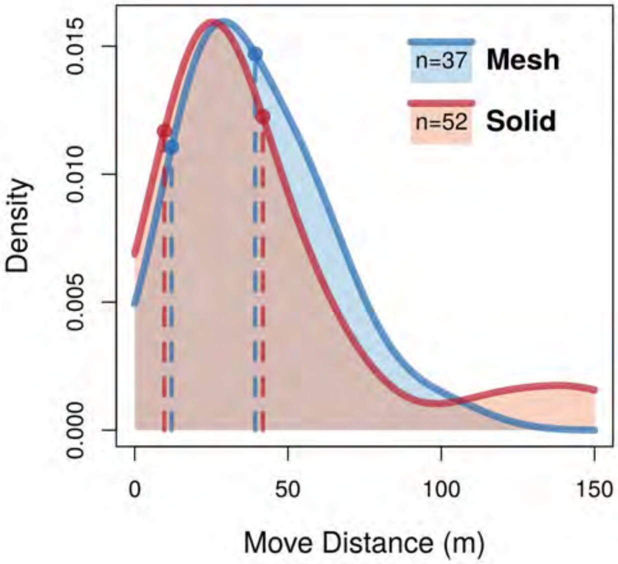

Figure 6. Distributions of Movement Distances by Fence Type. Lines Represent the Mean and Lower 90% Confidence Level Based on Cumulative Density of Observed Data.

The linear regression modeling indicates CTS moved longer distances if they encountered the fence farther away from the tunnel system. However, this was only if their initial direction choice was toward the tunnel system (Figure 7). There was no difference in predicted move distances for those CTS that encountered the fence and initially turned in the "wrong" direction

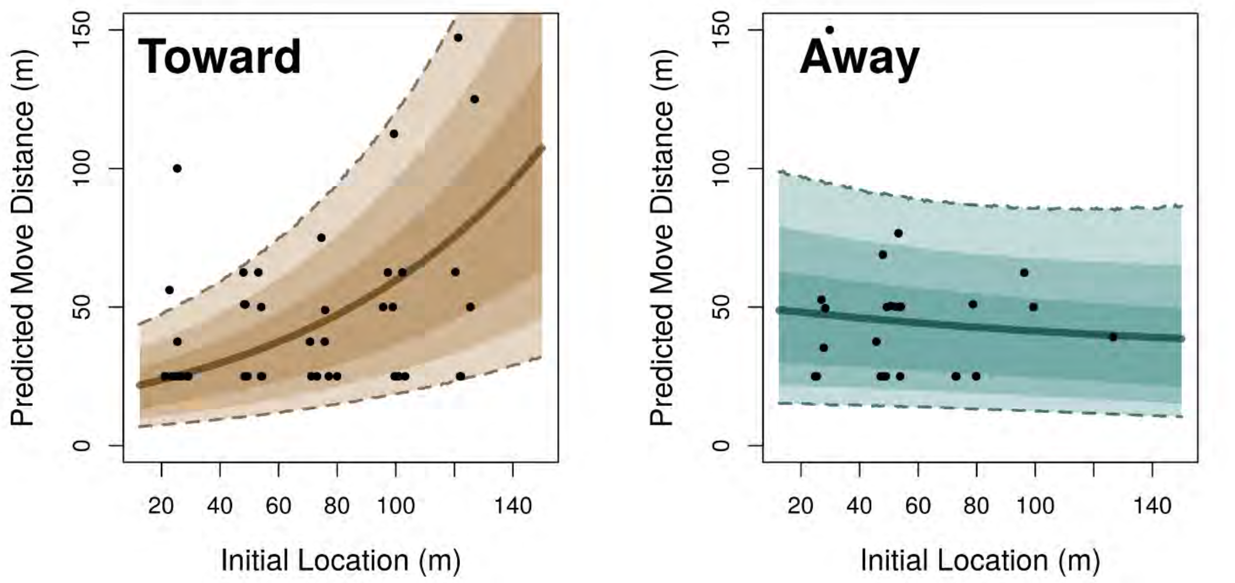

Figure 7. Movement Distance by Initial Location and Direction of Travel (Toward or Away from Underpass) with 90% Confidence Intervals.

The probability that CTS reached the tunnel system (0 m camera) decreased rapidly with increasing distance from the tunnels and was also highly dependent upon their initial direction choice. The average predicted probability of an individual reaching the tunnel system if the CTS encountered the fence at a distance of 25 m and was moving toward the tunnels was 0.48. This was reduced to only 0.15 if the CTS was initially moving away from the tunnels. Model estimated probabilities of success were lower along the mesh fencing than solid fencing, but fence type was not a significant predictor of success at reaching the underpass system (Table 2, Figure 8).

Table 2. Predicted Probabilities of Reaching Underpass by Initial Location and Direction of Travel (Toward or Away from Underpass)

	Solid Fencing				**Mesh Fencing**			
	TOWARD Underpass		**AWAY from Underpass**		**TOWARD Underpass**		**AWAY from Underpass**	
Initial Distance	Probability of Success	90% CI	Probability of Success	90% CI	Probability of Success	90% CI	Probability of Success	90% CI
12.5	.76	.57- .91	.35	.11- .64	.60	.37- .81	.20	.05- .42
25	.59	.38- .79	.21	.04- .46	.40	.21- .61	.11	.02- .24
50	.24	.08- .44	.07	.00- .25	.13	.04- .26	.03	.00- .10
75	.07	.01- .19	.03	.00-.15	.03	.00- .09	.01	.00- .06
100	.02	.00- .07	.02	.00-.10	.01	.00- .03	.01	.00- .04
125	.01	.00- .03	.01	.00- .06	.00	.00- .01	.00	.00- .02

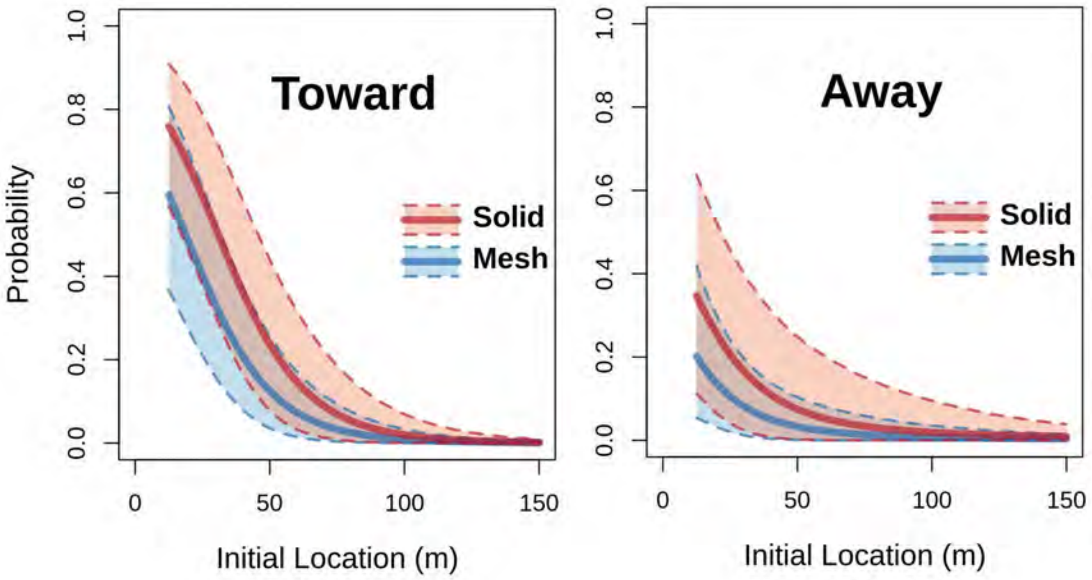

Figure 8. Probability of Reaching Underpass by Initial Location and Direction of Travel (Toward or Away from Underpass) with 90% Confidence Intervals.

Based upon timing, speed, and diagonal views of CTS entering and exiting the tunnels, we estimate that 5 to 11 out of the 51 CTS we documented traveling along the upland fence lines passed through the tunnel system from upland habitat toward the lake and 11 to 16 CTS entered the tunnels in the 20 m wide passage system without ever interacting with the fence. Once CTS entered a tunnel, there was a very high probability of them making it to the other side (0.89). Speed of passage through the tunnels was consistent with the speed at which CTS moved along the solid fencing (Table 3).

Table 3. Underpass System Permeability Metrics (2019)

No. CTS entered	**No. CTS turned around**	**No. CTS successful passage**	**Tunnel System Permeability**	**Average Individual Passage Time (min:sec)**		**Average Passage speed (m/min)**	
				Mean	90% CI	Mean	90% CI
41[a]	4	33[b]	0.89	6:33[c]	4:48- 8:18[c]	2.1[c]	1.5- 2.8[c]

[a] 4 CTS unknown if complete passage due to camera battery failure

[b] 22 CTS passed from upland to lake, 10 CTS passed from lake to upland, 1 CTS passed 3x from lake to upland to lake to upland

[c] a single passage time of 11 hours 18 min was excluded. Only CTS individual that spent day in passage.

Discussion

Our results showed that a relatively small proportion of the CTS that were documented migrating from upland habitat reached the passage system leading to breeding habitat at Lagunita Lake. CTS moved an average distance of 40 m along barrier fencing before “giving up” and their probability of making it to the passage system decreased rapidly with increasing distance from the tunnels.

The average distance moved by an individual CTS was 40 m. Approximately half of the individuals moved longer distances and half moved shorter distances before “giving up.” This did not mean that all individuals moved along the barrier fencing in one direction and then either made it to the tunnel or gave up. Many individuals moved back and forth along the fencing and the 40 m represents the average span of total fence distance moved. Although this was an average, we estimated a fence span distance of less than 12.5 m would encompass 90% of population movements from the movement density distribution. Because our cameras were set 25 m apart, we were unable to estimate the specific distance with high confidence. Our logistic model predicted that 66% of individuals encountering the fence at the median distance of 12.5 m would successfully reach the tunnel system if headed toward the passage. For suggesting minimum distances between passages across a migratory pathway, we assume that either direction a CTS turns, it will encounter a passage. Therefore, these results suggest that underpasses spaced less than 12.5 m from one another along CTS migratory pathways could provide a high level of connectivity to the population. Future studies with cameras placed closer together will allow for more precise estimates for targeted levels of permeability.

In addition to distance moved, the direction the salamanders turned when reaching the barrier fencing was a large factor in whether they reached the passage system. CTS that reached the barrier fencing and then travelled in the wrong direction (away from the passages) were significantly less likely to reach the crossing than CTS that made the correct initial direction choice. In fact, CTS that made the correct initial direction choice were also more likely to travel longer distances to reach the passages.

Other studies have estimated average movement distances of migrating long-toed salamanders along fencing to be 27 m or less (Allaback and Laabs 2003, Pagnucco et al. 2012). These results are consistent with our findings and it would be expected that CTS move farther based upon their larger body size and longer migration distances. It is possible that not all CTS were making migratory movements during our study, as they may have been foraging. However, in that case we would expect to document the same individuals on multiple dates along the fence line which was rare in our study (2 out of 91 individuals). This was the first study to passively monitor individual movements of amphibians along fencelines and tunnels using new active trigger camera traps (HALT; Hobbs and Brehme 2017).

Previous studies have employed capture-recapture by hand and with pitfall traps to actively track individuals (Allaback and Laabs 2003, Pagnucco et al. 2012, Ottburg and van der Ree 2019, Matos et al. 2019). These active methods can potentially alter animal behavior, direction, speed, movement distances and require subsampling over the active period of the target species. Matos

(2019) successfully used hand capture-recapture and fluorescent dye to track short distance foraging movements of newts (<26 m), however this method is not effective for monitoring movements over longer distances or time periods (e.g. Eggert 2002, Brehme et al. 2013). The use of these cameras coupled with individual identification by spot patterns allowed us to passively monitor species movements across the entire season along the fencing and underpasses unaffected by human presence. By calibrating cameras to atomic clocks, we were able to monitor not only distance but the precise speed of all individuals that passed by more than one camera.

It is also relevant to note that the barrier fencing was placed along a slightly curved road that created an approximate 10 to 20 degree angle leading to the passages and was perpendicular to the assumed main migratory path. Caltrans best management practices and others recommend installing barrier fencing at an angle into the habitat ("V" shaped toward the tunnel) in order to better lead migrating amphibians toward the tunnels (Federal Ministry of Transport 2000, Iuell et al. 2003, Schmidt and Zumbach 2008, Clevenger and Huijser 2011, Gunson et al. 2016, Langton and Clevenger 2020). There have not been any published studies we are aware of that directly compare the success of these configurations. However, the use of more directional fencing at a greater angle is expected reduce the proportion of individuals moving in the wrong direction away from the passage entrance. This configuration would also be expected increase movement distances along fencing because it is closer to the trajectory of the migrating amphibians. For these reasons, it is estimated that distances between passages can be farther apart with more directional fencing than with perpendicular fencing to accomplish the same level of permeability (e.g. Langton and Clevenger 2020). However, these "V" shaped configurations typically require planning of multiple passages that are spaced apart across an entire migratory pathway. In this case, there is a single crossing structure of 3 passages and placing fencing at greater angles would have excluded a substantial amount of upland CTS habitat.

If fencing must be set parallel to the roadway along an easement, it is possible that small turnarounds placed at frequent intervals along the fencing would be effective in turning individuals moving away from the tunnels in the right direction closer to the tunnel system (rather than only at fence ends). Turnarounds were shown to be effective for two out of three individuals that reached the fence ends in our study and have been shown to be effective at changing the initial trajectory of movement for lizards, snakes and toads in San Diego (Chapter 7). Future studies on the effects of multiple turnarounds are planned for this and other study sites.

The transparency of fencing (mesh vs. solid) did not significantly affect the movement distances or probability of CTS making it to the underpass system. However, the speed and time of travel were significant by fence type. CTS moving along solid fencing moved at almost twice the average speed and were 3 times less likely to turn around and repeatedly move back and forth. This indicates that CTS moving along fencing that they can see through results in them expending a higher amount of energy to make it to the crossing. We and others have shown in other studies (Ruby et al. 1994, Milburn-Rodríguez et al. 2016, Chapter 6) that animals interact with transparent fencing with behaviors such as poking, attempting to climb, and moving back and forth. Higher energy and time expenditures of these behaviors may have negative impacts on breeding success (Carr 2011, Navas et al. 2016). However, mesh fencing has benefits in ease of installation, increased permeability to wind and water, and reduced temperature and wind differentials from the surrounding environment (Boyle et al. 2019, Langton and Clevenger 2020). In concurrent studies on lizards, snakes and toads (Chapter 6), we have found that addition of a visual barrier along the bottom edge of the fence is effective in both reducing these fence interaction behaviors and increasing the speed of movement to that comparable to a full solid barrier. The potential use of visual barriers should allow flexibility in choosing fence materials for amphibian crossing systems. We intend to test this as part of a Before-After Control-Impact study at the Stanford CTS site.

Therefore, the likelihood by distance that animals reach a passage can inform the planning and spacing of crossing systems for migratory amphibians and other migratory species. Without considering this, it is possible that barrier effects of the mitigation could be worse to survivorship and connectivity than the original road mortality problem (Jaeger and Fahrig 2004, Ottburg and van der Grift 2017). This applies when high connectivity is important for the persistence of the population, such as with migratory amphibian species that must make population level movements between upland and breeding habitats (Semlitsch 2008, Hamer and McDonnell 2008, Hamer et al. 2015).

Finally, CTS that did reach the opening of the underpass system at Stanford University had a very high probability (89%) of making a complete crossing to the other side. The tunnels in our study were specially built for amphibians in that they are made of inert materials and incorporate a grid ceiling to allow natural light, moisture and rainfall to permeate the length of the passage. These have been shown to be highly permeable to amphibian movement in other locations, particularly throughout Europe (see review by Langton and Clevenger 2017). Maintenance of barrier fencing and tunnel systems is important for long term success. This includes regular inspection and repair of fencing, maintenance of vegetation by the fencing to prevent climbing, and clearing of excess debris from the tunnels (e.g. Schmidt and Zumbach 2008, van der Ree et al. 2015, Langton and Clevenger 2020).

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References

Allaback, ML. and DM Laabs. 2002. Effectiveness of road tunnels for the Santa Cruz long-toed salamander. Transactions of the Western Section of the Wildlife Society 38: 5–8.

Bolster BC. 2010. A status review of the California tiger salamander (*Ambystoma californiense*). Report to the Fish and Game Commission, State of California. Nongame Wildlife Program Report 2010–4.

Boyle, SP, R Dillon, JD Litzgus and D Lesbarrères. 2019. Desiccation of herpetofauna on roadway exclusion fencing. The Canadian Field-Naturalist 133(1): 43–48.

Brehme, CS, JA Tracey, LR McClenaghan and RN Fisher, 2013. Permeability of roads to movement of scrubland lizards and small mammals. Conservation Biology, 27(4), pp.710-720.

Brehme CS, SA Hathaway, and RN Fisher. 2018. An objective road risk assessment method for multiple species: Ranking 166 reptiles and amphibians in California. Landscape Ecology 33(6): 911–935.

Carr, JA. 2011. Stress and reproduction in amphibians. In Hormones and Reproduction of Vertebrates. Academic Press, pp. 99–116.

City of Menlo Park. 2017. Traffic Volume Data. *https://www.menlopark.org/1543/Traffic-volume-data*. Accessed May 13, 2020.

Clevenger, AP and MP Huijser. 2011. Wildlife crossing structure handbook: design and evaluation in North America (No. FHWA-CFL-TD-11-003). United States. Federal Highway Administration. Central Federal Lands Highway Division.

Congdon, P. 2006. Bayesian Statistical Modeling. 2nd ed. Wiley, West Sussex, England. 573 pages, see pp. 221–224.

Denwood, MJ. 2016. Runjags: An R package providing interface utilities, model templates, parallel computing methods and additional distributions for MCMC models in JAGS. Journal of Statistical Software 71(9): 1–25.

Eggert, C. 2002. Use of fluorescent pigments and implantable transmitters to track a fossorial toad (*Pelobates fuscus*). Herpetological Journal, 12(2): 69-74.

Eigenbrod F, SJ Hecnar and L Fahrig. 2008. The relative effects of road traffic and forest cover on anuran populations. Biological Conservation 141(1): 35–46.

Federal Ministry of Transport (Germany), Building and Housing, Road Engineering and Road Traffic. 2000. Merkblatt zum Amphibienschutz an Straßen 28 p. Germany [Guidelines for amphibian protection on roads, In German]

Gibbs JP. 1998. Amphibian movements in response to forest edges, roads, and streambeds in southern New England. Journal of Wildlife Management 62: 584–589.

Gunson, K, D Seburn, J Kintsch and J Crowley. 2016. Best Management Practices for Mitigating the Effects of Roads on Amphibian and Reptile Species at Risk in Ontario. Ontario Ministry of Natural Resources and Forestry. Queen’s Printer for Ontario. 112 pp.

Hamer, AJ and MJ McDonnell. 2008. Amphibian ecology and conservation in the urbanising world: a review. Biological Conservation, 141(10): pp. 2432–2449.

Hamer, AJ, TE Langton and D. Lesbarrères. 2015. Making a safe leap forward: mitigating road impacts on amphibians. Handbook of Road Ecology, pp. 261–270.

Helldin JO and SO Petrovan. 2019. Effectiveness of small road tunnels and fences in reducing amphibian roadkill and barrier effects at retrofitted roads in Sweden. PeerJ 7:e7518 *https://doi.org/10.7717/peerj.7518*.

Hobbs, MT and CS Brehme. 2017. An improved camera trap for amphibians, reptiles, small mammals, and large invertebrates. PLOS ONE, 12(10), p.e0185026.

Iuell, B, GJ Bekker, R Cuperus, J Dufek, G Fry, C Hicks, V Hlaváč, V Keller, B Rosell, T Sangwine and N Třrslřv. 2003. COST 341–Wildlife and traffic: a European handbook for identifying conflicts and designing solutions. URL: *https://www. milieuinfo. be/productie/beheerplone/nietacm/iene/cost-341/COST.*

Jaeger, JA and L Fahrig. 2004. Effects of road fencing on population persistence. Conservation Biology 18(6): 1651–1657.

Jochimsen DM, CR Peterson, KM Andrews, and J Whitfield Gibbons. 2004. A literature review of the effects of roads on amphibians and reptiles and the measures used to minimize those effects. Idaho Fish and Game Department and USDA Forest Service Report.

Langton, TE. 1989. Amphibians and roads; proceedings of the Toad Tunnel Conference, Rendsburg, Federal Republic of Germany, 7-8 January 1989. In Toad Tunnel Conference, 1989, Rendsburg, West Germany.

Langton, TES and AP Clevenger. 2017. Amphibian and Reptile Highway Crossings: State of the practice, gap analysis and decision support tool. Report prepared for the State of California, Department of Transportation, Division of Research, Innovation and System Information., Office of Materials and Infrastructure Research, June 2017.

Langton, TES and AP Clevenger. 2020. Measures to Reduce Road Impacts on Amphibians and Reptiles in California. Best Management Practices and Technical Guidance. Prepared by Western Transportation Institute for California Department of Transportation, Division of Research, Innovation and System Information.

Matos, C, SO Petrovan, PM Wheeler, and AI Ward. 2019. Short-term movements and behaviour govern the use of road mitigation measures by a protected amphibian. Animal Conservation 22(3): 285–296.

Milburn-Rodríguez JC, J Hathaway, K Gunson, D Moffat, S Béga and D Swensson. 2016. Road mortality mitigation: The effectiveness of Animex fencing versus mesh fencing. *https://animexfencing.com/whyanimex/animex-vs-mesh.*

Navas, CA, FR Gomes and EA De Domenico. 2016. Physiological ecology and conservation of anuran amphibians. Amphibian and Reptile Adaptations to the Environment: Interplay Between Physiology and Behavior. DV de Andrade, CR Bevier, and JE de Carvalho (eds.). CRC Press, Boca Raton, Florida, pp. 155–188.

Orłowski G. 2007. Spatial distribution and seasonal pattern in road mortality of the common toad *Bufo bufo* in an agricultural landscape of south-western Poland. Amphibia-Reptilia 28(1): 25–31.

Ottburg, FG and EA van der Grift. 2019. Effectiveness of road mitigation for common toads (*Bufo bufo*) in the Netherlands. Frontiers in Ecology and Evolution 7: 23.

Hamer, A.J. and McDonnell, M.J., 2008. Amphibian ecology and conservation in the urbanising world: a review. Biological Conservation, 141(10): 2432–2449.

Pagnucco KS, CA Paszkowski and GJ Scrimgeour. 2012. Characterizing movement patterns and spatio-temporal use of under-road tunnels by long-toed salamanders in Waterton Lakes National Park, Canada. Copeia 2012(2): 331–340. DOI 10.1643/CE-10-128.

Rasband, WS. ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, *https://imagej.nih.gov/ij/*, 1997–2018.

Ruby, DE, JR Spotila, SK Martin, and SJ Kemp. 1994. Behavioral responses to barriers by desert tortoises: implications for wildlife management. Herpetological Monographs 8: 144–160.

Semlitsch, RD. 1998. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. Conservation biology, 12(5), pp. 1113-1119.

Schmidt, BR and S Zumbach. 2008. Amphibian Road Mortality and How to Prevent It: A Review. In: Mitchell, JC; RE Jung Brown, and B Bartolomew. Urban Herpetology. St. Louis, Missouri, 157-167.Semlitsch, RD. 2008. Differentiating migration and dispersal processes for pond-breeding amphibians. Journal of Wildlife Management, 72(1): 260–267.

Trenham PC. 1998. Demography, migration, and metapopulation structure of pond-breeding salamanders. Ph.D. dissertation. University of California, Davis.

Trenham PC, WD Koenig, and HB Shaffer. 2001. Spatially autocorrelated demography and interpond dispersal in the salamander *Ambystoma californiense*. Ecology 82(12): 3519–3530.

Trenham PC, WD Koenig, MJ Mossman, SL Stark and LA Jagger. 2003. Regional dynamics of wetland-breeding frogs and toads: turnover and synchrony. Ecological Applications 13(6): 1522–1532.

Van Tienhoven AM, JE Den Hartog, RA Reijns, and VM Peddemors. 2007. A computer-aided program for pattern-matching of natural marks on the spotted raggedtooth shark *Carcharias taurus*. Journal of Applied Ecology 44: 273–280. *https://reijns.com/i3s/.*

van der Ree, R, JW Gagnon and DJ Smith. 2015. Fencing: a valuable tool for reducing wildlife-vehicle collisions and funneling fauna to crossing structures. Handbook of Road Ecology. Oxford: John Wiley & Sons, pp. 159–171.

Chapter 5. Movement of Yosemite Toads Along Barrier Fencing and a Novel Elevated Road Segment in Sierra National Forest, CA

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Introduction

Amphibians have been identified as being particularly susceptible to the negative effects of roads within their habitat (e.g. Forman et al. 2003, Rytwinski and Fahrig 2012, Andrews et al. 2015a, 2015b). Many are slow moving, do not avoid roads, and are simply too small for drivers to avoid. During rains many amphibians make long linear terrestrial movements regardless of the presence of intersecting roadways (Glista et al. 2008). In particular, pond breeding amphibians use both aquatic and terrestrial habitat for breeding, development, foraging, and overwintering, and therefore, require connectivity within and between aquatic and terrestrial habitats to support basic life history requirements. Increased mortality of amphibian populations from vehicles using roads that intersect breeding and upland habitat, if significant, can result in reduced population sizes and increased probability of extirpation (e.g. Hamer et al. 2008, Semlitsch 2008, Brehme et al. 2018, Ottburg and van der Grift 2019).

Bufonid toads can move large distances (>1 km) in both aquatic and terrestrial habitats to satisfy their annual resource requirements, and there is evidence that bufonid toads are particularly susceptible to negative impacts from roads (Trenham et al. 2003, Orłowski 2007, Eigenbrod et al. 2008). Endangered and threatened species are considered at risk of extirpation, often due to multiple stressors, and are thus thought to be less likely to be resilient to additional road impacts. Because of these attributes, the Yosemite toad ranked in the highest risk category for susceptibility to negative road impacts in a recent road risk assessment of 166 species of reptiles and amphibians in California (Brehme et al. 2018).

The Yosemite toad is a relatively long-lived toad (12–15 years) that inhabits high elevation, open, montane meadows, willow thickets, and adjoining forests in the Sierra Nevada, California. This species breeds in shallow edges of snowmelt pools and ponds or along edges of lakes and slow-moving streams. Some breeding sites dry up before larvae metamorphose. Females may breed every other year or once every three years. Although still distributed over most of its original range with many populations actively breeding and recruiting (Shaffer et al. 2000), the species has declined or disappeared from more than 50% of the sites from which it has been recorded (Jennings and Hayes 1994, Drost and Fellers 1996, USFWS 2014). Hypotheses for declines include habitat loss and degradation, disease (chytridiomycosis), airborne contaminants, livestock grazing, drought, fish predation, raven predation, road mortality and vehicle vibration effects (e.g. Hammerson et al. 2004, Davidson and Fellers 2005, USFWS 2014).

In 2017, the U.S. Forest Service, Sierra National Forest reported 126 Yosemite toads that had been run over and killed by vehicles on Forest Service roads. Of these, 92 subadults were found on the 9S09 road between June 24 and October 24. The Forest Service and U.S. Fish and Wildlife Service are particularly concerned about the potential for increased Yosemite toad road mortality due to increased vehicular traffic projected for these roads in the future.

Elevated Road Segment

A common road mitigation strategy for amphibians is to install small passages under the roadway in combination with attached barriers or fencing (1 to 2 feet or more high). The barriers are used to prevent animals from going out onto the roadway and to funnel them toward the passage(s). However, there is evidence that inadequate underpass spacing between uplands and breeding ponds may result in population declines in pond breeding amphibians (Ottburg and van der Grift 2019).

The life history of the Yosemite toad presented a unique challenge to this common mitigation strategy. Yosemite toad adults move from upland habitats to wetlands to breed during early snow melt in the spring, and then migrate back into the upland habitats shortly after breeding. Therefore, a passage-barrier system would likely only be effective for reducing road mortality during post breeding toad migrations to uplands after most of the snow has melted or during the summer migrations (including juveniles). Secondly, Yosemite toads have been shown to travel in straight line trajectories over wide areas, resulting in long lengths of roadways where they are susceptible to road mortality without any clearly defined “hot spots”.

Finally, the road is on a flat landscape, with an upland slope on one side and downward slope on the other. Burrowing passage(s) under the road would require a significant amount of grading and re-contouring on the upland slope side to make passage entrances accessible.

To meet these challenges, in June of 2018, we designed and installed a new road crossing structure in a high road mortality section of 9S09 (Figure 1). The crossing structure is an elevated roadway segment placed on top of the existing road surface and composed of hardwood laminated billet road mats that are designed for use by heavy equipment at construction sites (Emtek®). The road mats are approximately 6 in. thick and were installed on top of 8-in. high support bars installed on and perpendicular to the road, allowing for passage of small animals. They were built to meet codes and specifications for U.S. Forest Service, County, and City roads.

Diagram: Side view depiction of elevated road segment (rectangle with vertical lines) with barrier fencing (lines) and openings for toad passage underneath (solid rectangles); not to scale.

Figure 1. Diagram and Photos of Elevated Road Segment.

This proposed study is part of a larger USGS research program in collaboration with the Western Transportation Institute (WTI; Montana State University) for the California Department of Transportation (Caltrans). The larger study provides research to inform best management practices for barrier and crossing systems for sensitive amphibians and reptiles in California.

Movement along Barrier Fencing

The common toad, *Bufo bufo*, in the Netherlands turned around after an average of 50 m if they did not reach an underpass (Ottburg and van der Grift 2019). As with the California tiger salamander (Chapter 4), the distance Yosemite toads may travel along a barrier fence to find a passable crossing is unknown. Therefore, a study was warranted to determine toad movement distances along barriers to inform proper passage spacing for the Yosemite toad. There is also evidence that animals may spend more time trying to climb or get through opaque fencing compared to solid fencing (Milburn-Rodríguez et al. 2016). Therefore, we were also interested in whether fencing opacity affects the probability or speed at which the toads and other amphibians find wildlife crossings.

The results of this study will help to gauge effectiveness of this new road crossing structure, identify underpass spacing needs, evaluate barrier materials, and assess the effectiveness of fence end turnarounds for pond breeding amphibians.

Research questions:

1) What is the probability a Yosemite toad will reach an underpass based upon the distance from the underpass an animal first encounters the barrier wall?
2) How quickly do toads travel along the barrier wall toward the crossing structure?
3) How does the opacity of fencing effect the questions above?
    a. Solid barrier (high-density polyethylene (HDPE-2); Animex®)
    b. Semi-transparent barrier (water- permeable rigid polymer matrix; ERTEC® E-Fence, referred to hereon as “mesh”)
5) Is the elevated roadway segment effective in reducing road mortality while maintaining connectivity between breeding wetlands and uplands for the Yosemite toad?

Study Location:

U.S. Forest Service Road 9S09 in Sierra National Forest, CA between Yosemite toad breeding and upland habitat.

Methods

Field Study

We studied the movement of Yosemite toads adjacent to and under the ERS structure along 9S09 in Sierra National Forest, CA in the breeding seasons of 2018 and 2019. The road bisects a Yosemite toad breeding meadow and upland habitat (Figure 2).

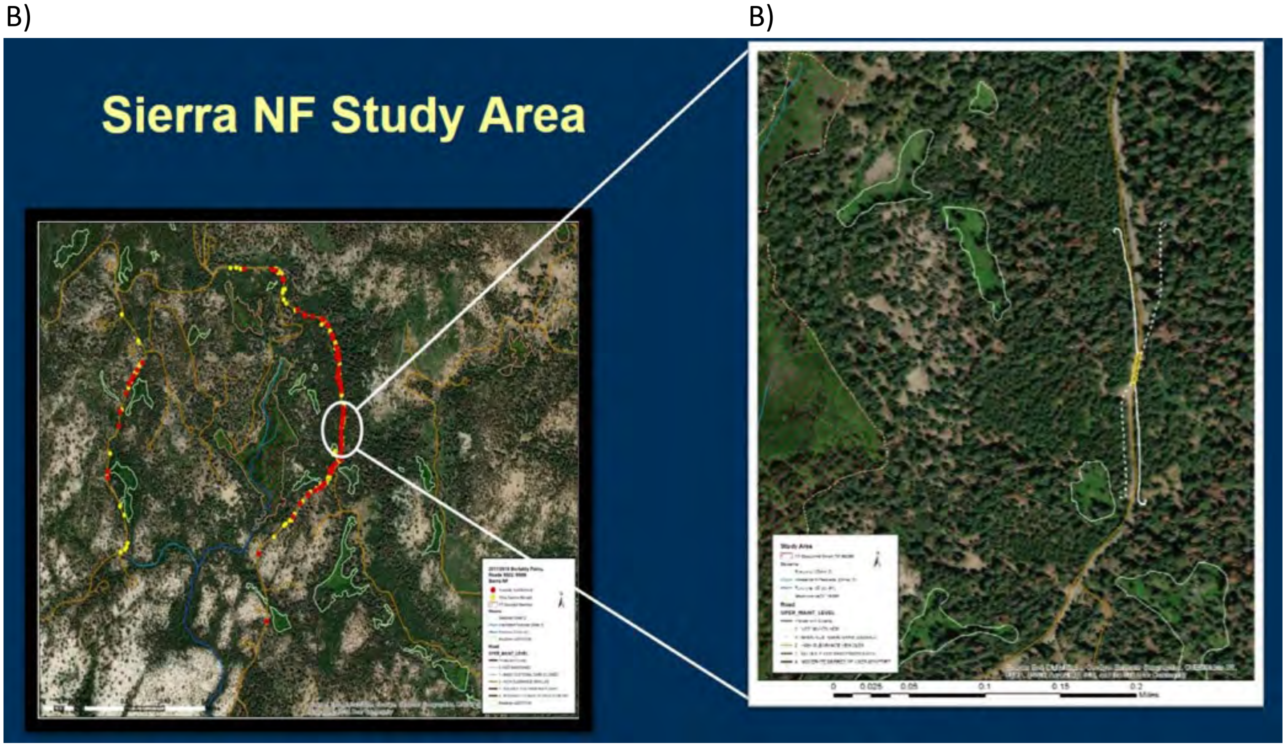


Figure 2. Maps of A) Yosemite Toad Road Mortality and B) Location of Barrier and Elevated Road Crossing in Sierra National Forest Between Upland and Breeding Habitat.

A total of approximately 480 m of barrier fencing was installed along the east and west sides of 9S09 (~120 m in each direction) connected to the ERS crossing. One portion of the fencing installed was semi-transparent (ERTEC ® rigid polymer matrix E-Fence^{TM}) and the other portion was solid (Animex® high-density polyethylene (HDPE-2)). Jump-outs (ERTEC® cones and high berms) were installed a minimum of every 10 m along the fence to provide toads and other small vertebrates a way to get back into the habitat if they ended up on the road side of the barrier fencing. At outer fence ends, turnarounds were installed to redirect animals away from the road and back toward the upland habitat in a U-shaped fashion. The turnarounds were approximately 2 m long and 1 m in width. Fencing was installed with the bottom buried in the ground according to manufacturers' guidelines.

HALT ® camera systems (Hobbs and Brehme 2017) were placed against the fencing every 20 m along the new fence lines from 0 to 100 m from the ERS (Figures 3 and 4). Each 0 m camera was approximately 8 m from the closest ERS opening to allow them to be shielded from the view of forest visitors. Cameras were set up on the wetland side as soon as possible after the road opened (spring) and were checked weekly to collect data on toads during their upland migration.

Figure 3. Schematic of Elevated Road Segment, Mesh Fencing (Dotted Lines), Solid Fencing (Lines), HALT Cameras (Circles), and Time Lapse Cameras (Black Circles); Not to Scale.

At fence end turnarounds, HALT camera systems were placed above the end terminal to record video of animals' movement trajectory after reaching the fence-ends (2018). Due to evidence of CTS turning around but not being recorded on video, in 2019, we narrowed the end of the turnaround so that the edge of the "U" was 0.4 m from the beginning of the turnaround creating a tear drop shape. This allowed us to install the trigger at the turnaround opening so that we could record animals entering and exiting the turnaround.

The extreme width of the ERS underpass made it impossible to sample completely; therefore, we had to subsample underpass activity in both space and time. For this, we placed HALT camera systems under both ERS intersections with the fence line on the west side to record tunnel entrances. We then set eight Reconyx cameras set to a time lapse of every 5 minutes on the upland side under the ERS to gather more data on animal movements.

All cameras were set as soon as the snow melted and road opened, and then checked on a weekly basis during the late spring and summer (May–Oct. 2018 and July–Oct 2019). Each time we set and checked the cameras, we took a photo of a battery powered atomic clock in order to calibrate exact minutes and seconds upon processing.

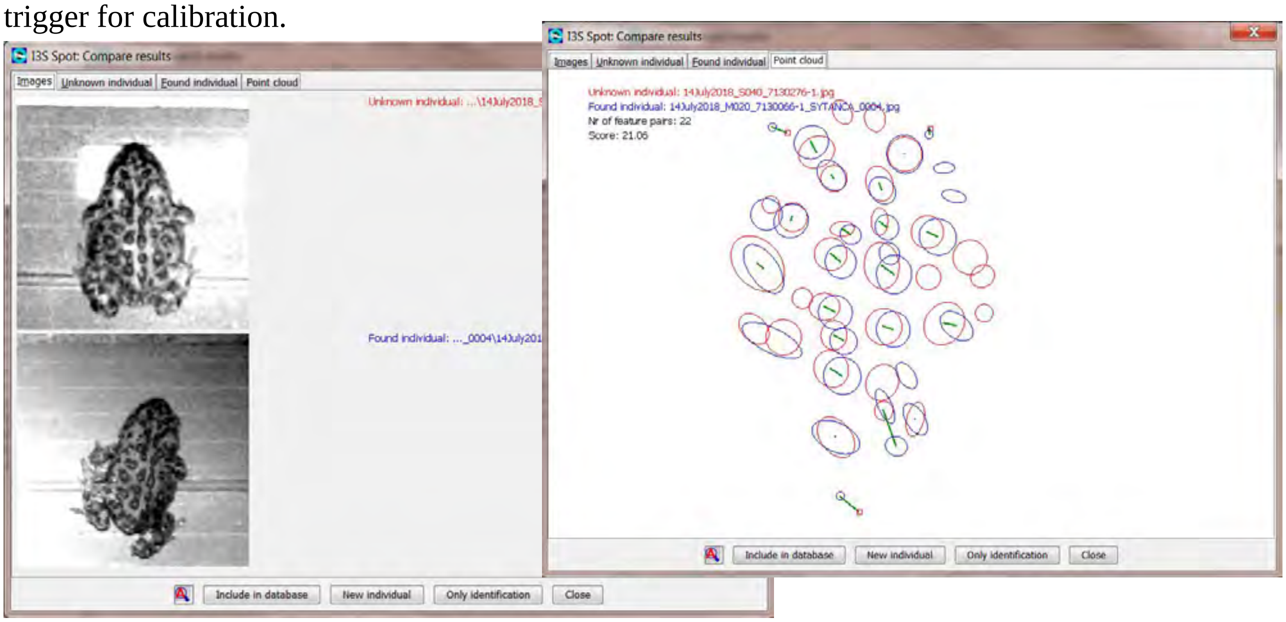
Road mortality surveys were conducted along 9S09 by the U.S. Forest Service.

Figure 4. Solid (A) and Mesh (B) Fence Lines. Along the Fences are Jump Outs and Cameras within Plastic Bins Facing Down Toward HALT Triggers.

Analysis

Movement along fence line

Photos of all Yosemite Toads were analyzed using pattern recognition software to identify individuals by their unique spot patterns (I^{3}S Spot; Van Tienhoven et al. 2007; Figure 5). Camera location, time, and direction of movement were recorded for each individual. Snout to vent length was measured with Program ImageJ (Rasband 1997-2018) using the 1 cm grids from the HALT trigger for calibration.



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Unknown individual: ...\14July2018_
Found individual: ..._0004\14July201
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Unknown individual: 14July2018_S040_7130276-1.jpg
Found individual: 14July2018_M020_7130066-1_SYTANCA_0004.jpg
Nr of feature pairs: 22
Score: 21.06
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Figure 5. Example of Yosemite Toad Identified to Individual Using i3s Software to Distinguish Spot Patterns.

For individual Yosemite Toads, we then calculated movement distances along the fence lines, numbers of turn arounds, speed, and “success” at reaching 0 m cameras next to underpass system. Because cameras were placed 20 m apart, our margin of error for estimating fence movement distance ranged between 0 and 20 m. For instance, if an animal was only detected at a single camera, then our average estimated distance was 20 m (10 m before reaching the camera and 10 m after exiting the camera). Similarly, if an individual was detected at multiple consecutive cameras moving in the same direction, our margin of error was typically 20 m. In the instances where individuals were detected at consecutive cameras, we also calculated the movement speed between segments. If such an individual then turned around and was re-detected at a camera while moving in the other direction, we estimated the distance travelled along the fence before turning around by multiplying the time between detections by its average speed. Because of this, if individuals travelled back and forth several times, we were able to more accurately estimate the total distance of fence line traversed (fence movement distance). If an individual reached the 0 m camera (where the experimental fence lines attached to the short length of existing fence), this was considered a “success” at reaching the passage system with no added error for distance moved afterward.

For models of movement along fence line, we used Markov Chain Monte Carlo (MCMC) implemented in the R programming language and the runjags package to interface with JAGS (Just Another Gibbs Sampler) to sample values of all unknown parameters from the joint posterior distribution. In each case, four chains were sampled to perform standard diagnostics for convergence. In all cases, non-informative prior distributions were used for all parameters.

Logistic Regression for Success in Reaching Underpass Opening

We modeled the probability of success of Yosemite toads in reaching the 0 m camera near the crossing opening. For this, we used a Bayesian approach to logistic regression modeling (Figure 6). The response was a Bernoulli random variable, where 0 indicates failure and 1 indicates success in being detected by the camera at the opening of the crossing (ReachedTunnel). The probability of success for the Bernoulli distribution is a logistic (i.e. $p = \exp(y)/(1 + \exp(y))$ function of the linear component of the model that consists of four predictors (FenceType, InitLoc, InitAway, InitLocAway) and five parameters that include an intercept and a regression coefficient corresponding to each of the predictors. FenceType is a binary variable where 0 indicates a mesh fence and 1 indicates a solid fence. InitLoc is the position along the fence where the animal was first detected in meters from the crossing opening (with error described in the previous paragraph), InitAway is a binary variable where 0 indicates that the animal was initially moving toward the crossing and 1 indicates it was initially moving away from the crossing, and InitLocAway is an interaction (product of) InitLoc and InitAway. All predictors were standardized (the mean subtracted from each value and then divided by the standard deviation) prior to modeling. The priors for the parameters were non-informative normal distributions with mean 0 and 0.001 precision (i.e. a variance of 1000). The parameters were sampled from their posterior distributions using MCMC (as described above) and described by mean, median, and quantiles of their marginal distributions. This allowed us to assess the effect of each predictor on the probability of success.

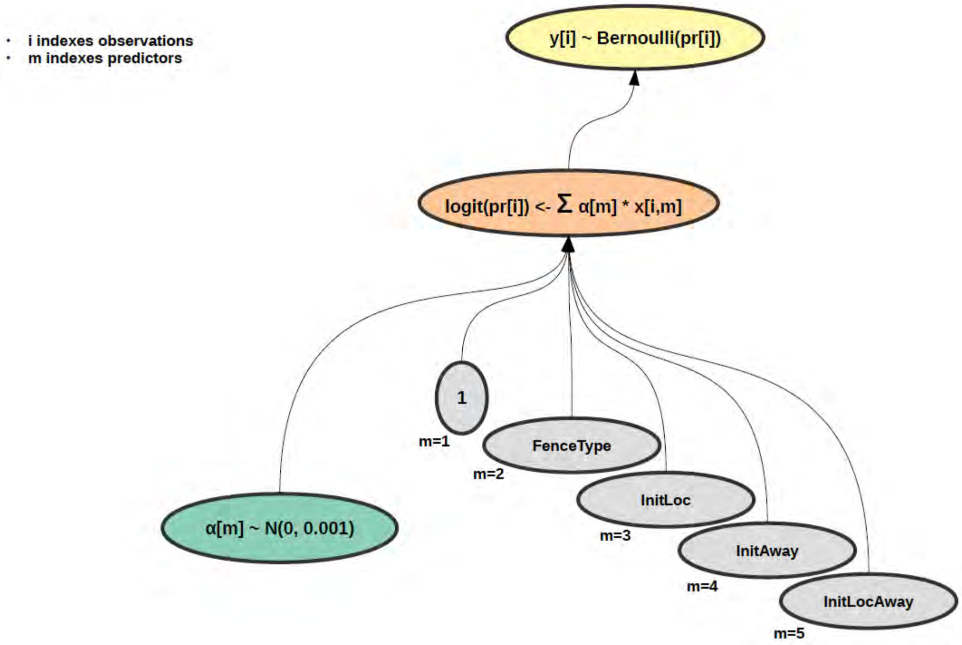

Figure 6. Logistic Regression for Success in Reaching Underpass Opening

Gamma Regression for Distance Moved Along Fence

We also modeled the distance that Yosemite toads moved along the fence. We used a Bayesian approach to regression modeling of the probability of successfully reaching the underpass opening (Figure 7). The response was assumed to be a gamma distributed random variable, which is a continuous positive variable representing the distance the animal moved along the fence as described. The gamma distribution has a shape parameter, which we assumed to be independent of any predictors, and a rate parameter that we model as an exponential (i.e. rate = exp(y)) function of the linear component of the model that consists of four predictors FenceType, InitLoc, InitAway, ReachedTunnel, InitLocAway and six parameters that include an intercept and a regression coefficient corresponding to each of the predictors. All predictors, except for ReachedTunnel, were standardized prior to modeling. The prior for the shape parameter was a non-informative exponential distribution with a rate of 0.00001. The priors for the regression parameters for the rate were normal distributions with mean 0 and 0.001 precision (i.e. a variance of 1000). The parameters were sampled from their posterior distributions using MCMC (as described above) and described by mean, median, and quantiles of their marginal distributions. This allowed us to assess the effect of each predictor on the distance moved along the fence.

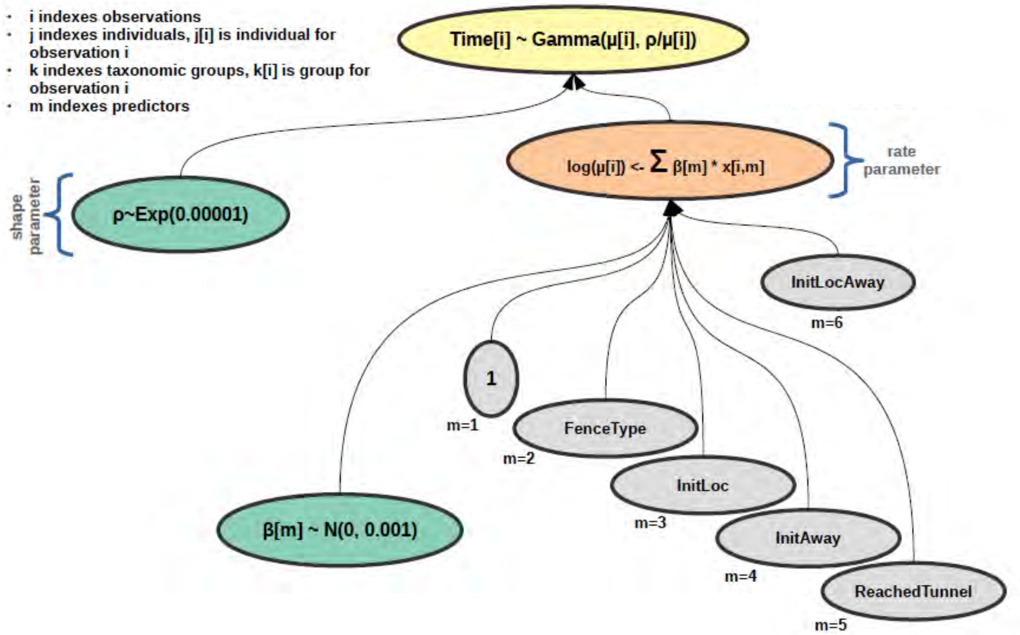

Figure 7. Gamma Regression for Distance Moved Along Fence

Elevated Road Segment Crossing

Because the ERS crossing system is so wide (>100 ft), it was not possible to monitor the entire underpass. Therefore, we subsampled by placing two HALT cameras along the fence lines underneath the ERS (wetland side) and eight Reconyx time lapse cameras underneath middle portions of the ERS on the upland side (Figure 1: not to scale). All active trigger camera images were considered a single species event if within one minute of each other. Because of the large number of time lapse images generated, they were only scanned for the presence of Yosemite toads during time periods they were detected with the HALT cameras along the fence lines.

To assess ERS crossing permeability, we analyzed the number of individual Yosemite toads monitored along the fence that reached the passage. For all species, we also compared the relative number of species detections immediately outside the ERS (red circles; 0 m cameras) vs. under the ERS on each side (yellow circles; Figure 8).

Red circles: HALT cameras immediately outside of ERS system
Yellow circles: HALT cameras underneath ERS adjacent to the fence line
Black open circles: Time lapse cameras placed underneath the ERS on the upland (terrestrial) side facing toward the wetland habitat side. Note: length of ERS not to scale and numbers of time lapse cameras greater than depicted (8).

Figure 8. Schematic of General Locations of Cameras Used to Monitor ERS Permeability (Red and Yellow Circles).

Results

Due to road closures during winter and spring months, we began monitoring upland toad movements immediately after snow melt and during the summer months when toads are typically active and moving during rainfall events. Total summer precipitation in nearby Huntington Lake during the monitoring periods was 1.12 in. for 2018 (June-Oct) and 0.59 in. for 2019 (July- Oct) after the snow melt (Huntington Lake Historical Weather; worldweatheronline). Both summer seasons were approximately 3.0 in. below average rainfall during these periods (Western Regional Climate Center 044176-5). Breeding and recruitment were documented by USFS in 2019; however, we likely missed most of the upland dispersal at the site due to the extended period of snowpack through June and lack of access to the site during this time.

Fence Movement

We documented a total of 37 individually identified Yosemite toads in 2018 (24 over 12 nights) and 2019 (13 over 6 nights) moving along the fence-line. Five or fewer individuals (5 photos) were not included in the initial analysis due to low confidence in these identifications. Of the 37 individuals in the analysis, 19 were subadults (<44 mm snout-to-vent length (SVL)) and 18 were adults (>44 mm SVL). Among fence types, eight subadults and 13 adults were recorded along the mesh and 11 subadults and five adults were recorded along the solid. We considered individual movements from 2018 to 2019 as independent in the analysis.

Because our sample size was low, confidence intervals are extremely wide for most parameters. We present averages and confidence intervals of fence distance, movement speed, and direction changes (i.e. back and forth movements) among fence types and age classes in Table 1.

Fence movement distances averaged approximately 52 m (Table 1, Figure 9) and did not significantly differ by fence type or age class, although mean distance moved was farther along the solid (63 m) than mesh (43 m) fencing. With these preliminary data, there were no significant differences in the response variables by fence type. Yosemite toads moved an average of 1 m/min and changed directions an average of 0.5 times per 20 m (i.e. per camera location). Adults were 71% faster than subadults and changed directions 75% more often, although not significantly.

Seven out of 10 Yosemite toads changed course at a turnaround back toward the fence line or out into habitat, and of these, four toads were subsequently documented on other cameras 40-80 m away continuing to move back along the fence line.

Table 1. Yosemite Toad Movement Metrics by Fence Type and Age Class

			Fence Distance Moved (m)		**Movement Speed (m/s)***		**Direction Changes per 20m**	
		Sample Size	Mean	90% CI	Mean	90% CI	Mean	90% CI
By Fence Type	Solid	16 (13*)	63.3	10- 109	1.0	0.7- 1.3	0.6	0.3- 0.9
	Mesh	21 (9*)	43.2	10- 105	0.9	0.6- 1.2	0.5	0.2- 0.8
By Age Class	Subadult	19 (13*)	48.9	38.3- 59.6	0.7	0.6- 0.9	0.4	0.2- 0.6
	Adult	18 (9*)	43.1	30.0- 56.3	1.2	1.0- 1.5	0.7	0.4- 1.0
All Toads		**37**	**52.3**	**10- 110**	**1.0**	**0.6- 1.3**	**0.5**	**0.3- 0.7**

*individuals that passed more than one camera where movement speed was calculated

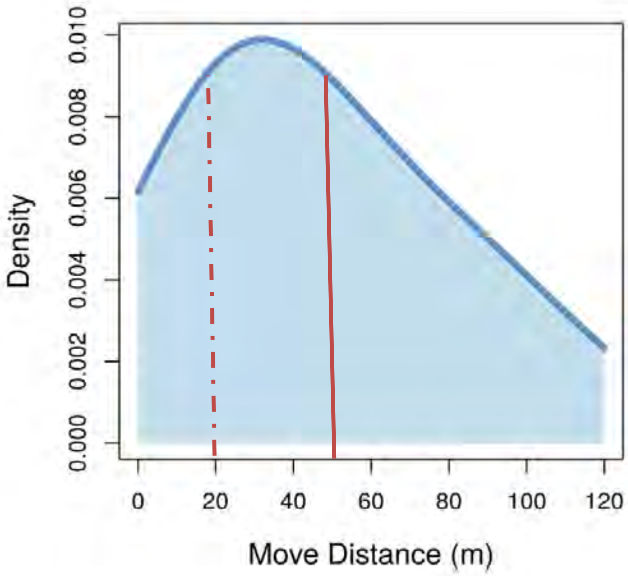

Figure 9. Distributions of Movement Distances. Lines Represent Mean (Solid) and Lower 90% Confidence Interval (Dashed).

The linear regression modeling showed a general pattern similar to that of CTS but with low slopes and low confidence. Yosemite toads moved shorter distances if they encountered the fence closer to the tunnel system and their initial direction was toward the tunnel system. There was no difference in predicted move distances for the toads that encountered the fence and turned in the "wrong" (away) direction (Figure 10).

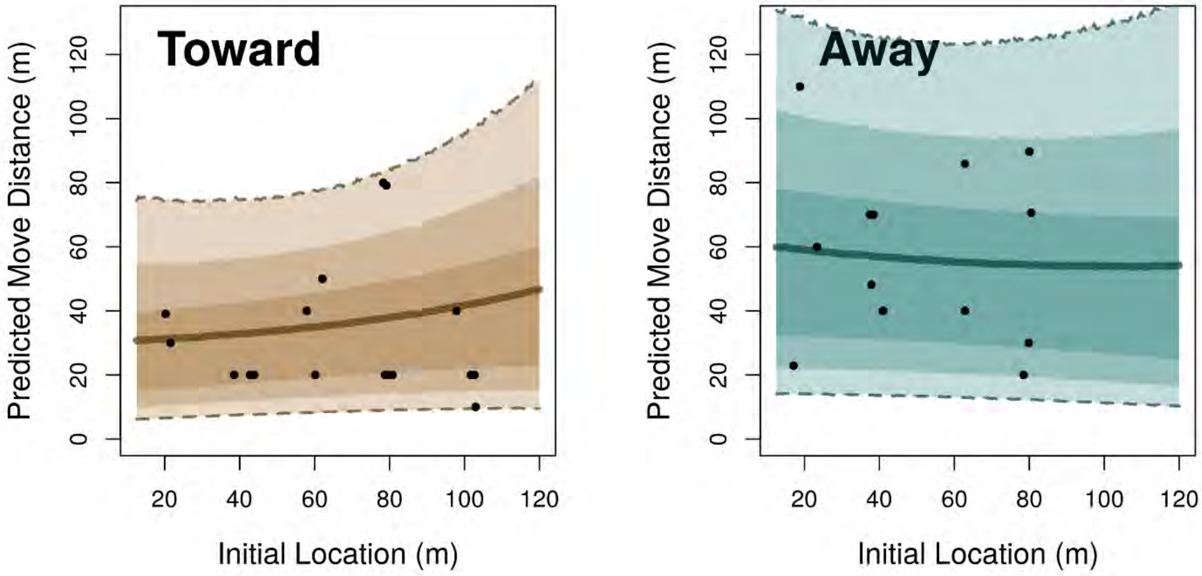

Figure 10. Movement Distance by Initial Location and Direction of Travel (Toward or Away from Underpass) with 90% Confidence Intervals.

The probability that Yosemite toads reached the tunnel system (0 m camera) decreased rapidly with increasing distance from the ERS system and was also highly dependent upon their initial direction choice. Yosemite toads had a high probability of reaching the ERS underpass if they encountered the fence at a distance of 20 m (mesh fencing) to 40 m (solid fencing) and were moving toward the ERS. Probabilities rapidly declined beyond those distances and were low if the toads were moving away from the ERS (Table 2, Figure 11). The estimates close to 1.0 and 0.0 indicated more data is needed to more accurately predict the probabilities of success in this system.

Table 2. Probability of Reaching Underpass by Initial Location, Direction of Travel (Toward or Away from Underpass), and Fence Type.

	Solid Fencing				Mesh Fencing			
	TOWARD Underpass		AWAY from Underpass		TOWARD Underpass		AWAY from Underpass	
Initial Location (m)	Probability of Success	90% CI	Probability of Success	90% CI	Probability of Success	90% CI	Probability of Success	90% CI
10	1.00	1.00- 1.00	.48	.21- .75	1.00	.99- 1.00	.01	.00- .06
20	1.00	1.00- 1.00	.44	.20- .70	.91	.41- 1.00	.01	.00- .05
40	.65	.00- 1.00	.37	.14- .63	.02	.00- .11	.01	.00- .04
60	.04	.00- .27	.32	.07-.63	.00	.00- .00	.01	.00- .03
80	.00	.00- .00	.28	.04-.68	.00	.00- .00	.00	.00- .02
100	.00	.00- .00	.25	.01-.72	.00	.00- .00	.00	.00- .02

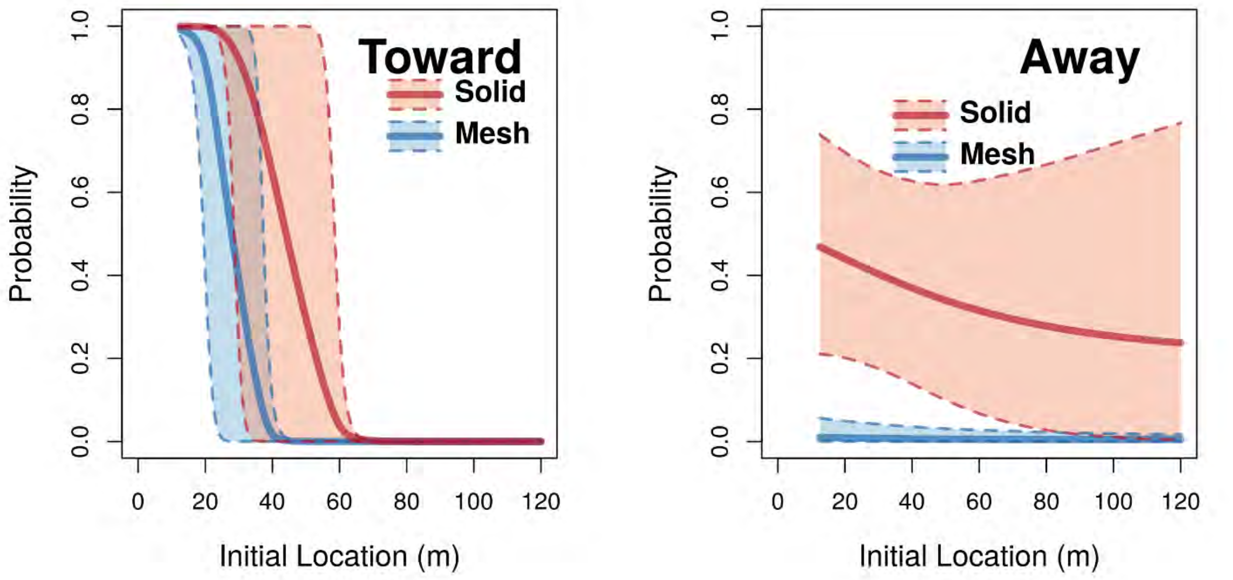

Figure 11. Probability of Reaching Underpass by Initial Location, Direction of Travel (Toward or Away from ERS), and Fence Type with 90% Confidence Intervals. Note that more samples are needed to better inform the models.

Underpass Permeability

Of the eight Yosemite toads that were tracked moving toward the ERS system at one of the “0 m” cameras (~5 m from the ERS entrance), three moved underneath at the first immediate right/left turn from the barrier fencing into the ERS and two moved along the length of the ERS (not underneath) to the barrier fencing on the other side. It is possible the other three toads moved under the bridge but not across a HALT trigger. Toads were detected on the time lapse cameras during the periods of their activity but could not be identified to individual.

Twenty-four other Yosemite toads that moved under the ERS were detected by one of the two HALT triggers (16 toads) or by a time lapse camera (8 toads). These data represent only a subsample of available linear width of the ERS system, so we suspect many more Yosemite toads passed under the crossing. At an average movement speed of 1 m/min and a field of depth of about 1 m, we estimate the eight time-lapse cameras subsampled toads across approximately 40% of the linear length of the ERS for 20% of the time. Because of this, we expect the total number of toads that moved under the ERS was likely closer to 100 during the time periods monitored.

The relative activity of Yosemite toads immediately inside vs. outside (~5 m from opening) of the ERS crossing system was almost equal (20 vs. 19 events; Table 3). The relative activity of other animals varied by species and groups. In general, mammals were detected at greater rates underneath vs. outside the ERS system (ratio 3.1), while reptiles and amphibians were detected at slightly lower rates underneath vs. outside the ERS system (ratios 0.70 and 0.83).

			RELATIVE ACTIVITY		
			Outside	Inside	Ratio
AMPH	Pacific Treefrog	*Hyla regilla*	209	174	0.83
	Yosemite Toad	***Anaxyrus californica***	**20**	**19**	0.95
	Sierra Nevada Ensatina	*Ensatina eschscholtzii platensis*	12	4	0.33
	Unknown salamander		0	3	na
		Subtotal Amphibians	241	200	0.83
REPT	Mountain Gartersnake	*Thamnophis elegans elegans*	25	14	0.56
	Rubber Boa	*Charina bottae*	6	4	0.67
	Sierra Alligator Lizard	*Elgaria multicarinata*	6	7	1.17
	Western Fence Lizard	*Sceloporus occidentalis*	6	2	0.33
	Unknown lizard		1	4	4.00
		Subtotal Reptiles	44	31	0.70
MAMMALS	Mice/Rats	*Family Rodentia*	165	534	3.24
	CA ground squirrel	*Otospermophilus beecheyi*	19	38	2.00
	Long-tailed Weasel	*Mustela frenata*	0	1	>1.0
	Spotted skunk	*Spilogale putorius*	0	4	>1.0
	American marten	*Martes americana*	0	2	>1.0
	Chipmunk	*Neotamias spp.*	3	1	0.33
	CA Vole	*Microtus californicus*	2	1	0.50
	Shrew	*Sorex spp.*	1	16	16.00
	Yellow-bellied Marmot	*Marmota flaviventris*	1	1	1.00
		Subtotal Mammals	191	598	3.13

Table 3. Relative Activity by Species Immediately Inside vs. Outside Elevated Road Segment.

Discussion

Although the sample size was low due to seasonal weather and sampling constraints, we found similarities between the fence movement behavior of Yosemite toads and CTS (Chapter 4). On average, Yosemite toads moved a distance of 52 m along barrier fencing before "giving up" and their probability of making it to the crossing decreased rapidly with increasing distance from the ERS. This is very close to the 50 m average that Ottberg and van der Grift (2019) reported for *Bufo bufo* in the Netherlands. Many individuals moved back and forth along the fencing and the average of 52 m represents the average span of total fence distance moved. Therefore, approximately half moved greater distances and half moved smaller distances with approximately 90% of toads estimated to move 20 m or more. Because our cameras were set 20 m apart, we were unable to estimate the specific distances with high confidence. However, these preliminary results suggest that passages spaced within 20 m of one another along Yosemite toad migratory pathways should provide connectivity to 90% of the population.

As with CTS, the likelihood that only some animals will reach a passage informs planning and monitoring of crossing systems for migratory amphibians and other migratory species. Without considering this in planning for distances between crossings, there is a potential for crossing systems constructed to reduce road mortality to become a barrier to population level movements.

In addition to distance moved, the direction Yosemite toads turned when reaching the barrier fencing was a large factor in whether they reached the crossing. Toads that reached the barrier fencing and then travelled in the wrong direction (away from the tunnels) were significantly less likely to reach the crossing than toads that made the correct initial direction choice. In fact, it appeared that, as with CTS, toads that made the correct initial direction choice were also more likely to travel longer distances to reach the tunnels.

It is possible that not all Yosemite toads were making migratory movements during our study, as they may have been foraging. However, in that case we would expect to document the same individuals on multiple dates along the fence line which was rare in our study.

The transparency of fencing (mesh vs. solid) did not significantly affect the movement distances or probability of making it to the underpass system, although the estimated probabilities were slightly less for the semi-transparent fencing. Unlike CTS, there was no apparent difference in speed or turnaround rates (moving back and forth) by fence type in the preliminary data for Yosemite toads.

We caution that a greater sample size is needed to accurately predict the probability of success by initial distance from passage, direction choice, and effects of fence type and age class on Yosemite toad movements along the fence lines. Continued data collection in future years and placement of additional cameras at 10 m along the fence lines will allow for higher confidence in these estimates.

Finally, initial results showed that the ERS crossing has a high potential to provide increased connectivity for Yosemite toads and a wide range of other amphibian, reptile, and small mammal species while greatly reducing road mortality (no road mortality of Yosemite toads has been documented in the project footprint since installation of the ERS; S. Barnes, USFS, pers. comm.). This new prototype crossing can be made to any length, creating a wide passage without constricting migratory movements to small tunnels. The prototype ERS also allows natural light, moisture and rainfall to permeate the length of the passage so that climate and moisture underneath is similar to that outside. The large width of the passage does present challenges in monitoring successful crossings due to the wide monitoring area. We are exploring the use of different camera systems, additional cameras, and wildlife tracking techniques to better monitor movements near and underneath the passage in the future.

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References

Andrews KM, P Nanjappa and SP Riley (eds), 2015a. Roads and ecological infrastructure: concepts and applications for small animals. JHU Press, Baltimore, MD.

Andrews KM, TA Langen and RPJH Struijk. 2015b. Reptiles: Overlooked but often at risk from roads. Handbook of Road Ecology. Wiley, New York, pp. 271–280.

Brehme, CS, SA Hathaway, and RN Fisher. 2018. An objective road risk assessment method for multiple species: ranking 166 reptiles and amphibians in California. Landscape Ecology 33(6): 911–935.

Davidson C and GM Fellers. 2005. *Bufo canorus*. In: Lannoo M (ed) Amphibian declines: the conservation status of United States species. University of California Press, Berkeley, pp. 430–432.

Drost, CA and GM Fellers. 1996. Collapse of a regional frog fauna in the Yosemite area of the California Sierra Nevada, USA. Conservation Biology 10: 414–425.

Eigenbrod F, SJ Hecnar and L Fahrig. 2008. The relative effects of road traffic and forest cover on anuran populations. Biological Conservation 141(1): 35–46.

Forman RT, D Sperling, JA Bissonette, AP Clevenger, CD Cutshall, VH Dale, L Fahrig, R France, CR Goldman, K Heanue and JA Jones. 2003. Road ecology. Science and Solutions. Island Press, Washington.

Glista DJ, TL DeVault and JA DeWoody. 2008. Vertebrate road mortality predominantly impacts amphibians. Herpetological Conservation and Biology 3(1): 77–87.

Hamer, AJ. and MJ McDonnell. 2008. Amphibian ecology and conservation in the urbanising world: a review. Biological Conservation 141(10): 2432–2449.

Hammerson, G, R Grasso and C Davidson. 2004. *Anaxyrus canorus*. The IUCN Red List of Threatened Species 2004: e.T3180A9659674. *https://dx.doi.org/10.2305/IUCN.UK.2004.RLTS.T3180A9659674.en.* Downloaded on 28 May 2020.

Hobbs, MT and CS Brehme. 2017. An improved camera trap for amphibians, reptiles, small mammals, and large invertebrates. PLOS ONE 12(10), p.e0185026.

Jennings, MR and MP Hayes. 1994. Amphibian and reptile species of special concern in California (p. 255). Rancho Cordova, CA: California Department of Fish and Game, Inland Fisheries Division.

Milburn-Rodríguez JC, J Hathaway, K Gunson, D Moffat, S Béga and D Swensson. 2016. Road mortality mitigation: The effectiveness of Animex fencing versus mesh fencing. *https://animexfencing.com/whyanimex/animex-vs-mesh*.

Orłowski G. 2007. Spatial distribution and seasonal pattern in road mortality of the common toad *Bufo bufo* in an agricultural landscape of south-western Poland. Amphibia-Reptilia 28(1): 25–31.

Ottburg, FG and EA van der Grift. 2019. Effectiveness of road mitigation for common toads (*Bufo bufo*) in the Netherlands. Frontiers in Ecology and Evolution 7: 23.

Hamer, AJ and McDonnell, MJ, 2008. Amphibian ecology and conservation in the urbanising world: a review. Biological Conservation 141(10): 2432–2449.

Rasband, WS. 1997–2018. ImageJ,. US. National Institutes of Health, Bethesda, Maryland, USA, *https://imagej.nih.gov/ij/.*

Rytwinski T and L Fahrig. 2012. Do species life history traits explain population responses to roads? A meta-analysis. Biological Conservation 147(1): 87–98.

Semlitsch, RD. 2008. Differentiating migration and dispersal processes for pond-breeding amphibians. Journal of Wildlife Management 72(1): 260–267.

Shaffer, HB and GM Fellers, A Magee and SR Voss. 2000. The genetics of amphibian declines: population substructure and molecular differentiation in the Yosemite toad *Bufo canorus* (Anura, Bufonidae) based on the single-strand conformational polymorphism analysis (SSCP) and mitochondrial DNA sequence data. Molecular Ecology 9: 245–257.

Trenham PC, WD Koenig, MJ Mossman, SL Stark and LA Jagger. 2003. Regional dynamics of wetland-breeding frogs and toads: turnover and synchrony. Ecological Applications 13(6): 1522–1532.

U.S. Fish and Wildlife Service. 2014. Endangered Species Status for Sierra Nevada Yellow-Legged Frog and Northern Distinct Population Segment of the Mountain Yellow-Legged Frog, and Threatened Species Status for Yosemite Toad; Final Rule. Federal Register, Vol. 29, No. 82, April 29, 2014. 81 FR 59045 59119.

Van Tienhoven AM, JE Den Hartog, RA Reijns and VM Peddemors. 2007. A computer-aided program for pattern-matching of natural marks on the spotted ragged tooth shark *Carcharias taurus*. Journal of Applied Ecology 44, 273–280. *https://reijns.com/i3s/*.

Chapter 6. Effect of Fence Opacity on the Movement of Reptiles and Amphibians and the Effectiveness of Two Jump-out Designs.

Authors: Cheryl Brehme[1], Jeff A. Tracey[1], Jennifer Kingston[1], Jeremy Sebes[1], Tristan Edgarian[1], Robert Fisher[1]
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Introduction

Options for road barrier materials vary greatly from solid concrete, composites, and plastics to transparent and semi-transparent wire and plastic meshes. Meshes are typically easy to work with and are permeable to water and air movement; however, there is some evidence that animals may spend more time trying to climb or get through transparent fencing than solid fencing (Milburn-Rodriguez et al. 2016). Thus, opacity could influence both barrier effectiveness and the probability and speed with which an animal finds a wildlife crossing.

"Jump-outs" are commonly built along road barrier fencing to ensure that large animals can escape if they get caught within the road barrier sections (Clevenger and Huijser 2011, van der Ree et al. 2015, Hopkins et al. 2018). However, few jump-outs have been designed, tested, or used for allowing the escape of herpetofauna back into the habitat if they become trapped along a road with barrier fencing on both sides.

We conducted studies at the Rancho Jamul Ecological Reserve (RJER) in Jamul, California, to compare the behavior and movement speed of herpetofauna in relation to transparent, semi-transparent, and solid fencing. In addition, we tested the effectiveness of two jump-out designs. The results of these studies will help to inform transportation agencies on these important components of road barrier and crossing systems.

Herpetofauna Groups Targeted: Snakes, lizards, toads
Research questions:

1. Are transparent, semi-transparent mesh, and solid barriers equally effective as barriers to movement?
2. How quickly do individuals travel along barriers of differing opacity?
3. Are jump-outs of differing designs effective in allowing herpetofauna to escape if trapped within the roadway?

Methods

Field Study

At Rancho Jamul Ecological Reserve, we set up a multi-faceted fenced enclosure to study the behavior and speed of animals along different fence materials and the effectiveness of jump-outs (Figure 1). The fenced behavioral enclosure was installed along a habitat edge between riparian scrub and coastal scrub habitat in the reserve. The behavioral enclosure consisted of a 12 m long, 45 cm wide linear "runway" with 2 m long alternating segments of hardware cloth, black plastic mesh (ERTEC® rigid polymer matrix fence with climbing barrier at top), and solid black (Animex® high-density polyethylene (HDPE-2)) barrier fencing 60 inches in original height buried to a depth of 10–15 cm. The alternating segments contained the same barrier fencing on both sides of the runway and each fence type was randomly repeated two times along the runway. To prevent bias based upon the location of the fencing, the order of the fencing types was changed during the middle of the study. The bare soil floor of the enclosure was tamped down with a steel dirt tamper to prevent digging and hiding behaviors. We also buried 1 in. PVC pipes ¾ in. deep along the floor in between each fence segment perpendicular to the runway to provide a white strip between segments. This allowed us to easily discern when an animal moved from one segment to another.

We built a 4 m introduction section made of white solid fencing for introduction and habituation of test animals before they made the decision to start moving along the test runway. At the end of the runway, we built an exit section with four jump outs. Two "high" jump outs were built as earthen ramps leading up to the top of the fence, with an approximate 50 cm drop to jump out into the habitat. Two "low" jump-outs were modified rectangular cones (ERTEC®) with a diameter of 22 cm installed halfway up the barrier fencing with a small earthen ramp and an approximate 20 cm drop into the habitat (Figure 2). The cones were modified by increasing the size of the opening on the exit side to a diameter of approximately 10 cm. An outer fence around the exit section allowed us to capture animals once they exited the jump-out and return them to the original place of capture. The entire behavioral enclosure was covered on top at a height of approximately 1.5 m with shade sail cloth to prevent spots of sunlight and shade from influencing animal behaviors.

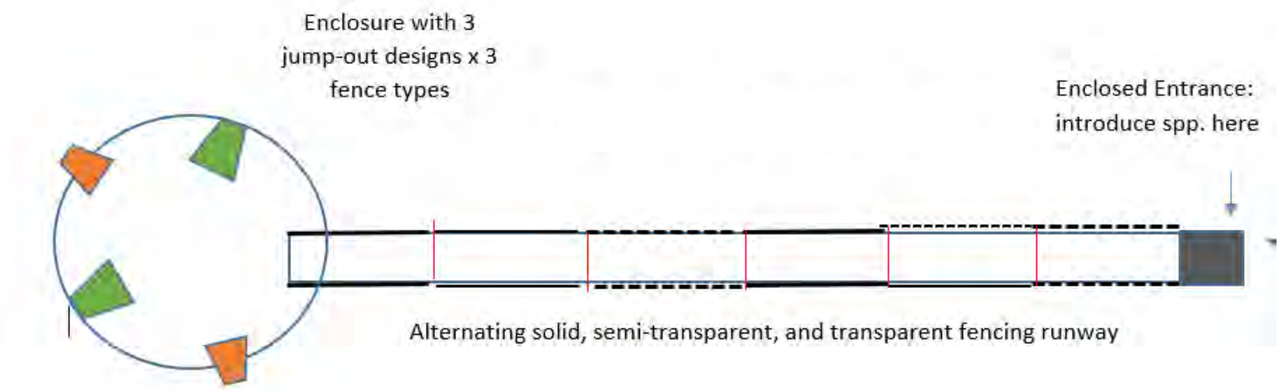

Figure 1. Graphic of Behavioral Enclosure

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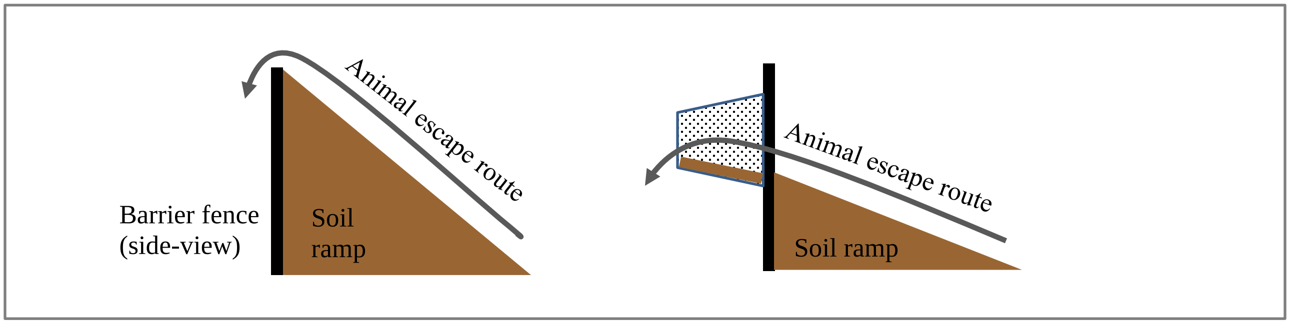

Figure 2. Diagram of Jump-Out Configurations a) Over Fence and b) Through Fence.

Trials were run in spring and summer months from June through September in 2018 and March through June in 2019. To determine if animals would respond differently to the transparent and semi-transparent fencing in the presence of a visual barrier, from late August through September of 2018 and June of 2019, we placed black duct tape along the bottom of the first segments of hardware cloth and mesh fencing approximately 15 cm (6 in.) in height.

We captured animals using visual searching and linear trap arrays with pitfall traps and snake traps within 150 m of the behavioral enclosure as described in Fisher et al. (2008). The traps were set in the early morning, checked throughout the day, and closed at mid-day. Some snakes were also opportunistically collected if observed while checking the pitfall arrays. Each animal included in the trials was weighed, measured, temporarily marked with ink (Sharpie®), placed into a holding bag (snake bag/pillowcase) and brought to the enclosure.

Captured animals were placed one at a time within the introduction section approximately 2 m from the first fence segment. Observers were stationed behind camouflage netting at the entrance and exit sides of the behavioral enclosure. The first observer on the exit side operated a stationary video camera on a tripod to record all animal movements within the enclosure and was behind camouflage netting throughout the entire trial. The second observer gently released each animal from its holding bag or snake trap into the enclosure approximately 2 m from the first fence trial segment while behind the camouflage netting. Each animal was then observed until it left the behavioral enclosure or for 30 minutes (if it did not complete the trial). Examples of reptiles moving through the enclosure are provided in Figure 3. After the trial, each animal was immediately released to its original place of capture. Once back at the field office, the observers uploaded videos and recorded the following:

- Direction and pathway of all movements
- Time spent along each fence segment
- Whether a solid visual barrier was present (on mesh or HC fencing)
- Behaviors observed at each fence segment: Poking, climbing, moving back and forth, sitting
- Number of fence segments completed
- Whether animals escaped by climbing over fencing
- What exits were approached and used

Figure 3. Photos of A) California Striped Racer (*Masticophis lateralis*) Poking at Hardware Cloth, B) Orange-Throated Whiptail (*Aspedoscelis hyperythrus*) Poking at Hardware Cloth, C) Rosy Boa (*Lichanura trivirgata)* Moving Through Runway Toward Exit Structures, D) Orange-Throated Whiptail Exiting High Ramp and E) Red-Diamond Rattlesnake (*Crotalus ruber*) Exiting Escape Funnel.

Analysis

Only data from individual animals that completed at least three fence segments (one of each type) were used in the analysis. Many animals turned around one or more times during their trial and travelled by the same fence lines on repeated occasions. We used all data where a complete pass was made and accounted for this with a covariate "FirstSegment" indicating whether it was the individuals first encounter with that fence type.

Movement Time along Fence Types: Logistic Regression:

We first modelled the probabilities of fence interaction behaviors using logistic regression. For this we only used the individuals first encounter with each fence type (Hardware Cloth, Mesh, Solid +/- Visual Barrier). To determine whether the probability of fence interaction behaviors differed across fence types and by taxonomic group (lizards, snakes, toads) and the effect of a visual barrier, we fitted a general linear model with a binomial distribution and logit-link function (Program R):

Fence Interaction Behavior (0/1) ~ FenceType*VisualBarrier + TaxonomicGroup

Movement Time along Fence Types: Linear Regression:

Individuals of different species and taxonomic groups had widely varying times along the fence lines within the behavioral enclosure. To minimize this variation and to determine whether speed of movement was affected by fence type, we did two things. First, we removed records of segment passes where the behavior "sitting" was recorded. This behavior was not considered an interaction with the fence but represented varying, and sometimes long, periods of time where an animal would "freeze." Second, we standardized all time data to z-distributions by individual (mean= 0, data as number of standard deviations from the mean). As an example, an individual with times of 5, 10, and 15 min across fences A, B, and C would be transformed to -1, 0, 1. Likewise, another individual with times of 1, 2, and 3 min across fences A, B, and C would be transformed to -1, 0, 1. This allowed us to account for the wide variability of speed among individuals and focus on their relative responses to the different fence types.

We then modelled the data using linear regression fitted by least squares to determine whether time differed across fence types and if the installation of a visual barrier affected time spent along the fence types by taxonomic group (lizards, snakes, toads)(Program R):

Standardized Time ~ FenceType*VisualBarrier + TaxonomicGroup + FirstSegment

For both types of models described, we also ran mixed model versions based on maximum likelihood with the individual as a random variable; the mixed models had convergence issues due to the large number of parameters (i.e. overparameterization). However, the model coefficients and standard error estimates were very similar between the general linear and mixed model types. Further analyses of this study will be conducted using Bayesian methods for a manuscript.

Results

We captured a total of 174 individuals to use in our trials. Of these, 66% (114) completed at least one full set of fence types and thus were used in the behavioral modelling. Eighty individuals completed moving through all fence lines to the exit arena and of these, 87.5% (70) exited using one of the jump-outs (Table 1).

Table 1. Numbers of Species Used in Trials with Outcomes

		Number	Fence lines passed (out of 6)			Number
Taxon	Species	Escaped	<3	3-5*	6*	exited
Frog	*SubTotal*			1		
	Pseudacris regilla			1		
Lizard	*SubTotal*		46	24	57	49
	Aspidoscelis hyperythrus		23	7	42	38
	Aspidoscelis tigris		1	2	2	2
	Elgaria multicarinata		2	1	2	1
	Sceloporus occidentalis		11	13	6	5
	Sceloporus orcutti				1	
	Uta stansburiana		9	1	3	2
	Plestiodon skiltonianus	1	1		0	
Snake	*SubTotal*		6	6	21	20
	Crotalus ruber				3	3
	Crotalus oreganus				2	2
	Lampropeltis getula				2	2
	Lichanura trivirgata				1	1
	Coluber fuliginosus				2	1
	Coluber lateralis		3	2	5	5
	Pituophis catenifer		2	3	5	5
	Tantilla planiceps		1		0	
	Thamnophis hammondii			1	2	2
Toad	*SubTotal*		6	3	2	1
	Anaxyrus boreas		2	2	2	1
	Spea hammondii		4	1	0	
	Grand Total	1	59	34	80	70

*used in modelling

All behavioral models showed that fence type was significant in predicting the probability that herpetofauna would exhibit fence interaction behaviors (Tables 2–4, Figures 4–6). Poking, moving back and forth, and climbing behaviors were more common as the transparency of the fence increased (solid > mesh> hardware cloth). Across taxonomic groups, toads showed higher probabilities of fence interaction behaviors than lizards and snakes, although the variability in the data was greater for toads. Along with the greater probability of these behaviors, the time it took for herpetofauna to pass each fence type increased as the transparency of the fence increased (Table 5, Figure 7).

The addition of a 15 cm (6 in) visual barrier along the bottom of the mesh and hardware cloth fencing reduced the probability of poking and back and forth movements among all taxa and was particularly significant in reducing poking behaviors of lizards and snakes. When a visual barrier was present, there was little difference in the probability of fence interaction behaviors among the fence types. Similarly, a visual barrier significantly reduced the time it took for individuals to move along the mesh and hardware cloth fencing so that there was little difference in individual speed among all fence types.

Table 2. Effect of Fence Type on Animal Behavior: Poking and Looking

Coefficients:	Estimate	Std. Error	t-value	Pr(>|t|)	
(Intercept= Solid)	-3.215	0.412	-7.811	5.65E-15	***
FenceTypeMesh	2.482	0.425	5.847	5.01E-09	***
FenceTypeHC	3.582	0.430	8.325	< 2e-16	***
VB011	-1.228	1.150	-1.067	0.286	
TypeSnake	0.281	0.262	1.074	0.283	
TypeToad	3.044	0.734	4.150	3.32E-05	***
FirstSegType1	0.232	0.252	0.918	0.359	
FenceTypeMesh:VB011	-0.885	1.313	-0.674	0.500	
FenceTypeHC:VB011	-0.640	1.236	-0.518	0.604	

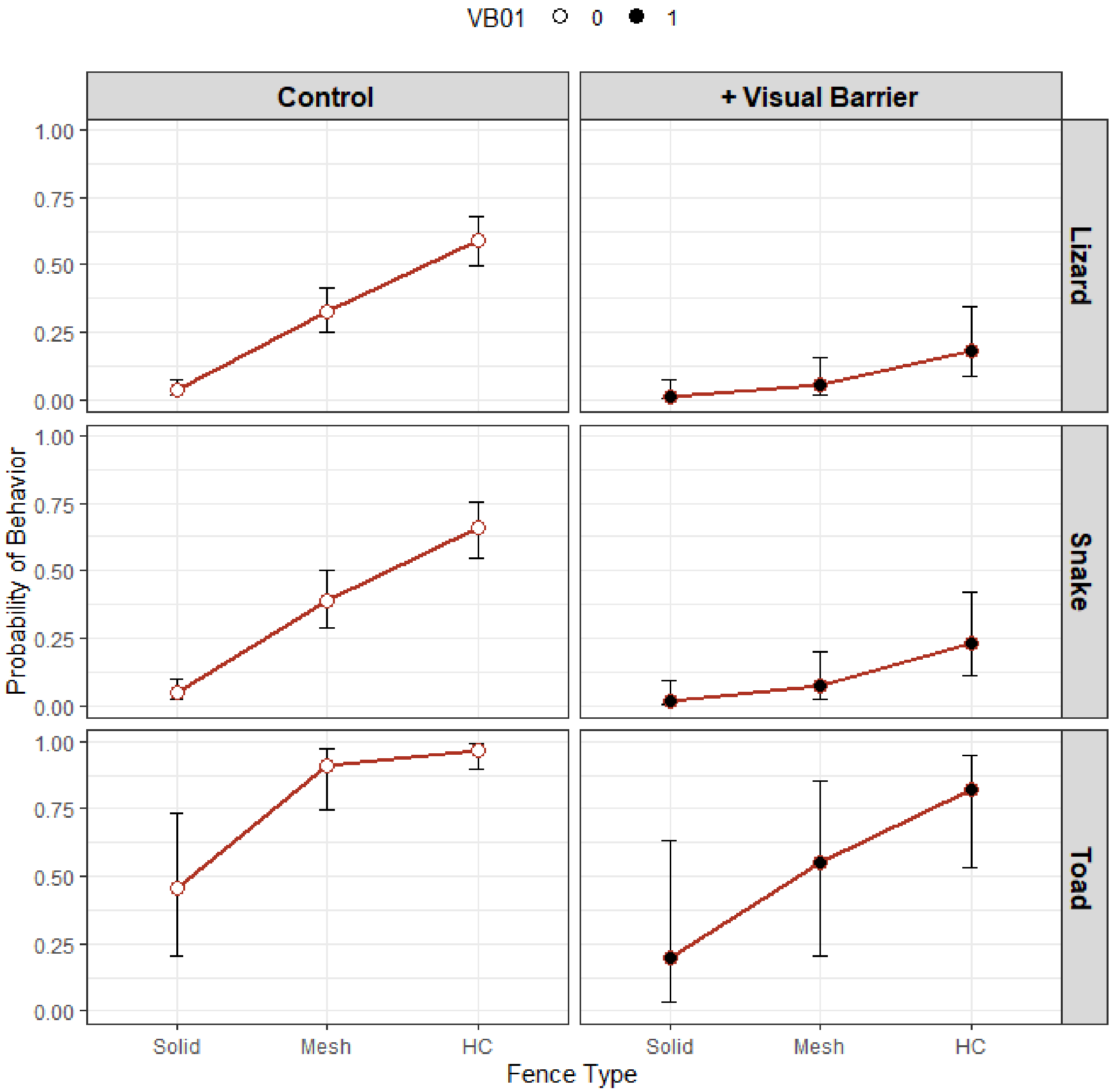

Figure 4. Effect of Fence Type on Animal Behavior: Poking and Looking

VB= visual barrier, HC= hardware cloth

Table 3. Effect of Fence Type on Animal Behavior: Back and Forth Movements

Coefficients:	Estimate	Std. Error	t-value	Pr(>|t|)	
(Intercept= Solid)	*-2.928*	*0.418*	*-7.001*	*2.53E-12*	***
FenceTypeMesh	*1.606*	*0.452*	*3.552*	*3.83E-04*	***
FenceTypeHC	*2.245*	*0.444*	*5.053*	*4.36E-07*	***
VB011	*-0.715*	*1.102*	*-0.649*	*0.516*	
TypeSnake	*-0.752*	*0.338*	*-2.225*	*0.026*	*
TypeToad	*1.076*	*0.742*	*1.451*	*0.147*	
FirstSegType1	*0.075*	*0.284*	*0.265*	*0.791*	
FenceTypeMesh:VB011	*0.020*	*1.235*	*0.016*	*0.987*	
FenceTypeHC:VB011	*-1.265*	*1.334*	*-0.948*	*0.343*	

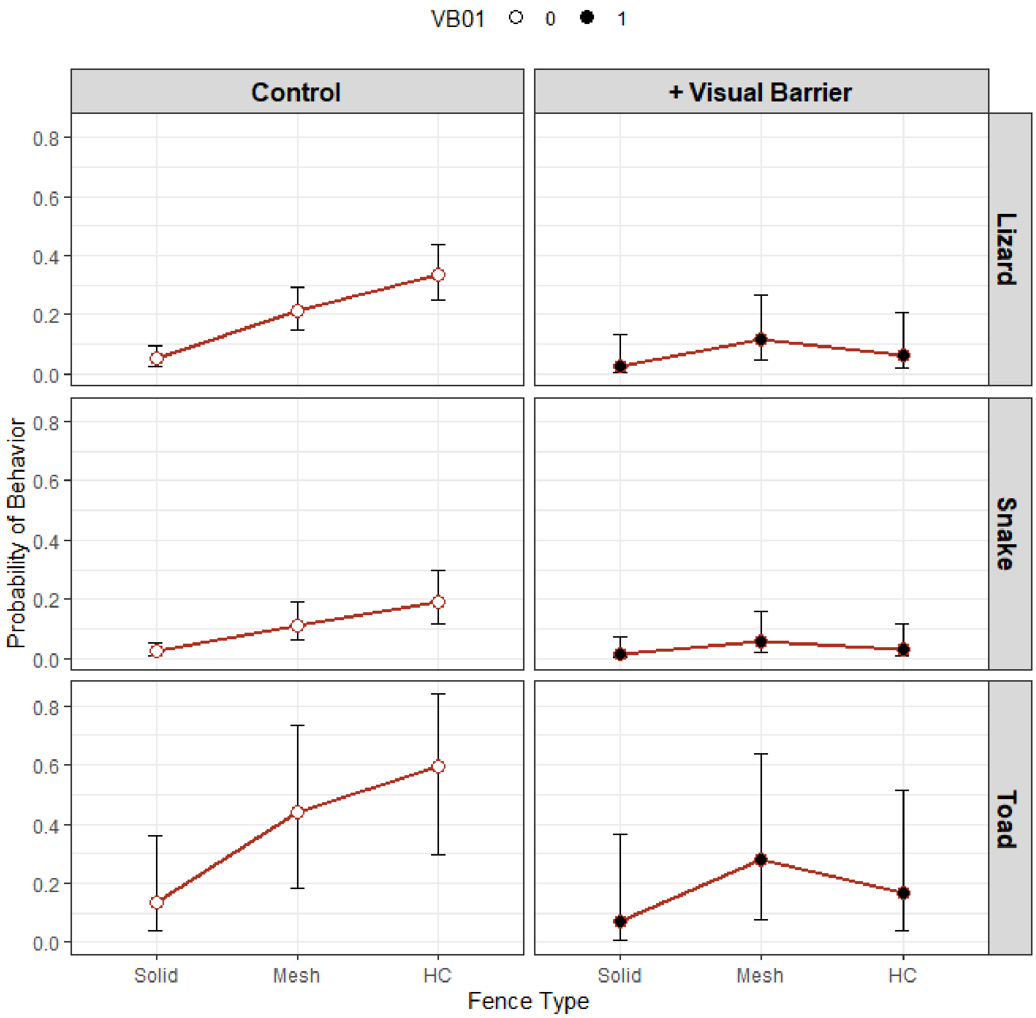

Figure 5. Effect of Fence Type on Animal Behavior: Back and Forth Movements

VB= visual barrier, HC= hardware cloth

Table 4. Effect of Fence Type on Animal Behavior: Climbing

Coefficients:	Estimate	Std. Error	t-value	Pr(>|t|)	
(Intercept= Solid)	*-3.319*	*0.521*	*-6.373*	*0.000*	***
FenceTypeMesh	*1.105*	*0.576*	*1.917*	*0.055*	.
FenceTypeHC	*1.662*	*0.561*	*2.963*	*0.003*	**
VB011	*-16.458*	*1711.284*	*-0.010*	*0.992*	
TypeSnake	*-1.850*	*0.745*	*-2.484*	*0.013*	*
TypeToad	*2.020*	*0.790*	*2.558*	*0.011*	*
FirstSegType1	*0.102*	*0.390*	*0.261*	*0.794*	
FenceTypeMesh:VB011	*-0.938*	*2465.362*	*0.000*	*1.000*	
FenceTypeHC:VB011	*14.523*	*1711.284*	*0.008*	*0.993*	

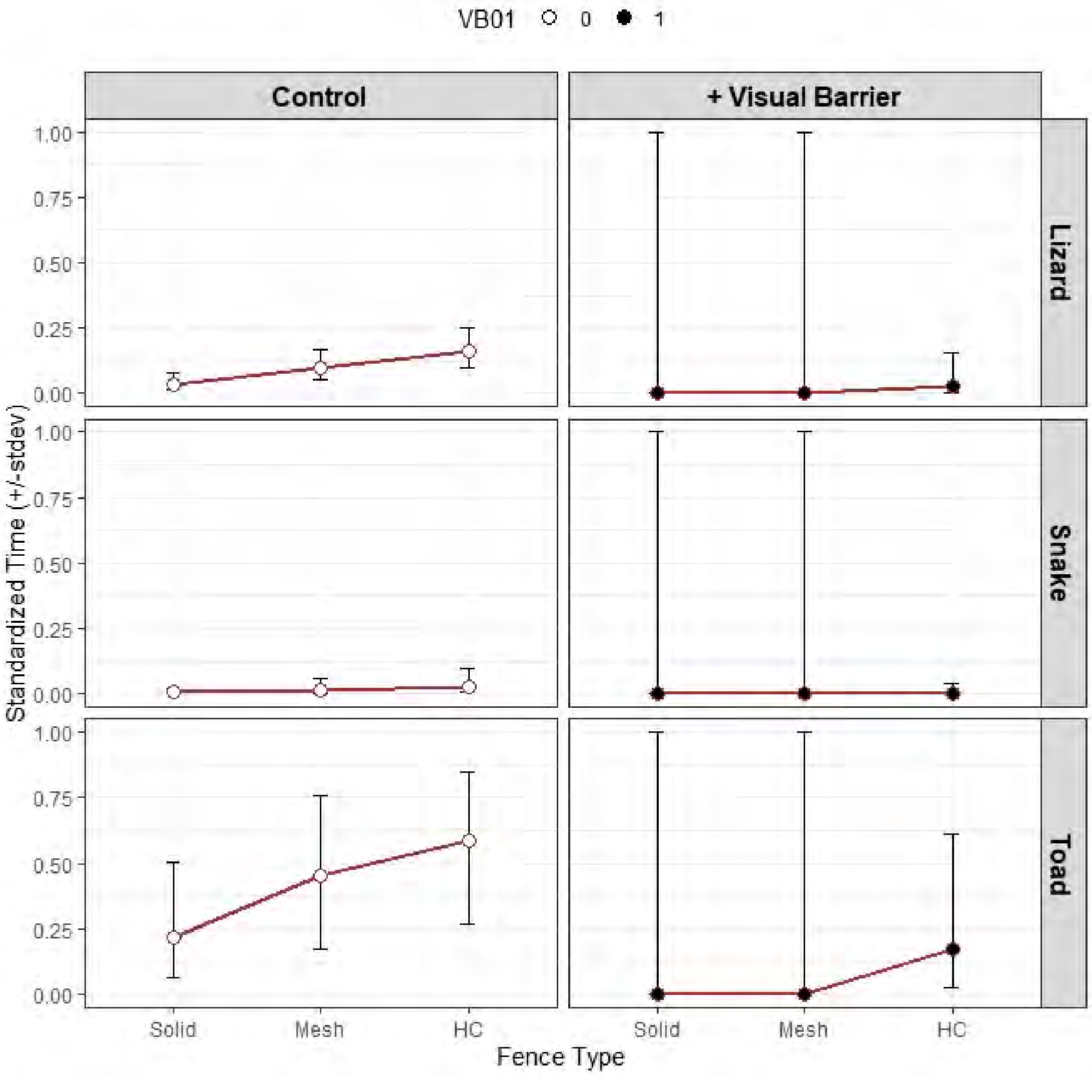

Figure 6. Effect of Fence Type on Animal Behavior: Climbing

VB= visual barrier, HC= hardware cloth

Table 5. Effect of Fence Type on Relative Movement Time

Coefficients:	Estimate	Std. Error	t-value	Pr(>|t|)	
(Intercept= Solid)	*-0.31719*	*0.06641*	*-4.776*	*2.11E-06*	***
FenceTypeMesh	*0.24439*	*0.09012*	*2.712*	*0.00683*	**
FenceTypeHC	*0.72434*	*0.09106*	*7.955*	*5.71E-15*	***
VB011	*0.56038*	*0.1081*	*5.184*	*2.72E-07*	***
TypeSnake	*0.04315*	*0.08091*	*0.533*	*0.59394*	
TypeToad	*-0.02768*	*0.17773*	*-0.156*	*0.87626*	
FirstSegType1	*-0.13039*	*0.07296*	*-1.787*	*0.07427*	.
FenceTypeMesh:VB011	*-0.4652*	*0.16574*	*-2.807*	*0.00512*	**
FenceTypeHC:VB011	*-1.01179*	*0.15753*	*-6.423*	*2.22E-10*	***

*Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1*

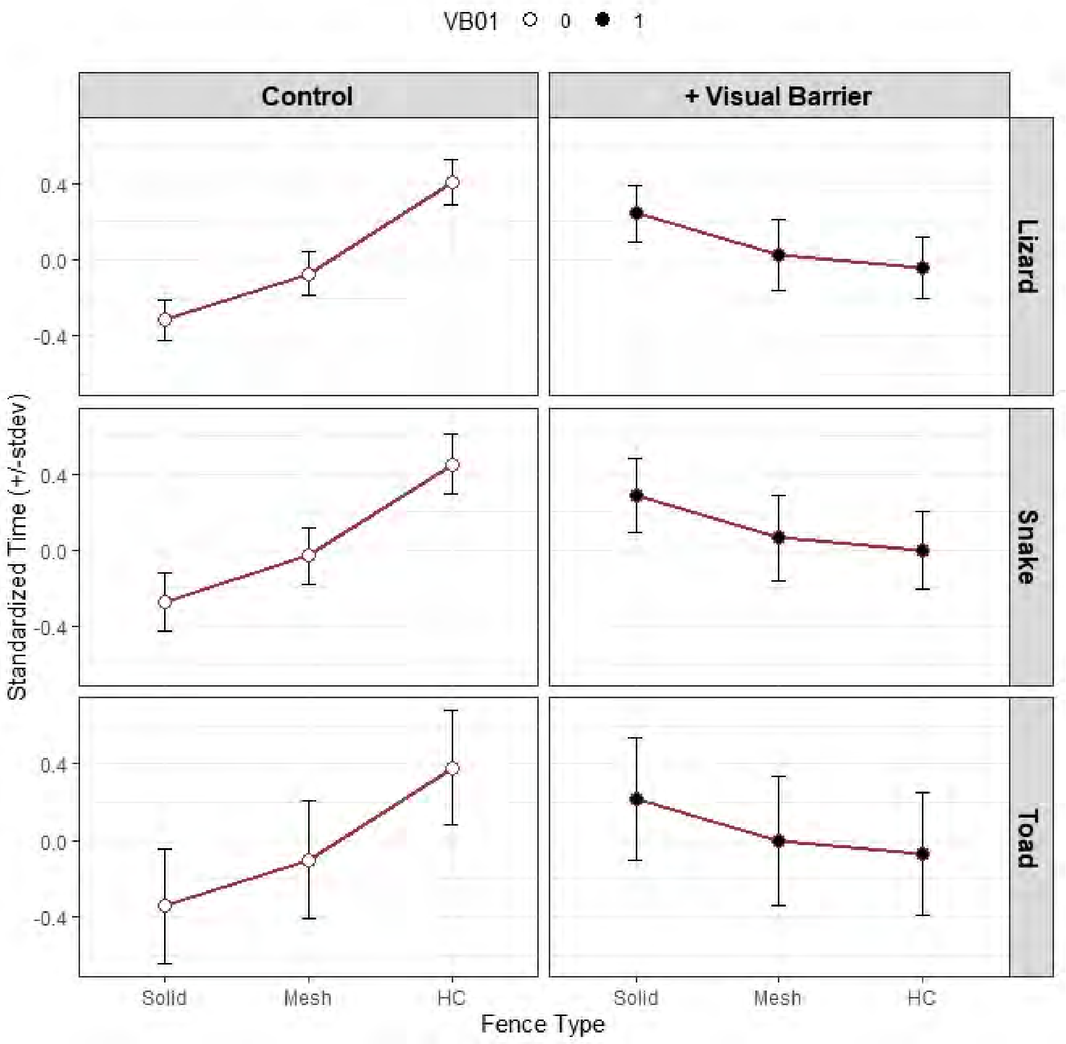

Figure 7. Effect of Fence Type on Relative Movement Time

Effectiveness of jump-outs

A total of 75% of lizards (43/57), 95% of snakes (20/21), and 50% of toads (1/2) used a jump-out to escape the enclosure. There was little difference between the use of the high ramp and low funnel jump-outs by lizards and snakes (Figure 8). We observed that lizards often sat on top of the high ramp for long periods of time before jumping to the ground, whereas there was little hesitation with the low jump-outs. A higher proportion of lizards (16–23%) did not exit via the jump-outs. Many of these sat in the exit arena until they timed out or moved back in the direction of the entrance.

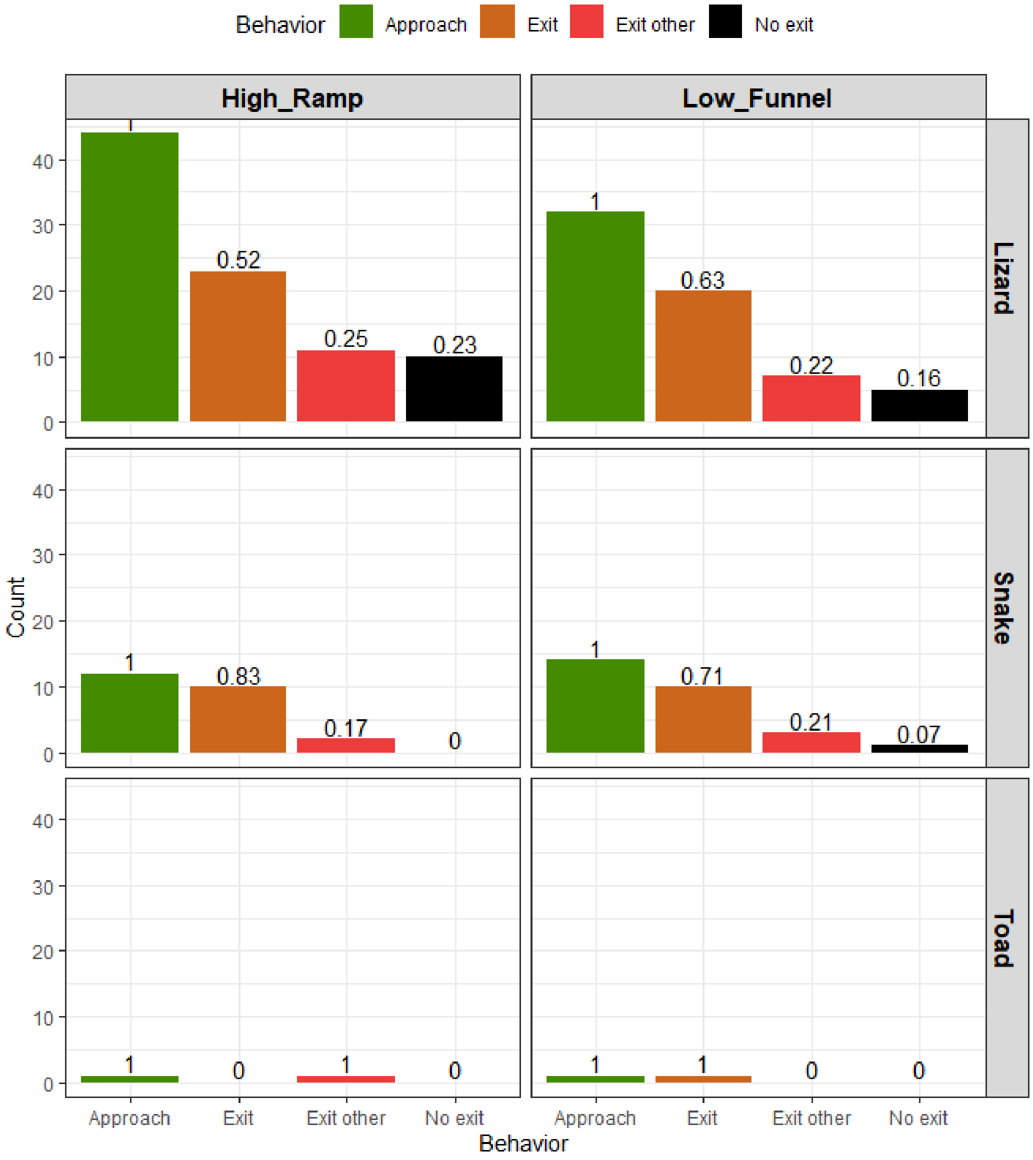

Figure 8. Proportion of Herpetofauna Groups that Approached and Used 2 Jump-Out Designs.

Discussion

Our results provide evidence that herpetofauna are more likely to interact with the transparent and semi-transparent fences by poking it with their noses, pacing back and forth, and attempting to climb. The transparent and semi-transparent fencing types used in this study are not only see-through but are permeable to the movement of air. Because sight and chemoreception senses are typically well developed in reptiles, it is not clear to what extent these different senses are driving fence interaction behaviors. However, animals exhibiting these behaviors appear to be trying to find a way through the fence to the other side.

Although fence interaction behaviors have been documented elsewhere in comparing hardware cloth and solid fencing (Ruby et al. 1994, Milburn-Rodríguez et al. 2016), our study shows a gradation of response from solid to semi-transparent to transparent fencing in all taxa studied. In addition, our study shows that these behaviors result in animals moving slower, or spending more time, along transparent/permeable fencing in comparison to solid fencing. This may not be a concern when the purpose of the fence is primarily to exclude animals. However, effect of fence opacity on movement rates should be considered when a dual objective is to lead species toward a road crossing structure, particularly when high permeability and population connectivity across the structure is desired (Simlitsch 2008, Hamer et al. 2015, Brehme et al. 2018).

There are reasons why hardware cloth, mesh, or solid barriers may be desirable in particular landscapes, habitats, and climates with considerations that include rain and wind permeability, durability, and aesthetics (Langton and Clevenger 2020). Our study is the first to show that addition of a simple visual barrier at ground level (6 inches our study) can result in substantial decreases in fence interaction behaviors and in increased rates of movement. For most response measures, herpetofauna responses to mesh and hardware cloth fencing with a visual barrier were not significantly different than to the solid barrier. This may allow for more flexibility in the decision-making and planning processes for barrier systems for herpetofauna. With any barrier or fencing system, proper maintenance is extremely important for its continued success (Hamer et al. 2015, Baxter-Gilbert et al. 2015, Langton and Clevenger 2020).

Finally, we showed that two jump-out configurations were largely effective in allowing animals trapped on the wrong side of the barriers to escape back into the habitat. Animals can easily get trapped on the wrong (road) side of barrier fencing by entering through a tear or opening in the fencing or by entering the roadway at the end of the exclusion fencing. Although jump-outs are commonly built structures along wildlife fencing for large mammals, they have not commonly been incorporated into transportation planning for small animal barriers. Jump-outs for herpetofauna can be provided at regular intervals along barriers with interval distances determined by target species movement distances. It is also important that any jump-out design for herpetofauna consider the safety of other wildlife. For short barrier fencing, most other wildlife can simply jump over the barrier. For larger barrier systems, escape routes may include multiple size jump-outs for a wider variety of species.

Acknowledgements

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References

Baxter-Gilbert, JH, JL Riley, D Lesbarrères and JD Litzgus. 2015. Mitigating reptile road mortality: fence failures compromise ecopassage effectiveness. PLOS ONE 10(3), p.e0120537.

Brehme CS, SA Hathaway and RN Fisher. 2018. An objective road risk assessment method for multiple species: Ranking 166 reptiles and amphibians in California. Landscape Ecology 33(6): 911–935.

Clevenger, AP and MP Huijser. 2011. Wildlife Crossing Structure Handbook, Design and Evaluation in North America, Publication No. FHWA-CFL/TD-11-003. Department of Transportation, Federal Highway Administration, Washington D.C., USA.

Fisher, R, D Stokes, C Rochester, C Brehme, S Hathaway and T Case. 2008. Herpetological monitoring using a pitfall trapping design in southern California. U.S. Geological Survey Techniques and Methods Vol. 2:A5. *https://pubs.usgs.gov/tm/tm2a5/pdf/tm2a5.pdf.*

Hamer, AJ, TE Langton, and D Lesbarrères. 2015. Making a safe leap forward: mitigating road impacts on amphibians. Handbook of road ecology, Van Der Ree, R, DJ. Smith, and C Grilo (eds). Handbook of Road Ecology. John Wiley & Sons, pp. 261–270.

Hopkins, CB, JS Johnson, SR Kuchta, , DS McAvoy, VD Popescu, SC Porter, WM Roosenburg, GP Sisson, BR Sperry, MT Trainer and RL Wiley. 2018. Effectiveness of Wildlife Mitigation Treatments along the Nelsonville Bypass (No. FHWA/OH-2018-8).

Langton, TES, and AP Clevenger. 2020. Measures to Reduce Road Impacts on Amphibians and Reptiles in California. Best Management Practices and Technical Guidance. Prepared by Western Transportation Institute for California Department of Transportation, Division of Research, Innovation and System Information.

Milburn-Rodríguez JC, J Hathaway, K Gunson, D Moffat, S Béga and D Swensson. 2016. Road mortality mitigation: The effectiveness of Animex fencing versus mesh fencing. *https://animexfencing.com/whyanimex/animex-vs-mesh*.

Ruby, DE, JR Spotila, SK Martin and SJ Kemp. 1994. Behavioral responses to barriers by desert tortoises: implications for wildlife management. Herpetological Monographs 8: 144–160.

Semlitsch, RD. 2008. Differentiating migration and dispersal processes for pond-breeding amphibians. Journal of Wildlife Management 72(1): 260–267.

van der Ree, R, JW Gagnon and DJ Smith. 2015. Fencing: a valuable tool for reducing wildlife-vehicle collisions and funneling fauna to crossing structures. Handbook of Road Ecology. Oxford: John Wiley & Sons, pp. 159–171.

Chapter 7. Effectiveness of Turnarounds in Changing the Trajectory of Reptiles and Amphibians in San Diego, CA.

Authors: Cheryl Brehme[1], Jeff A. Tracey[1], Jennifer Kingston[1], Jeremy Sebes[1], Tristan Edgarian[1], Robert Fisher[1]

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Introduction

It is common practice to install ‘turnarounds’ at fence ends and where barriers are unable to span across private road entries and easements (e.g. Clevenger and Huijser 2011, Ontario Ministry of Natural Resources and Forestry 2016, Langton and Clevenger 2020). For this, road barriers end in a “U” shape and are designed to redirect animals back in the opposite direction at fence ends and keep them off the roadway. Although they are recommended in many countries and in guidance documents (e.g. Iuell et al. 2003, Clevenger and Huijser 2011, Gunson et al. 2016), there are no systematic studies to our knowledge that have addressed the relative effectiveness of turnarounds (Langton and Clevenger 2017).

We conducted studies at the Rancho Jamul Ecological Reserve in Jamul, California to test the effectiveness of turnarounds in changing the trajectory of movement for herpetofauna and small mammals. We also compared effectiveness and time spent within the turnarounds based upon fence type: transparent, semi-transparent, and solid fencing. The results of these studies will help to inform transportation agencies on these important components of road barrier and crossing systems.

Research questions:

1. Are fence end turnarounds effective in redirecting the trajectory of animal movement?
2. Is the effectiveness of turnarounds influenced by the opacity of barrier fencing?

Methods

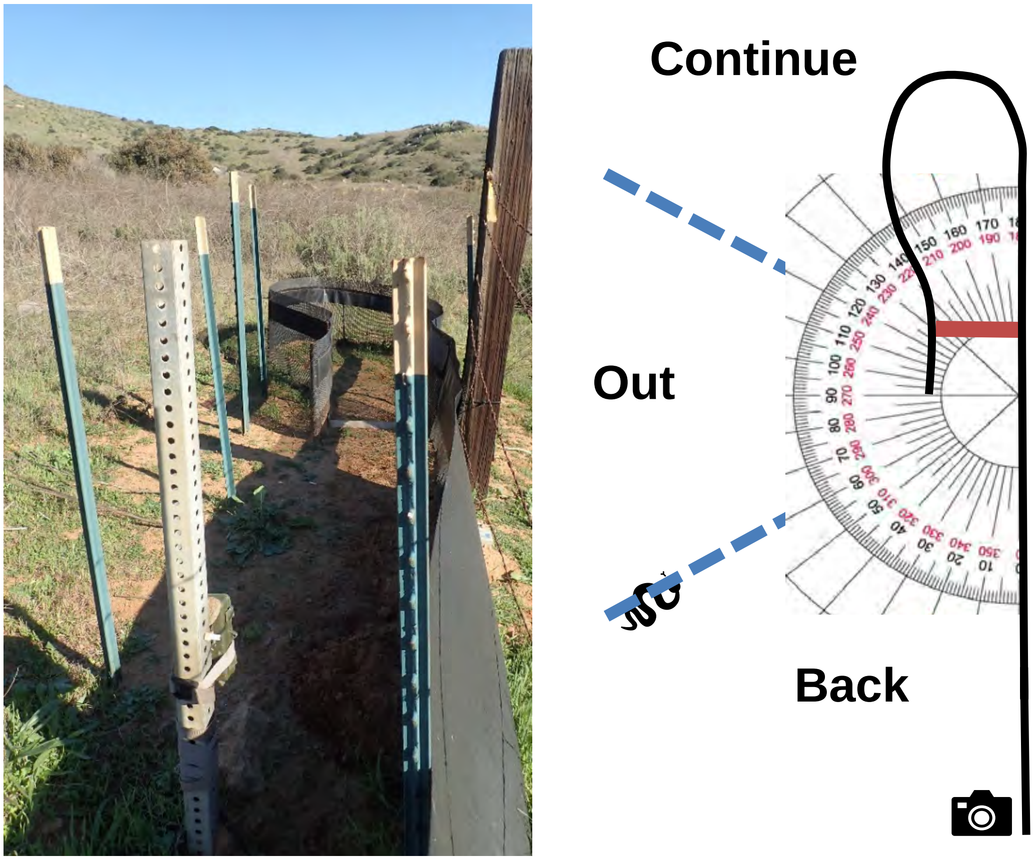
We installed three 20 m segments of solid barrier fencing within coastal sage scrub habitat in RJER adjacent to a dirt road. At the ends of each segment, we installed another 4 m of fencing and a turn-around approximately 1.5 m long and 1 m wide. The turnarounds ended approximately 0.4 m from the fence lines and extended another 0.4 m parallel to the fence (Figure 1). We used three materials with increasing opacity; hardware cloth (0.25 inch), mesh (ERTEC® rigid polymer matrix E-Fence), or solid fencing (Animex® high-density polyethylene (HDPE-2)). The placement of the turnarounds was mixed so that each segment ended with two of the different fence type materials. At the opening of each turnaround, we installed a HALT® active infrared trigger and camera system that allowed us to document animals going into and out of the turnarounds, as well as determine their trajectory upon leaving the turnaround. The cameras were placed 4.25 m from the end of the turnaround (2.25 m from trigger) with a frame of view that allowed us to follow the movement of animals for approximately 1 m in any direction and were set to record video for 25 seconds upon an animal activating the trigger. Cameras were set with 32-64GB SD cards and left on and checked on a weekly or biweekly basis from March 1 to Sept. 8, 2019.

Analysis

We watched all videos and recorded the following:

- Turnaround Fence Type and Segment number
- Species
- Time of entry and exit
- Distance and direction of travel

Individuals were only included in the analysis if the animals moved at least 0.7 m away from the end of the turnaround. If the same individual moved in and out of the turnaround more than once, only their final trajectory was recorded. Final direction of travel was recorded as three categories: Continue, Out, and Back (Figures 1 and 2). We also did not include data where an individual encountered another individual that may have affected the direction of travel.



Note: Extra stakes in ground to keep cows away from turnaround

Figure 1. Example of A) Turnaround with Camera and Trigger Set Up and B) Direction of Movement Categories.

Figure 2. Example of A) Cottontail Rabbit (*Sylvilagus audubonii*) Continuing in the Same Direction, B) Red-Diamond Rattlesnake (*Crotalus ruber*) Moving Away into the Habitat, and C) Western Toad (*Anaxyrus boreas*) Moving Back along the Fenceline after Leaving the Turnaround. Screenshots taken from Videos Showing Animals Continuing in the Same Direction Out of View.

To determine if the turnarounds were successful in changing the trajectory of movement among taxonomic groups and fence types, we analyzed the choice made by each subject after they reached the turnaround using a multinomial logit choice model (Figure 3). Each individual had a choice of turning back (1, "back"), exiting out of the structure (2, "out"), or continuing in the same direction of travel (3, "continue"). This model is a multinomial generalization of the logistic model which models a binomial response (with one trial, hence a Bernoulli random variable). For each choice, we first calculate a "probability potential." The first choice (back) is a "reference" and is assigned a probability potential of "1" in all cases. The remaining two responses have probability potentials that are an exponential (i.e. rate = exp(y)) function of the linear component of the model that depend on two predictor variables that encode fence type and three variables for taxonomic group, a response-specific intercept and two regression coefficients. The final probabilities for each choice were calculated as the probability potential for that choice divided by the sum of all the probability potentials. This ensured that sum of the probabilities for the choice made for each observation added to one. The taxon-specific parameters were drawn from normal distributions with means and precisions based on parameters drawn from "all taxa" hyper-prior distributions. The hyperprior means were drawn from a normal distribution with mean 0 and 0.001 precision. The precisions were calculated as one over a squared standard deviation, with the standard deviation drawn from a uniform distribution on an interval from 0 to 1000. The parameters were sampled from their posterior distributions using MCMC (as described above) and described by mean, median, and quantiles of their marginal distributions. This allowed us to assess the effect of turn around fence type on the choice made by each subject.

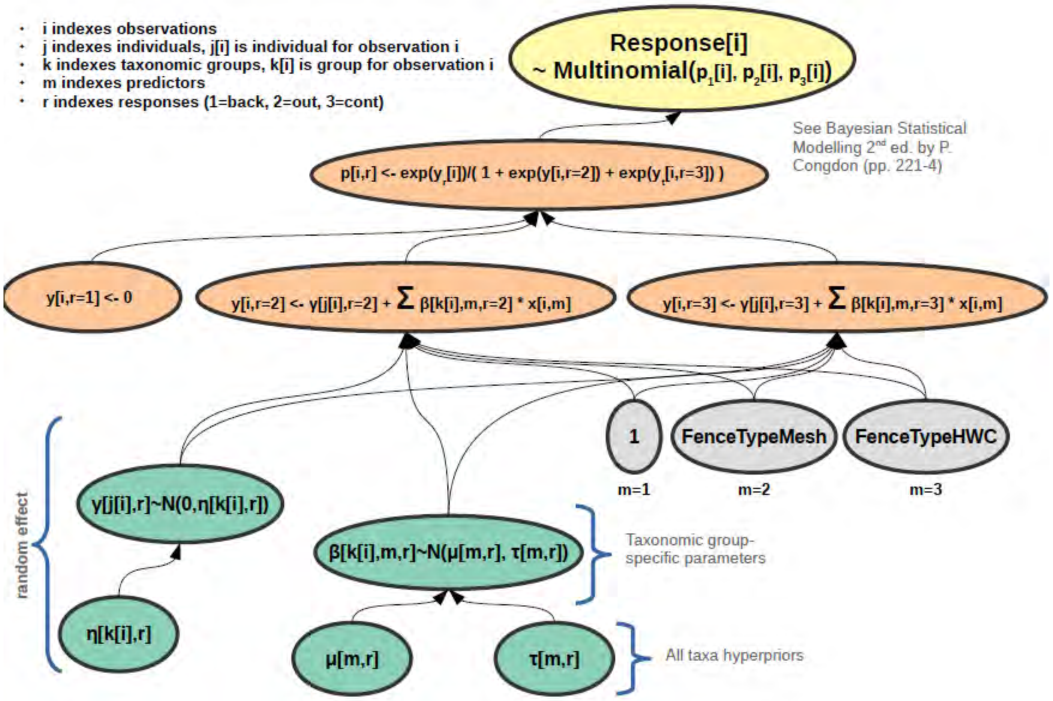


Figure 3. Turn Around Study: Multinomial Logit Choice Model for Response to Turn Around Structure

Time Spent in Turnarounds: Linear Regression:

We modelled time spent in the turnarounds using linear regression fitted by least squares to determine if time differed across fence types and taxonomic group (lizards, snakes, toads, and small mammals)(Program R):

Time ~ FenceType* TaxonomicGroup

Results

We captured useable video of 790 individual turnaround encounters that met our distance criteria. This represented 264 lizard, 96 snake, 59 toad, one frog, and 370 small mammal movements (Table 1). Among all herpetofauna, 92% changed course back toward the fence line or back out into the habitat. A total of 64% of lizard, 68% of snake, 80% of toads and 43% of small mammal movements were made back along the original fence line after encountering a turnaround.

Table 1. Species Documented Using Turnarounds and Movement Trajectory Results

		Fence lines passed (out of 6)			Proportion
Taxon	Species	Continued	Out	Back	Back+ Out
Lizard	*SubTotal*	26	69	169	0.90
	Aspidoscelis hyperythrus	12	53	69	0.91
	Aspidoscelis tigris			2	1.00
	Elgaria multicarinata			1	1.00
	Plestiodon gilberti			1	1.00
	Plestiodon skiltonianus		1		1.00
	Sceloporus occidentalis	3	1	15	0.84
	Uta stansburiana	11	14	79	0.89
	Unknown lizard			2	1.00
Snake	*SubTotal*	1	30	65	0.99
	Coluber fuliginosus		2	12	1.00
	Coluber lateralis	1	9	23	0.97
	Coluber flagellum		6	9	1.00
	Crotalus oreganus		6	5	1.00
	Crotalus ruber		2	1	1.00
	Lampropeltis getula		2	3	1.00
	Pituophis catenifer		2	11	1.00
	Salvadora hexalepis		1		1.00
	Unknown snake			1	1.00
Toad/Frog	*SubTotal*	5	8	47	0.92
	Anaxyrus boreas	4	5	31	0.90
	Pseudacris regilla			1	1.00
	Unknown anuran	1	3	15	0.95
Small Mammal	*SubTotal*	120	91	159	0.68
	Chaetodipus spp.	3	15	33	0.94
	Dipodomys simulans	29	22	36	0.67
	Microtus californicus	3	2	2	0.57
	Neotoma spp.	5	2		0.29
	Notiosorex crawfordii	1	1	2	0.75
	Otospermophilus beecheyi	41	16	35	0.55
	Peromyscus spp.	37	30	47	0.68
	Reithrodontomys megalotis		1	1	1.00
	Thomomys bottae		2	1	1.00
	Unknown rodent	1		2	0.67
	Grand Total	152	198	440	0.81

Across fence types, results of the multinomial logit choice model showed high probabilities (ρ) that lizards, snakes, and toads changed their trajectory of movement (back, out) after encountering and exiting a turnaround (Lizard ρ= 0.88, 90% CI 0.70–1.00, Snakes ρ= 0.98, 90% CI 0.77–1.00, Toad ρ= 0.90, 90% CI 0.62–1.00). Responses by lizards and toads, but not snakes, varied by fence type (Figure 4). Lizards and toads were generally more likely to change their trajectory (back, out) after encountering mesh and hardware cloth turnarounds in comparison to solid turnarounds.

Mammals had an overall lower probability than herpetofauna of changing their trajectory after exiting turnarounds (back and out ρ= 0.59, 90% CI 0.41–0.84). By fence type, mammals were more likely to change their trajectory (back, out) after encountering hardware cloth turnarounds in comparison to solid and mesh turnarounds.

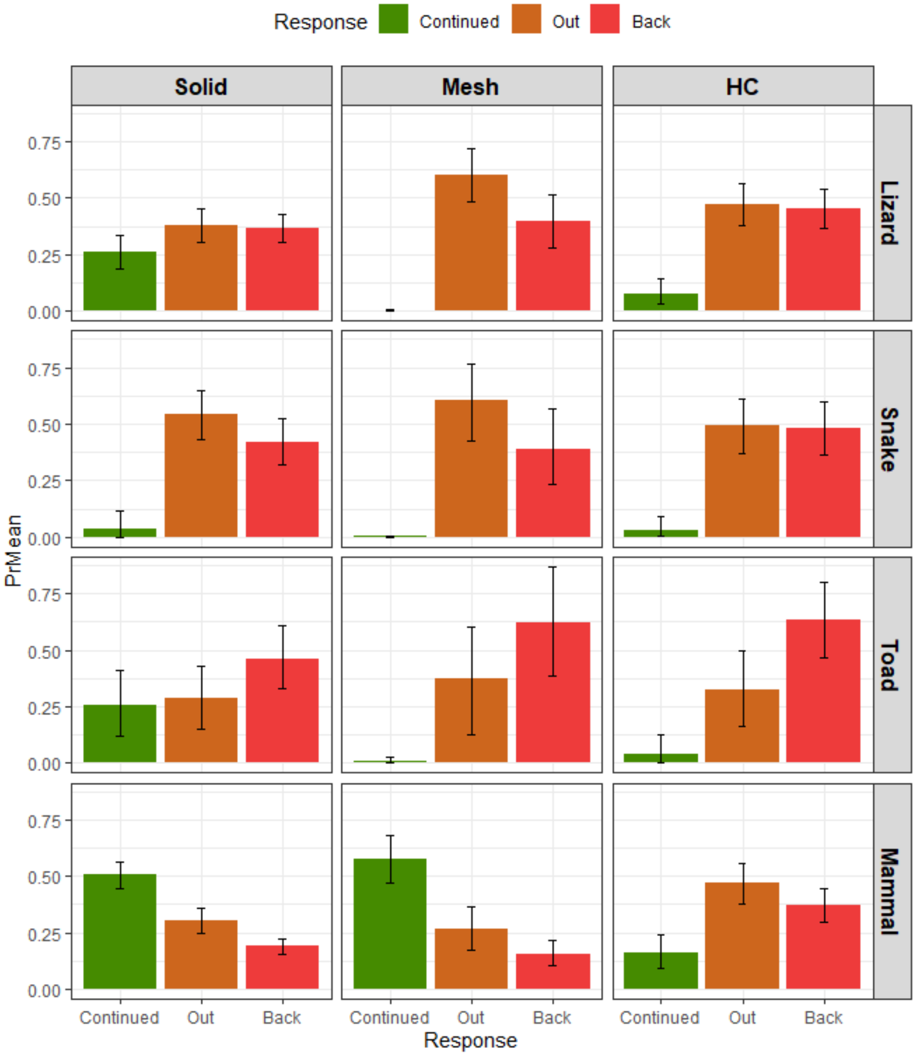


Figure 4. Directional Probabilities After Exiting Turnaround by Taxonomic Group and Fence Type (+/- 90% CI)

By Fence Type, all groups except toads spent significantly less time in the solid turnarounds than in the hardware cloth turnarounds (p<0.001; Table 2, Figure 5). Overall by taxon, mammals spent the least time in turnarounds (ave. model estim.=0.4 min), followed by snakes (ave. model estim=1.9 min), lizards (ave. model estim= 2.7 min), and toads (ave. model estim=3.0 min).

Table 2. Effects and Interactions of Fence Type and Taxon on Time spent in Turnaround

Coefficients:	Estimate	Std. Error	t-value	Pr(>|t|)	
(Intercept= Solid/Lizard)	*0.105*	*0.136*	*0.777*	*0.437*	
FenceTypeMesh	*1.083*	*0.286*	*3.788*	*1.65E-04*	***
FenceTypeHC	*1.240*	*0.218*	*5.683*	*1.96E-08*	***
TaxGroup1Mammal	*-1.424*	*0.177*	*-8.063*	*3.31E-15*	***
TaxGroup1Snake	*-0.009*	*0.275*	*-0.032*	*0.974*	
TaxGroup1Toad	*0.698*	*0.307*	*2.271*	*0.023*	*
FenceTypeMesh:TaxGroup1Mammal	*-0.926*	*0.371*	*-2.498*	*0.013*	*
FenceTypeHC:TaxGroup1Mammal	*-0.587*	*0.298*	*-1.971*	*0.049*	*
FenceTypeMesh:TaxGroup1Snake	*-0.699*	*0.560*	*-1.248*	*0.212*	
FenceTypeHC:TaxGroup1Snake	*-0.263*	*0.400*	*-0.658*	*0.511*	
FenceTypeMesh:TaxGroup1Toad	*-0.498*	*0.665*	*-0.748*	*0.454*	
FenceTypeHC:TaxGroup1Toad	*-1.030*	*0.500*	*-2.059*	*0.040*	*
(Intercept= Solid/Lizard)	*0.105*	*0.136*	*0.777*	*0.437*	

*Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1*

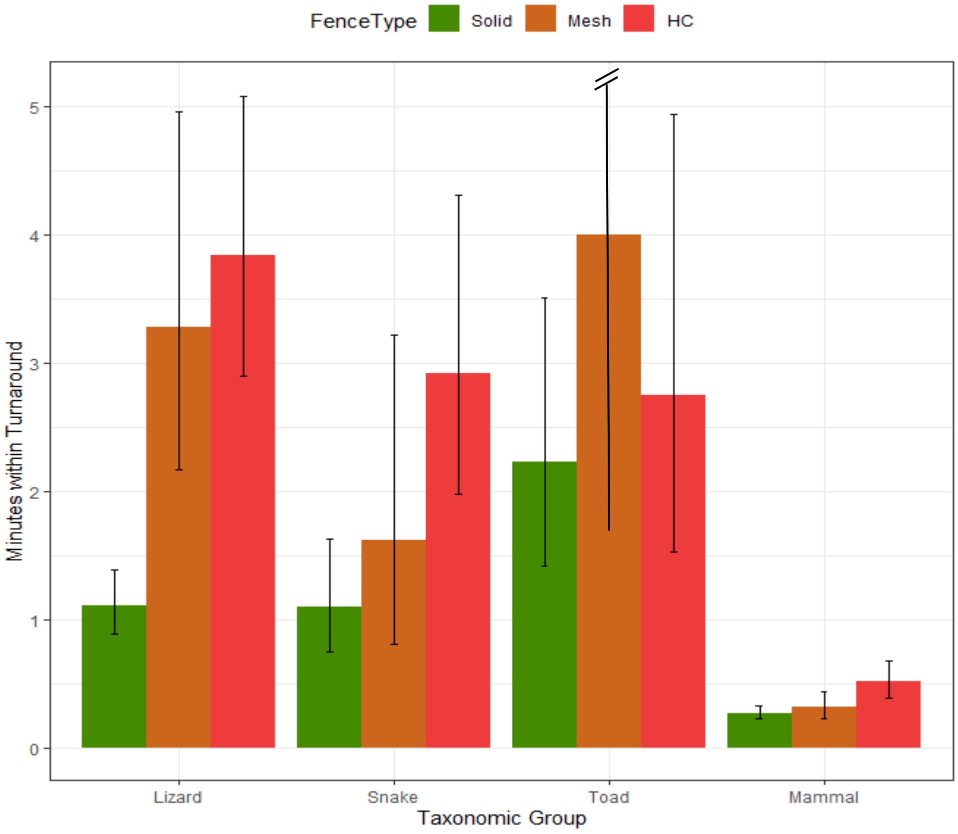


Figure 5. Estimated Time Spent in Turnaround by Taxonomic Group and Fence Type (+/- 90% CI)

Discussion

Our study is the first to show that small turnarounds at fence ends can be effective in changing the trajectory of movement for a majority of herpetofauna and small mammals. We documented that over 90% of herpetofauna (lizards, snakes and toads), as well as 69% of small mammals, changed course after leaving the turnaround. Of these 67% of herpetofauna and 43% of small mammals moved back along the original fence line. We (Chapter 5), and others (Ruby et al. 1994, Milburn-Rodríguez et al. 2016) have shown that animals spend more time interacting with fencing that they can see and smell through (e.g. poking, back and forth movements, climbing). We observed this in the turnaround study as well, as lizards, snakes and small mammals spent increased amounts of time in transparent/permeable and semi-transparent/permeable turnarounds than solid turnarounds.

Turnarounds made of solid fencing appeared to be less effective in changing the movement trajectory of lizards and toads in comparison to mesh and hardware cloth fencing. In addition, both solid and semi-transparent mesh fencing appeared to be less effective in changing the trajectory of small mammals in comparison to more transparent hardware cloth. These results could be related to animals interacting with the fencing and spending more time in the more transparent turnarounds, so that they were less likely to remember and continue on their original trajectory. The results may also be related to the different types of spatial learning and memory used for navigation when animals are subjected to solid barriers (egocentric) in comparison to transparent barriers (allocentric) as has been shown in maze-food trials with rodents (Violle et al. 2009, Vorhees and Williams 2014). Validation of these findings in other locations and possibly more specific research studies addressing spatial learning and movement responses in reptiles, amphibians, and small mammals in their natural environments would be needed to further our understanding of these results.

We did not compare different sizes or shapes of turnarounds in our study; however, we hypothesize that having the end of the turnaround close to the original fence line (or turning back in toward the fence line) may help to steer animals back to the original barrier in the other direction. We chose not to install large turnarounds as we wanted to reduce the probability of animals becoming stressed or ‘trapped’ in the turnarounds for long periods of time. However, longer turnarounds or larger turnarounds encompassing smaller turnarounds may increase the probability that animals do not make it onto the roadways (Langton and Clevenger 2020). Our study also suggests the use of transparent or semi-transparent fencing for turnarounds may potentially increase their effectiveness.

In this study, we only documented animal movement for up to 1 m (3.4 feet) after leaving the turnaround. It is entirely possible that animals changed course again after they left the field of view of the video camera. In our Stanford and Sierra movement studies (Chapters 3 and 4), two out of three CTS that presumably reached a turnaround at the fence end were subsequently documented on another camera 25-125 m away moving back along the fence line. Preliminary results suggest seven out of 10 Yosemite toads changed course at a turnaround, while three continued in the direction past the fence ends. Of the seven toads that changed course, four were subsequently documented on another camera 40-80 m away moving back along the fence line toward the passage. Further studies using more cameras and/or tracking methods are needed to better understand how turnarounds affect movement of animals over a longer distances and time frames. Higher mortality of herpetofauna has been well documented at fence ends even with turnarounds (Gunson et al. 2014, Langton and Clevenger 2017, Helldin and Petrovan 2019). However, the high proportion of herpetofauna that changed directions in our study supports the use of turnarounds in attempts to reduce the chances that small animals go out onto the roadway at fence ends and potentially to help 'steer' them back toward to a crossing structure.

In our migrating California tiger salamander (Chapter 4) and Yosemite toad studies (Chapter 5), we also found that these amphibian species were much less likely to encounter a crossing structure if they started out in the 'wrong' direction (i.e. moving away from the crossing after encountering a barrier). Many animals "gave up" before reaching the fence ends. These results suggest that more regularly placed turnarounds along the fence lines may allow them to correct their trajectory sooner and possibly increase their chances of making it to crossing structures. If effective, this strategy may help to increase the permeability of crossing structures to individual and population movements of reptiles and amphibians (and small mammals). These studies are currently in the planning stages.

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References

Clevenger, AP and MP Huijser. 2011. Wildlife Crossing Structure Handbook, Design and Evaluation in North America, Publication No. FHWA-CFL/TD-11-003. Department of Transportation, Federal Highway Administration, Washington D.C., USA.

Gunson, KE, DC Seburn and D. Lesbarrères. 2014. Monitoring turtle movements on Highways 7 & 41; 2012 and 2013. Final report submitted to the Ministry of Transportation, Kingston, Ontario.

Gunson, K, D Seburn, J Kintsch and J Crowley. 2016. Best Management Practices for Mitigating the Effects of Roads on Amphibian and Reptile Species at Risk in Ontario. Ontario Ministry of Natural Resources and Forestry. Queen's Printer for Ontario. 112 pp.

Helldin, JO and SO Petrovan. 2019. Effectiveness of small road tunnels and fences in reducing amphibian roadkill and barrier effects at retrofitted roads in Sweden. PeerJ, 7, p.e7518.

Iuell, B., GJ Bekker, R Cuperus, J Dufek, G Fry, C Hicks, V Hlaváč, V.Keller, B Rosell, T Sangwine and N Třrslřv. 2003. COST 341–Wildlife and traffic: a European handbook for identifying conflicts and designing solutions. URL: *https://www. milieuinfo. be/productie/beheerplone/nietacm/iene/cost-341/COST.*

Langton, TES and AP Clevenger. 2017. Amphibian and Reptile Highway Crossings: State of the practice, gap analysis and decision support tool. Report prepared for the State of California, Department of Transportation, Division of Research, Innovation and System Information, Office of Materials and Infrastructure Research, June 2017

Langton, TES and AP Clevenger. 2020. Measures to Reduce Road Impacts on Amphibians and Reptiles in California. Best Management Practices and Technical Guidance. Prepared by Western Transportation Institute for California Department of Transportation, Division of Research, Innovation and System Information.

Milburn-Rodríguez JC, J Hathaway, K Gunson, D Moffat, S Béga and D Swensson. 2016. Road mortality mitigation: The effectiveness of Animex fencing versus mesh fencing. *https://animexfencing.com/whyanimex/animex-vs-mesh*.

Ontario Ministry of Natural Resources and Forestry. April 2016. Best Management Practices for Mitigating the Effects of Roads on Amphibians and Reptile Species at Risk in Ontario. Queen’s Printer for Ontario. 112 pp.

Ruby, DE, JR Spotila, SK Martin and SJ Kemp. 1994. Behavioral responses to barriers by desert tortoises: implications for wildlife management. Herpetological Monographs 8: 144–160.

Vorhees, CV and MT Williams. 2014. Assessing spatial learning and memory in rodents. ILAR Journal 55(2): 310–332.

Violle, N, F Balandras,Y Le Roux, D Desor. and H Schroeder. 2009. Variations in illumination, closed wall transparency and/or extramaze space influence both baseline anxiety and response to diazepam in the rat elevated plus-maze. Behavioural Brain Research 203(1): 35–42.

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How does climate change cause extinction?

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How does climate change cause extinction?

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Anthropogenic climate change is predicted to be a major cause of species extinctions in the next 100 years. But what will actually cause these extinctions? For example, will it be limited physiological tolerance to high temperatures, changing biotic interactions or other factors? Here, we systematically review the proximate causes of climate-change related extinctions and their empirical support. We find 136 case studies of climatic impacts that are potentially relevant to this topic. However, only seven identified proximate causes of demonstrated local extinctions due to anthropogenic climate change. Among these seven studies, the proximate causes vary widely. Surprisingly, none show a straightforward relationship between local extinction and limited tolerances to high temperature. Instead, many studies implicate species interactions as an important proximate cause, especially decreases in food availability. We find very similar patterns in studies showing decreases in abundance associated with climate change, and in those studies showing impacts of climatic oscillations. Collectively, these results highlight our disturbingly limited knowledge of this crucial issue but also support the idea that changing species interactions are an important cause of documented population declines and extinctions related to climate change. Finally, we briefly outline general research strategies for identifying these proximate causes in future studies.

1. Introduction

Anthropogenic climate change is recognized as a major threat to global biodiversity, one that may lead to the extinction of thousands of species over the next 100 years [1–7]. Climate change is an especially pernicious threat, as it may be difficult to protect species from its effects, even within reserves [8,9]. Furthermore, climate change may have important interactions with other anthropogenic impacts (e.g. habitat loss [2,6]). Given this, understanding the responses of species to modern climate change is one of the most pressing issues facing biologists today.

But what do we actually know about how climate change causes extinction? It might seem that limited physiological tolerances to high temperatures should be the major factor that causes climate change to threaten the persistence of populations and species, and many studies have justifiably focused on these tolerances [10–13]. However, there may be many other proximate causes of extinction, even when anthropogenic climate change is the ultimate cause. These proximate factors include negative impacts of heat-avoidance behaviour [14], the climate-related loss of host and pollinator species [15,16] and positive impacts of climate change on pathogens and competitors [17,18], among others. The relative importance of these factors is unclear and has not, to our knowledge, previously been reviewed, despite increasing interest in mechanisms underlying the impacts of climate change [19].

Identifying these proximate causes may be critical for many reasons. For example, different proximate factors may call for different conservation strategies to ameliorate their effects [20]. These different proximate factors may also influence the accuracy with which the impacts of climate change are predicted and may drive populations to extinction at different rates.

In this paper, we address three topics related to how anthropogenic climate change causes extinction. First, we briefly review and categorize the many proposed factors that potentially lead to extinction from climate change. Second, we argue that there is already abundant evidence for current local extinctions as a result of climate change, based on the widespread pattern of range contractions at the warm edges of species' ranges (low latitude and low elevation). Third, and most importantly, we perform to the best of our knowledge, the first large-scale review of empirical studies that have addressed the proximate causes of local extinctions related to climate change. This review reveals some unexpected results. We find that despite intensive research on the impacts of climate change, only a handful of studies have demonstrated a proximate cause of local extinctions. Further, among those studies that have identified a proximate cause, very few implicate limited physiological tolerance to high temperatures as the main, direct cause. Instead, a diverse set of factors are supported, with species interactions being particularly important. Finally, we outline some of the research approaches that can be used to examine the proximate factors causing extinction from climate change.

2. Proximate factors causing extinction from climate change

We briefly review and categorize the diverse proximate factors that may cause extinctions due to climate change. We organize these factors by distinguishing between abiotic and biotic factors (following the literature on species range limits [21]). However, all factors are ultimately related to abiotic climate change.

We make several caveats about this classification. First, we emphasize broad categories of factors, so some specific factors may not be included. Second, some factors are presently hypothetical and have not yet been demonstrated as causes of extinction. Third, we recognize that these factors are not mutually exclusive and may act synergistically to drive extinction. They may also interact with other, non-climatic factors (e.g. habitat modification [2,6]) and many different ecological and demographic factors may come into play as populations approach extinction [22]. Finally, we do not address factors that impede climate-induced dispersal.

(a) Abiotic factors

(i) Temperature (physiological tolerances)

Many effects of anthropogenic climate change follow from an increase in temperature. The most obvious proximate factor causing extinction is temperatures that exceed the physiological tolerance of the species [10,12]. This factor may be most important in sessile organisms and those with limited thermoregulatory ability, and in regions and time scales in which temperature increase is greatest.

The impacts of temperature may also be more indirect, but still related to physiological tolerances. For example, in spiny lizards (*Sceloporus*), local extinctions seem to occur because higher temperatures restrict surface activity during the spring breeding season to a daily time window that is overly short [23]. Similarly, increased air temperatures may both decrease activity time and increase energy maintenance costs, leading organisms to die from starvation rather than from overheating [14]. In aquatic organisms, increased water temperatures may lead to increased metabolic demand for oxygen while reducing the oxygen content of the water [24]. Variability in temperature may also be an important proximate cause of extinction [25], including both extreme events and large differences over the course of a year. In temperate and polar latitudes, a mismatch between photoperiod cues and temperature may be important, with fixed photoperiod responses leading to activity patterns that are inappropriate for the changed climate [26]. Here, both low and high temperatures could increase mortality rates and lead to population extinction.

(ii) Precipitation (physiological tolerances)

Anthropogenic changes are also modifying precipitation patterns [27], and these changes may drive extinction in a variety of ways. For example, decreasing precipitation may lead directly to water stress, death and local extinction for terrestrial species [28], and loss of habitat for freshwater species or life stages [29,30]. There may also be synergistic effects between heat and drought stress (e.g. in trees [31]). Changing precipitation may be more important to some species than changing temperature, sometimes leading to range shifts in the direction opposite to those predicted by rising temperatures [32].

(iii) Other abiotic factors

Other abiotic, non-climatic factors may drive extinctions that are ultimately caused by climate change. For example, climate change can increase fire frequency, and these fires may be proximate causes of extinction (e.g. in South African plants [33]). Similarly, increases in temperature lead to melting ice-caps and rising sea levels [27], which may eliminate coastal habitats and modify the salinity of freshwater habitats [34].

(b) Biotic factors

The biotic factors that are the proximate causes of extinction from climate change can be placed in three general categories.

(i) Negative impacts on beneficial species

Climate change may cause local extinction of a given species by causing declines in a species upon which it depends. These may include prey for predators [35], hosts for parasites and specialized herbivores [16], species that create necessary microhabitats [36] and species that are essential for reproduction (e.g. pollinators [15]).

(ii) Positive impacts on harmful species

Alternately, climate change may cause extinction through positive effects on species that have negative interactions with a focal species, including competitors [37,38], predators [39,40] and pathogens [41–43]. Warming temperatures can also benefit introduced species, exacerbating their negative effects on native flora and fauna [44].

(iii) Temporal mismatch between interacting species

Climate change may also create incongruence between the activity times of interacting species [45]. These phenological mismatches may occur when interacting species respond to different environmental cues (e.g. temperature versus photoperiod for winter emergence) that are not congruently influenced by climate change [46]. We consider this category to be distinct from the other two because the differences in activity times are not necessarily negative or positive impacts on the species that are interacting with the focal species.

3. Are there current extinctions due to climate change?

Our goal is to understand which proximate factors cause extinctions due to climate change. However, we first need to establish that such extinctions are presently occurring. Few global species extinctions are thought to have been caused by climate change. For example, only 20 of 864 species extinctions are considered by the International Union for Conservation of Nature (IUCN) [47] to potentially be the result of climate change, either wholly or in part (using the same search criteria as a recent review [9]), and the evidence linking them to climate change is typically very tenuous (see the electronic supplementary material, table S1). However, there is abundant evidence for local extinctions from contractions at the warm edges of species' ranges. A pattern of range shifts (generally polewards and upwards) has been documented in hundreds of species of plants and animals [48,49], and is one of the strongest signals of biotic change from global warming. These shifts result from two processes: cold-edge expansion and warm-edge contraction (see the electronic supplementary material, figure S1). Much has been written about cold-edge expansions [21,50], and these may be more common than warm-edge contractions [51]. Nevertheless, many warm-edge contractions have been documented [52–58], including large-scale review studies spanning hundreds of species [48,59]. These warm-edge populations are a logical place to look for the causes of climate-related extinctions, especially because they may already be at the limits of their climatic tolerances [60]. Importantly, this pattern of warm-edge contraction provides evidence that many local extinctions have already occurred as a result of climate change.

We generally assume that the proximate factors causing local extinction from climate change are associated with the death of individuals. However, others factors may be involved as well. These include emigration of individuals into adjacent localities, declines in recruitment, or a combination of these and other factors. The question of whether climate-related local extinctions occur through death, dispersal or other processes has received little attention (but see [61,62]), and represents another important but poorly explored area in climate-change research.

4. What causes extinction due to climate change? current evidence

Given that there are many different potential causes of extinction as a result of climate change, and given that many populations have already gone extinct (as evidenced by warm-edge range contractions), what proximate causes of climate-related extinction have actually been documented? We conducted a systematic review of the literature to address this question.

(a) Causes of extinction: methods

We conducted three searches in the ISI Web of Science database, using the following keywords: (i) (('locally extinct' OR 'local extinction' OR 'extinc*') AND (caus*) AND ('climate change' OR 'global warming')); (ii) (('locally extinct' OR 'local extinction') AND ('climate change' OR 'global warming')); and (iii) (('extinc*' OR 'extirpat*') AND ('climate change' OR 'global warming' OR 'changing climate' OR 'global change')). The first two were conducted on 7 December 2011 and the third on 4 February 2012. Each search identified a partially overlapping set of studies (687 unique studies overall). We then reduced this to 136 studies which suggested that climate change is associated with local extinctions or declines (see the electronic supplementary material, appendix S1).

Among these 136 studies, we then identified those that reported an association between local extinction and climatic variables and that also identified a specific proximate cause for these extinctions (see the electronic supplementary material, appendix S1). The evidence linking these proximate causes to anthropogenic climate change varied considerably, but included studies integrating experimental and correlative results [23,63], and those that also accounted for factors unrelated to climate change [64]. Although we did not perform a separate, comprehensive search for all studies of climate-related declines, we also include studies of population declines that were connected to potential local extinctions as a second category of studies. Studies of declines should also be informative, given that the factors causing population declines may ultimately lead to extinctions [65]. All studies reported declines in abundance but some also considered declines in other parameters (e.g. fecundity). We also included studies of impacts from natural oscillations (such as the El Niño-Southern Oscillation, ENSO) as a third category of results.

(b) Causes of extinction: results

(i) Proximate causes of local extinctions

Of 136 studies focusing on local extinctions associated with climate change (see the electronic supplementary material, appendix S1), only seven identified the proximate causes of these extinctions (table 1 and figure 1*a*). Surprisingly, none of the seven studies shows a straightforward relationship between local extinction and limited tolerances to high temperature. For example, for the two studies that relate extinctions most directly to changing temperatures, the proximate factor is related either to how temperature limits surface activity time during the breeding season [23] or to a complex relationship between extreme temperatures (both cold and hot), precipitation and physiology [25,63]. Most studies (four of seven) implicate species interactions as the proximate cause, especially decreases in food availability [35,64,66]. Many authors have predicted that altered species interactions may be an important cause of extinction resulting from climate change (e.g. [67,68]), and our results empirically support the importance of these interactions (relative to other factors) among documented cases of local extinction.

(ii) Proximate causes of population declines

Seven studies identified proximate causes of population declines (table 2). The frequency of different proximate causes is intriguingly similar to those for population extinctions (figure 1*a*,*b*). Specifically, species interactions are the

Table 1. Studies documenting the proximate causes of local extinction due to anthropogenic climatic change.

species	location	hypothesized proximate cause of local extinction	reference
American pika (*Ochotona princeps*)	Great Basin region, USA	limited tolerance to temperature extremes (both high and low)	[25,63]
planarian (*Crenobia alpina*)	Wales, UK	loss of prey as result of increasing stream temperatures	[35]
desert bighorn sheep (*Ovis canadensis*)	California, USA	decrease in precipitation leading to altered plant community (food)	[64]
checkerspot butterfly (*Euphydryas editha bayensis*)	San Francisco Bay area, CA, USA	increase in variability of precipitation corresponding with reduction of temporal overlap between larvae and host plants	[66]
fish (*Gobiodon* sp. A)	New Britain, Papua New Guinea	destruction of obligate coral habitat due to coral bleaching caused by increasing water temperatures	[36]
48 lizard species (genus *Sceloporus*)	Mexico	increased maximum air temperature approaches physiological limit, seemingly causing decreased surface activity during the reproductive season	[23]
Adrar Mountain fish species	Mauritania	loss of water bodies due to drought	[30]

proximate cause of declines in the majority of studies, with declines in food availability being the most common cause [69,71,72], along with disease [70]. Drying of aquatic habitats is the cause in one study [29]. Two studies show physiological tolerances to abiotic factors as responsible for declines, with the declines being due to desiccation stress in desert trees [28], and due to oxygen limitation at high temperatures in a fish [24]. However, we find again that no studies show a straightforward relationship between population declines and temperatures exceeding the critical thermal limits of physiological tolerance.

(iii) Proximate causes of extinction due to 'natural' climatic oscillations

Among the 136 studies, four documented proximate causes of climate-change related extinctions that were associated with climatic oscillations (table 3). These oscillations may increase in frequency and severity due to anthropogenic impacts ([77], but see [78]). All four studies reinforce the importance of species interactions as the proximate cause of many extinctions attributable to climate change (figure 1*c*), including climate-related losses of food resources [73,75], loss of an algal symbiont ('coral bleaching'; [74]) and pathogen infection [76].

Two of the most widely discussed examples of climate-change related extinctions involve chytrid fungus in amphibians and coral bleaching (including many examples given above [36,70,74,75]). In both cases, local extinctions are strongly connected to natural climatic oscillations (e.g. [74]), but the links to anthropogenic climate change are still uncertain. For example, Pounds *et al.* [42] concluded that chytrid-related declines and extinctions in the frog genus *Atelopus* are related to anthropogenic warming, but Rohr & Raffel [70] subsequently suggested that chytrid spread in *Atelopus* was largely due to El Niño events. The link between anthropogenic climate change and local extinction of coral populations through bleaching also remains speculative [79]. For example, severe climate anomalies can cause bleaching and coral mortality [80], but bleaching itself does not always lead to mass mortality [81].

(c) Proximate causes of extinction: synthesis

Our review of the proximate causes of population extinctions and declines due to climate change reveals three main results, which are concordant across the three categories of studies (extinctions, declines and climatic oscillations). First, very few studies have documented proximate factors (18 of 136). Second, a diversity of proximate causes are empirically supported. Third, changing interspecific interactions are the most commonly demonstrated causes of extinctions and declines (figure 1). Specifically, changes in biotic interactions leading to reduced food availability are the single most common proximate factor (figure 1). In contrast, limited physiological tolerances to high temperatures are supported only infrequently and indirectly (figure 1). Interestingly, the impacts of species interactions may be particularly difficult to document, inviting underestimation. However, we caution that these generalizations are based on few studies. For example, all three datasets (tables 1–3) are dominated by vertebrates, with only one plant study represented. Thus, the frequencies of documented proximate causes may change as the pool of studies becomes more taxonomically representative.

Finally, we note that we did not specifically address global species extinctions associated with climate change in our review. However, IUCN lists 20 species as extinct or extinct in the wild that potentially declined because of climate change (see the electronic supplementary material, table S1). Of these 20 species, seven are frogs that were possibly infected by chytrid fungus, which may be facilitated by climate change (see above). Four are snails, which may have become extinct as a result of drought. Two are freshwater fishes that lost their habitats because of drought. Among the six birds, two were also potentially affected by drought. The other four birds are island species possibly impacted by storms (the severity of which may be related to climate change), but these all had clear non-climatic threats. A similar pattern occurs in one island rodent species. In almost all cases, the links between extinction and anthropogenic climate change are speculative (but see [82]), which is why these cases were not included previously in our review. Intriguingly, none of the 20 is clearly related to

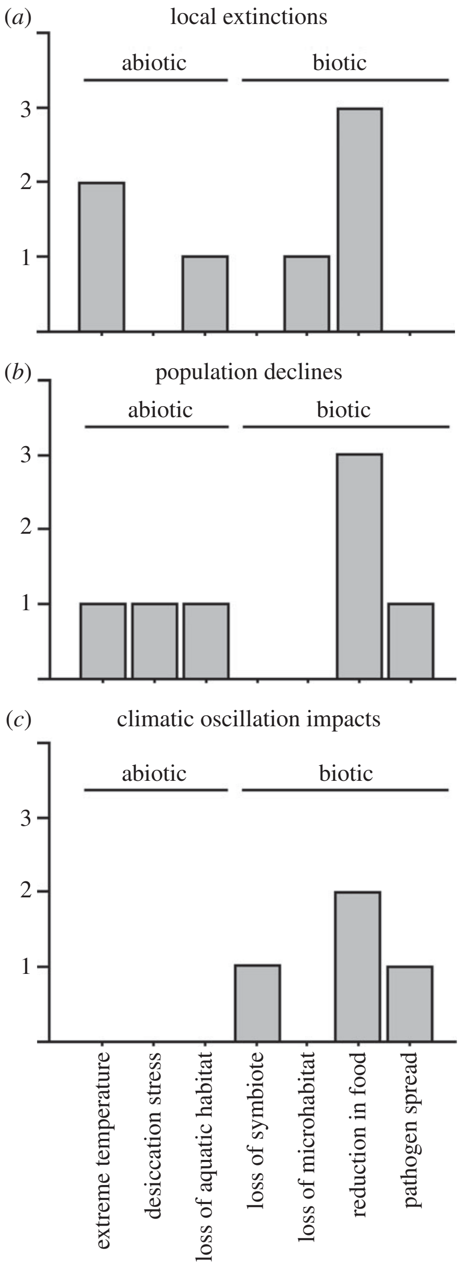

Figure 1. Summary of the frequency of different proximate causes of extinction due to climate change, among published studies. (*a*) 'local extinctions' refers to studies of local extinctions related to anthropogenic climate change (table 1), (*b*) 'population declines' refers to studies of declines in population abundance related to anthropogenic climate change (table 2), whereas (*c*) 'climatic oscillation impacts' refers to studies showing declines related to natural climatic oscillations (table 3) (but these oscillations may also be influenced by human factors, see relevant text). We note that there is some ambiguity in assigning some studies to a single, simple category.

limited tolerances to high temperatures (see the electronic supplementary material, table S1).

5. Approaches for finding the proximate causes of climate-related extinction

Our review demonstrates that disturbingly little is known about the proximate causes of extinctions due to recent climate change. How can this important gap be filled? Many approaches are possible, and we very briefly summarize two general frameworks that are beginning to be used. One focuses on individual species at multiple localities [23,25,63], the other on species assemblages at a particular locality [83–85]. These approaches are summarized graphically in the electronic supplementary material, figure S2.

Focusing on individual species (see the electronic supplementary material, figure S2), one must first document local extinctions or declines. To test whether populations have gone extinct, the present and past geographical ranges of the species can be compared. These analyses need not require surveying the entire species range, but could focus on a more limited series of transects (e.g. near the lowest latitudes and elevations, where ranges may already be limited by climatic factors [69,86]). The historical range can be determined from literature records and/or museum specimen localities [87]. These latter data are becoming increasingly available through online databases (e.g. GBIF; http://www.gbif.org/). Next, the species range (or select transects) should be resurveyed to document which populations are extant [23,56]. Evaluating whether populations persist is not trivial, and recent studies [56,88] have applied specialized approaches (e.g. occupancy modelling [89]). Furthermore, resurveys should account for false absences that may be misinterpreted as extinctions and for biases created by unequal sampling effort in space and time [87,90,91].

Documenting climate-related declines presents different challenges than documenting extinctions, given that most species lack data on population parameters over time. Some populations have been the focus of long-term monitoring, facilitating detailed studies of climate change impacts [86,92]. Large-scale databases on population dynamics through time are now becoming available. For example, the Global Population Dynamics Database [93] contains nearly 5000 time-series datasets. However, for many species, resurveying ranges to document local extinctions may be a necessary first step instead.

Given demonstrable local extinctions or declines, the next step is to determine whether these are related to large-scale trends in global climate change. Peery *et al.* [94] summarize six approaches that can be used to relate environmental factors to population declines [95]. These same approaches can be applied to connect global climate change and local extinctions. Relationships between changes in climate over time and population extinction versus persistence can be tested using GIS-based climatic data for relatively fine time scales (e.g. each month and year; PRISM; [96]). These analyses should preferably include data on other potential causes of local extinction not directly related to climate change, such as human habitat modification [64]. These analyses should help establish whether the observed local extinctions or declines are indeed due to climate change. If so, the next step is to understand their proximate causes.

Correlative analyses can be carried out to generate and test hypotheses about which proximate causes may be involved. Biophysical modelling [97] may be especially useful for these analyses, as it can incorporate many important factors, such as microclimate [98] and related variables (e.g. shade, wind speed, cloudiness, humidity) and relevant behavioural, ecological, demographic and physiological parameters [14,23]. Dissecting the specific aspects of climate that are most strongly associated with local extinctions may be important (e.g. is it warmer temperatures in the hottest part of the year, or the coldest?). Correlative studies can also test potential biotic factors, including the association between population extinctions or declines and the abundance of other species with negative impacts on the species in question (e.g. competitors, pathogens) or reductions in

Table 2. Studies documenting the proximate causes of declines in abundance due to anthropogenic climatic change.

species	location	hypothesized proximate cause of decline	reference
aloe tree (*Aloe dichotoma*)	Namib desert	desiccation stress owing to decreasing precipitation	[28]
four species of amphibians	Yellowstone National Park, USA	increasing temperature and decreasing precipitation cause a decline in habitat availability (pond drying)	[29]
plover (*Pluvialis apricaria*)	United Kingdom	high summer temperatures reduce abundance of craneflies (prey)	[69]
eelpout (*Zoarces viviparus*)	Baltic Sea	oxygen limitation at high temperatures	[24]
frogs (genus *Atelopus*)	Central and South America	climate change facilitates spread of pathogen (chytrid fungus)	[70]
grey jay (*Perisoreus canadensis*)	Ontario, Canada	warm autumns cause rotting in hoarded food, compromising overwinter survival and breeding success in the following year	[71]
Cassin's auklet (*Ptychoramphus aleuticus*)	California, USA	changes in upwelling timing and strength lower both adult survival and breeding success by changing food availability	[72]

Table 3. Studies that report proximate causes of declines in abundance or fitness associated with El Niño-Southern Oscilliation (ENSO) events.

species	location	hypothesized proximate cause of decline	reference
fig wasps (Hymenoptera: Agonidae)	Borneo	ENSO event causes obligate host trees (*Ficus* sp.) to fail to produce inflorescences, resulting in local extinction of pollinating wasps	[73]
corals	Panama and Ecuador	high sea surface temperatures cause bleaching and mortality	[74]
butterflyfish	Indian Ocean	climate-related loss of coral food source	[75]
toad (*Bufo boreas*)	Western USA	warming reduces water depth in ponds, which increases ultraviolet-B exposure of embryos, which in turn increases risk of fungal infection	[76]

species necessary for persistence (e.g. prey, hosts). Two-species occupancy models [99] could be applied to test for the impacts of these and other types of interspecific interactions. Identifying the particular interactions that are responsible for climate-related extinctions may be challenging, given the diversity of interactions and species that may be involved. However, our results suggest that changing biotic interactions may be the most common proximate causes of climate-related extinction (figure 1).

Once potential factors are identified with correlative studies, these can be tested with mechanistic analyses. These could include experimental tests of physiological tolerances to relevant temperature and precipitation regimes [10,24,86,100], and laboratory and field tests of species interactions [39]. Transplant experiments that move individuals from extant populations into nearby localities where the species has recently gone extinct [100] may be particularly useful (for species in which this is practical). In many ways, experimental analyses can provide the strongest tests of the hypothesized causes of local extinctions. However, these should be informed by broader correlative studies. For example, simply testing the physiological tolerances of a species to extremely high temperatures may say little about the causes of climate-associated local extinction in that species if those extinctions are actually caused by warmer temperatures in winter or the spread of a competitor.

The second major approach (see the electronic supplementary material, figure S2) is to focus on species assemblages at single localities over time [83–85], rather than analysing multiple localities across the range of one or more species. Given data on species composition at different points in time, the local extinctions or declines of certain species can be tested for association with temporal changes in climate. These losses can then be related to specific biological traits (e.g. greater loss of species with temperature-cued flowering times versus those using photoperiod, or species for which the site is near their southern versus northern range limits [84]). These relationships can then point the way to more mechanistic and experimental studies.

6. Questions for future research

Understanding the proximate factors that cause climate-related extinctions should be an urgent priority for future research and should open the door to many additional applied and basic questions. Are there specific conservation and management strategies that can be matched to specific extinction causes? Are there phylogenetic trends or life-history correlates [20] of these factors that may allow researchers to predict which factors will be important in a species without having to conduct lengthy studies within that species? Do different factors influence the ability of niche models to accurately predict range shifts and extinctions due to climate change (e.g. physiological tolerances versus species interactions)? Can species adapt to some potential causes of extinction and not others?

7. Conclusions

Climate change is now recognized as a major threat to global biodiversity, and one that is already causing widespread local extinctions. However, the specific causes of these present and future extinctions are much less clear. Here, we have reviewed the presently available evidence for the proximate causes of extinction from climate change. Our review shows that only a handful of studies have focused specifically on these factors, and very few suggest a straightforward relationship between limited tolerance to high temperatures and local extinction. Instead, a diverse set of factors is implicated, including effects of precipitation, food abundance and mismatched timing with host species. Overall, we argue that understanding the proximate causes of extinction from climate change should be an urgent priority for future research. For example, it is hard to imagine truly effective strategies for species conservation that ignore these proximate causes. We also outline some general approaches that may be used to identify these causes. However, we make the important caveat that the relative importance of different proximate causes may change radically over the next 100 years as climate continues to change, and limited physiological tolerances to high temperatures may become the dominant cause of extinction. Nevertheless, our review suggests the disturbing possibility that there may be many extinctions due to other proximate causes long before physiological tolerances to high temperatures become predominant.

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References

1. Thomas CD *et al*. 2004 Extinction risk from climate change. *Nature* **427**, 145–148. (doi:10.1038/nature02121)
2. Jetz W, Wilcove DS, Dobson AP. 2007 Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biol.* **5**, 1211–1219. (doi:10.1371/journal.pbio.0050157)
3. Leadley P *et al*. 2010 Biodiversity scenarios: projections of 21st century change in biodiversity and associated ecosystem services. Secretariat of the Convention on Biological Diversity, Montreal, 2010.
4. Pereira HM *et al*. 2010 Scenarios for global biodiversity in the 21st century. *Science* **330**, 1496–1501. (doi:10.1126/science.1196624)
5. Dawson TP, Jackson ST, House JI, Prentice IC, Mace GM. 2011 Beyond predictions: biodiversity conservation in a changing climate. *Science* **332**, 53–58. (doi:10.1126/science.1200303)
6. Hof C, Araujo MB, Jetz W, Rahbek C. 2011 Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature* **480**, 516–519. (doi:10.1038/nature10650)
7. Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F. 2012 Impacts of climate change on the future of biodiversity. *Ecol. Lett.* **15**, 5–377. (doi:10.1111/j.1461-0248.2011.01736.x)
8. Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD. 2009 The velocity of climate change. *Nature* **462**, 1052–1055. (doi:10.1038/nature08649)
9. Monzón J, Moyer-Horner L, Palamar MB. 2011 Climate change and species range dynamics in protected areas. *BioScience* **61**, 752–761. (doi:10.1525/bio.2011.61.10.5)
10. Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR. 2008 Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl Acad. Sci. USA* **105**, 6668–6672. (doi:10.1073/pnas.0709472105)
11. Huey RB, Deutsch CA, Tewksbury JJ, Vitt LJ, Hertz PE, Perez HJA, Garland T. 2009 Why tropical forest lizards are vulnerable to climate warming. *Proc. R. Soc. B* **276**, 1939–1948. (doi:10.1098/rspb.2008.1957)
12. Somero GN. 2010 The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine ‘winners’ and ‘losers’. *J. Exp. Biol.* **213**, 912–920. (doi:10.1242/jeb.037473)
13. Somero GN. 2011 Comparative physiology: a ‘crystal ball’ for predicting consequences of global change. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* **301**, R1–R14. (doi:10.1152/ajpregu.00719.2010)
14. Kearney M, Shine R, Porter WP. 2009 The potential for behavioral thermoregulation to buffer ‘cold-blooded’ animals against climate warming. *Proc. Natl Acad. Sci. USA* **106**, 3835–3840. (doi:10.1073/pnas.0808913106)
15. Memmott J, Craze P, Waser N, Price M. 2007 Global warming and the disruption of plant–pollinator interactions. *Ecol. Lett.* **10**, 710–717. (doi:10.1111/j.1461-0248.2007.01061.x)
16. Schweiger O, Heikkinen RK, Harpke A, Hickler T, Klotz S, Kudrna O, Kühn I, Pöyry J, Settele J. 2012 Increasing range mismatching of interacting species under global change is related to their ecological characteristics. *Glob. Ecol. Biogeogr.* **21**, 88–99. (doi:10.1111/j.1466-8238.2010.00607.x)
17. Tylianakis JM, Didham RK, Bascompte J, Wardle DA. 2008 Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* **11**, 1351–1363. (doi:10.1111/j.1461-0248.2008.01250.x)
18. Bonelli S, Cerrato C, Loglisci N, Balletto E. 2011 Population extinctions in the Italian diurnal Lepidoptera: an analysis of possible causes. *J. Insect Conserv.* **15**, 879–890. (doi:10.1007/s10841-011-9387-6)
19. Beever JA, Belant JL. (eds) 2012 *Ecological consequences of climate change. Mechanisms, conservation, and management*. Boca Raton, FL: CRC Press.
20. Beever JA, Belant JL. 2012 Ecological consequences of climate change: synthesis and research needs. In *Ecological consequences of climate change. Mechanisms, conservation, and management* (eds JA Beever, JL Belant), pp. 285–294. Boca Raton, FL: CRC Press.
21. Sexton JP, McIntyre PJ, Angert AL, Rice KJ. 2009 Evolution and ecology of species range limits. *Annu. Rev. Ecol. Evol. Syst.* **40**, 415–436. (doi:10.1146/annurev.ecolsys.110308.120317)
22. Brook BW, Sodhi NS, Bradshaw CJA. 2008 Synergies among extinction risks under global change. *Trends Ecol. Evol.* **23**, 453–460. (doi:10.1016/j.tree.2008.03.011)
23. Sinervo B *et al*. 2010 Erosion of lizard diversity by climate change and altered thermal niches. *Science* **328**, 894–899. (doi:10.1126/science.1184695)
24. Pörtner HO, Knust R. 2007 Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* **315**, 95–97. (doi:10.1126/science.1135471)
25. Beever EA, Ray C, Wilkening JL, Brussard PF, Mote PW. 2011 Contemporary climate change alters the pace and drivers of extinction. *Glob. Change Biol.* **17**, 2054–2070. (doi:10.1111/j.1365-2486.2010.02389.x)
26. Bradshaw WE, Holzapfel CM. 2010 Light, time, and the physiology of biotic response to rapid climate

change in animals. *Annu. Rev. Physiol.* **72**, 147–166. (doi:10.1146/annurev-physiol-021909-135837)

27. IPCC 2007 Climate change 2007, synthesis report. In *Contributions of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climage Change* (eds Core Writing Team, R. K. Pachauri, A Reisinger), pp. 104. Geneva, Switzerland: IPCC.
28. Foden W *et al.* 2007 A changing climate is eroding the geographical range of the Namib Desert tree aloe through population declines and dispersal lags. *Divers. Distrib.* **13**, 645–653. (doi:10.1111/j.1472-4642.2007.00391.x)
29. McMenamin SK, Hadley EA, Wright CK. 2008 Climatic change and wetland desiccation cause amphibian decline in Yellowstone National Park. *Proc. Natl Acad. Sci. USA* **105**, 16 988–16 993. (doi:10.1073/pnas.0809090105)
30. Trape S. 2009 Impact of climate change on the relict tropical fish fauna of Central Sahara: threat for the survival of Adrar Mountains fishes, Mauritania. *PLoS ONE* **4**, e4400. (doi:10.1371/journal.pone.0004400)
31. Adams HD, Guardiola-Claramonte M, Barron-Gafford GA, Villegas JC, Breshears DD, Zou CB, Troch PA, Huxman TE. 2009 Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global change-type drought. *Proc. Natl Acad. Sci. USA* **106**, 7063–7066. (doi:10.1073/pnas.0901438106)
32. Crimmins SM, Dobrowski SZ, Greenberg JA, Abatzoglou JT, Mynsberge AR. 2011 Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science* **331**, 324–327. (doi:10.1126/science.1199040)
33. Keith DA, Akçakaya HR, Thuiller W, Midgley GF, Pearson RG, Phillips SJ, Regan HM, Araújo MB, Rebelo TG. 2008 Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biol. Lett.* **4**, 560–563. (doi:10.1098/rsbl.2008.0049)
34. Jones AR. 2012 Climate change and sandy beach ecosystems. In *Ecological consequences of climate change. Mechanisms, conservation, and management* (eds JA Beever, JL Belant), pp. 133–159. Boca Raton, FL: CRC Press.
35. Durance I, Ormerod SJ. 2010 Evidence for the role of climate in the local extinction of a cool-water triclad. *J. N. Am. Benthol. Soc.* **29**, 1367–1378. (doi:10.1899/09-159.1)
36. Munday PL. 2004 Habitat loss, resource specialization, and extinction on coral reefs. *Glob. Change Biol.* **10**, 1642–1647. (doi:10.1111/j.1365-2486.2004.00839.x)
37. Wethey DS. 2002 Biogeography, competition, and microclimate: the barnacle *Chthamalus fragilis* in New England. *Integr. Comp. Biol.* **42**, 872–880. (doi:10.1093/icb/42.4.872)
38. Suttle KB, Thomsen MA, Power ME. 2007 Species interactions reverse grassland responses to changing climate. *Science* **315**, 640–642. (doi:10.1126/science.1136401)
39. Goddard JHR, Gosliner TM, Pearse JS. 2011 Impacts associated with the recent range shift of the aeolid nudibranch *Phidiana hiltoni* (Mollusca, Opisthobranchia) in California. *Mar. Biol.* **158**, 1095–1109. (doi:10.1007/s00227-011-1633-7)
40. Harley CDG. 2011 Climate change, keystone predation, and biodiversity loss. *Science* **334**, 1124–1127. (doi:10.1126/science.1210199)
41. Benning TL, LaPointe D, Atkinson CT, Vitousek PM. 2002 Interactions of climate change with biological invasions and land use in the Hawaiian Islands: modeling the fate of endemic birds using a geographic information system. *Proc. Natl Acad. Sci. USA* **99**, 14 246–14 249. (doi:10.1073/pnas.162372399)
42. Pounds JA *et al.* 2006 Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* **439**, 161–167. (doi:10.1038/nature04246)
43. Ytrehus B, Bretten T, Bergsjø B, Isaksen K. 2008 Fatal pneumonia epizootic in musk ox (*Ovibos moschatus*) in a period of extraordinary weather conditions. *Ecohealth* **5**, 213–223. (doi:10.1007/s10393-008-0166-0)
44. Stachowicz JJ, Terwin JR, Whitlach RB, Osman RW. 2002 Linking climate change and biological invasions: ocean warming facilitates nonindigenous species invasions. *Proc. Natl Acad. Sci. USA* **99**, 15 497–15 500. (doi:10.1073/pnas.242437499)
45. Visser ME, van Noordwijk AJ, Tinbergen JM, Lessells CM. 1998 Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proc. R. Soc. Lond. B* **265**, 1867–1870. (doi:10.1098/rspb.1998.0514)
46. Visser ME, Holleman LJM. 2001 Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proc. R. Soc. Lond. B* **268**, 289–294. (doi:10.1098/rspb.2000.1363)
47. IUCN 2012 *The IUCN red list of threatened species*. Version 2012.1. See http://www.iucnredlist.org (accessed 19 June 2012).
48. Parmesan C, Yohe G. 2003 A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42. (doi:10.1038/nature01286)
49. Thomas CD. 2010 Climate, climate change, and range boundaries. *Divers. Distrib.* **16**, 488–495. (doi:10.1111/j.1472-4642.2010.00642.x)
50. Angert AL, Crozier LG, Rissler LJ, Gilman SE, Tewksbury JJ, Chunco AJ. 2011 Do species' traits predict recent shifts at expanding range edges? *Ecol. Lett.* **14**, 677–689. (doi:10.1111/j.1461-0248.2011.01620.x)
51. Parmesan C, Gaines S, Gonzalez L, Kaufman DM, Kingsolver J, Peterson AT, Sagarin R. 2005 Empirical perspectives on species borders: from traditional biogeography to global change. *Oikos* **108**, 58–75. (doi:10.1111/j.0030-1299.2005.13150.x)
52. Hickling R, Roy DB, Hill JK, Thomas CD. 2005 A northward shift of range margins in the British Odonata. *Glob. Change Biol.* **11**, 502–506. (doi:10.1111/j.1365-2486.2005.00904.x)
53. Perry AL, Low PJ, Ellis JR, Reynolds JD. 2005 Climate change and distribution shifts in marine species. *Science* **308**, 1912–1915. (doi:10.1126/science.1111322)
54. Wilson JW, Gutierrez D, Martinez D, Agudo R, Monserrat VJ. 2005 Changes to the elevational limits and extent of species ranges associated with climate change. *Ecol. Lett.* **8**, 1138–1146. (doi:10.1111/j.1461-0248.2005.00824.x)
55. Thomas CD, Franco AMA, Hill JK. 2006 Range retractions and extinctions in the face of climate warming. *Trends Ecol. Evol.* **21**, 415–416. (doi:10.1016/j.tree.2006.05.012)
56. Moritz C, Patton JL, Conroy CJ, Parra JL, White GC, Beissinger SR. 2008 Impact of a century of climate change on small-mammal communities in Yosemite National Park, USA. *Science* **322**, 261–264. (doi:10.1126/science.1163428)
57. Hawkins SJ *et al.* 2009 Consequences of climate-driven biodiversity changes for ecosystem functioning of North European rocky shores. *Mar. Ecol. Prog. Ser.* **396**, 245–259. (doi:10.3354/meps08378)
58. Jones SJ, Lima FP, Wethey DS. 2010 Rising environmental temperatures and biogeography: poleward range contraction of the blue mussel, *Mytilus edulis* L., in the western Atlantic. *J. Biogeogr.* **37**, 2243–2259. (doi:10.1111/j.1365-2699.2010.02386.x)
59. Chen IC, Hill JK, Ohlemuller R, Roy DB, Thomas CD. 2011 Rapid range shifts of species associated with high levels of climate warming. *Science* **333**, 1024–1026. (doi:10.1126/science.1206432)
60. Anderson BJ, Akçakaya HR, Araújo MB, Fordham DA, Martinez-Meyer E, Thuiller W, Brook BW. 2009 Dynamics of range margins for metapopulations under climate change. *Proc. R. Soc. B* **276**, 1415–1420. (doi:10.1098/rspb.2008.1681)
61. Gilchrist HG, Mallory ML. 2005 Declines in abundance and distribution of the ivory gull (*Pagophila eburnea*) in Arctic Canada. *Biol. Conserv.* **121**, 303–309. (doi:10.1016/j.biocon.2004.04.021)
62. Tyler NJC. 2010 Climate, snow, ice, crashes, and declines in populations of reindeer and caribou (*Rangifer tarandus* L.). *Ecol. Monogr.* **80**, 197–219. (doi:10.1890/09-1070.1)
63. Beever EA, Ray C, Mote PW, Wilkening JL. 2010 Testing alternative models of climate-mediated extirpations. *Conserv. Biol.* **20**, 164–178. (doi:10.1890/08-1011.1)
64. Epps CW, McCullough D, Wehausen JD, Bleich VC, Rechel JL. 2004 Effects of climate change on population persistence of desert-dwelling mountain sheep in California. *Conserv. Biol.* **18**, 102–113. (doi:10.1111/j.1523-1739.2004.00023.x)
65. Caughley G. 1994 Directions in conservation biology. *J. Anim. Ecol.* **63**, 215–244. (doi:10.2307/5542)
66. McLaughlin JF, Hellmann JJ, Boggs CL, Ehrlich PR. 2002 Climate change hastens population extinctions. *Proc. Natl Acad. Sci. USA* **99**, 6070–6074. (doi:10.1073/pnas.052131199)
67. Gilman SE, Urban MC, Tewksbury J, Gilchrist GW, Holt RD. 2010 A framework for community interactions under climate change. *Trends Ecol. Evol.* **25**, 325–331. (doi:10.1016/j.tree.2010.03.002)
68. Urban M, Tewksbury JJ, Sheldon KS. 2012 On a collision course: competition and dispersal

differences create no-analogue communities and cause extinctions during climate change. *Proc. R. Soc. B* **279**, 2072–2080. (doi:10.1098/rspb.2011.2367)

69. Pearce-Higgins JW, Dennis P, Whittingham MJ, Yalden DW. 2010 Impacts of climate on prey abundance account for fluctuations in a population of a northern wader at the southern edge of its range. *Glob. Change Biol.* **16**, 12–23. (doi:10.1111/j.1365-2486.2009.01883.x)
70. Rohr JR, Raffel TR. 2010 Linking global climate and temperature variability to widespread amphibian declines putatively caused by disease. *Proc. Natl Acad. Sci. USA* **107**, 8269–8274. (doi:10.1073/pnas.0912883107)
71. Waite TA, Strickland D. 2006 Climate change and the demographic demise of a hoarding bird living on the edge. *Proc. R. Soc. B* **273**, 2809–2813. (doi:10.1098/rspb.2006.3667)
72. Wolf SG, Snyder MA, Doak DF, Croll DA. 2010 Predicting population consequences of ocean climate change for an ecosystem sentinel, the seabird Cassin's auklet. *Glob. Change Biol.* **16**, 1923–1935. (doi:10.1111/j.1365-2486.2010.02194.x)
73. Harrison RD. 2000 Repercussions of El Niño: drought causes extinction and the breakdown of mutualism in Borneo. *Proc. R. Soc. Lond. B* **267**, 911–915. (doi:10.1098/rspb.2000.1089)
74. Glynn PW, Mate JL, Baker AC, Calderon MO. 2001 Coral bleaching and mortality in Panama and Ecuador during the 1997-1998 El Niño-Southern Oscillation event: spatial/temporal patterns and comparisons with the 1982–1983 event. *Bull. Mar. Sci.* **69**, 79–109.
75. Graham NAJ, Wilson SK, Pratchett MS, Polunin NVC, Spalding MD. 2009 Coral mortality versus structural collapse as drivers of corallivorous butterflyfish decline. *Biodivers. Conserv.* **18**, 3325–3336. (doi:10.1007/s10531-009-9633-3)
76. Kiesecker JM, Blaustein AR, Belden LK. 2001 Complex causes of amphibian population declines. *Nature* **410**, 681–684. (doi:10.1038/35070552)
77. Timmermann A, Oberhuber J, Bacher A, Esch M, Latif M, Roeckner E. 1999 Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature* **398**, 694–697. (doi:10.1038/19505)
78. Collins M *et al*. 2010 The impact of global warming on the tropical Pacific Ocean and El Niño. *Nat. Geosci.* **3**, 391–397. (doi:10.1038/ngeo868)
79. Pandolfi JM, Connolly SR, Marshall DJ, Cohen AL. 2011 Projecting coral reef futures under global warming and ocean acidification. *Science* **333**, 418–422. (doi:10.1126/science.1204794)
80. Hoegh-Guldberg O. 1999 Climate change, coral bleaching and the future of the world's coral reefs. *Mar. Freshwater Res.* **50**, 839–866. (doi:10.1071/MF99078)
81. Eakin CM *et al*. 2010 Caribbean corals in crisis: record thermal stress, bleaching, and mortality in 2005. *PLoS ONE* **5**, e13969. (doi:10.1371/journal.pone.0013969)
82. Gerlach J. 2007 Short-term climate change and the extinction of the snail *Rhachistia aldabrae* (Gastropoda: Pulmonata). *Biol. Lett.* **3**, 581–584. (doi:10.1098/rsbl.2007.0316)
83. Sagarin RD, Barry JP, Gilman SE, Baxter CH. 1999 Climate-related change in an intertidal community over short and long time scales. *Ecol. Monogr.* **69**, 465–490. (doi:10.1890/0012-9615(1999)069[0465:CRCIAI]2.0.CO;2)
84. Willis CG, Ruhfel B, Primack RB, Miller-Rushing AJ, Davis CC. 2008 Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proc. Natl Acad. Sci. USA* **105**, 17 029–17 033. (doi:10.1073/pnas.0806446105)
85. Wethey DS, Woodin SA, Hilbish TJ, Jones SJ, Lima FP, Brannock PM. 2011 Response of intertidal populations to climate: effects of extreme events versus long term change. *J. Exp. Mar. Biol. Ecol.* **400**, 132–144. (doi:10.1016/j.jembe.2011.02.008)
86. Dahlhoff EP, Fearnley SL, Bruce DA, Gibbs AG, Stoneking R, McMillan DM, Deiner K, Smiley JT, Rank NE. 2008 Effects of temperature on physiology and reproductive success of a montane leaf beetle: implications for persistence of native populations enduring climate change. *Physiol. Biochem. Zool.* **81**, 718–732. (doi:10.1086/590165)
87. Tingley MW, Beissinger SR. 2009 Detecting range shifts from historical species occurrences: new perspectives on old data. *Trends Ecol. Evol.* **24**, 625–633. (doi:10.1016/j.tree.2009.05.009)
88. Tingley MW, Monahan WB, Beissinger SR, Moritz C. 2009 Birds track their Grinnellian niche through a century of climate change. *Proc. Natl Acad. Sci. USA* **106**, 19 637–19 643. (doi:10.1073/pnas.0901562106)
89. MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey LL, Hines JE. 2006 *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence.* Burlington, MA: Academic Press.
90. Charmantier A, McCleery RH, Cole LR, Perrins C, Kruuk LEB, Sheldon BC. 2008 Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science* **320**, 800–803. (doi:10.1126/science.1157174)
91. Boakes EH, McGowan PJK, Fuller RA, Chang-qing D, Clark NE, O'Connor K, Mace GM. 2010 Distorted views of biodiversity: spatial and temporal bias in species occurrence data. *PLoS Biol.* **8**, e1000385. (doi:10.1371/journal.pbio.1000385)
92. Botts EA, Erasmus BFN, Alexander GJ. 2011 Geographic sampling bias in the South African Frog Atlas Project: implications for conservation planning. *Biodivers. Conserv.* **20**, 119–139. (doi:10.1007/s10531-010-9950-6)
93. NERC Centre for Population Biology, Imperial College 2010 The global population dynamics database version 2. See http://www3.imperial.ac.uk/cpb/research/patterns andprocesses/gpdd.
94. Peery MZ, Beissinger SR, Newman SH, Burkett EB, Williams TD. 2004 Applying the declining population paradigm: diagnosing causes of poor reproduction in the marbled murrelet. *Conserv. Biol.* **18**, 1088–1098. (doi:10.1111/j.1523-1739.2004.00134.x)
95. Beissinger SR, Wunderle Jr JM, Meyers JM, Saether BE, Engen S. 2008 Anatomy of a bottleneck: diagnosing factors limiting population growth in the Puerto Rican parrot. *Ecol. Monogr.* **78**, 185–203. (doi:10.1890/07-0018.1)
96. Daly C, Gibson WP, Taylor GH, Johnson GL, Pasteris P. 2002 A knowledge-based approach to the statistical mapping of climate. *Clim. Res.* **22**, 99–113. (doi:10.3354/cr022099)
97. Buckley LB, Urban MC, Angilletta MJ, Crozier LG, Rissler LJ, Sears MW. 2010 Can mechanism inform species distribution models? *Ecol. Lett.* **13**, 1041–1054. (doi:10.1111/j.1461-0248.2010.01479.x)
98. Helmuth B *et al*. 2006 Mosaic patterns of thermal stress in the rocky intertidal zone: implications for climate change. *Ecol. Monogr.* **76**, 461–479. (doi:10.1890/0012-9615(2006)076[0461:MPOTSI]2.0.CO;2)
99. Richmond OMW, Hines JE, Beissinger SR. 2010 Two-species occupancy models: a new parameterization applied to co-occurrence of secretive rails. *Ecol. Appl.* **20**, 2036–2046. (doi:10.1890/09-0470.1)
100. Jones SJ, Mieszkowska N, Wethey DS. 2009 Linking thermal tolerances and biogeography: *Mytilus edulis* (L.) at its southern limit on the east coast of the United States. *Biol. Bull.* **217**, 73–85.

California Department of Forestry and Fire Protection

Emergency Fund
Fire Suppression Expenditures

Fiscal Year	Expenditures
1979—1980	$11,978,000
1980—1981	$21,178,000
1981—1982	$12,582,000
1982—1983	$8,619,000
1983—1984	$12,358,000
1984—1985	$16,847,000
1985—1986	$35,510,000
1986—1987	$14,799,000
1987—1988	$56,769,000
1988—1989	$57,983,000
1989—1990	$39,345,000
1990—1991	$70,825,000
1991—1992	$22,524,000
1992—1993	$85,591,000
1993—1994	$65,679,000
1994—1995	$69,858,000
1995—1996	$60.4 million
1996—1997	$107 million
1997—1998	$47.7 million
1998—1999	$43.8 million
1999—2000	$178.5 million

Fiscal Year	Expenditures
2000—2001	$114 million
2001—2002	$166 million
2002—2003	$135 million
2003—2004	$252 million
2004—2005	$170 million
2005—2006	$117 million
2006—2007	$206 million
2007—2008	$524 million
2008—2009	$499 million
2009—2010	$274+ million
2010—2011	$90.1 million
2011—2012	$140 million
2012—2013	$310 million
2013—2014	$242 million
2014—2015	$402 million
2015—2016	$608 million
2016—2017	$534 million
2017—2018	$773 million
2018—2019*	$635 million (EST)
2019—2020**	$ 91 million (EST)

October 2019
www.fire.ca.gov

*E-fund expenditures for FY 2018-19 are estimates. Final numbers are pending.

**E-fund expenditures for FY 2019-20 are YTD estimates. Numbers are updated at the beginning of each month.

INDEPENDENT EXTERNAL SPRINKLERS
to protect your home during a wildfire

From the California Chaparral Institute

We've been investigating external sprinklers for quite some time. The idea requires a paradigm shift for people because sprinklers have traditionally been for the protection of lives inside a structure. Now that we increasingly facing a different threat, wind-driven fire from the outside, we need to look at structure protection from a new perspective. Other countries outside of the United States, notably Australia and Canada, have employed external sprinklers in the wildland-urban-interface (WUI) with success.

The basic idea is that <u>a wet house is nearly impossible to ignite</u>.


From platypussprinkler.com

EXAMPLES

The first time we encountered the idea was right after the 2003 Cedar Fire in San Diego County, California. The owners of a home in Wildcat Canyon were convinced the under-eave misters they installed allowed the structure to survive the wildfire. The rural canyon in which they lived was one of the hardest hit. The owners had turned on the gravity fed system supplied by a 5,000-gallon water tank just before they evacuated. When they returned, their home was one

of the few structures left standing in the canyon. The misters had soaked an area of about six feet wide all around the home. They wrote a full description of their experience. It is available here:
http://www.californiachaparral.org/images/Conniry_Story.pdf

The idea has been slowly catching on.

Another family in San Diego County built a more elaborate under-eave misting system that actually uses wind to help distribute the water. The builder, Dr. Joseph Mitchell, has a complete description of his system on his website here:
http://www.mbartek.com/weeds-info

Dr. Mitchell has also published a paper in the Fire Safety Journal than provides design and performance details on his mister system. It is available here:
http://www.californiachaparral.org/images/Mitchell_JW_Ex_Sprinklers_WEEDS_2006.pdf

A couple in Santa Barbara claimed their external sprinklers saved their home during the 2009 Jesusita Fire while they sheltered in place. Most of the homes around them burned. They were interviewed by a local news station:
https://youtu.be/g0PGC0YEjZY

During interviews after the 2017 Thomas Fire, we have encountered several people who were convinced that the external sprinklers they had installed played an important role in saving their homes. In fact, the National Fire Protection Association and Firewise USA are both beginning to produce educational materials about external sprinklers for people in the WUI. There is a sample of one of their handouts at the end of this summary paper.

INSTALLERS

There are a few start-up companies in the US that are promoting the idea. For example:

Roof Saver Sprinklers
www.roofsaversprinklers.com
waveGuard
https://www.waveguardco.com/

The larger, more established companies we are familiar with are either Canadian or Australian. However, in conversations with these companies, they indicated they had investigated marketing their systems in the states, but decided against it because of the tendency for Americans to file liability claims. Here is one of the bigger firms in Canada:
SPIEDR: https://www.spiedr.com/spiedr-structure-protection-sprinklers/

There are a multitude of videos available on YouTube describing external sprinkler systems. One of the best is a detailed explanation of an innovative, computer-controlled system from Australia:
https://youtu.be/y2z-sQfMHko

RECOMMENDATIONS

There's a lot of potential for these systems.

Unfortunately, when the idea of external sprinklers is brought up, many seem to misunderstand the concept and immediately cite power failures and water pressure as limiting factors. To function properly, external sprinklers must be independent. This means the water source needs to be a backyard pool, or as in the case of the family in Wildcat Canyon, a 5,000-gallon water tank. The water has to be either gravity fed or on an independent gas or diesel-powered pump. These systems can be turned on when the owner evacuates, or remotely by cell phone or other electronic device. Based on our own observations, we believe many of the homes that burned in eastern Ventura during the 2017 Thomas Fire could have been likely saved if they had properly designed external sprinkler systems protecting them.

Policy makers should consider requiring new homes built in the WUI have independent external sprinkler systems. Clusters of homes could be served by a single system. Where realistic, communities already built in very high fire hazard zones could be given 10 years to retrofit homes (singly or in group). Pre-disaster FEMA grants could be made available for the most vulnerable communities as they have been for the mountain towns of Big Bear and Idyllwild, California, to retrofit flammable building features.

For more on how to protect your home from wildfire, please visit our webpage at:
http://www.californiachaparral.org/bprotectingyourhome.html

WILDFIRE RESEARCH FACT SHEET

EXTERIOR SPRINKLER SYSTEMS

Are exterior sprinkler systems an option for protecting a home during a wildfire, after residents have evacuated the property?

Functionality and Installation

The function of an exterior sprinkler system is to minimize the opportunity for ignition by wetting the home and surrounding property. Sprinkler systems should be able to protect a home against the three basic wildfire exposures: wind-blown embers, radiant heat and direct flame contact.

Sprinklers systems can be mounted in one or more locations, including:

- The roof (Photo 1).
- Under the eave at the edge of the roof.
- On the property, in which case the sprinklers are directed at the home from multiple locations surrounding it.

Ember ignition of combustibles located on or near the home can result in a radiant and/or flame contact exposure (Photo 2). Water should reach all vulnerable areas for the system to have maximum effect both on and near the home (Photo 3).

Potential Issues

Post-fire assessments have shown exterior sprinkler systems can be effective in helping a home survive a wildfire, but potential issues exist with their use. These issues include:

- The water supply should be adequate to deliver water, when needed, for the time embers could threaten a home. This period could be up to 8 hours.
  - Check with your local fire department if your sprinkler system uses water from a municipal supply; they may have suggestions to help minimize water consumption.
- The effectiveness of a sprinkler system is questionable when a neighboring home is burning, since this would result in an extended radiant heat and/or contact exposure to the home.
- These systems can be activated manually or by an automated device, such as a sensor that detects heat or flame, or by an SMS-enabled cell phone. The ability of these systems to activate based strictly on an ember exposure has not been determined. Since wind-blown embers can be transported for up to a mile from the flame front of a wildfire, this may be a limitation.
- The most threatening wildfires occur during high-wind events and the homeowner should consider how the distribution/transport of water droplets may be influenced by elevated wind speeds.

Recommendations

Given the potential issues regarding performance, it's recommended that use be a supplement to, and not a replacement for, already proven mitigation strategies, such as the reduction of potential fuels throughout the home ignition zones, along with removal of roof and gutter debris, and use of noncombustible and fire/ember-ignition resistant building materials and installation design details.

Photo 1. Roof mounted sprinkler.

Photo 2. In order to be effective, external sprinklers must be able to wet all areas where ignition can occur, or be sufficiently effective in quenching embers that approach the home so they won't have enough energy to ignite combustible items.

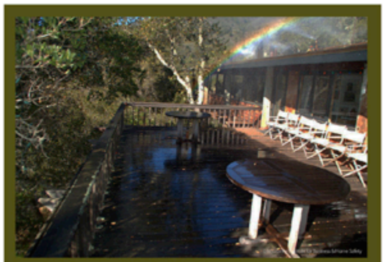

Photo 3. Roof-edge mounted sprinkler. Note these sprinklers did not deliver water in the near-home area. With this scenario, a sufficient number of wind-blown embers would have to be quenched in order to avoid ignition of the siding and decking in this zone, particularly at the deck-to-wall intersection.

Insurance Institute for Business & Home Safety

NFPA | FIREWISE USA® RESIDENTS REDUCING WILDFIRE RISKS

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PG&E OUTAGES: Bay Area Power Outage Survival Guide

KPIX CBS SF BayArea ≡ MENU NEWS WEATHER SPORTS BEST OF VIDEO KPIX 5 ON AIR

Power Outage Results In Multiple Crashes, Injuries At Santa Rosa Intersections

October 9, 2019 at 2:47 pm **Filed Under:** Car crashes, PG&E, Power Outage, public safety power shutoff

SANTA ROSA (CBS SF) — Widespread power outages in the North Bay have resulted in a number of auto accidents at intersections where traffic signals were not working, according to authorities.

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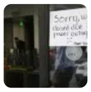
Delayed PG&E Power Shutdown Begins In East Bay, South Bay, Santa Cruz County

PG&E Confirms It Will Shut Off Power To Quarter Million Bay Area Customers



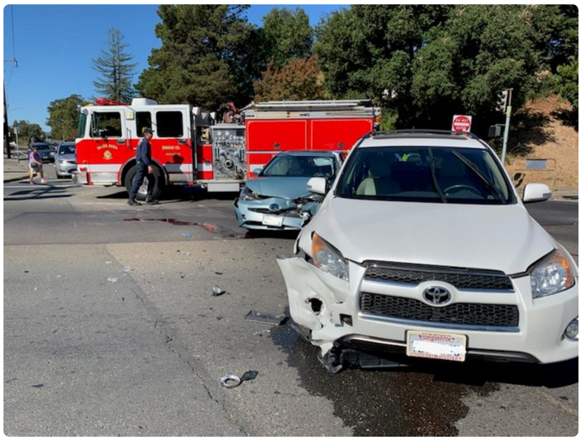
Bay Area Power Outage Survival Guide

The City of Santa Rosa said in a tweet on Wednesday that there have been "multiple" traffic collisions at intersections without power, including five crashes that resulted in injuries.

Drivers were urged to slow down and reminded to treat intersections without power as four-way stops.

City of Santa Rosa
@CityofSantaRosa

City of Santa Rosa Police and Fire Departments have responded to multiple traffic collisions, including five with injuries, at intersections without power. Please slow down and treat all intersections without power as a four way stop.



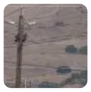
16 12:16 PM - Oct 9, 2019

18 people are talking about this

PG&E has shut off power in parts of Sonoma, Solano, Marin and Napa counties as part of a Public Safety Power Shutoff, designed to prevent deadly wildfires during dangerous wind conditions Wednesday and Thursday.

Power shutdowns have been postponed until at least 8 p.m. for the East Bay, the South Bay and the Peninsula, according to officials.

The utility is currently under Chapter 11 bankruptcy protection after its power lines ignited several massive wildfires in Northern California since 2017. Victims of those fires have filed millions of dollars in damage lawsuits against the utility.

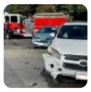


San Jose Residents Brace For Evening Power Outages, Nightmare Commute

Fire Crews Gain Upper Hand On San Bruno Mountain Brush Fire

UC Berkeley, Several Other Bay Area Schools Cancel Wednesday Classes

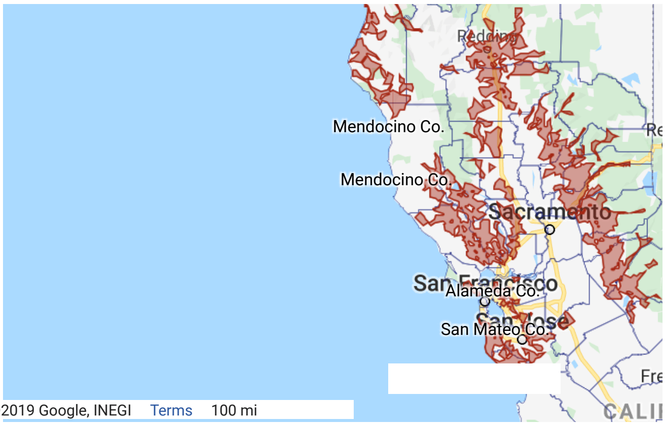
2 Flights Forced To Make Emergency Landings At San Francisco Int'l Airport



Power Outage Results In Multiple Crashes, Injuries At Santa Rosa Intersections

Newsom: Californians Should Be 'Outraged' Over PG&E Power Shutoffs

Planned power s... ☆



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ALSO READ:

- **Bay Area Power Outage Survival Guide**
- Emergency Centers Activated Ahead Of Power Shutoffs
- PG&E Web Page On Power Outages Crashes From High User Volume
- Bay Area Schools Cancel Classes Amid Mass Power Outages

Comments

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State Senator Calls For Clear Standards In Future PG&E Shutoffs

Amid the unprecedented power shutoffs by Pacific Gas & Electric Co., a Bay Area lawmaker is seeking to restrict such outages

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Population persistence in landscapes fragmented by roads: Disentangling isolation, mortality, and the effect of dispersal

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Barrier effect
Mortality
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ABSTRACT

Linear infrastructures, one of several forms of land-use, are a major driver of biodiversity loss. Roads impact populations at many levels, with direct road mortality and barrier effect contributing to decreased population abundance, higher isolation and subdivision, and therefore to increased extinction risk. In this paper, we compared the effect of road mortality and of the barrier effect on population isolation, persistence and size, and assessed the interaction of these effects with dispersal. We used a spatially explicit, process-based model of population dynamics in landscapes fragmented by varying levels of road density. We modelled a barrier effect independently from road mortality by varying the probability with which individuals avoid crossing roads. Both road mortality and the barrier effect caused population isolation. While road mortality alone had stronger negative effects than the barrier effect without extra mortality, the latter also resulted in decreased population size. Yet, road avoidance could, in some cases, rescue populations from extinction. Populations with a large dispersal distance were more negatively affected as road mortality increased. However, when there was no road mortality they maintained larger sizes than populations with a short dispersal distance. Our results highlight the much higher relative importance of road mortality than the barrier effect for population size and persistence, and the importance of assessing relevant species traits for effective long-term transportation planning and conservation management. Our model can be used in species-specific situations and with real landscape configurations in applications such as conservation planning.

1. Introduction

The current biodiversity crisis is mainly driven by land-use change (Pereira et al., 2012; Maxwell et al., 2016). Roads, one of many forms of land-use, cause major impacts on populations. As the road network is predicted to strongly increase in the coming years (van der Ree et al., 2015), it is crucial to assess its impact on populations, in order to apply suitable mitigation measures, and improve conservation and road planning.

Roads cause habitat loss and fragmentation, and decrease habitat quality. Roads also cause direct mortality through wildlife collisions with vehicles, and act as a barrier to movement (van der Ree et al., 2015). These direct and indirect impacts of roads can contribute to population isolation and subdivision, to decreases in population abundance, and therefore can increase population extinction risk (van der Ree et al., 2015; Ascensão et al., 2016), although there are also positive effects for some species (e.g., see Rytwinski and Fahrig, 2012, 2013).

Species traits can also influence population-level responses to land-use change (Pereira and Daily, 2006), and should be considered when assessing the effects of roads. Specifically, dispersal has been identified as an important factor but its influence on population persistence is still not fully understood. For example, while the role of dispersal is beneficial in metapopulation models (e.g., Hanski, 1998), because more patches can be colonized if dispersal is large, in source-sink models or reaction-diffusion models (e.g., Skellam, 1951; Pulliam, 1988) dispersal affects populations negatively, because it can lead to colonization of habitats where population growth rates are negative (sink habitats) (Pereira and Borda-de-Água, 2013). Moreover, dispersal can be associated with increased mortality risk (e.g., Nathan et al., 2012), with some studies suggesting there is an optimal intermediate dispersal rate

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for persistence in disturbed habitats (Casagrandi and Gatto, 1999).

The detrimental effect of dispersal in disturbed habitats is supported by several empirical studies (e.g., fragmented forests: Gibbs, 1998; Van Houtan et al., 2007). In the specific case of roads, a higher mobility has been related to negative effects of roads in mammal and bird species (Rytwinski and Fahrig, 2012). Furthermore, using a theoretical approach, Borda-de-Água et al. (2011) predicted that the larger the mean dispersal distance in a population, the larger would be the minimum area necessary for this population to persist in a landscape fragmented by roads.

In this paper we focus on dispersal movement as the process whereby individuals leave their initial location, move across a more or less suitable environment, and settle in a new location (Clobert et al., 2012; Matthysen, 2012). Our model does not currently include other types of movement (such as daily movements).

Direct road mortality introduces an additional source of mortality besides natural mortality. In addition, roads can also act as a barrier that does not introduce additional mortality, when the animals do not cross the roads. This barrier effect can be due to physical structures (such as fences) or to road avoidance behavior (e.g., Jaeger and Fahrig, 2004; Grilo et al., 2012), and for simplicity in this paper we refer to it simply as barrier effect. Although this can rescue individuals from road mortality to some extent, the negative consequences of habitat loss and fragmentation may be higher when such barrier effect is present, since road avoidance can lead to population isolation and to higher exposure to demographic and environmental stochasticity (Rytwinski and Fahrig, 2012; Ascensão et al., 2016). Moreover, the effects of road mortality and of road avoidance can be confounded and are still to be properly disentangled. For example, reduced population abundance near roads may be due to direct road mortality, or due to road avoidance behavior (e.g., Fahrig et al., 1995).

Although there is evidence that the effects of roads on population abundance are in general negative (Rytwinski and Fahrig, 2015), the impact of roads on population persistence has not been so commonly addressed (but see, for example Borda-de-Água et al., 2014 and Ceia-Hasse et al., 2017).

The key issue addressed in this paper was to disentangle the influence of an additional source of mortality (direct road mortality) versus the influence of a barrier effect to movement that does not introduce such additional mortality on population isolation, persistence and size, as well as the influence of dispersal, in fragmented landscapes. We addressed this using roads. We use a spatially explicit, process-based model of population dynamics. Our questions were: (1) What is the importance of road mortality versus isolation, for population persistence and size in landscapes fragmented by roads?; (2) How does dispersal influence the size and the persistence of populations under varying levels of road mortality and of a barrier effect?

2. Materials and methods

We used an individual-based toy model of population dynamics to perform a theoretical study on the effects of road mortality, barrier effect and dispersal on population isolation, size and persistence of a virtual species. Our study is not based on any empirical data and thus is more appropriately considered under the virtual ecology rationale (e.g., Grimm, 1999; Zurell et al., 2010).

2.1. Model description

The model description follows the ODD (Overview, Design concepts, Details) protocol for describing agent-based models (Grimm et al., 2006, 2010). The model was implemented as an ANSI C++ program, which can be downloaded from https://github.com/anaceiahasse/landsim.

2.1.1. Purpose

The purpose of the model is to simulate population dynamics in fragmented landscapes. Specifically, in this study, the model simulated population dynamics in landscapes fragmented by roads, with special emphasis on the effects of road mortality, of a barrier effect without mortality, and on the influence of dispersal distance.

2.1.2. Entities, state variables, and scales

The entities of the model are the landscape and the individuals, i.e., the model keeps track of the features of the landscape and of the female population (the model only considers female individuals for simplicity).

The landscape is a two-dimensional grid of N x N square cells with reflecting boundaries. An alternative approach to deal with edge effects would have been to consider periodic boundary conditions (i.e., torus geometry) instead of reflecting boundaries. However, given a dispersal step size of only one cell and the large size of the grid, both approaches can lead to similar outcomes. Each cell of the landscape is assigned to one of n possible types with values varying between 0 and 1. In the present case, each cell belongs to one of two possible types, "high-quality" habitat (non-road) or "road", with values of "1″ and "0″, respectively. We generated several landscapes with different proportions of road cells, where roads were placed perpendicularly to one another (Fig. 1, Table 1). We used simple hypothetical regular road networks because our main objective was to disentangle the effects of sink mortality versus those of a barrier effect that does not introduce additional mortality. Sink mortality here corresponds to road mortality, and it is the probability that an individual dies when crossing a road (see Section 2.1.7.3 below). Our goal was to derive general principles that can be the basis to understanding and model more specific or complex cases.

Individuals are characterized by the following state variables: age, developmental stage (juvenile or adult), position in the landscape; and by the following attributes: fecundity, age at first breeding, natural survival probability, home range size, dispersal distance, road mortality probability, road avoidance probability (Table 1).

2.1.3. Process overview and scheduling

Each simulation time step consists of the following sequential events (Fig. 2, Table 1): reproduction; natural mortality; dispersal of juveniles; juvenile density-dependent mortality. Section 2.1.7 describes the submodels implementing these processes. Juveniles that establish a home range are inserted into the adult population at the end of each simulation time step, thereby updating population size and landscape cell availability for the following time step. At the beginning of each simulation time step, the age of each individual is updated (increased by 1), and the sequential steps listed above ensue.

2.1.4. Design concepts

2.1.4.1. Basic principles. Roads can contribute to population isolation, decreased size and increased extinction risk through direct mortality and barrier effects (e.g., van der Ree et al., 2015; Ascensão et al., 2016). Dispersal can also influence how roads impact populations (e.g., Borda-de-Água et al., 2011; Rytwinski and Fahrig, 2012). The model allows assessing the relative importance of these factors for population isolation, persistence and size, which is not yet fully understood.

2.1.4.2. Emergence. Population dynamics emerges from the model (i.e. from the set of rules defined, parameter values used and landscape configuration).

2.1.4.3. Adaptation. Juveniles choose the direction in which they disperse according to cell type (road versus high-quality habitat cell) and occupancy (they may avoid dispersing into road cells with a given probability and they do not disperse to occupied cells, respectively).

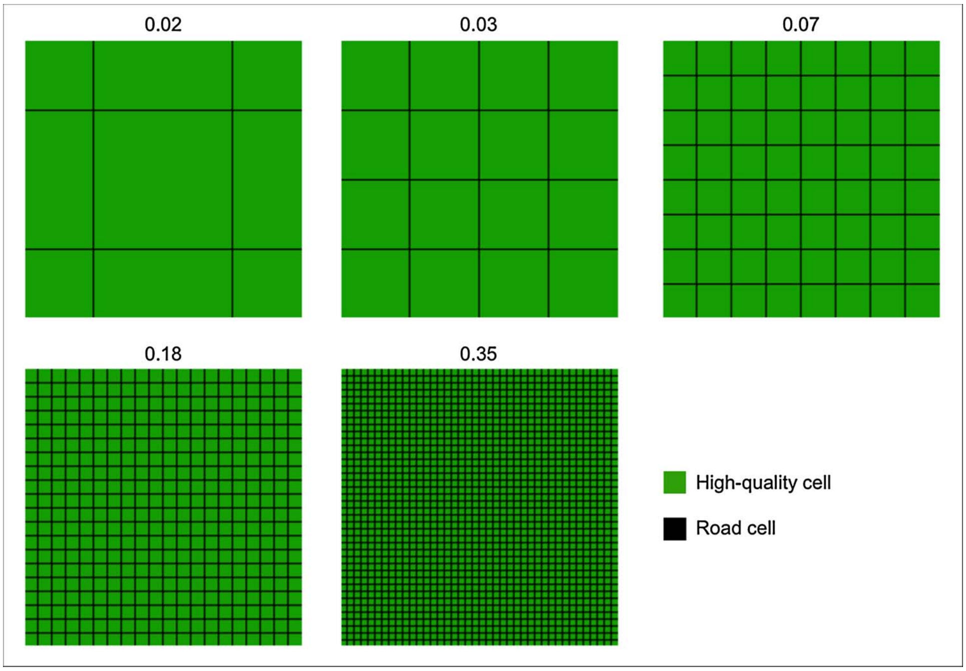

Fig. 1. Landscape configurations used in simulations. Each landscape is a grid of 200 × 200 cells composed of high-quality habitat cells, and road cells. Numbers on top of each panel indicate the proportion of road cells in each landscape.

Table 1
Model parameters and values used in the simulations.

Parameter	Value	
	1st set of simulations	2nd set of simulations
Landscape size (N x N)	200 × 200 cells	
Initial population size	10 individuals	
Number of replicates	100	
Number of time steps	1000	
Fecundity (b_i)	2	
Survival probability (s)	0.4	
Dispersal distance (d)	5 or 50 cells	
Road mortality, Road avoidance (m_{RM}, p_{RA})	(0.0, 0.0); (0.0, 1.0); (1.0, 0.0)	varied from 0 to 1 in steps of 0.1
Proportion of road cells in the landscape	0.02, 0.03, 0.07, 0.18, 0.35	0.07, 0.35

2.1.4.4. Sensing. During dispersal, juveniles evaluate cell type (road versus non-road cell) and occupancy.

2.1.4.5. Interaction. Juveniles do not disperse through cells that are already occupied.

2.1.4.6. Stochasticity. Stochasticity was incorporated in several processes (reproduction, natural mortality, dispersal of juveniles); see Section 2.1.7 for details.

2.1.4.7. Observation. For each model run, we recorded population size at the end of each simulation and averaged population size across replicates. We calculated the probability of extinction as the proportion of replicates in which populations went extinct before the end of the simulation.

2.1.5. Initialization

The model starts by settling an initial population of females at breeding age in the landscape. After the initial population is created, each simulation time step consists of the events described in Section 2.1.7 (Submodels). In all simulations, the initial population size was 10 individuals, set at random in the landscape. See Table 1 for the remaining parameter values used in the simulations and Fig. 3 for a representation of the settlement of the initial population in the landscape and of the colonization of the landscape.

2.1.6. Input data

The model does not import data of driving environmental variables.

2.1.7. Submodels

2.1.7.1. Reproduction. Females reproduce after one year and once they have established their home range. The number of female juveniles that a breeding female produces follows a Poisson distribution with mean equal to its fecundity b_i.

2.1.7.2. Natural mortality. Adults and juveniles die with probability (1 - s). When an individual dies it is removed from the population and its home range cell is made available for dispersing individuals.

2.1.7.3. Dispersal of juveniles. In our model adults do not move, and do not get killed by direct road mortality. Only juveniles disperse. Each juvenile disperses a fixed number of cells from its mother cell. A dispersal step is always to one of the four neighboring cells (von Neumann neighborhood), and is composed of the following events (Fig. 2b): (1) the individual evaluates whether its four neighboring cells are occupied or free, and does not disperse to occupied cells; (2) the individual evaluates whether the free neighboring cells correspond to roads or not, and can avoid dispersing through road cells with probability p_{RA}; (3) if the individual disperses through a road cell, sink dispersal mortality (road mortality) is applied with probability m_{RM}. The dispersal process is not stopped when the individual finds a first suitable empty cell; instead it continues until the individual either dies (due to road mortality), or disperses over his dispersal distance, d. An individual is allowed to move back to a cell it has previously visited. Therefore, two neighboring unoccupied cells are sufficient for an individual to survive over any number of dispersal steps. Moreover, each juvenile disperses from its mother cell, but given natural mortality that cell may be freed, and in that case it can be occupied by a juvenile. The default probability of dispersing to any neighboring cell is 1. However, if all four neighboring cells are occupied, and since

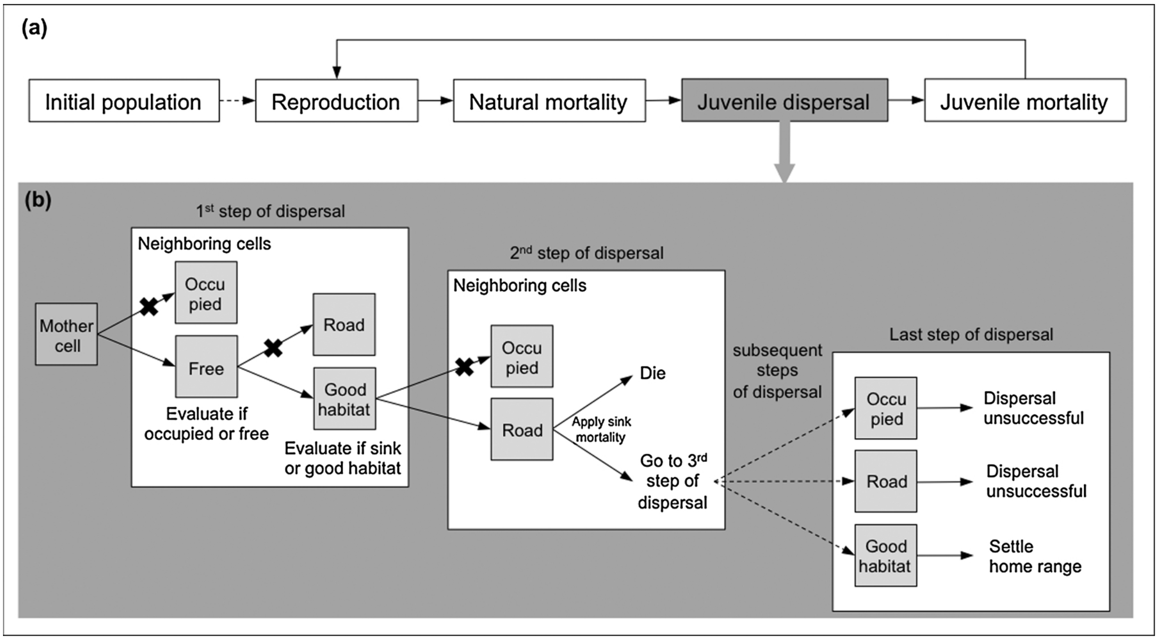

Fig. 2. Scheme of the model. (a) Schematic representation of the complete model simulation steps. (b) Schematic representation of juvenile dispersal. The x in (b) indicate that the individual does not disperse to occupied cells, and that it will disperse to a good habitat cell over a road cell.

individuals do not disperse to occupied cells, then the individual cannot move and dispersal is unsuccessful. If the cell in which the individual is at the end of dispersal is a road, dispersal is also unsuccessful. If dispersal is successful, the individual can settle a home range. In this study, we set the home range size to one cell and only one individual can establish its home range in each cell.

2.1.7.4. Juvenile density-dependent mortality. Following unsuccessful

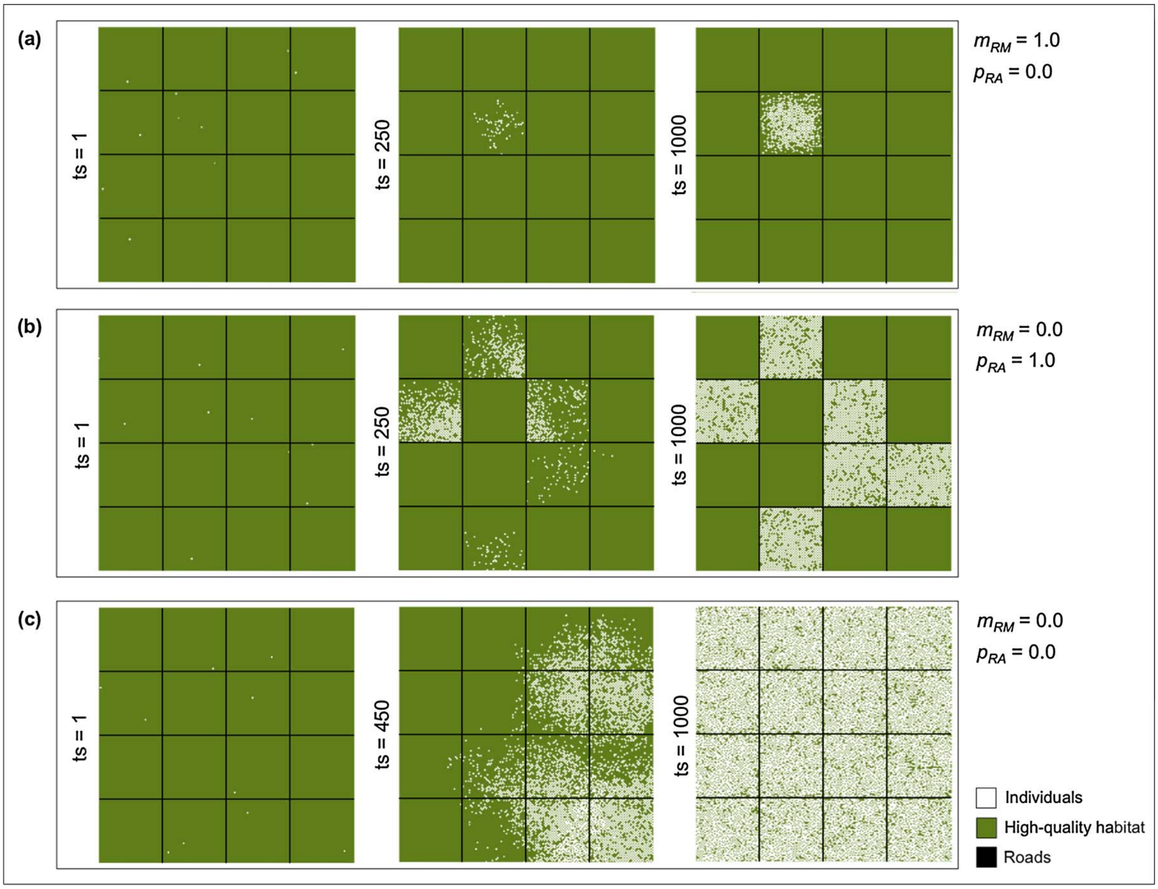

Fig. 3. Representation of the colonization of the landscape by a population under different combinations of values of road mortality probability (m_{RM}) and of road avoidance probability (p_{RA}), in different time steps (ts) of a model run. In the example shown, the dispersal distance is set to 50 cells (i.e. large dispersal) and the proportion of road cells in the landscape is 0.03.

dispersal, juveniles that did not establish their home range are removed from the population.

2.2. Simulations

We created five landscapes of 200 × 200 cells with perpendicular roads, each with a different proportion of road cells (Fig. 1, Table 1). We used two dispersal distances: short (5 cells), and large (50 cells), the latter of which we deemed reasonable considering the total size of the grid (40,000 cells). We modelled a barrier effect independently from sink mortality by varying the probability with which individuals do not cross roads while dispersing.

We performed two sets of simulations. In the first set of simulations, we assessed the effect of different extreme scenarios of road mortality and of road avoidance in landscapes with different proportions of road cells: (i) road mortality probability was one and there was no road avoidance; (ii) road avoidance probability was one and there was no road mortality; (iii) road mortality and road avoidance probabilities were both zero, for each dispersal distance and each road density. To assess the combined effects of road mortality and of road avoidance, in the second set of simulations we varied road mortality and road avoidance probabilities both at the same time independently from 0 to 1 in steps of 0.1 (i.e., using all combinations possible), for each dispersal distance (Table 1).

In all simulations, we used fixed values of the remaining parameters (Table 1), simulating the dynamics of hypothetical animal populations in hypothetical landscapes, because our main objective was to obtain general predictions on the differential effects of road mortality versus a barrier effect that did not introduce additional mortality (due to road avoidance behavior or physical structures such as fences), under different levels of dispersal.

We ran each simulation for 1000 time steps, to ensure that population size did not vary by more than 10% between consecutive simulation time steps, for at least the last 10 simulation time steps, and ran 100 replicates for each combination of values of parameters (Table 1).

Our computer program was extensively debugged, thus we are confident that the program is reproducing accurately the intended model. Being an individual-based model computer simulation, we performed our simulations under a set of assumptions that we deemed reasonable, and we tested them for a wide range of parameter values, obtaining the expected results.

Our model takes as input the model parameters and a two-dimensional matrix with the landscape. It produces a file containing the location of the home range of each adult in the landscape at each time step, and the population age structure at each time step. To apply the model to other species and landscape configurations, users can choose the values of the parameters specific to the species or population of interest, and a matrix with the desired landscape configuration.

3. Results

In our simulations, isolation occurred due to road mortality or to road avoidance (Fig. 3). With complete road mortality and no avoidance (Fig. 3a), or with complete avoidance and no road mortality (Fig. 3b), the landscape was only partially occupied. In contrast, when there was no mortality and no avoidance (Fig. 3c), the whole landscape was occupied.

When there was no road mortality and no road avoidance, the probability of extinction was higher and the population size was smaller at higher road densities, suggesting an effect due to habitat loss (Fig. 4). Nevertheless, with no road mortality and no road avoidance, the probability of extinction was zero or close to zero, even with high road density (Fig. 4a); and the population size was considerably larger than with either complete road avoidance, or complete road mortality (Fig. 4b). These results suggest that in such cases there was an effect of road avoidance or of road mortality, respectively.

The probability of extinction was higher and the population size was smaller when there was road mortality alone, than when there was road avoidance alone, except at the highest road density (Fig. 4). However, population size was much smaller at all road densities when there was road avoidance than in the case with no road avoidance and no road mortality (Fig. 4b).

When assessing the combined effects of road mortality and of road avoidance for different dispersal distances at the highest road density, the probability of extinction increased and the population size decreased with increasing road mortality (horizontal lines in Fig. 5). For a constant value of road mortality (vertical lines in Fig. 5), probability of extinction decreased and population size increased with increasing road avoidance. However, at this road density, the good habitat patches delimited by roads were small (16 cells), and populations went extinct when road avoidance was complete, even without road mortality.

The role of dispersal varied with road mortality. The probability of extinction increased and the population size decreased much faster with increasing road mortality for the large than for the short dispersal distance. However, when there was no road mortality, the probability of extinction was higher (Fig. 5a) and the population size was smaller (Fig. 5b) for the short dispersal distance.

Similar patterns were observed when assessing these effects at a lower road density (proportion of road cells in the landscape = 0.07; Fig. S1 in Appendix). However, they were less obvious than in the case of high road density, especially for the short dispersal distance: the probability of extinction was low, and the population sizes varied less. Nevertheless, population size strongly decreased with complete road avoidance, or with complete road mortality, for both dispersal distances, as in the case of high road density (Fig. 5).

Note that for the short dispersal distance and also for most of the large dispersal distance simulations in Fig. S1, while the probability of population extinction is close to zero, the population size is low, both when road mortality is one, and when road avoidance is one. This is because many individuals die on roads (when road mortality is one), or the population can only occupy part of the landscape (when road avoidance is one).

4. Discussion

Our results allow to make inferences about the differential effects of sink mortality versus those of a barrier effect without additional mortality, and the role of dispersal, on population persistence, isolation and size, which were the goals of this study. While habitat amount was kept constant when road mortality probability and road avoidance probability were varied with a same road density, it should nevertheless be taken into account that by generating landscapes with habitats and roads as grid cells, and by using a regular road network pattern, landscapes with higher road densities have lower total habitat amount and smaller habitat patches. In this sense, there were three effects present (i.e., road mortality, road avoidance, and habitat amount change).

4.1. Importance of road mortality versus a barrier effect without mortality for population persistence and size

Road mortality alone had a stronger negative effect on the probability of persistence and on population size than road avoidance alone. Road avoidance could also in some cases rescue populations under low to moderate road mortality from extinction, as suggested by other authors, since road avoidance decreases the probability that individuals cross roads, therefore reducing mortality caused by collision with vehicles (Jaeger and Fahrig, 2004; Rytwinski and Fahrig, 2013). Previous studies also suggest that the genetic effects of road mortality are stronger than those of the barrier effect without road mortality (e.g., Jackson and Fahrig, 2011; Ascensão et al., 2013).

In our simulations, population isolation occurred both when there was road mortality, or when there was a barrier effect without

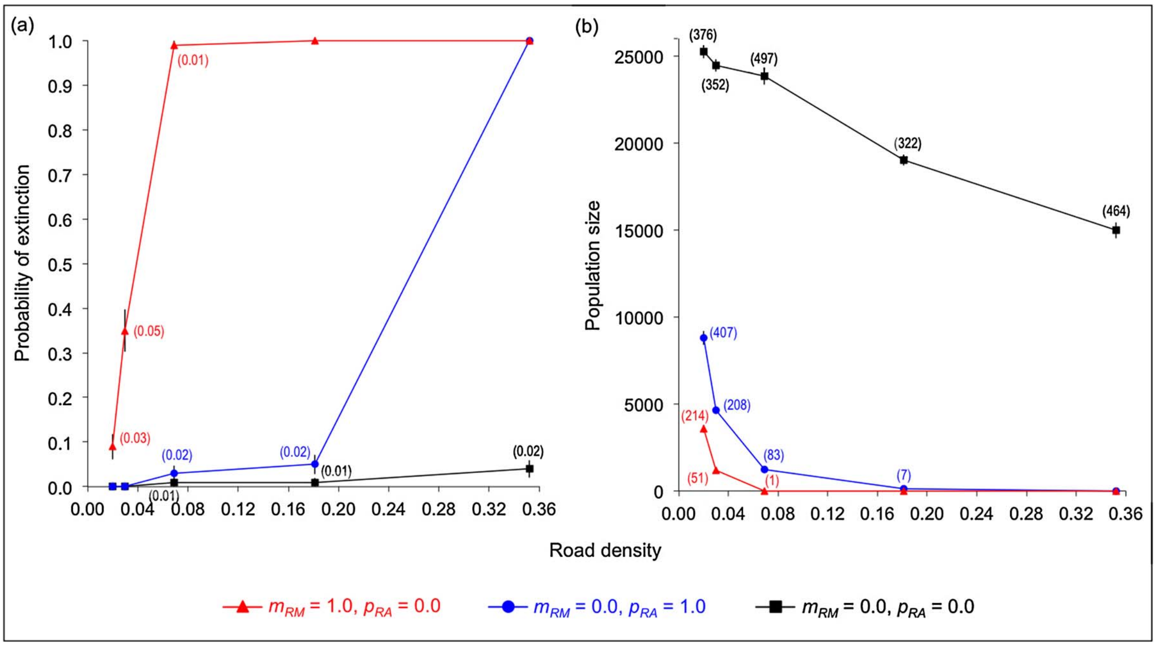

Fig. 4. Probability of population extinction (a) and population size (b) for the different proportions of road cells in the landscape, for different combinations of values of road mortality probability (m_{RM}) and of road avoidance probability (p_{RA}). Results shown are for the large dispersal distance (50 cells). Error bars correspond to the standard error of the mean, whose values are indicated in brackets (when different from zero).

additional mortality. Populations persisted even when road avoidance was very high, provided that the road mortality was low to moderate. Only complete road avoidance led populations to extinction, when road density was the highest. In those cases, individuals were isolated within the small patches of good habitat that were bounded by roads, and the resulting small populations exhibited an increased extinction risk due to demographic stochasticity (Lande, 1993).

Habitat fragmentation impairs species persistence and ecosystem functions. Moreover, the several effects of fragmentation are interlinked and can operate over long time scales (Haddad et al., 2015). In our analysis, population sizes were negatively affected when road avoidance was complete regardless of the road density, even if there was no road mortality. Population sizes were much smaller when compared to the cases with no road avoidance (and no road mortality). This may influence population persistence in the long-term, especially if other factors of disturbance come into play. For example, we did not vary habitat quality (all non-road cells had maximum habitat quality), because our aim was to obtain general predictions on the differential effects of road mortality versus those of a barrier effect without mortality. However, habitat quality can influence how roads affect populations (e.g., Grilo et al., 2014) and therefore the habitat quality of the non-road cells could be varied in more detailed studies, for example by including species-specific information on habitat preferences.

Moreover, although not included explicitly in our analysis, traffic volume is also important to consider when assessing the effects of roads on populations and in landscape connectivity studies, since traffic intensity may influence both road mortality and road avoidance, and thus population persistence (Jaeger et al., 2006; Jaeger, 2007; Charry and Jones, 2009; van Langevelde and Jaarsma, 2009; van Strien and Grêt-Regamey, 2016). Several studies suggest that road mortality may be higher at intermediate traffic volumes than high traffic volumes, because at higher traffic volumes road avoidance will be higher for many species (e.g., Seiler 2005; Grilo et al., 2015).

However, the focus of our analysis was on comparing the effects of road mortality vs. those of a barrier that does not introduce additional mortality, which can be due to road avoidance behavior but also due to physical structures such as fences (e.g., Jaeger and Fahrig, 2004; Grilo et al., 2012). Hence we modeled these directly as the probability of an individual dying on a road while crossing it, and the probability of an individual not crossing a road, regardless of the cause (e.g., road surface avoidance behavior, road avoidance due to traffic, fences), and therefore we did not consider traffic volume explicitly.

Additionally, while in our simulations individuals only evaluated their immediate neighboring cells in each step of dispersal, some species avoid roads from a distance (e.g., Jaeger et al., 2005), which may exacerbate the effects of habitat loss and fragmentation. Including microevolution in our individual-based model, which is fundamental to capture the response of organisms to changing conditions (Grimm and Berger, 2016), would also allow analysing eco-evolutionary responses to fragmentation (Haddad et al., 2015).

4.2. *Influence of dispersal distance on population persistence and size*

The role of dispersal distance varied depending on the values of road mortality. In fragmented landscapes, as was the case in all our simulations since roads were always present, populations with a larger dispersal distance showed a lower probability of extinction and maintained larger sizes, provided an additional source of mortality due to roads was not present. However, a large dispersal distance was detrimental for population size and persistence as road mortality increased.

We used fixed dispersal distances in our simulations. However, dispersal distance is usually stochastic (e.g., Nathan et al., 2012), and therefore it would not only be interesting but also add realism to the model by implementing dispersal kernels to determine dispersal distances (e.g., Austerlitz et al., 2004; Chipperfield et al., 2011), instead of using fixed dispersal distances.

Furthermore, in our simulations, dispersing individuals only evaluated their immediate four neighboring cells in each dispersal step, which can be considered as a biased random walk (e.g., Turchin 1998). While this has been a common choice to model movement with an orientation component (e.g., Börger et al., 2008), expanding the perceptive range of dispersing individuals would increase the realism and facilitate the transferability of the model to concrete situations.

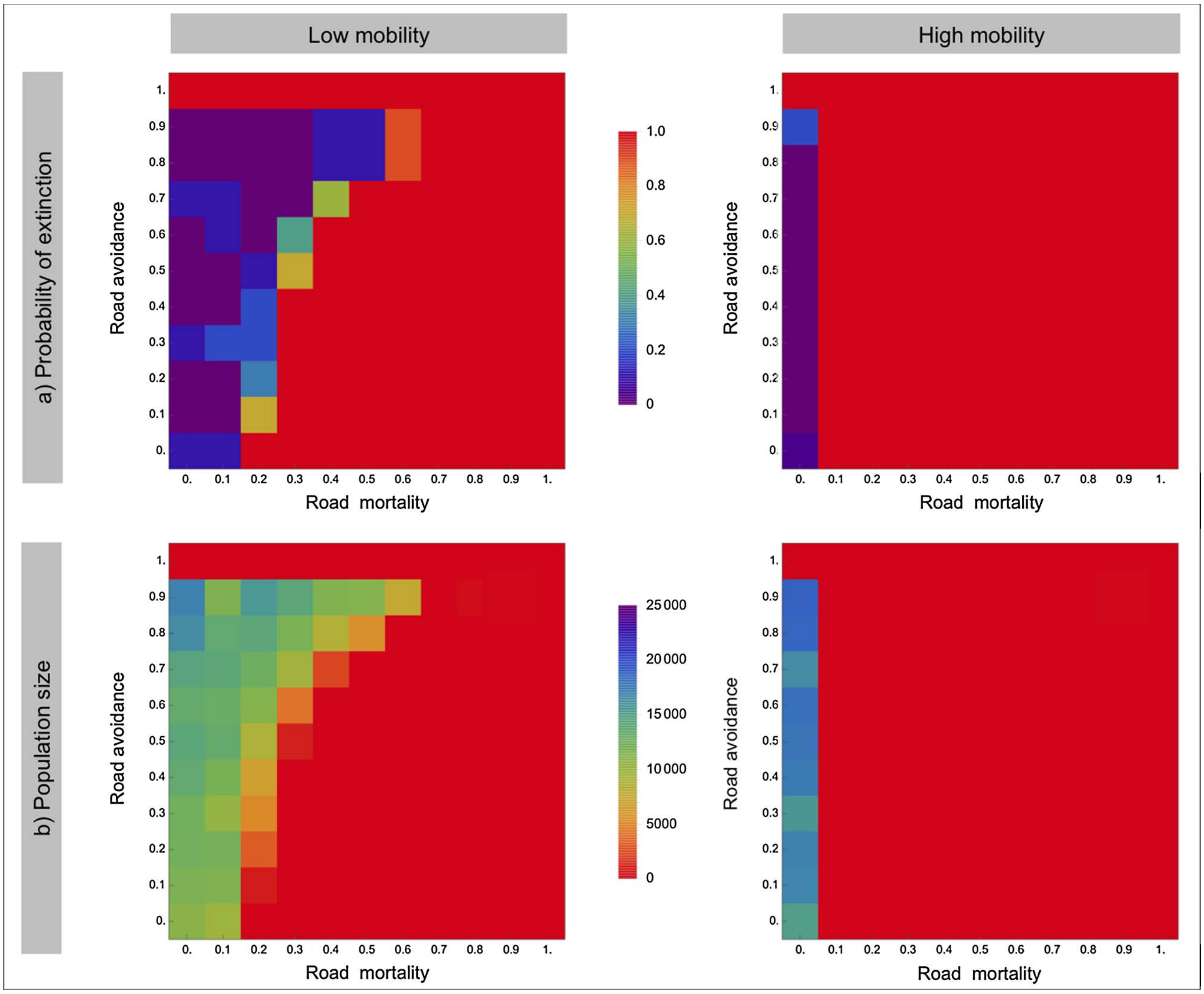

Fig. 5. Probability of population extinction (a) and population size (b) as a function of road mortality and road avoidance, for different dispersal distances (Low mobility = 5 cells; High mobility = 50 cells) in the landscape with the highest proportion of road cells in the landscape (0.35).

4.3. Limitations

The type of movement (juvenile dispersal) considered in our paper can have a large influence on individual fitness and population structure (Matthysen, 2012). However, our model does not currently include other types of movement (such as daily movements), and thus adults do not get killed due to road mortality. This is a simplification, because in real contexts animals will encounter roads during other types of movement as well. Therefore, it would be important to include such types of movement in the analysis.

Furthermore, in our model each juvenile disperses over a fixed number of cells, which implies that individuals may end their dispersal movement on a road (or right of way). This could correspond to situations where there are no other options for dispersal, e.g., all neighboring areas already occupied or corresponding to unsuitable habitat, but it should be considered as a simplification of real cases.

We used two dispersal distances in our simulations because we wanted to ensure that we were comparing the roles of contrasting dispersal distances, i.e., a short vs. a large dispersal distance. Including a wider range of dispersal distances could help further understand the role of dispersal in these fragmented landscapes, as some studies suggest there is an optimal intermediate dispersal rate for persistence in disturbed habitats (Casagrandi and Gatto, 1999).

We used a virtual species and simple hypothetical regular road networks because our main goal was to disentangle the effects of road mortality versus those of a barrier effect without such mortality. However, this implies that our results hold for the virtual species in the regular road network used.

4.4. Conclusions and future research directions

Our results highlight the much higher relative importance of road mortality than the barrier effect (without road mortality), and of assessing relevant species traits such as dispersal distance. We emphasize three results of our study: first, that even though population persistence was not impaired when road avoidance was complete (except when suitable habitat patches became too small to sustain viable populations), population size was considerably decreased, which is important to consider in long-term conservation management; secondly, that a large dispersal distance is not necessarily always detrimental for population size and persistence in fragmented landscapes if mortality in unsuitable habitats is low, which calls for further investigation; and thirdly, that population isolation occurred in extreme cases (i.e., complete road mortality or a complete barrier effect without road mortality). These may be especially important for species expected (Rytwinski and Fahrig, 2013) or observed (e.g., some snakes and turtles; Shepard et al., 2008) to avoid roads, and for species for which road avoidance increases with increasing traffic volume (e.g., carnivores and ungulates; Dyer et al., 2002; Alexander et al., 2005; Leblond et al., 2013).

Finally, our model can stimulate other studies, either theoretical or empirical. Our results hold for the virtual species in the regular road network used, but our model can be applied to species-specific situations, by using the specific trait values of the species or population of interest. Information on model parameter values (initial population size, fecundity, age at first breeding, survival probability, home range size, dispersal distance, road mortality, or road avoidance) can be obtained from published databases, individual studies, or derived from related or ecologically similar species, and using allometric relationships (e.g., Jones et al., 2009; Borda-de-Água et al., 2014; Salguero-Gómez et al., 2016; Ceia-Hasse et al., 2017). For example, data on population density can be used to determine the initial population size. Data availability is usually higher for vertebrates and within these for mammals, followed by birds. This is also true for data on road mortality, and especially on road avoidance behavior, for which species-specific information is lacking for many species (Rytwinski and Fahrig, 2012).

Furthermore, although we used only simple hypothetical regular road networks in our simulations, the modelled landscape can represent real landscapes with real road configurations, and can hence also be used to evaluate the impact of different mitigation options for increasing population persistence, in environmental impact assessments, and for conservation planning.

Acknowledgments

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ecolmodel.2018.01.021.

References

Alexander, S.M., Waters, N.M., Paquet, P.C., 2005. Traffic volume and highway permeability for a mammalian community in the Canadian Rocky Mountains. Can. Geogr./Géographe Can. 49, 321–331.

Ascensão, F., Clevenger, A., Santos-Reis, M., Urbano, P., Jackson, N., 2013. Wildlife–vehicle collision mitigation: is partial fencing the answer? An agent-based model approach. Ecol. Model. 257, 36–43.

Ascensão, F., Mata, C., Malo, J., Ruiz-Capillas, P., Silva, C., Silva, A., Santos-Reis, M., Fernandes, C., 2016. Disentangle the causes of the road barrier effect in small mammals through genetic patterns. PLoS One 11, e0151500.

Austerlitz, F., Dick, C., Dutech, C., Klein, E., Oddou-Muratorio, S., Smouse, P., Sork, V., 2004. Using genetic markers to estimate the pollen dispersal curve. Mol. Ecol. 13, 937–954.

Borda-de-Água, L., Grilo, C., Pereira, H.M., 2014. Modeling the impact of road mortality on barn owl (Tyto alba) populations using age-structured models. Ecol. Model. 276, 29–37.

Borda-de-Água, L., Navarro, L., Gavinhos, C., Pereira, H.M., 2011. Spatio-temporal impacts of roads on the persistence of populations: analytic and numerical approaches. Landsc. Ecol. 26, 253–265.

Börger, L., Dalziel, B.D., Fryxell, J.M., 2008. Are there general mechanisms of animal home range behaviour? A review and prospects for future research. Ecol. Lett. 11, 637–650.

Casagrandi, R., Gatto, M., 1999. A mesoscale approach to extinction risk in fragmented habitats. Nature 400, 560–562.

Ceia-Hasse, A., Borda-de-Água, L., Grilo, C., Pereira, H.M., 2017. Global exposure of carnivores to roads. Glob. Ecol. Biogeogr. 26, 592–600.

Charry, B., Jones, J., 2009. Traffic volume as a primary road characteristic impacting wildlife: a tool for land use and transportation planning. In: Wagner, P.J., Nelson, D., Murray, E. (Eds.), Proceedings of the 2009 International Conference on Ecology and Transportation, pp. 159–172.

Chipperfield, J., Holland, E., Dytham, C., Thomas, C., Hovestadt, T., 2011. On the approximation of continuous dispersal kernels in discrete-space models. Methods Ecol. Evol. 2, 668–681.

Clobert, J., Baguette, M., Benton, T.G., Bullock, J.M. (Eds.), 2012. Dispersal Ecology and Evolution. Oxford University Press, Oxford, UK.

Dyer, S.J., O'Neill, J.P., Wasel, S.M., Boutin, S., 2002. Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. Can. J. Zool. (80), 839–845.

Fahrig, L., Pedlar, J., Pope, S., Taylor, P., Wegner, J., 1995. Effect of road traffic on amphibian density. Biol. Conserv. (74), 177–182.

Gibbs, J.P., 1998. Distribution of woodland amphibians along a forest fragmentation gradient. Landsc. Ecol. 13, 263–268.

Grilo, C., Reto, D., Filipe, J., Ascensão, F., Revilla, E., 2014. Understanding the mechanisms behind road effects: linking occurrence with road mortality in owls. Anim. Conserv. 17, 555–564.

Grilo, C., Sousa, J., Ascensão, F., Matos, H., Leitão, I., Pinheiro, P., Costa, M., Bernardo, J., Reto, D., Lourenço, R., Santos-Reis, M., Revilla, E., 2012. Individual spatial responses towards roads: implications for mortality risk. PLoS One 7, e43811.

Grilo, C., Smith, D.J., Klar, N., 2015. Carnivores: struggling for survival in roaded landscapes. In: van der Ree, R., Smith, D.J., Grilo, C. (Eds.), Handbook of Road Ecology. John Wiley & Sons, Ltd, Chichester, UK, pp. 300–312.

Grimm, V., 1999. Ten years of individual-based modelling in ecology: what have we learned, and what could we learn in the future? Ecol. Model. 115, 129–148.

Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J., Goss-Custard, J., Grand, T., Heinz, S., Huse, G., Huth, A., Jepsen, J.U., Jørgensen, C., Mooij, W.M., Müller, B., Pe'er, G., Piou, C., Railsback, S.F., Robbins, A.M., Robbins, M.M., Rossmanith, E., Rüger, N., Strand, E., Souissi, S., Stillman, R.A., Vabø, R., Visser, U., DeAngelis, D.L., 2006. A standard protocol for describing individual-based and agent-based models. Ecol. Model. 198, 115–126.

Grimm, V., Berger, U., DeAngelis, D.L., Polhill, J.G., Giske, J., Railsback, S.F., 2010. The ODD protocol: a review and first update. Ecol. Model. 221, 2760–2768.

Grimm, V., Berger, U., 2016. Structural realism, emergence, and predictions in next-generation ecological modelling: synthesis from a special issue. Ecol. Model. 326, 177–187.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R., Melbourne, B.A., Nicholls, A.O., Orrock, J.L., Song, D.-X., Townshend, J.R., 2015. Habitat fragmentation and its lasting impact on earth's ecosystems. Sci. Adv. 1, e1500052.

Hanski, I., 1998. Metapopulation dynamics. Nature 396, 41–49.

Jackson, N.D., Fahrig, L., 2011. Relative effects of road mortality and decreased connectivity on population genetic diversity. Biol. Conserv. 144, 3143–3148.

Jaeger, J., 2007. Effects of the configuration of road networks on landscape connectivity. In: Irwin, C.L., Nelson, D., McDermott, K.P. (Eds.), Proceedings of the 2007 International Conference on Ecology and Transportation, pp. 267–280.

Jaeger, J., Fahrig, L., Ewald, K., 2006. Does the configuration of road networks influence the degree to which roads affect wildlife populations? In: Irwin, C.L., Garrett, P., McDermott, K.P. (Eds.), Proceedings of the 2005 International Conference on Ecology and Transportation, pp. 151–163.

Jaeger, J.A.G., Bowman, J., Brennan, J., Fahrig, L., Bert, D., Bouchard, J., Charbonneau, N., Frank, K., Gruber, B., von Toschanowitz, K.T., 2005. Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. Ecol. Model. 185, 329–348.

Jaeger, J.A.G., Fahrig, L., 2004. Effects of road fencing on population persistence. Conserv. Biol. 18, 1651–1657.

Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., Orme, C.D.L., Safi, K., Sechrest, W., Boakes, E.H., Carbone, C., Connolly, C., Cutts, M.J., Foster, J.K., Grenyer, R., Habib, M., Plaster, C.A., Price, S.A., Rigby, E.A., Rist, J., Teacher, A., Bininda-Emonds, O.R.P., Gittleman, J.L., Mace, G.M., Purvis, A., 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90, 2648.

Lande, R., 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. Am. Nat. 142, 911–927.

Leblond, M., Dussault, C., Ouellet, J.–P., 2013. Avoidance of roads by large herbivores and its relation to disturbance intensity. J. Zool 289, 32–40.

Matthysen, E., 2012. Multicausality of dispersal: a review. In: Clobert, J., Baguette, M., Benton, T.G., Bullock, J.M. (Eds.), Dispersal Ecology and Evolution. Oxford University Press, Oxford, UK, pp. 3–18.

Maxwell, S., Fuller, R., Brooks, T., Watson, J., 2016. Biodiversity: the ravages of guns, nets and bulldozers. Nature 536, 143–145.

Nathan, R., Klein, E., Robledo-Arnuncio, J., Revilla, E., 2012. Dispersal kernels: review. In: Clobert, J., Baguette, M., Benton, T.G., Bullock, J.M. (Eds.), Dispersal Ecology and Evolution. Oxford University Press, Oxford, UK, pp. 187–210.

Pereira, H.M., Borda-de-Água, L., 2013. Modelling biodiversity dynamics in countryside and native habitats. Encyclopedia of Biodiversity. Elsevier, New York, pp. 321–328.

Pereira, H.M., Daily, G.C., 2006. Modeling biodiversity dynamics in countryside landscapes. Ecology 87, 1877–1885.

Pereira, H.M., Navarro, L.M., Martins, I.S., 2012. Global biodiversity change: the bad, the good, and the unknown. Annu. Rev. Environ. Resour. 37, 25–50.

Pulliam, H.R., 1988. Sources, sinks, and population regulation. Am. Nat. 132, 652–661.

Rytwinski, T., Fahrig, L., 2015. The impacts of roads and traffic on terrestrial animal populations. In: van Der Ree, R., Smith, D.J., Grilo, C. (Eds.), Handbook of Road Ecology. John Wiley & Sons, Ltd, Chichester, UK, pp. 237–246.

Rytwinski, T., Fahrig, L., 2013. Why are some animal populations unaffected or positively affected by roads? Oecologia 173, 1143–1156.

Rytwinski, T., Fahrig, L., 2012. Do species life history traits explain population responses to roads? A meta-analysis. Biol. Conserv. 147, 87–98.

Salguero-Gómez, R., Jones, O.R., Archer, C.R., Bein, C., de Buhr, H., Farack, C., Gottschalk, F., Hartmann, A., Henning, A., Hoppe, G., Römer, G., Ruoff, T., Sommer, V., Wille, J., Voigt, J., Zeh, S., Vieregg, D., Buckley, Y.M., Che-Castaldo, J., Hodgson, D., Scheuerlein, A., Caswell, H., Vaupel, J.W., 2016. COMADRE: a global data base of animal demography. J. Anim. Ecol. 85, 371–384.

Seiler, A., 2005. Predicting locations of moose–vehicle collisions in Sweden. J. Appl. Ecol. 42, 371–382.

Shepard, D.B., Kuhns, A.R., Dreslik, M.J., Phillips, C.A., 2008. Roads as barriers to animal movement in fragmented landscapes. Anim. Conserv. 11, 288–296.

Skellam, J.G., 1951. Random dispersal in theoretical populations. Bull. Math. Biol. 53, 135–165.

Turchin, P., 1998. Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants, Weimar and Now. Sinauer, pp. 13.

van der Ree, R., Smith, D.J., Grilo, C., 2015. The ecological effects of linear infrastructure and traffic. In: van Der Ree, R., Smith, D.J., Grilo, C. (Eds.), Handbook of Road Ecology. John Wiley & Sons, Ltd, Chichester, UK, pp. 1–9.

Van Houtan, K.S., Pimm, S.L., Halley, J.M., Bierregaard, R.O.J., Lovejoy, T.E., 2007. Dispersal of Amazonian birds in continuous and fragmented forest. Ecol. Lett. 10, 219–229.

van Langevelde, F., Jaarsma, C., 2009. Modeling the effect of traffic calming on local animal population persistence. Ecol. Soc. 14, 39.

van Strien, M., Grêt-Regamey, A., 2016. How is habitat connectivity affected by settlement and road network configurations? Results from simulating coupled habitat and human networks. Ecol. Model. 342, 186–198.

Zurell, D., Berger, U., Cabral, J.S., Jeltsch, F., Meynard, C.N., Münkemüller, T., Nehrbass, N., Pagel, J., Reineking, B., Schröder, B., Grimm, V., 2010. The virtual ecologist approach: simulating data and observers. Oikos 119, 22–635.

Los Angeles Times

CALIFORNIA

PG&E power outages bring darkness, stress and debt to California's poor and elderly

Michele Newton, left, and her daughter, Brenna Delwisch, have evacuated to a hotel at their own expense because Newton requires electricity to run a breathing machine at night. (Anita Chabria / Los Angeles Times)

By ANITA CHABRIA, TARYN LUNA

OCT. 11, 2019
11:21 AM

CLEARLAKE, Calif. — When PG&E cut power to her family's remote Northern California ranch just after midnight Tuesday, Brenna Delwisch fought to stay awake.

She was afraid if she slept, her mom would die.

A few years ago, her mother, Michele Newton, suffered a stroke and an aortic dissection, an explosion of heart arteries that can be fatal. Ever since, Newton has been afflicted with severe sleep apnea. At night, she wears a continuous positive airway pressure machine that keeps her breathing normally.

Without it, said Delwisch, "it's like [her] chest is arguing with whether to breathe or not. It looks like a struggle."

Delwisch, 33, watched that struggle, until she simply couldn't stay awake any longer. Around 5 a.m., exhausted from anxiety, she gave up.

"I am not vigilant enough anymore," she told Newton, a single mom who worked at gas stations and restaurants to raise her two kids. "You have to wake up."

Delwisch and Newton are among the 65,000 people in Lake County, one of the most impoverished in the state, who are learning by trial what happens when utilities cut power to people living on the edge.

This week, as Pacific Gas & Electric Co. shut off electricity to hundreds of thousands to reduce wildfire risks, many Lake County residents discovered they weren't ready, despite warnings that the cuts were coming. There were too many loose ends in their often complicated and precarious lives that hadn't been accounted for by themselves or government agencies.

CALIFORNIA

PG&E's blackouts were 'not surgical by any stretch.' Its systems may be to blame

Oct. 11, 2019

Few understood what the challenges would be until they were in the dark: A mom who couldn't refill her son's medication for bipolar disorder; a schizophrenic man who couldn't quiet the voices in his head without the television on; the people on dialysis who had to travel to another town.

Even little things became hard. Ice and charcoal were scarce, making it difficult to keep food cold or cook a meal. Freezing showers were too intimidating for elderly nursing home residents as fall arrives with 45-degree nights here.

"You don't know until it happens how it's really going to affect you," said Tara Drolma, 72, who was watching the power fade on her emergency battery, and wondering if she would have to choose between charging her electric wheelchair or her heart monitor.

The planned outages are meant to save lives and property. Many in Lake County, which has endured multiple fires in recent years, including the Mendicino Complex fire last year, are too familiar with the risk of an errant spark.

The landlocked county butts up against Sonoma and Napa on its south end, and is swallowed by the Mendocino National Forest to the north. In between, Clear Lake, the largest freshwater lake in the state, is the heart of the county. Most people live in scattered towns along its banks.

Around its bucolic waters, charred remains of trees fill the rolling hills like desolate gray cenotaphs. Almost everyone here has been evacuated or lost a home from fire. Some have lost loved ones.

Even so, after two days of darkness, many now see the outages as bitter medicine. While a blackout might mean just spoiled food and inconvenience in places with more resources and money, Lake County is poor — its poverty rate is close to double the state average — and many residents say the last few days have compounded their challenges.

The county has 2,200 people who receive in-home services because of age or disabilities, higher than the per-capita state average. Some are now accumulating new credit card debt as they purchase generators and backup batteries, check into hotels and upgrade wireless data plans to stay informed.

All the time, they are working to keep medical devices such as oxygen tanks functioning, and find basic necessities. There seemed to be little in the way of a safety net beyond inexpensive meals at the senior centers and charging stations around the lake set up by PG&E. Many complained reliable information was hard to find.

“Clearly [the power cuts] are really impacting a certain segment of the population and have the potential to be disastrous,” said Crystal Markytan, director of social services for Lake County. “It’s not a little thing. You don’t realize how dependent you are on power.”

Gov. Gavin Newsom on Thursday night broadly criticized PG&E for its handling of the cuts, saying: “What has occurred in the last 48 hours is unacceptable. … You’ve got people that can’t even access water, or medical supplies. We’re seeing a scale and scope of something that no state in the 21st century should experience.”

CALIFORNIA

Full coverage: California power outages

Oct. 9, 2019

Little help has been given to address the individual hardships of people such as Delwisch, Newton and Drolma, who all said they felt more aid should be provided if power is cut. The state included $75 million in its most recent budget to address emergency response to outages, and PG&E contacted customers in its database of medically fragile customers, as well as providing charging stations and other aid in some places before the recent cutoff.

But Democratic Sen. Mike McGuire, who represents a swath of Northern California, including Lake County, said both PG&E and the state must do more.

“We need to rethink everything about this shutdown and how to take care of the most vulnerable in our communities,” McGuire said. “These shutdowns can be life and death.”

McGuire said he believes the state should require PG&E to open its own office of emergency services; dedicate a budget to providing emergency services; and create a reliable list of vulnerable Californians who may need aid in a blackout. McGuire said the current reliance on lists of customers who have reduced rates for medical reasons is not accurate. Renters without their own PG&E accounts or residents of some mobile home parks, for example, would not be on it.

“PG&E has made a large assumption by utilizing their care database, but it is wildy inaccurate and doesn’t do the job to keep the most vulnerable in their service territory safe,” said McGuire.

Outages are not considered the same as natural disasters such as fires, said Markytan, and despite the state funding, there are not the same resources to fund shelters or disaster aid on the level of a fire evacuation. That means individuals and counties are largely on their own to bear the expense and disruption of a shut-off.

Markytan said “the crux of my concern” is explaining that difference to people who don’t differentiate between being displaced by fire or power outages.

The county worked hard to inform residents that outages were coming, and provided what aid it could, she said. Her agency worked with the fire department to provide four extra people to help answer non-urgent 911 calls, but she said she “can’t even imagine” what would happen during an extended outage.

She said there is no county funding dedicated to power cuts, and no shelter sites. If the county found money to open a shelter, it wouldn’t be equipped with a generator. Markytan said she hopes lessons learned from this shut-off can help improve responses if there is a next one.

“This is the first big one,” she said. “It’s really piecemeal at this point.”

In the meantime, the power shut-offs have further exposed the divide between the haves and the have-nots here. Delwisch’s brother, a Navy contractor in Hawaii, gave his sister money to book her, Newton and two of their Chihuahuas into an Econolodge a few hours away, where there was still power. That cost about $350.

They spent another $300 on Amazon buying a backup battery for the breathing machine. Delwisch called the sums “astronomical” and said she’s lucky to have a sibling who can help.

She wondered if others are as fortunate. Is PG&E “forcing people to leave their houses and wind up someplace they are more vulnerable?” Delwisch asked.

Tara Drolma, 72, said her backup battery is running low and she may have to choose between charging her electric wheelchair or her heart monitor if power is not restored soon. (Anita Chabria / Los Angeles Times)

In a house that requires traversing four gravel roads off the main highway to reach, Drolma said the outage had left her with few options other than waiting it out. Her backup battery was down to 59% on Thursday afternoon. In spring, after a threatened outage that never happened, she purchased a pair of solar panels, putting the $2,500 on a credit card and hoping to pay it off slowly. But they are still in boxes, waiting for someone to help her set them up.

With her computer dead, she paid to increase her cellular data plan, which she considers her only lifeline to information. For meals, she has been eating bread and canned tuna, and a cold potato left over from before the power went out.

“If I had money this would be a non-issue,” said Drolma.

A few miles away in Clearlake, about 250 people came through an electrical charging station set up by PG&E in a back room of the senior center on Thursday. The day before, about 150 used it, said PG&E representative Conrad Asper.

Liz Taft walked a half-mile pushing her brother-in-law's oxygen machine to recharge it for him at a senior center after PG&E cut power in Lake County. (Anita Chabria/Los Angeles Times)

One of those sitting at the long tables was Liz Taft. She had put her brother-in-law's oxygen machine in a red cart and pulled it a half-mile here to recharge it. About 3 feet tall, the machine provides him with about 16 hours of oxygen, and it isn't light. It ran empty about 9 a.m. Thursday, but he needs it for his chronic obstructive pulmonary disease. Around noon, Taft was worried what the hours without it would do to him.

"It may mean he may wind up at the hospital," said Taft, wondering why the shut-offs had hit so many so hard. "It's ridiculous."

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Living near major roads and the incidence of dementia, Parkinson's disease, and multiple sclerosis: a population-based cohort study

Hong Chen, Jeffrey C Kwong, Ray Copes, Karen Tu, Paul J Villeneuve, Aaron van Donkelaar, Perry Hystad, Randall V Martin, Brian J Murray, Barry Jessiman, Andrew S Wilton, Alexander Kopp, Richard T Burnett

Summary

Background Emerging evidence suggests that living near major roads might adversely affect cognition. However, little is known about its relationship with the incidence of dementia, Parkinson's disease, and multiple sclerosis. We aimed to investigate the association between residential proximity to major roadways and the incidence of these three neurological diseases in Ontario, Canada.

Methods In this population-based cohort study, we assembled two population-based cohorts including all adults aged 20–50 years (about 4·4 million; multiple sclerosis cohort) and all adults aged 55–85 years (about 2·2 million; dementia or Parkinson's disease cohort) who resided in Ontario, Canada on April 1, 2001. Eligible patients were free of these neurological diseases, Ontario residents for 5 years or longer, and Canadian-born. We ascertained the individual's proximity to major roadways based on their residential postal-code address in 1996, 5 years before cohort inception. Incident diagnoses of dementia, Parkinson's disease, and multiple sclerosis were ascertained from provincial health administrative databases with validated algorithms. We assessed the associations between traffic proximity and incident dementia, Parkinson's disease, and multiple sclerosis using Cox proportional hazards models, adjusting for individual and contextual factors such as diabetes, brain injury, and neighbourhood income. We did various sensitivity analyses, such as adjusting for access to neurologists and exposure to selected air pollutants, and restricting to never movers and urban dwellers.

Findings Between 2001, and 2012, we identified 243 611 incident cases of dementia, 31 577 cases of Parkinson's disease, and 9247 cases of multiple sclerosis. The adjusted hazard ratio (HR) of incident dementia was 1·07 for people living less than 50 m from a major traffic road (95% CI 1·06–1·08), 1·04 (1·02–1·05) for 50–100 m, 1·02 (1·01–1·03) for 101–200 m, and 1·00 (0·99–1·01) for 201–300 m versus further than 300 m (*p* for trend=0·0349). The associations were robust to sensitivity analyses and seemed stronger among urban residents, especially those who lived in major cities (HR 1·12, 95% CI 1·10–1·14 for people living <50 m from a major traffic road), and who never moved (1·12, 1·10–1·14 for people living <50 m from a major traffic road). No association was found with Parkinson's disease or multiple sclerosis.

Interpretation In this large population-based cohort, living close to heavy traffic was associated with a higher incidence of dementia, but not with Parkinson's disease or multiple sclerosis.

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Introduction

Dementia, Parkinson's disease, and multiple sclerosis are among the most common neurodegenerative diseases, with devastating effects on individuals, families, and society. Globally, about 55 million people have these disorders, with rising numbers expected given increasing longevity.[1,2] Without cures, identification of modifiable risk factors is important.

Despite the mounting global effect of these neurodegenerative diseases, their cause remains largely unknown.[3–5] Concern is growing that exposures associated with traffic such as air pollution and noise might contribute to neurodegenerative pathology.[6,7] Results of studies showed that air pollutants and diesel exhaust induce oxidative stress and neuroinflammation,[8] activate microglia,[9] and stimulate neural antibodies.[10] Exposure to more noise also impairs cognitive abilities in rats.[11] Similarly, a few epidemiologic studies[12–14] linked traffic-related noise and air pollution to cognitive decline and increased incidence of Parkinson's disease[15] and Alzheimer's disease.[16] Traffic exposure might affect various neurodegenerative processes.

Studies also showed that living near roads was associated with reduced white matter hyperintensity volume[17] and cognition,[18,19] but its effect on the incidence of dementia, Parkinson's disease, and multiple sclerosis is unknown. Living near traffic is a multifaceted exposure representing heightened exposure to nitrogen oxides, ultrafine particles, fine particulate matter (≤2·5 μm in diameter or $\text{PM}_{2\cdot5}$), heavy metals, polycyclic aromatic hydrocarbons, volatile organic compounds, noise, and other factors. Because hundreds of millions of people

Research in context

Evidence before this study

We searched the MEDLINE and Embase databases for epidemiological studies of the associations between exposure to roadway traffic and the risk in adults (older than 18 years of age) of developing dementia, Parkinson's disease, or multiple sclerosis. Studies published in the peer-review literature up to Feb 1, 2016, were included, regardless of the language of publication. We perused the bibliographies of these articles and of previously published reviews. We searched the bibliographic databases using the keywords traffic exposure, mobile source, roadway, proximity or near, air pollution, and with the following health outcomes: dementia; Alzheimer's disease; cognition; Parkinson's disease; multiple sclerosis. A few studies found an association between living close to major roadways and cognitive decline and changes in the brain structure. There is also some evidence linking traffic-related noise and air pollution to cognitive decline and the incidence of dementia, and to a lesser degree, Parkinson's disease. No study has so far investigated the onset of all three major neurodegenerative diseases (dementia, Parkinson's disease, and multiple sclerosis) in association with near-road exposure. Moreover, the few existing studies involved relatively small study populations and nearly half were cross-sectional.

Added value of this study

We report that living close to heavy traffic is associated with increased incidence of dementia. Using the same populations and methods, however, we did not find an association between residential proximity to traffic and Parkinson's disease or multiple sclerosis. The cause of these major neurodegenerative diseases remains largely unclear. This study sheds important insights into a possible role of near-road exposure on the development of dementia. Our study overcomes several limitations of previous studies, since it has large cohorts comprising almost the entire adult population in Ontario, the most populous province in Canada, and lagged exposure up to 10 years to reduce concerns about reverse causality. With demographic characteristics similar to the USA and many European countries, findings from this study will be highly generalisable to populations in many other regions.

Implications of all the available evidence

Increasing population growth and continuing urbanisation globally has placed many people close to heavy traffic. With the widespread exposure to traffic and growing population with dementia, even a modest effect from near-road exposure can pose an enormous public health burden. This study suggests that improvements in environmental health policies and land use planning aimed at reducing traffic exposure can have considerable potential for prevention of dementia, which would lead to a broad public health implication. This study adds weight to previous observations suggesting that roadway traffic is an important source of environmental stressors that could give rise to neurological disorders and that future investigation targeting the effects of different aspects of traffic such as traffic-related air pollutants and noise on neurological health is merited.

worldwide live close to major roads, we sought to investigate the association between exposure to traffic, measured by residential proximity to major roadways, and the incidence of dementia, Parkinson's disease, and multiple sclerosis in a large population-based cohort in Ontario, Canada.

Methods

See Online for appendix

Study design

We did a population-based cohort study of all Ontario adults to determine the incidence of dementia, Parkinson's disease, and multiple sclerosis. Eligible participants were, as of April 1, 2001, Ontario residents for 5 years or longer, aged 20–85 years, and Canadian-born. We created the study population using Ontario's Registered Persons Database, a registry of all residents who have ever had health insurance. This database covers virtually all Ontario residents.[20]

Because dementia and Parkinson's disease onset occurs predominantly in people aged 55 years or older, whereas multiple sclerosis onset is most common in adults younger than 50 years, we separated the study population into two analytical cohorts: individuals aged 20–50 years (multiple sclerosis cohort); and individuals aged 55–85 years (dementia or Parkinson's disease cohort). We further excluded individuals with any of these three disorders at baseline, yielding a total of 4 372 720 and 2 165 268 participants in each cohort.

The Research Ethics Board of Sunnybrook Health Sciences Centre, Toronto, approved the study.

We ascertained incident diagnoses of dementia, Parkinson's disease, and multiple sclerosis using validated databases (see appendix). Details of these databases are available elsewhere.[20] These databases have been validated previously using chart review, with sensitivity of 78–84% and specificity of 99–100%.[21–23] They were created using hospital discharge abstracts from the Canadian Institute for Health Information, physician service claims from the Ontario Health Insurance Plan database, and prescription medication claims from the Ontario Drug Benefits programme database. Hospital, laboratory, and physician services in Ontario are funded by the provincial government through a single-payer universal medicare system that covers virtually all residents.[20] Drug coverage is provided to those aged 65 years or older, and social assistance recipients. We linked the cohorts to these databases using encrypted unique identifiers to ascertain incident cases.

Residential proximity to roads

We calculated residential proximity to major roadways or highways based on 6-character postal-code addresses in 1996, 5 years before cohort inception. Postal codes in urban areas represent the centroid of the blocks or single large buildings in which cohort members lived. Distance (m) was measured using ArcGIS. Major traffic roads include primary urban roads and arterial roads (ie, a major thoroughfare with medium to large traffic capacity with a combination of controlled access and intersections at grade level) whereas highways include expressways and primary and secondary highways, according to Ontario Government Road Network Data Standards. Consistent with previous studies,[17,24] we created five distance categories: less than 50 m from major traffic road, 50–100 m, 101–200 m, 201–300 m, and more than 300 m. We also considered a continuous measure of distance.

Covariates

We selected accepted or suspected risk factors for neurodegenerative pathology, including age, sex, pre-existing comorbidities, and socioeconomic status.[3–5] The comorbidities included traumatic brain injury, diabetes, hypertension, stroke, coronary heart disease, congestive heart failure, and arrhythmia. We ascertained the presence of comorbidities at baseline using hospital discharge abstracts, physician service claims, and validated chronic disease databases (appendix).

Several individual-level socioeconomic status and behavioural factors, such as education, smoking, and physical activity are also implicated in neurological health,[3–5] but were unavailable. Since neighbourhood-level socioeconomic status is strongly associated with these factors,[25,26] we derived four neighbourhood-level variables: income quintile, a measure of relative household income accounting for household size and community; percentage of population aged 15 years or older with less than high school education; unemployment rate; and percentage of recent immigrants, using 2001 Canadian Census dissemination area data. A dissemination area (with 400–700 people) is the smallest census geographic area for which census data are disseminated. We further derived neighbourhood-level deprivation based on the Ontario Marginalization Index that quantifies the degree of marginalisation in health and social wellbeing (appendix).

To control for regional differences in the incidence of dementia, Parkinson's disease, and multiple sclerosis, we created a variable for urban residence (yes/no), density of neurologists using the ICES Physician Database to represent accessibility to neurological care, and the latitude of residence given the reported latitude gradient with multiple sclerosis.[3] Additionally, we created a dichotomous variable classifying Ontario into the Greater Toronto Area, a densely-populated urban mega-region, and all other areas. Toronto tends to differ from other areas with respect to sociodemographic characteristics, health care access, and population health status.

To explore whether exposure to air pollutants, especially nitrogen dioxide (NO_2) and $PM_{2·5}$ might explain the roadway proximity-outcome association, we obtained long-term measures of $PM_{2·5}$ and NO_2 for all participants (appendix). Briefly, estimates of ground-level concentrations of $PM_{2·5}$ were derived from satellite observations of aerosol optical depth in combination with outputs from a global atmospheric chemistry transport model (GEOS-Chem CTM).[27] The $PM_{2·5}$ estimates were further adjusted using information on urban land cover, elevation, and aerosol composition using a geographically weighted regression. We used estimates between 1998 (the earliest year with available data) and 2001 (the year of cohort inception), thus producing four-year mean concentration of $PM_{2·5}$ at a spatial resolution of 1×1 km and covering all North America below 70°N, which includes all of Ontario. These

	Multiple sclerosis cohort* (n=4 372 720)		Dementia/Parkinson's disease cohort* (n=2 165 268)	
	Subject count	%	Subject count	%
Age at entry (years); mean (SD)	35·9 (8·7)	..	66·8 (8·2)	..
20–29	1 198 499	27·4	..	..
30–39	1 475 303	33·7	..	..
40–50	1 698 918	38·9	..	..
55–64	..	..	978 235	45·2
65–74	..	..	731 685	33·8
75–85	..	..	455 348	21·0
Sex				
Male	2 178 448	49·8	1 013 010	46·8
Female	2 194 272	50·2	1 152 258	53·2
Pre-existing comorbidity†				
Coronary heart disease	21 957	0·5	213 071	9·8
Stroke	6005	0·2	66 241	3·1
Congestive heart failure	4687	0·1	120 550	5·6
Diabetes	105 088	2·4	323 544	15·0
Hypertension	295 996	6·8	1 038 119	48·0
Arrhythmia	11 717	0·3	93 495	4·3
Traumatic brain injury	302 869	6·9	90 694	4·2
Area-level risk factors‡				
Low-income cutoff quintile				
Lowest	784 958	18·0	400 839	18·5
Lower middle	867 694	19·8	447 184	20·7
Middle	903 386	20·7	437 336	20·2
Upper middle	915 524	20·9	420 427	19·4
Upper	901 158	20·6	459 482	21·2
Percentage of rural residents	724 024	16·6	410 575	19·0
Percentage of recent immigrants	..	3·6	..	3·3
Percentage ≥15 years of age with less than high school education	..	25·5	..	26·9
Percentage ≥15 years of age without employment	..	6·2	..	6·2

Data are n or %, unless otherwise specified. *Multiple sclerosis cohort comprised all adults aged 20–50 years and dementia/Parkinson's disease cohort comprised all adults aged 55–85 years in Ontario, Canada, in 2001. †In the 10 years before cohort onset. ‡From Canadian Census 2001, at the census dissemination area level.

Table 1: **Baseline characteristics of the study population**

	Incidence of dementia (n=243611)‡			Incidence of Parkinson's disease (n=31577)‡			Incidence of multiple sclerosis (n=9247)‡		
	HR	95% CI	p_{trend}	HR	95% CI	p_{trend}	HR	95% CI	p_{trend}
Distance† by category									
<50 m	1·07	1·06–1·08	0·0349	1·01	0·98–1·04	0·12	1·02	0·95–1·09	0·72
50–100 m	1·04	1·02–1·05	··	1·01	0·97–1·05	··	0·93	0·86–1·01	··
101–200 m	1·02	1·01–1·03	··	0·99	0·96–1·03	··	1·01	0·95–1·08	··
201–300 m	1·00	0·99–1·01	··	0·99	0·96–1·02	··	1·01	0·94–1·08	··
>300 m	Reference	··	··	Reference	··	··	Reference	··	··
Log(distance)§	0·91	0·89–0·92	··	0·99	0·97–1·01	··	1·00	0·98–1·02	··

Cox proportional hazards model with age as the time-scale, stratified by an indicator for living in the Greater Toronto Area or not, adjusted for sex, history of diabetes, hypertension, coronary heart disease, stroke, congestive heart failure, arrhythmia, and traumatic brain injury, income quintile, urban/rural indicator, census division-level unemployment rate, education, recent immigrants, as well as the subtraction of these variables at the census dissemination level from their census division. For multiple sclerosis, the model was also adjusted for latitude. †Major traffic roads include primary urban roads and arterial roads whereas highways include expressways and primary and secondary highways, as defined by Ontario Government Road Network Data Standards. ‡Incidence of dementia and Parkinson's disease was analysed among all adults aged 55–85 years (dementia/Parkinson's disease cohort) whereas incidence of multiple sclerosis was analysed among all adults aged 20–50 years (multiple sclerosis cohort). §Distance was fitted as a continuous variable, using natural logarithm of distance. Hazard ratios (HRs) expressed per IQR increase in distance (dementia/Parkinson's disease cohort: 310 m and multiple sclerosis cohort: 320 m).

***Table 2*: Hazard ratios and 95% CIs for the associations between residential proximity to major roadways in 1996 and the risks of incident dementia, Parkinson's disease, and multiple sclerosis in Ontario, during the follow-up period 2001–12**

satellite-based estimates of $PM_{2·5}$ closely agree with ground measurements at fixed-site monitoring stations across North America (R^2 0·82, n=1440).[27] Similarly, we derived long-term exposure to NO_2 from a national land-use regression (LUR) model developed from Environment Canada's National Air Pollution Surveillance Network monitoring data, 2005–11 satellite NO_2 estimates, area of industrial land use, road length, and mean summer rain fall.[28] The estimates were further calibrated by incorporating local-scale variations of NO_2 from vehicle emissions by applying spatially-varying multipliers that represented distance-decay gradient in NO_2. The final LUR model explained 73% of the variation in annual 2006 measurements of NO_2, with a root mean square error of 2·9 parts per billion (ppb).[28] The resulting LUR NO_2 estimates were available for each year between 1998 and 2001, after applying temporal adjustment.

Statistical analysis

We used Cox proportional hazards models with age as the time-scale to assess the relationship between residential proximity to major roadways and the incidence of dementia, Parkinson's disease, and multiple sclerosis. For each outcome, follow up time (in days) was measured from April 1, 2001 until diagnosis date, ineligibility for provincial health insurance, death, or March 31, 2012.

Separate models were developed for each disease. All models were stratified by region (living in Toronto or not), and adjusted for sex, comorbidities, urban residency, and neighbourhood-level income, education, unemployment, and immigration status. To adjust for regional variations in the neighbourhood-level variables across Ontario, we included them as the average for each census division (equivalent to county), and as the difference between the values for each census dissemination area and the census division mean. We further adjusted for latitude for multiple sclerosis cohort. The analyses were repeated using distance as categorical and continuous variables.

We routinely tested for deviation from the proportional hazards assumption by adding the cross-product of each variable with the natural logarithm of the time variable, but we did not find any violation of this assumption ($p>0·05$). We calculated adjusted hazard ratios (HRs) and 95% CIs for each category of roadway proximity compared with the furthest category (>300 m). Linear trend was assessed by assigning the median distance (in natural log) to each category and fitting the term as a continuous variable in a regression model. In analyses with distance as a continuous variable, we considered the natural log of distance because this exposure has been linearly related to mortality and morbidity outcomes in Ontario and elsewhere.[17,24]

Sensitivity analyses

We controlled for access to neurologists, deprivation index, and a North/South indicator (appendix). We also adjusted for a linear term for time to account for potential changes in the risk of the three disorders over time.

We assessed whether HR might be influenced by any spatial dependence among participants. We fitted models with a frailty term for census division (ie, county) to account for the possibility that participants in the same community could share similar risk factors than those living in different locations. We assumed a gamma distribution for the frailties, with an exchangeable correlation structure within county.

We assessed the potential influence of unmeasured individual-level socioeconomic status and behavioural variables, especially education, smoking, obesity, and

	Main model ‡		Indirectly adjusted for smoking		Further indirectly adjusted for BMI, physical activity		Further indirectly adjusted for education	
	Hazard ratio	95% CI	Hazard ratio	95% CI	Hazard ratio	95% CI	Hazard ratio	95% CI
Distance† by category								
<50 m	1·07	1·06–1·08	1·06	1·05–1·08	1·06	1·05–1·08	1·06	1·05–1·08
50–100 m	1·04	1·02–1·05	1·03	1·02–1·05	1·03	1·02–1·05	1·04	1·02–1·06
101–200 m	1·02	1·01–1·03	1·01	1·00–1·02	1·01	1·00–1·03	1·02	1·01–1·04
201–300 m	1·00	0·99–1·01	1·00	0·98–1·01	1·00	0·99–1·02	1·01	0·99–1·03
>300 m	Reference	··	Reference	··	Reference	··	Reference	··
Log (distance)§	0·91	0·89–0·92	0·92	0·90–0·93	0·92	0·90–0·93	0·92	0·90–0·93

Indirect adjustment for smoking, body-mass index (BMI), physical activity, and attained education. Data of smoking, BMI, physical activity, and educational attainment were obtained from Ontario respondents to the 1996 cycle of National Population Health Survey and the 2000–01, 2003 cycles of Canadian Community Health Survey, and who were 50 to 85 years old at the time of the surveys (n=16 441). †Major traffic roads include primary urban roads and arterial roads whereas highways include expressways and primary and secondary highways, as defined by Ontario Government Road Network Data Standards. ‡Cox proportional hazards model with age as time axis, stratified by an indicator for living in the Greater Toronto Area or not, adjusted for sex, history of diabetes, hypertension, coronary heart disease, stroke, congestive heart failure, arrhythmia, and traumatic brain injury, income quintile, urban/rural indicator, census division-level unemployment, education, and recent immigrants, as well as the subtraction of these variables at the census dissemination level from their census division. §Distance was fitted as a continuous variable, using natural logarithm of distance. The hazard ratios were expressed per interquartile-range increase in distance (310 m).

***Table 3*: Hazard ratios and 95% CI for associations between residential proximity to major roadways in 1996 and the risk of incident dementia in Ontario during the follow-up period 2001–12**

	Parkinson's disease				Multiple sclerosis			
	Main model‡		Indirectly adjusted for smoking and physical activity||		Main model‡		Indirectly adjusted for smoking||	
	Hazard ratio	95% CI	Hazard ratio	95% CI	Hazard ratio	95% CI	Hazard ratio	95% CI
Distance† by category								
<50 m	1·01	0·98–1·04	1·01	0·98–1·05	1·02	0·95–1·09	1·00	0·93–1·07
50–100 m	1·01	0·97–1·05	1·02	0·98–1·06	0·93	0·86–1·01	0·93	0·86–1·01
101–200 m	0·99	0·96–1·03	0·99	0·96–1·03	1·01	0·95–1·08	1·00	0·93–1·06
201–300 m	0·99	0·96–1·02	1·00	0·97–1·03	1·01	0·94–1·08	1·00	0·93–1·07
>300 m	Reference	··	Reference	··	Reference	··	Reference	··
Log (distance)§	0·99	0·97–1·01	1·00	0·98–1·02	1·00	0·98–1·02	0·99	0·97–1·02

Indirect adjustment for smoking and physical activity for Parkinson's disease, and for smoking for multiple sclerosis. Data of smoking and physical activity were obtained from Ontario respondents to the 1996 cycle of National Population Health Survey and the 2000–01 and 2003 cycles of Canadian Community Health Survey. For Parkinson's disease, respondents aged 50–85 years at the time of the surveys were included (n=16 441) and for multiple sclerosis, those who were 20–55 years old were included (n=31 635). †Major traffic roads include primary urban roads and arterial roads whereas highways include expressways and primary and secondary highways, as defined by Ontario Government Road Network Data Standards. ‡Cox proportional hazards model with age as time axis, stratified by an indicator for living in the Greater Toronto Area or not, adjusted for sex, history of diabetes, hypertension, coronary heart disease, stroke, congestive heart failure, arrhythmia, and traumatic brain injury, income quintile, urban/rural indicator, census division-level unemployment, education, and recent immigrants, as well as the subtraction of these variables at the census dissemination level from their census division. For multiple sclerosis, the model was also adjusted for latitude. §Distance was fitted as a continuous variable, using natural logarithm of distance. HRs expressed per interquartile-range increase in distance (dementia/Parkinson's disease cohort: 310 m and multiple sclerosis cohort: 320 m). ||For Parkinson's disease, p_{trend}=0·38 and for multiple sclerosis, p_{trend}=0·53.

***Table 4*: Hazard ratios and 95% CI for associations between residential proximity to major roadways in 1996 and risk of incident Parkinson's disease and multiple sclerosis in Ontario, during the follow-up period 2001–12**

physical activity on our results. To do this, we used a method to mathematically adjust HR for these variables while simultaneously controlling for all variables available in the model (ie, age, sex, comorbidities, and socioeconomic status; appendix). Details of this method are presented elsewhere.[29] Briefly, this method requires spatial associations between the unmeasured and observed variables from an auxiliary dataset. Following previous Canadian studies,[30] we obtained the relationships using data from the 1996–97 cycle of the National Population Health Survey and the 2000–01 and 2003 cycles of the Canadian Community Health Survey, which constituted a representative sample of the study cohorts (appendix). This information along with estimated associations between these unmeasured variables and incident dementia, Parkinson's disease, and multiple sclerosis from the literature, were used to estimate their effect on HR. Based on systematic reviews of dementia, Parkinson's disease, and multiple sclerosis, we considered all four variables in our analysis with dementia, smoking and physical activity with Parkinson's disease, and smoking with multiple sclerosis (appendix).

Furthermore, we additionally adjusted for $PM_{2·5}$ and NO_2, excluded events occurring in the first 2 and 5 years

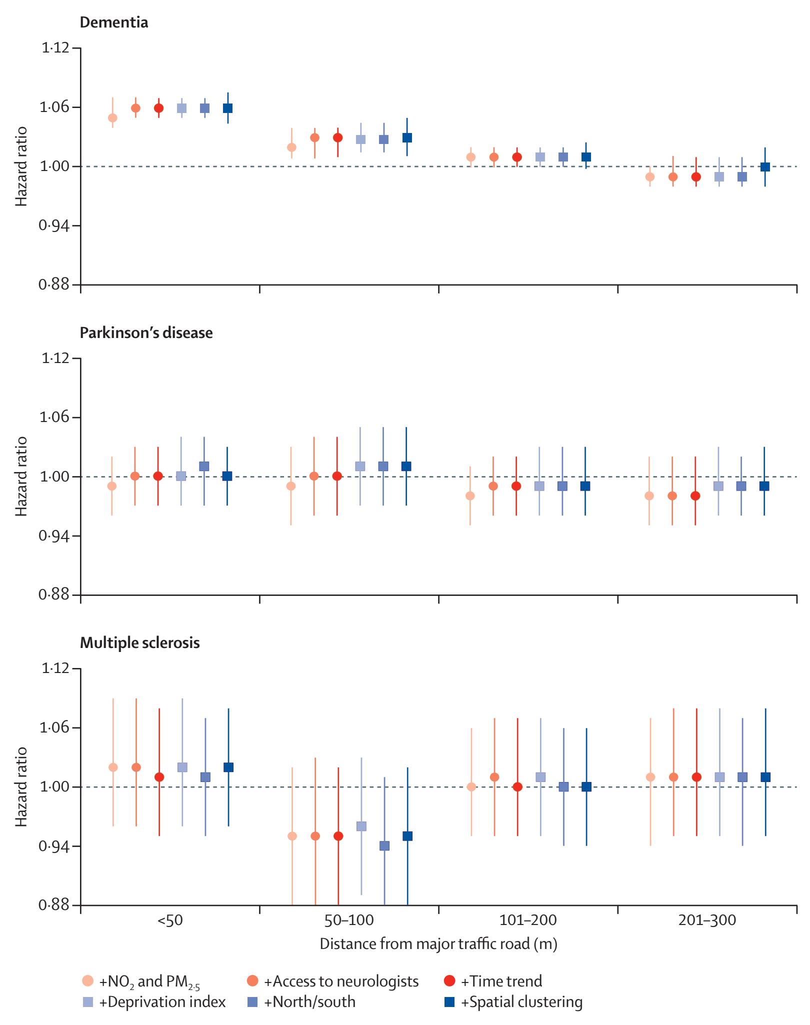

Figure 1: **Estimated associations between residential proximity to major roadways in 1996 and the risk of incident dementia, Parkinson's disease, multiple sclerosis in Ontario, 2001–12**

Measured by six sensitivity analyses to further control for potential confounding factors. Model further adjusted for exposure to NO$_2$ and PM$_{2·5}$ access to neurologists, time trend, deprivation, an indicator for North/South Ontario, and a frailty term to account for potential spatial clustering.

during follow-up to lag exposure up to 10 years, excluded people residing in long-term care facilities (often located near major roadways) at baseline, and restricted the dementia/Parkinson's disease cohort to those aged 65 years or older because drug information was unavailable for younger adults. Lastly, we further adjusted for rurality index and neighbourhood-level percentage of visible minority, and restricted the analysis to people who never moved since 1996, to urban residents, and to residents of six major urban centres in Ontario (Toronto, Hamilton, Ottawa, London, Windsor, and Sarnia) (appendix).

Role of the funding source

The funder had no role in study design, data collection, data analysis, data interpretation, or writing of the report. The corresponding author had full access to all the data in the study and had final responsibility for the decision to submit for publication.

Results

The multiple sclerosis cohort comprised 46·7 million person-years of observations and the dementia/Parkinson's disease cohort contributed 20·1 million person-years. At baseline, the mean age was 35·9 years (SD 8·7 years) for the multiple sclerosis cohort and 66·8 years (8·2 years) for the dementia/Parkinson's disease cohort (table 1). Of the multiple sclerosis cohort, 50% were male, 17% were rural residents, 2% had diabetes, and 7% had hypertension, whereas 47% of the dementia/Parkinson's disease cohort were male, 19% were rural residents, 15% had diabetes, and 48% had hypertension. Average unemployment among census dissemination areas was 6% and the mean percentage of population with less than high school education was about 26% in both cohorts.

Nearly half of the cohorts lived within 200 m from a major road and 95% were within 1000 m (appendix). Of the cohorts, the average concentration of PM$_{2·5}$ according to participants' residences in 1996, 5 years before cohort inception, was 9·7 μg/m³ (range 1·3–19·8 μg/m³), while the average concentration of NO$_2$ was 15·4 ppb (2·2–62·0 ppb). Between 2001–12, we identified 243 611 incident cases of dementia, 31 577 incident cases of Parkinson's disease, and 9247 incident cases of multiple sclerosis.

In both categorical and continuous analyses, living closer to a major road was associated with increased incidence of dementia, with fully adjusted HR of 1·07 (95% CI 1·06–1·08) for people living less than 50 m, 1·04 (1·02–1·05) for people living 50–100 m, 1·02 (1·01–1·03) for people living 101–200 m, and 1·00 (0·99–1·01) for people living 201–300 m away from a major roadway versus more than 300 m from a major roadway (P_{trend}=0·0349; table 2). An interquartile-range increase in residential proximity to a major road was associated with a 9% (95% CI 8–11%) lower incidence of dementia. In contrast, there was no evidence linking traffic proximity to Parkinson's disease or multiple sclerosis (HR 1·00 for both; table 2).

The association between traffic exposure and dementia was insensitive to additional controls for smoking, obesity, physical activity, and education (HR 1·06 for living <50 m away from a major road, 1·04 for 51–100 m, and 1·02 for 101–200 m; table 3). Similarly, the associations between traffic exposure and Parkinson's disease and multiple sclerosis remained unchanged after adjusting for smoking and physical activity (table 4).

Further adjustment for access to neurologists, deprivation, time trend, and a North/South indicator did not alter the associations, nor did adding a frailty term in the survival model to account for potential spatial clustering (figure 1). Adjustment for NO$_2$ and PM$_{2·5}$ modestly attenuated the association between traffic proximity and dementia (HR 1·05 for living <50 m away from a major road and HR 1·02 for 51–100 m away from a major road *vs* 1·07 and 1·04 without adjustment). Importantly, NO$_2$ was significantly associated with dementia, whereas PM$_{2\cdot5}$ was associated with both dementia and Parkinson's disease (appendix).

In sensitivity analyses, the magnitude of associations were similar after further excluding the first 2 and 5 years of follow-up, restricting to people aged 65 years or older, excluding those living in long-term care facilities, or considering other sensitivity analyses (figure 2 and appendix). However, the association between living less than 50 m from a major roadway and dementia appeared stronger among participants who lived in urban areas, who lived in one of the six major cities, or who never moved (HR 1·09–1·12, depending on the analysis).

Discussion

In this large population-based cohort, living near major roadways was associated with increased dementia incidence. The associations seemed stronger among urban residents, especially those living in major urban centres and those who never moved. Although the increase in risk might appear moderate (eg, HRs varied from 1·07–1·12 for living <50 m away from a major road, depending on the region), this translates to 7–11% of dementia cases in patients who live near major roads attributable to traffic exposure (appendix). The associations were robust to various sensitivity analyses, except for additional adjustment for PM$_{2\cdot5}$ and NO$_2$ which led to a modest attenuation. It is noteworthy that both NO$_2$ and PM$_{2\cdot5}$ were positively associated with dementia. Lastly, we found no association between roadway proximity and incidence of Parkinson's disease or multiple sclerosis.

To our knowledge, this is the first study to investigate the onset of three major neurodegenerative diseases in association with near-roadway exposure. Previous studies have linked living near roadways to cognitive decline in cohorts of older adults in Boston MA, USA[18] and in the Ruhr area, Germany,[19] and to smaller white matter hyperintensity volume in the Framingham Offspring cohort.[17] Living near major roads substantially increases an individual's exposure to traffic-related air pollution (eg, ultrafine particles, nitrogen oxides, and particles from wear of tyres and friction materials), and noise.[17] Although the mechanisms through which traffic exposure might affect brain health are unknown, systemic inflammation arising from traffic-related air pollution is probably important. In studies of both experimental animals and in autopsy samples of sudden accidental deaths in human beings, particulates and diesel exhaust provoke oxidative stress and systemic inflammatory responses, disrupt the blood-brain barrier, precipitate Aβ peptides, and activate microglia.[8,9] Ultrafine particles have also been found in the olfactory bulb and the frontal cortical areas in the brain of highly exposed dogs and human beings.[8] Furthermore, emerging epidemiologic evidence relates nitrogen oxides and black carbon, markers for traffic-related pollution, to dementia incidence[12] and cognitive impairment.[14] We observed that exposures to NO$_2$ and PM$_{2\cdot5}$ were related to dementia and that adjusting for these two pollutants attenuated its association with roadway proximity, suggesting that the effect of traffic exposure might, at least in part, operate through this mechanism. Given the potentially significant implications of exposure to traffic-related pollutants on dementia risk, understanding their effects merit further investigation.

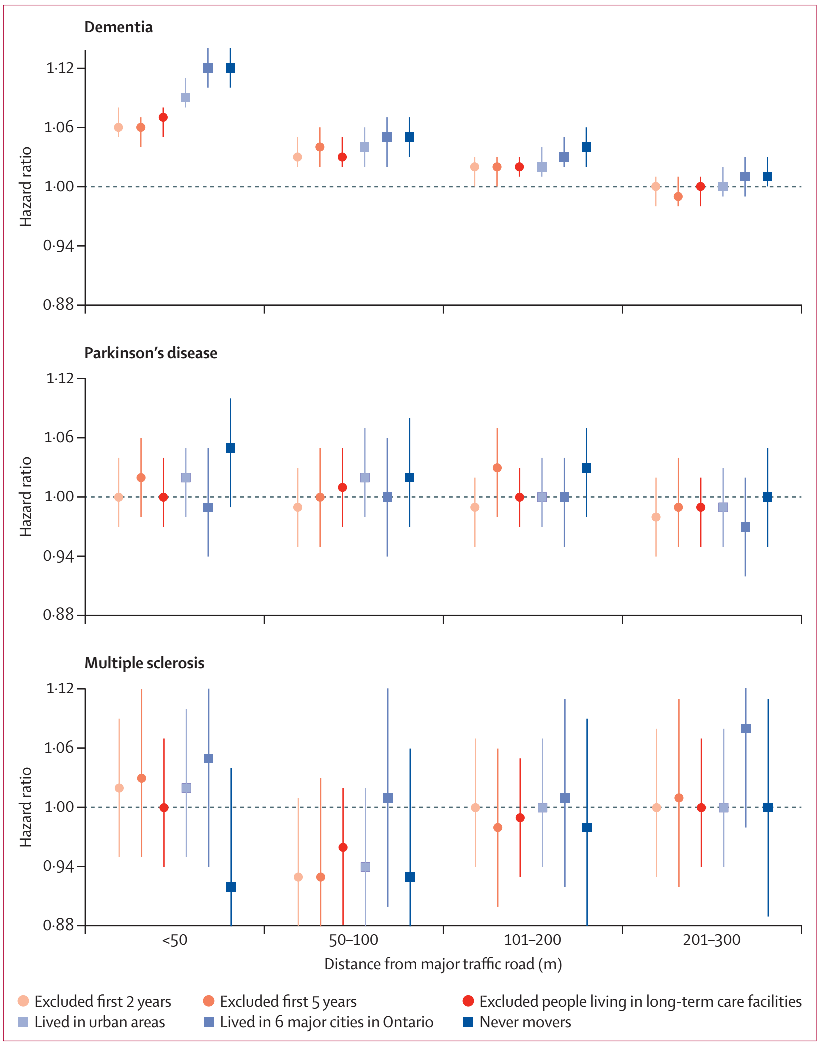

***Figure 2*: Association between residential proximity to major roadways in 1996 and the risk of incident dementia, Parkinson's disease, multiple sclerosis in Ontario, 2001–12**

Hazard ratios and 95% CIs from six additional sensitivity analyses (excluding first 2 years of follow-up, excluding first 5 years of follow-up, excluding people living in long-term care facilities, restricting to urban residents, restricting to six major cities in Ontario, and restricting to those who did not move after 1996).

The fact that PM$_{2\cdot5}$ and NO$_2$ did not fully explain the near-road effect on dementia suggests that additional pollutants or other factors such as noise might play a role. Although we were unable to directly examine these factors, traffic-related noise has been linked to cognitive impairment in a cohort in Germany.[13] In rat models, noise exposure directly impaired cognition.[11] Additionally, sleep loss from noise contributes to sleep fragmentation, which is associated with reduced cognition.[5] Living near busy roads might also reduce physical activity, which could subsequently affect neurological health. However, we found little change in our results after indirect adjustment for this variable.

Compared with dementia, less is known about the effect of traffic exposure on Parkinson's disease and multiple sclerosis. Only three studies have examined the relationship between traffic exposure and Parkinson's disease: a positive association between NO_2 and incident Parkinson's disease was reported in a case-control study in Denmark,[15] whereas in another case-control study in the USA, no association with NO_2 was found.[31] Additionally, in a cross-sectional study in Ontario, Parkinson's disease prevalence was not associated with roadway proximity nor NO_2.[32] For multiple sclerosis, one time-series study found a relationship between daily hospital admissions and particulate pollution,[33] but no studies have assessed the effect of living close to traffic. In this study, we observed an association only between traffic proximity and dementia, which might be attributable to relatively few cases of Parkinson's disease and multiple sclerosis. Another possibility is that traffic exposure could augment neurodegeneration through pathways that are related to dementia but not Parkinson's disease or multiple sclerosis.[3–5]

Our study has some limitations. First, we could not identify undiagnosed cases of dementia, Parkinson's disease, and multiple sclerosis. However, the estimates were unchanged when we adjusted for access to neurologists, a North/South indicator, deprivation, and time trends. With universal health care in Ontario, incomplete diagnosis might lead to underestimation of the true effect because this measurement error was probably independent of the exposure.

Second, we did not have information on medications that might potentially influence dementia risk (eg, anti-inflammatory medication and NSAIDs), although it is unclear whether these factors would be associated with traffic exposure. Furthermore, we lacked information on individual socioeconomic status and behavioural variables. To control for these unmeasured variables, we adjusted for neighbourhood socioeconomic status and comorbidities. Since neighbourhood socioeconomic status is strongly associated with individual socioeconomic status and behavioural variables,[25,26] and comorbidities and neurodegenerative diseases share some common behavioural factors, adjusting for these variables should reduce the influence of these unmeasured variables on HR (appendix). We further controlled indirectly for these variables, and found similar results. Although we cannot rule out residual confounding, the null findings for Parkinson's disease and multiple sclerosis do not support this possibility.

Third, our exposure assessment was based on postal-code addresses, which do not completely reflect personal exposure. $PM_{2.5}$ is a complex mixture with a secondary aerosol component that might not originate from vehicle emissions. Finally, roadway proximity does not account for traffic density and meteorological conditions that might influence exposure to air pollution and noise. Given the inherent imprecision of this exposure, our assessment of near-road exposure was probably subject to non-differential misclassification that probably attenuated our results.

The strengths of this study include the large cohorts made up of almost the entire adult population in Ontario. The many cases ascertained from validated registries enabled us to investigate fine-scale changes in traffic exposure and to examine the effect from exposures lagged up to 10 years. Our study also benefited from quantifying and comparing the effects on three major neurodegenerative diseases from traffic exposures using the same methods. Furthermore, the availability of detailed information on medical and residential history allowed us to control for important risk factors (eg, head trauma) and assess the influence of residential mobility.

Conclusions

In this large cohort, living near major roadways was associated with higher incidence of dementia, but not Parkinson's disease or multiple sclerosis. Given the potentially significant implications of traffic exposure on dementia risk, understanding the effect of different aspects of traffic merits further investigation.

Contributors

HC, RTB, JCK, PJV, KT, BJM, RC, and BJ contributed to the study design. HC, ASW, and AK prepared and cleaned the data. HC, AvD, PH, and RVM contributed to the exposure assessment. RTB provided substantial scientific input in statistical methods and interpretation of the results. HC, RTB, JCK, PJV, KT, BJM, ASW, and AK contributed to the data analyses. HC took the lead in drafting the manuscript. All authors contributed to interpretation of data, provided critical revisions to the manuscript, and approved the final draft.

Declaration of interests

We declare no competing interests.

Acknowledgements

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References

1 Prince M, Guerchet M, Prina M. The epidemiology and impact of dementia: current state and future trends. Geneva, World Health Organization, 2015. http://www.who.int/mental_health/neurology/dementia/dementia_ thematicbrief_epidemiology.pdf (accessed June 18, 2016).

2 World Health Organization. Neurological disorders: public health challenges. Geneva, World Health Organization, 2006. http://www.who.int/mental_health/neurology/neurodiso/en/ (accessed June 18, 2016).

3 O'Gorman C, Lucas R, Taylor B. Environmental risk factors for multiple sclerosis: a review with a focus on molecular mechanisms. *Int J Mol Sci* 2012; **13:** 11718–52.

4 Wirdefeldt K, Adami HO, Cole P, Trichopoulos D, Mandel J. Epidemiology and etiology of Parkinson's disease: a review of the evidence. *Eur J Epidemiol* 2011; **26** (suppl 1): S1–58.

5 Baumgart M, Snyder HM, Carrillo MC, Fazio S, Kim H, Johns H. Summary of the evidence on modifiable risk factors for cognitive decline and dementia: a population-based perspective. *Alzheimers Dement* 2015; **11:** 718–26.

6 Block ML, Elder A, Auten RL, et al. The outdoor air pollution and brain health workshop. *Neurotoxicology* 2012; **33:** 972–84.

7 Tzivian L, Winkler A, Dlugaj M, et al. Effect of long-term outdoor air pollution and noise on cognitive and psychological functions in adults. *Int J Hyg Environ Health* 2015; **218:** 1–11.

8 Calderon-Garciduenas L, Solt AC, Henriquez-Roldan C, et al. Long-term air pollution exposure is associated with neuroinflammation, an altered innate immune response, disruption of the blood-brain barrier, ultrafine particulate deposition, and accumulation of amyloid beta-42 and alpha-synuclein in children and young adults. *Toxicol Pathol* 2008; **36:** 289–310.

9 Block ML, Wu X, Pei Z, et al. Nanometer size diesel exhaust particles are selectively toxic to dopaminergic neurons: the role of microglia, phagocytosis, and NADPH oxidase. *FASEB J* 2004; **18:** 1618–20.

10 Calderon-Garciduenas L, Vojdani A, Blaurock-Busch E, et al. Air pollution and children: neural and tight junction antibodies and combustion metals, the role of barrier breakdown and brain immunity in neurodegeneration. *J Alzheimers Dis* 2015; **43:** 1039–58.

11 Cui B, Wu M, She X, Liu H. Impulse noise exposure in rats causes cognitive deficits and changes in hippocampal neurotransmitter signaling and tau phosphorylation. *Brain Res* 2012; **1427:** 35–43.

12 Oudin A, Forsberg B, Adolfsson AN et al. Traffic-related air pollution and dementia incidence in northern Sweden: a longitudinal study. *Environ Health Perspect* 2016; **124:** 306–12.

13 Tzivian L, Dlugaj M, Winkler A, et al. Long-term air pollution and traffic noise exposures and mild cognitive impairment in older adults: a cross-sectional analysis of the Heinz Nixdorf recall study. *Environ Health Perspect* 2016; **124:** 1361–68.

14 Power MC, Weisskopf MG, Alexeeff SE, Coull BA, Spiro A III, Schwartz J. Traffic-related air pollution and cognitive function in a cohort of older men. *Environ Health Perspect* 2011; **119:** 682–87.

15 Ritz B, Lee PC, Hansen J, et al. Traffic-related air pollution and Parkinson's disease in Denmark: a case-control study. *Environ Health Perspect* 2016; **124:** 351–56.

16 Jung CR, Lin YT, Hwang BF. Ozone, particulate matter, and newly diagnosed Alzheimer's disease: a population-based cohort study in Taiwan. *J Alzheimers Dis* 2015; **44:** 573–84.

17 Wilker EH, Preis SR, Beiser AS, et al. Long-term exposure to fine particulate matter, residential proximity to major roads and measures of brain structure. *Stroke* 2015; **46:** 1161–66.

18 Wellenius GA, Boyle LD, Coull BA, et al. Residential proximity to nearest major roadway and cognitive function in community-dwelling seniors: results from the MOBILIZE Boston Study. *J Am Geriatr Soc* 2012; **60:** 2075–80.

19 Ranft U, Schikowski T, Sugiri D, Krutmann J, Kramer U. Long-term exposure to traffic-related particulate matter impairs cognitive function in the elderly. *Environ Res* 2009; **109:** 1004–11.

20 Chen H, Kwong JC, Copes R, et al. Cohort Profile: The Ontario population health and environment cohort (ONPHEC). *Int J Epidemiol* 2016; published online April 20. DOI:10.1093/ije/dyw030.

21 Butt DA, Tu K, Young J, et al. A validation study of administrative data algorithms to identify patients with Parkinsonism with prevalence and incidence trends. *Neuroepidemiology* 2014; **43:** 28–37.

22 Jaakkimainen RL, Bronskill SE, Tierney MC, et al. Identification of physician-diagnosed Alzheimer's disease and related dementias in population-based administrative data: a validation study using family physicians' electronic medical records. *J Alzheimers Dis* 2016; **54:** 337–49.

23 Widdifield J, Ivers NM, Young J, et al. Development and validation of an administrative data algorithm to estimate the disease burden and epidemiology of multiple sclerosis in Ontario, Canada. *Mult Scler* 2015; **21:** 1045–54.

24 Chen H, Goldberg MS, Burnett RT, Jerrett M, Wheeler AJ, Villeneuve PJ. Long-term exposure to traffic-related air pollution and cardiovascular mortality. *Epidemiology* 2012; **24:** 35–43.

25 Janssen I, Boyce WF, Simpson K, Pickett W. Influence of individual- and area-level measures of socioeconomic status on obesity, unhealthy eating, and physical inactivity in Canadian adolescents. *Am J Clin Nutr* 2006; **83:** 139–45.

26 Gan WQ, Davies HW, Koehoorn M, Brauer M. Association of long-term exposure to community noise and traffic-related air pollution with coronary heart disease mortality. *Am J Epidemiol* 2012; **175:** 898–906.

27 van Donkelaar A, Martin RV, Spurr RJ, Burnett RT. High-resolution satellite-derived PM2.5 from optimal estimation and geographically weighted regression over North America. *Environ Sci Technol* 2015; **49:** 10482–91.

28 Hystad P, Setton E, Cervantes A, et al. Creating national air pollution models for population exposure assessment in Canada. *Environ Health Perspect* 2011; **119:** 1123–29.

29 Shin HH, Cakmak S, Brion O, et al. Indirect adjustment for multiple missing variables applicable to environmental epidemiology. *Environ Res* 2014; **134:** 482–87.

30 Crouse DL, Peters PA, Hystad P, et al. Ambient PM2.5, O3, and NO2 exposures and associations with mortality over 16 years of follow-up in the Canadian census health and environment cohort (CanCHEC). *Environ Health Perspect* 2015; **123:** 1180–86.

31 Liu R, Young MT, Chen JC, Kaufman JD, Chen H. Ambient air pollution exposures and risk of Parkinson disease. *Environ Health Perspect* 2016; published online June 10, 2016. DOI:10.1289/EHP135.

32 Finkelstein MM, Jerrett M. A study of the relationships between Parkinson's disease and markers of traffic-derived and environmental manganese air pollution in two Canadian cities. *Environ Res* 2007; **104:** 420–32.

33 Angelici L, Piola M, Cavalleri T, et al. Effects of particulate matter exposure on multiple sclerosis hospital admission in Lombardy region, Italy. *Environ Res* 2016; **145:** 68–73.

Relative Sensitivities of Mammalian Carnivores to Habitat Fragmentation

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Abstract: *I examined the effects of habitat fragmentation on the distribution and abundance of mammalian carnivores in coastal southern California and tested the prediction that responses to fragmentation varied with the body size of carnivore species. I conducted track surveys for nine native and two exotic carnivore species in 29 urban habitat fragments and 10 control sites. Fragment area and isolation were the two strongest landscape descriptors of predator distribution and abundance. Six species were sensitive to fragmentation, generally disappearing as habitat patches became smaller and more isolated; three species were enhanced by fragmentation, with increased abundance in highly fragmented sites; and two species were tolerant of fragmentation, with little to no effect of landscape variables on their distribution and abundance. Within urban habitat fragments, the carnivore visitation rate increased at sites with more exotic cover and closer to the urban edge, a pattern driven largely by the increased abundance of fragmentation-enhanced carnivores at edge sites. Finally, body size, in conjunction with other ecological characteristics, partially accounted for the heterogeneity in responses to fragmentation among carnivore species. These differential sensitivities are useful criteria for choosing appropriate focal species for ecological research and conservation planning, a choice that depends on the scale of fragmentation in a region and the commensurate responses of carnivore populations at that scale.*

Sensibilidad Relativa a la Fragmentación del Hábitat de Mamíferos Carnívoros

Resumen: *Examiné los efectos de la fragmentación del hábitat sobre la distribución y abundancia de mamíferos carnívoros en la costa del sur de California y evalué la predicción de que las respuestas a la fragmentación variaban con el tamaño corporal de carnívoros. Se realizaron muestreos de huellas para nueve especies nativas y dos exóticas en 29 fragmentos de hábitat urbano y 10 sitios control. El área fragmentada y su aislamiento fueron los dos principales descriptores de la distribución y abundancia de depredadores. Seis especies fueron sensibles a la fragmentación, generalmente las especies desaparecían conforme los fragmentos eran más pequeños y aislados, tres especies fueron favorecidas por la fragmentación, con incremento en su abundancia en sitios altamente fragmentados, y dos especies fueron tolerantes a la fragmentación con poco o ningún efecto de las variables del paisaje sobre su distribución y abundancia. Dentro de los fragmentos de hábitat urbano, las tasas de presencia de carnívoros incrementaron en sitios con mayor cobertura exótica y cercanos al borde urbano, un patrón dirigido principalmente por el incremento en la abundancia de carnívoros favorecidos por la fragmentación en el borde de los sitios. Finalmente, el tamaño corporal, conjuntamente con otras características ecológicas, fueron parcialmente responsables de la heterogeneidad en respuestas a la fragmentación entre especies de carnívoros. Estas sensibilidades diferenciales son un criterio útil para seleccionar especies focales apropiadas para investigaciones ecológicas y la planeación de la conservación, una selección que depende de la escala de fragmentación en una región y de las respuestas apropiadas de las poblaciones de carnívoros a esa escala.*

Introduction

The destruction of habitat has been targeted as one of the most serious threats to biological diversity world-

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wide (Wilcove et al. 1998), and in areas with increasing urbanization, the loss and fragmentation of habitat is virtually inevitable. Mediterranean scrub habitats in coastal southern California are particularly threatened. Intensive development in the region over the past century has destroyed all but 10% of the native coastal sage scrub habitat (McCaull 1994). This habitat loss has created a "hotspot" of endangerment and extinction for the highly endemic biota in the region (Dobson et al. 1997). Mammalian carnivores are thought to be particularly vulnerable to local extinction in fragmented landscapes because of their relatively large ranges, low numbers, and direct persecution by humans (Noss et al. 1996; Woodroffe & Ginsberg 1998). The decline and extirpation of top predators from fragmented systems may generate trophic cascades that alter the structure of ecological communities (Crooks & Soulé 1999). Indeed, the persistence of these environmentally sensitive and ecologically pivotal species may be indicative of the integrity of entire ecosystems (Noss et al 1996). As such, mammalian carnivores can serve as useful tools for the study of ecological disturbances or for conservation planning and reserve design (Soulé & Terborgh 1999).

Mammalian predators are difficult to study, however, because of their low densities, nocturnal and secretive habits, and wariness of humans (Sargeant et al. 1998). As a result, the ecology of many carnivore species and their responses to ecological disturbances such as fragmentation are often poorly understood. Although considered members of the same ecological guild, carnivores may vary in their responses to fragmentation. In particular, differences in body size among carnivore species have been proposed as an important determinant of extinction probability (Brown 1986; Belovsky 1987). The relationship between body size and extinction risk in animals is complex, however, and has been the subject of considerable debate, with studies predicting and reporting positive, negative, or no relation of body size to extinction probability (reviewed by Johst & Brandl 1997). Few studies have evaluated if, how, or why carnivore species differ in their relative sensitivities to fragmentation effects.

My goal was to analyze the effects of the loss and fragmentation of habitat on mammalian carnivores in the urbanizing landscape of coastal southern California. Habitat fragmentation must be viewed as a multiscale problem, with fragmentation effects depending on the scale of fragmentation and the movement patterns of target species (Andren 1994). I therefore surveyed a suite of carnivore species that occur across a range of fragmentation levels and evaluated their responses to fragmentation at two spatial scales: (1) landscape-level heterogeneity among fragments and (2) local heterogeneity at sites within fragments. To allow for a more comprehensive assessment of relative sensitivities to fragmentation, I not only documented the presence or absence of each carnivore species, but also measured their relative abundance at each site. Finally, I tested the prediction that responses to fragmentation vary with body size in carnivore species, explored other ecological traits of these predators that may contribute to extinction risk, and used these differential sensitivities to evaluate the utility of mammalian carnivores as focal species with which to assess the degree of functional landscape connectivity.

Methods

Study Areas

I conducted carnivore surveys in 29 urban habitat fragments in coastal San Diego County from Fall 1995 through Summer 1997. Twenty-eight of these fragments were originally studied by Soulé et al. (1988). The fragments, completely surrounded by human-modified landscapes, are typically dendritic canyons dissecting coastal mesas, although a few also contain mesa-top habitat. The fragments support a mosaic of shrub habitat, including mixed chaparral, chamise chaparral, maritime succulent shrub, and coastal sage scrub, the dominant assemblage in most sites. Disturbed areas within fragments were typically dominated by ruderal weed species, ornamental plants invading from surrounding residences, fire-retardant ground cover such as South African iceplant (*Carpobrotus edulis*), and non-native trees (e.g., palms and species of *Eucalyptus* and *Acacia*) (Alberts et al. 1993).

From Fall 1995 through Summer 2000, I conducted carnivore surveys in less disturbed areas in coastal southern California to act as controls to the small, urban habitat remnants. These control areas varied in size and degree of isolation (Table 1), ranging from relatively small reserves isolated within urban developments (e.g., Point Loma Ecological Reserve) to large blocks of habitat relatively continuous with larger natural areas (e.g., Miramar Marine Corps Air Station).

Carnivore Surveys

I assessed the distribution and relative abundance of nine native and two non-native predator species through track surveys. Native species were the mountain lion (*Felis concolor*), bobcat (*Felis rufus*), coyote (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), badger (*Taxidea taxus*), raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), western spotted skunk (*Spilogale gracilis*), and long-tailed weasel (*Mustela frenata*). Non-native target species were the domestic cat (*Felis catus*) and Virginia opossum (*Didelphis virginiana*), a marsupial introduced to California around 1910 (Jameson & Peeters 1988).

Table 1. Landscape variables and distributions of 11 mammalian carnivore species for 10 control sites and 29 urban habitat fragments in coastal southern California (1, present; 0, absent).

	Area (ha)	*Age (yrs)*	*Distance Y (m)*	*Distance Z (m)*	*Long-tailed weasel*	*Spotted skunk*	*Badger*	*Mountain lion*	*Bobcat*	*Coyote*	*Gray fox*	*Striped skunk*	*Raccoon*	*Opossum*	*Domestic cat*
Control sites															
Miramar Marine Corps Air Station	5806	0	0	0	0	0	0	1	1	1	0	1	1	1	0
Chino Hills State Park	4452	0	200	200	1	0	1	1	1	1	1	1	1	1	0
Limestone Canyon/Whiting Ranch	4450	0	15	15	0	0	1	1	1	1	1	1	1	1	0
San Joaquin Hills	4219	22	5353	2930	0	1	0	0	1	1	1	1	1	1	0
Weir Canyon	1923	0	69	69	0	0	0	1	1	1	1	1	0	1	0
Santa Margarita Ecological Reserve	1763	0	30	30	0	0	0	1	1	1	1	0	1	0	0
Starr Ranch	1548	0	0	0	0	1	0	1	1	1	1	1	1	1	0
Tenaja	1191	0	0	0	1	0	1	1	1	1	1	1	1	1	0
Torrey Pines State Reserve	428	0	68	68	0	0	0	0	1	1	1	1	1	1	0
Point Loma Ecological Reserve	264	45	5700	5700	0	0	0	0	0	1	1	1	1	0	1
Urban fragments															
Florida	102	59	2100	233	0	0	0	0	0	1	1	0	0	0	0
Torrey Pines Extenstion	74	20	91	91	0	0	0	0	1	1	1	1	1	1	1
Balboa Terrace	56	43	121	117	0	0	0	0	0	1	1	1	1	1	1
Alta La Jolla	34	23	121	93	0	0	0	0	0	1	1	1	1	1	1
Kate Sessions	31	25	121	93	0	0	0	0	0	1	1	1	1	1	1
Zena	15	45	2865	467	0	0	0	0	0	1	1	1	0	1	1
Canon	12	67	1219	1167	0	0	0	0	0	0	1	1	1	1	1
Laurel	10	88	1554	350	0	0	0	0	0	1	1	1	1	1	1
32nd Street South	10	65	304	233	0	0	0	0	0	1	0	0	0	0	1
Pottery	10	23	45	70	0	0	0	0	0	1	1	1	1	1	0
Washington	9	83	365	187	0	0	0	0	0	1	1	1	1	1	1
Syracuse	9	27	40	70	0	0	0	0	0	1	1	1	0	1	1
Baja	8	40	670	70	0	0	0	0	0	1	1	1	1	1	1
Raffee	8	28	61	163	0	0	0	0	0	1	1	1	1	1	1
Solana	8	20	550	187	0	0	0	0	0	1	1	0	1	1	0
Acuna	7	31	110	47	0	0	0	0	0	1	1	1	0	1	1
Juan	7	32	228	70	0	0	0	0	0	1	1	1	1	1	1
Chollas	6	45	1005	467	0	0	0	0	0	1	1	1	1	1	1
Mil Cumbres	6	20	550	23	0	0	0	0	1	1	1	1	0	1	1
Chateau	6	29	110	47	0	0	0	0	0	1	1	0	0	1	1
Oak Crest	6	15	400	140	0	0	0	0	0	1	0	0	0	1	1
54th	4	29	609	187	0	0	0	0	0	1	1	1	1	1	1
60th	4	46	335	350	0	0	0	0	0	1	0	0	0	1	0
Spruce	4	95	1767	93	0	0	0	0	0	1	1	1	1	1	1
Titus	3	86	280	163	0	0	0	0	0	1	1	1	1	1	1
Montanosa	3	11	91	93	0	0	0	0	0	1	0	0	0	1	1
El Mac	2	41	883	163	0	0	0	0	0	1	1	1	1	0	1
Poinsettia	2	59	350	350	0	0	0	0	0	0	1	0	1	1	1
Talbot	2	64	1219	933	0	0	0	0	0	0	1	1	1	1	1
Urban fragment occupancy					0	0	0	0	2	26	25	21	19	26	25
Total occupancy					2	2	3	7	11	36	34	30	28	34	26

I established a series of track-detection stations at approximately 250-m intervals along dirt roads or trails (human and/or wildlife) along the main axis of each study area (Linhart & Knowlton 1975; Conner et al. 1983; Sargeant et al. 1998). Each track station consisted of a 1-m-diameter, 1-cm-deep, circle of freshly sifted gypsum baited with a liquid carnivore scent lure (Russ Carman's Pro-Choice and Canine Call, Sterling Fur & Tool, Sterling, Ohio) every other day. Track transects were checked and reset daily for 5 consecutive days. Tracks on each station were measured and identified to species; tracks with ambiguous identifications were omitted from analyses. Track surveys were conducted once each sampling quarter: fall (September–November), winter (December–February), spring (March–May), and summer (June–August). Each site was sampled for 1–2 years.

The track index of each carnivore species in each quarterly sampling session was expressed as the total number of visits recorded for a species, divided by the total sampling effort. I defined a visit as at least one track of a species on a track station (Conner et al. 1983). Mathematically, the track index (I) was calculated as

$$I = \ln[\{v_j/(s_j n_j)\} + 1],$$

where v_j is the number of stations visited by a species in transect j, s_j is the number of stations in transect j, and n_j is the number of nights that stations were operative in transect j. Thus, I for each species represents the visitation rate per track station per night in each study area. Although this index cannot be directly translated into numbers of individuals and hence does not measure absolute densities, it does provide an index of the relative abundance of a species at each sampling point (Conner et al. 1983; Sargeant et al. 1998). For each species, I averaged track indices across quarterly sampling sessions to derive a mean index at each study area for the duration of the study. Indices were log-transformed to meet normality assumptions in the statistical analyses. Overall, track surveys totaled 6540 station-nights (s_j n_j) among all study sites.

Landscape Variables

I used area, age, and isolation to assess the effects of landscape-level fragmentation on carnivore populations (Table 1). I measured the total area of each fragment based on digitized images of scaled aerial photographs taken in 1995. Total area of each control site was defined as the reserve boundaries within which the surveys were conducted. Because control sites were often adjacent to unfragmented habitat, area approximations represent minimum estimates.

Fragment age, defined as the number of years since isolation of the habitat fragment by urban development, was based on dated aerial photographs and building permit records (Soulé et al. 1988). Because fragment age is highly negatively correlated to the proportion of native shrub cover within fragments (Suarez et al. 1998; Crooks et al. 2001), I used age to measure a time effect per se in the fragments and to represent the cumulative loss of native habitat in the entire fragment since isolation. Age was scored as zero for control sites that were directly adjacent to larger natural areas (Miramar Marine Corps Air Station, Starr Ranch Audubon Sanctuary, Tenaja Corridor) or that were separated from such areas by only a roadway and not by urban development (Chino Hills State Parks, Limestone Canyon/Whiting Ranch, Santa Margarita Ecological Reserve, Torrey Pines State Reserve, Weir Canyon).

Two variables were calculated to characterize the degree of isolation of each site: distance Y, the distance to the closest habitat patch (measured from patch edge to patch edge) of equal or larger size (Soulé et al. 1988), and distance Z, the shortest distance to any other habitat fragment, reserve, or possible movement linkage to such sites (e.g., riparian channels, power line easements, golf courses). Isolation was scored as zero for control sites directly adjacent to a larger natural area and as the width of the roadway for control sites isolated from larger habitat blocks by a roadway.

All landscape variables were log-transformed to meet normality assumptions in the statistical analyses. When only the urban habitat fragments were considered, fragment age was positively related to distance Y ($r = 0.564$, $p = 0.001$) and distance Z ($r = 0.526$, $p = 0.003$), and distance Y was positively related to distance Z ($r = 0.362$, $p = 0.053$). When both habitat fragments and control areas were included, area was negatively related to age ($r = -0.813$, $p < 0.001$), distance Y ($r = -0.467$, $p = 0.003$), and distance Z ($r = -0.299$, $p = 0.065$); age was positively related to distance Y ($r = 0.741$, $p < 0.001$) and distance Z ($r = 0.597$, $p < 0.001$); and distance Y was positively related to distance Z ($r = 0.761$, $p < 0.001$).

SPECIES RICHNESS AND DISTRIBUTION

Island biogeography theory predicts that landscape variables such as size and isolation should help determine the number of species on islands (MacArthur & Wilson 1967). To test this prediction, I calculated two measures of carnivore species richness for each study area: (1) the number of carnivore species detected at the site during the course of the study and (2) the number of native carnivore species detected, excluding the non-native opossum and domestic cat. A species was present in a study area if it was detected on track stations within the site at least once during the course of the study. Presence was verified with a combination of remotely triggered cameras, scat surveys, and opportunistic visual sightings. Presence of a species does not necessarily imply that the site can support resident animals or populations. Likewise, failure to detect a species at a site does not indicate that the species has never visited the area, but rather that it was not recorded during sampling sessions.

I used backward-elimination multiple regression to identify which landscape variables (size, age, and isolation) were the best predictors of carnivore species richness in a study site. Independent variables with $p < 0.15$ were included in all regression models to minimize exclusion of important predictors from the model, and tolerance values were set at 0.10 throughout to control for multicollinearity (Tabachnick & Fidell 1996). Comparison-wide error rates were examined in all statistical analyses (Mead 1988; Stuart-Oaten 1995) ($p < 0.05$, statistically significant; $0.05 < p < 0.10$, marginally significant). I first conducted the multiple-regression analyses including only the 29 urban habitat fragments and then including all 39 study sites.

I used logistic-regression analyses to evaluate the effect of landscape variables on the distribution of individual carnivore species. First, I constructed bivariate logistic-regression models to evaluate the separate effects of area and isolation (distance *Z*) on the probability of occurrence for each species across all 39 study sites. Area and distance *Z* were chosen because preliminary analyses indicated that they were the two strongest predictors of carnivore distribution. For species with significant area and isolation effects, I plotted logistic-regression curves of the probability of occurrence of each species as a function of area, holding isolation constant by substituting its median value into a two-way (area × isolation) logistic model. Likewise, I constructed isolation curves after holding area constant by substituting its median value into the two-way logistic model. From these curves, I calculated the area and isolation at which the probability of occurrence of the species equaled 50% and used these estimates to represent the relative area and isolation requirements for each species (following Crooks et al. 2001). Finally, I used multiple-logistic-regression models to graphically evaluate the combined effect of area and isolation on probability of occurrence for each species.

Logistic-regression estimates of probability of occurrences and relative area and isolation requirements are not intended, however, to represent the actual fragment size or isolation necessary to ensure the long-term persistence of a population (Hinsley et al. 1996). Rather, probability of occurrence measures the probability of an individual visiting the study area at least once during the course of the study, and the area and isolation estimates generated are intended to function only as relative indices of sensitivity to fragmentation. Area and isolation estimates are likely to be more accurate for those species with the most detections.

RELATIVE ABUNDANCE

I used backward-elimination regression models to identify which landscape variables were the best predictors of the track indices of each species in each study area. The analyses were first conducted including only the 29 urban habitat fragments. Mountain lions, spotted skunks, badgers, and long-tailed weasels were omitted from these analyses because they were not detected in any urban habitat fragments. Bobcats, detected in only two fragments, were also omitted.

I repeated the multiple-regression analyses across all 39 fragments and control sites, including mountain lions and bobcats in the analyses. Spotted skunks, badgers, and long-tailed weasels were again omitted due to low detection rates. Because the track indices for mountain lions and bobcats were zero for many sites, the results of these regressions must be interpreted with caution. The final regression models were determined largely by the patterns of species' presence or absence across sites and not by variation in relative abundance among sites where they occurred. Nevertheless, I report regression models for mountain lions and bobcats to allow for further evaluation of the effects of landscape variables on these species and for further comparisons of their fragmentation sensitivities to those of other carnivore species.

Local Variables

Habitat heterogeneity within these urban habitat fragments is an important determinant of the persistence of native scrub-breeding birds (Soulé et al. 1988), rodents (Bolger et al. 1997), and invertebrates (Suarez et al. 1998; Bolger et al. 2000), all potential prey for carnivore species. I measured three variables to investigate the effect of habitat heterogeneity on carnivore populations: distance to the urban edge, percent cover of native shrubs, and percent cover of exotic vegetation. I estimated the distance of each track station to the nearest urban edge (the backyards of the houses bordering the fragment) and log-transformed these values to meet normality assumptions in the statistical analyses. I used a Braun-Blanquet categorical scale (Kent & Coker 1992) to estimate the percent cover of native shrubs and of total exotic cover within a 20-m radius around each track station. The cover scale was 0 (<1%), 1 (1–5%), 2 (6–25%), 3 (26–50%), 4 (51–75%), and 5 (76–100%). Distance to edge was positively related to shrub cover ($r = 0.281$, $p = 0.007$) and negatively related to exotic cover ($r = -0.341$, $p = 0.001$), and shrub cover was negatively related to exotic cover ($r = -0.694$, $p < 0.001$).

SPECIES RICHNESS AND RELATIVE ABUNDANCE

I calculated the total number of carnivore species and the number of native carnivore species detected at each track station in the 29 urban habitat fragments during the course of the study; two exotic species (opossum and domestic cat) and five native species (bobcat, coyote, gray fox, striped skunk, and raccoon) were detected in the urban fragments and were hence included in the analyses. I then used backward-elimination multiple regression to identify which local variables were the best predictors of carnivore species richness at each station.

I calculated the mean track index for each species at each track station in the 29 urban habitat fragments to generate relative abundance indices. Again, mountain lions, spotted skunks, long-tailed weasels, badgers, and bobcats were omitted from these analyses due to low detection rates within fragments. I then used backward-elimination multiple regression to identify which local variables were the best predictors of the relative abundance of each species at a station. Some species were absent from some fragments, however, an absence driven in part by landscape variables such as area, age, and isolation. I therefore conducted the regressions for each species after excluding from the analyses all fragments where that species was never detected. By excluding these fragments I could account for the effects of landscape-level fragmentation on the presence or absence of a species and therefore more fully analyze the effects of local variables within fragments where that species occurred.

To further evaluate the effect of the urban edge on carnivores within fragments, for each species I graphed the mean track index at each station as a function of the distance of that station from the urban edge. Edge distances were classified into five categories: 0–24 m (n = 14 stations), 25–49 m (n = 35), 50–99 m (n = 16), 100–199 (n = 19), and >200 m (n = 7). Direct comparisons of track indices between species can be misleading, because the response of species to track stations may differ (Conner et al. 1983; Sargeant et al. 1998). To allow for more meaningful comparisons of track indices, I standardized the index for each species by dividing each value by the maximum track index recorded for that species. Therefore, these standardized track indices for each species ranged on a scale of 0 to 1.

Body Size and Fragmentation Sensitivity

I evaluated the relationship between body mass and sensitivity to fragmentation among carnivore species through linear-regression analysis. As an index of sensitivity to fragmentation, I calculated the average area of study sites occupied by each species, multiplying the area of each study site by the standardized track index (scale 0 to 1) of that species at that site. With area weighted by relative abundance per sampling point, the indices accounted not just for occupancy but also for differences in the relative abundance of a species among study sites. For example, for a given species, some study sites supported resident populations, whereas other study sites were only visited temporarily during the course of the study. Average area weighted by relative abundance accounted for such differences. In addition, I also compared body mass to typical home-range sizes and population densities reported in the literature for these species.

Results

Landscape Heterogeneity: Comparisons among Fragments

SPECIES RICHNESS AND DISTRIBUTION

The distribution of carnivore species varied across study sites (Table 1). Coyotes, opossums, gray foxes, domestic cats, striped skunks, and raccoons were detected in most urban fragments. Bobcats were detected in 9 of the 10 control sites but in only 2 urban habitat fragments, and mountain lions were detected in only 7 control sites and no urban fragments. I recorded few to no visits of mountain lions and bobcats in the habitat fragments, despite higher sampling intensity per unit area (station-nights/total area of site) in the 29 fragments (mean = 8.30 station-nights/ha, SE = 0.910) than in the 10 control sites (mean = 0.43 station-nights/ha, SE = 0.158) ($t = 4.58$, $p < 0.001$). Detections of spotted skunks, long-tailed weasels, and badgers were rare and occurred only in the larger habitat blocks.

Among the 29 urban habitat fragments, no landscape variables were retained as predictors of the total number of carnivore species in backward-elimination regression models (Table 2). When the opossum and domestic cat were excluded, however, the species richness of native carnivores exhibited a weak negative trend with fragment isolation (distance Z) and a weak positive trend with fragment age. When control sites were included in the analyses, both total carnivore species richness and native carnivore species richness increased with the area of the study site.

Logistic-regression models for each species indicated that the probability of occurrence across all sites was positively related to fragment area for coyotes ($\chi^2 = 5.57$, $p = 0.018$), bobcats ($\chi^2 = 29.85$, $p < 0.001$), mountain lions ($\chi^2 = 27.35$, $p < 0.001$), spotted skunks ($\chi^2 = 5.85$, $p = 0.016$), long-tailed weasels ($\chi^2 = 5.37$, $p = 0.021$), and badgers ($\chi^2 = 9.73$, $p = 0.002$). In contrast to these native carnivores, the probability of occurrence of domestic cats was higher in smaller fragments ($\chi^2 = 22.63$, $p < 0.001$). Area was not a significant predictor of probability of occurrence for gray foxes ($\chi^2 = 0.24$, $p = 0.627$), striped skunks ($\chi^2 = 1.81$, $p = 0.178$), raccoons ($\chi^2 = 2.02$, $p = 0.155$), or opossums ($\chi^2 = 0.357$, $p = 0.550$).

Logistic-regression models indicated that probability of occurrence across all sites decreased with fragment isolation (distance Z) for coyotes ($\chi^2 = 6.92$, $p = 0.008$), bobcats ($\chi^2 = 11.57$, $p < 0.001$), and mountain lions ($\chi^2 = 11.88$, $p < 0.001$). In contrast, probability of oc-

Table 2. Backward-elimination regression models of the effects of landscape variables on carnivore species richness and relative abundance among 29 urban habitat fragments and 10 control sites in coastal southern California.[a]

Variables	R^2	*Whole-model* p	*Coefficient*	p
Urban habitat fragments				
total species richness				
n.s.[b]				
native species richness	0.146	0.129		
distance *Z*			−0.408	0.067
age			+0.374	0.091
coyote	0.133	0.052		
area			+0.365	0.052
gray fox	0.114	0.074		
area			−0.336	0.074
domestic cat	0.393	0.002		
area			−0.550	0.001
distance *Z*			+0.246	0.122
opossum	0.164	0.029		
area			−0.405	0.029
striped skunk				
n.s.				
raccoon				
n.s.				
All sites				
total species richness	0.194	<0.001		
area			+0.440	<0.001
native species richness	0.372	<0.001		
area			+0.610	<0.001
coyote	0.15	0.015		
area			+0.388	0.015
bobcat	0.595	<0.001		
age			−0.921	<0.001
distance *Y*			+0.607	0.004
distance *Z*			−0.376	0.030
mountain lion	0.277	<0.001		
age			−0.526	<0.001
gray fox	0.197	0.005		
area			−0.444	0.005
raccoon	0.081	0.081		
area			−0.284	0.081
domestic cat	0.335	<0.001		
area			−0.579	0.001
opossum	0.241	0.002		
area			−0.491	0.002
striped skunk				
n.s.				

[a] *Independent variables are fragment area, age, and isolation (distance* Y *and distance* Z*). Independent variables with* $p < 0.15$ *were included in the final regression models.*

[b] *No independent variables were retained in the regression model (*$p > 0.15$*); n.s., not significant.*

currence was higher in more isolated fragments for domestic cats ($\chi^2 = 4.25, p = 0.039$). Isolation was not a significant predictor of probability of occurrence for gray foxes ($\chi^2 = 0.35, p = 0.553$), opossums ($\chi^2 = 1.88, p = 0.171$), spotted skunks ($\chi^2 = 0.18, p = 0.671$), striped skunks ($\chi^2 = 0.69, p = 0.407$), raccoons ($\chi^2 = 0.06, p = 0.811$), long-tailed weasels ($\chi^2 = 1.74, p = 0.187$), or badgers ($\chi^2 = 2.62, p = 0.106$).

After I controlled for isolation effects, the estimated area at which probability of occurrence was 50% was 1 ha for coyotes, 1.8 km^2 for bobcats, and 23 km^2 for mountain lions (Fig. 1a). The probability of occurrence for domestic cats dropped below 50% in fragments larger than 1.4 km^2; cats were never detected in the interior of control sites, and few if any feral cats occurred in these sites.

After I controlled for area effects, the estimated fragment isolation (distance *Z*) at which probability of occurrence was 50% was 883 m for coyotes and 6 m for bobcats (Fig. 1b). The probability of occurrence for mountain lions was <50% across the entire isolation range of fragments. In contrast, the probability of occurrence for domestic cats was >50% across the entire range of fragment isolation.

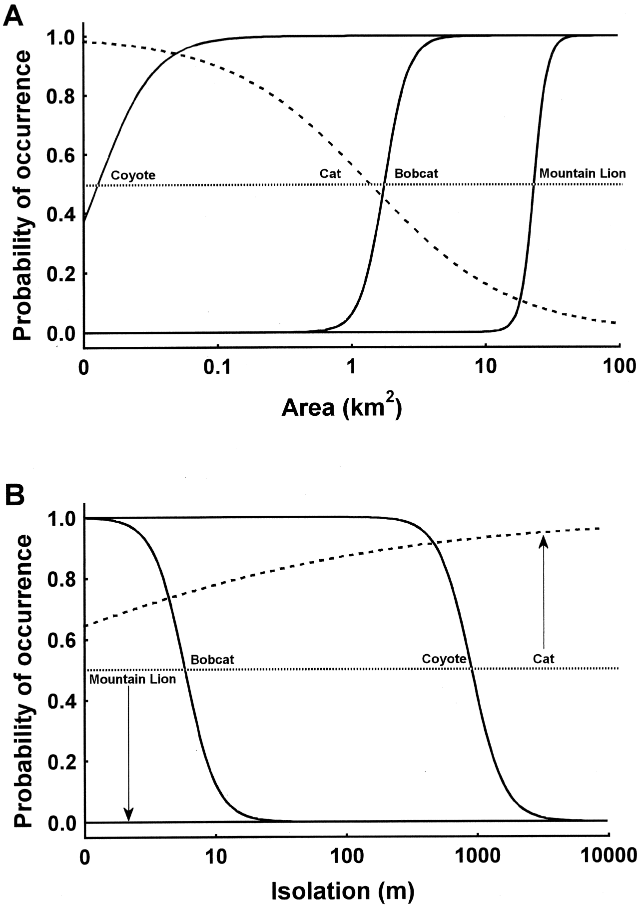

Figure 1. Logistic-regression models of the probability of occurrence of native (solid lines) and exotic (dashed line) carnivores as a function of (a) fragment area and (b) isolation. Area and isolation curves were constructed after the other independent variable was held constant by substituting its median values into a two-way (area × isolation) logistic-regression model. Only species with significant area and isolation effects are presented. Dotted line represents 50% probability of occurrence.

Multiple logistic-regression models of the combined effect of area and isolation on mountain lions, bobcats, and coyotes generated "extinction surfaces" that consisted of plateaus of occupancy at larger and less isolated sites that declined to basins of local extinctions at small and isolated fragments (Fig. 2). The effect of the area-isolation interaction, and hence the contour of the extinction surfaces, varied among species. The plateau for mountain lions was small and occurred only in the largest unfragmented sites, with large basins across all other study areas. The plateau for bobcats spanned a wider range of sites, but probability of occurrence dropped to zero in sites that were both small and isolated. Bobcats occurred in relatively small sites, but only those with little to no isolation. The plateau of coyotes was large, with a low probability of occurrence in only the smallest, most isolated urban fragments. Domestic cats exhibited a surface that was the inverse of these native predators. Their probability of occurrence was high in small and isolated fragments but lower in larger, less fragmented sites.

It should be emphasized, however, that the probability of residency or long-term viability of populations is undoubtedly lower than these probabilities of occurrence, particularly in smaller and isolated sites. For example, coyotes visited some fragments only temporarily during the course of the study. In some quarterly sampling sessions they were detected and in others they were not. Although the plateau of occupancy for coyotes encompassed most combinations of area and isolation, residency declined with fragment area. The average area of the 13 fragments in which coyotes came and went (mean = 0.75 [5.6 ha back-transformed], SD = 0.20) was smaller ($t = 3.01, p = 0.006$) than the average area of the 13 fragments in which coyotes were detected in every quarterly sampling session (mean = 1.19 [15.6 ha back-transformed], SD = 0.95).

RELATIVE ABUNDANCE

When only the 29 urban habitat fragments were included in the analyses, the relative abundance of coyotes at each sampling point was higher in larger fragments, whereas track indices of gray foxes, domestic cats, and opossums were higher in smaller fragments (Table 2). No variables were retained in the final model for raccoons and striped skunks ($p > 0.15$).

When control sites were also included in the regressions, coyote track indices at each sampling point again tended to be higher in larger sites. In contrast, the track indices of gray foxes, domestic cats, opossums, and raccoons were higher in smaller sites (Table 2). No landscape variables were retained in the models for the relative abundance of striped skunks.

When control sites were included in the regression models, fragment age was retained as the most significant predictor of the relative abundance of mountain lions and bobcats (Table 2); both species were less abundant in older sites. Mountain lions and bobcats were detected in relatively few sites, most of which were control areas not isolated by urban development (age = 0) and, for bobcats, a couple of recently isolated fragments (Table 1). This pattern generated the significant, negative slope between relative abundance and age for the two species.

The relative abundance of bobcats decreased with distance to the nearest movement linkage or natural area (distance Z) but, paradoxically, increased with distance to the nearest habitat patch of equal or larger size (distance Y). Bobcats were detected at sites that were relatively distant from larger natural areas (high values of

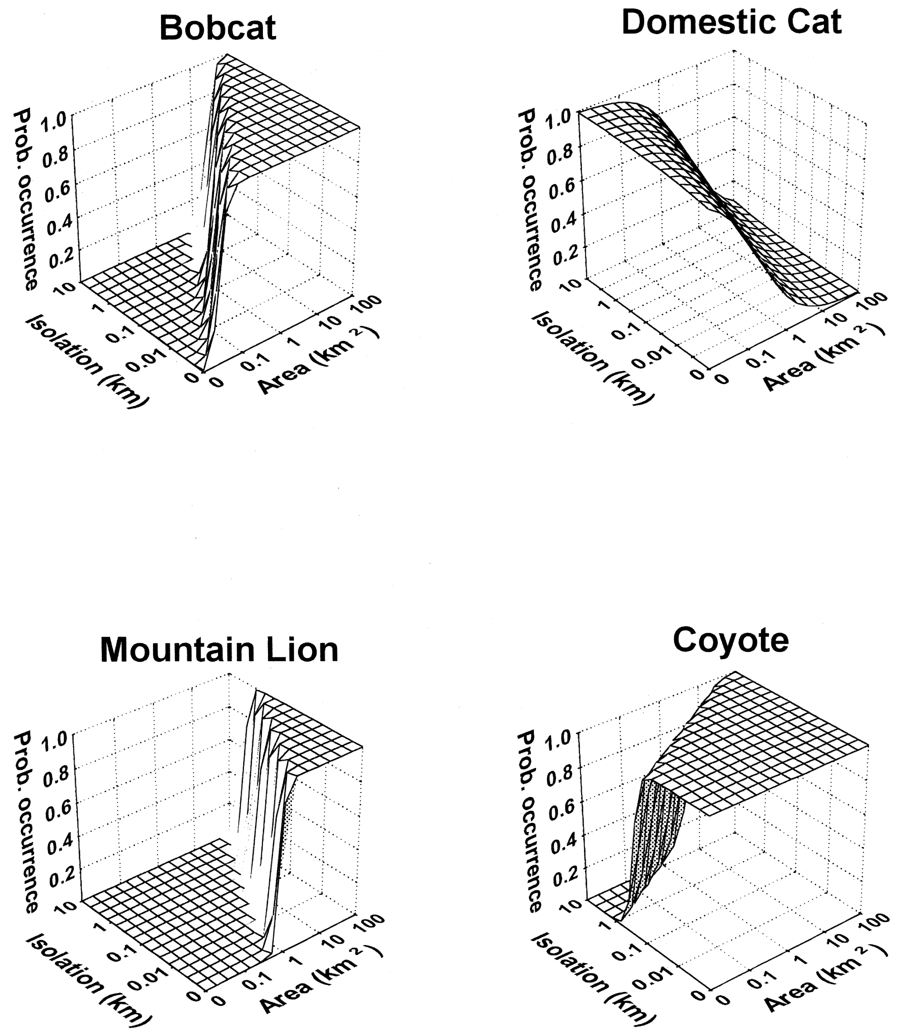

Figure 2. Multiple logistic-regression models of the probability of occurrence of mountain lions, bobcats, coyotes, and domestic cats as a function of fragment area and isolation. Only species with significant area and isolation effects are presented.

distance *Y*), but only if they were large or were near movement linkages to larger habitat blocks (low value of distance *Z*). For example, bobcats have persisted in the San Joaquin Hills, an isolated (distance *Y* = 5353 m) but large (4219 ha) habitat block. Bobcats were also detected in Mil Cumbres, a small (6 ha) urban fragment that was isolated from larger natural areas (distance *Y* = 550 m) but that was near a golf course (distance *Z* = 23 m), which likely served as a movement linkage to natural areas to the east.

Local Heterogeneity: Comparisons within Fragments

SPECIES RICHNESS AND RELATIVE ABUNDANCE

The number of carnivore species detected was greater at track stations closer to the urban edge (Table 3). This pattern was largely determined by non-native species. When exotic predators (domestic cats, opossums) were excluded from the analyses, the number of native species detected at each station did not vary significantly with any local variables.

The relative abundance of gray foxes and opossums was higher at track stations near the urban edge within fragments where each species occurred (Table 3). The abundance of domestic cat exhibited a weak negative trend with distance to urban edge. The relative abundance of striped skunks tended to be higher at greater distances from the urban edge. Domestic cats and raccoons tended to be more abundant at stations with more exotic cover. No local variables entered the model for the relative abundance of coyotes.

A graphical analysis revealed that the coyote rate of visitation to track stations was high both near the urban edge and into the interior of the urban habitat fragments (Fig. 3). The abundance of striped skunks also was relatively high in the interior of fragments. In contrast, the abundance of opossums, gray foxes, domestic cats, and raccoons was relatively high within 50 m from urban development, but then tended to decline into the interior of the habitat fragment.

Body Size and Fragmentation Sensitivity

When all species were included in the regression, the relationship between body mass (Table 4) and the average

Table 3. Backward-elimination regression models of the effects of local habitat variables on carnivore species richness and relative abundance at 92 track stations within 29 urban habitat fragments in southern California.[a]

Variables	R^2	*Whole-model* p	*Coefficient*	p
Total species richness	0.049	0.036		
edge			−0.222	0.036
Native species richness				
n.s.[b]				
Coyote (87 stations)				
n.s.				
Gray fox (85)	0.146	<0.001		
edge			−0.382	<0.001
Striped skunk (69)	0.042	0.095		
edge			0.205	0.095
Raccoon (62)	0.056	0.066		
exotic			0.237	0.066
Domestic cat (73)	0.143	0.005		
exotic			0.242	0.057
edge			−0.205	0.105
Opossum (79)	0.079	0.013		
edge			−0.281	0.013

[a] *Independent variables are distance to urban edge, native shrub cover, and total exotic cover. Independent variables with* $p < 0.15$ *were included in the final regression models. For each species, stations were included only in analyses for those fragments where the species was detected.*

[b] *No independent variables were retained in the regression model* ($p > 0.15$)*; n.s., not significant.*

area of study sites occupied by each carnivore species, weighted by the standardized track index of each species at each site, was not significant ($r = -0.392$, $p = 0.233$) (Fig. 4a). Spotted skunks, long-tailed weasels, and badgers, however, appeared to be outliers to an otherwise positive relationship between body size and average area of sites occupied. When these three species were excluded from the regression, the positive relationship was significant ($r = 0.725$, $p = 0.042$). Body mass was also positively related to typical home-range sizes (Fig. 4b: $r = 0.720$, $p = 0.012$) and negatively related to typical population densities (Fig. 4c: $r = -0.705$, $p = 0.015$) recorded for these species (Table 4).

Discussion

Landscape Heterogeneity and Carnivore Populations

Fragment area and isolation were the two strongest landscape predictors of predator distribution and abundance. Badgers, long-tailed weasels, spotted skunks, mountain lions, bobcats, and coyotes appear to be the species most sensitive to fragmentation, with a lower probability of occurrence and relative abundance per unit area in smaller and more isolated habitat patches. In contrast, the probability of occurrence and relative abundance of domestic cats, gray foxes, and opossums tended to decrease with fragment area and increase with fragment isolation. Landscape descriptors had relatively little effect on the distribution and abundance of raccoons and striped skunks. Because some carnivores were fragmentation-sensitive, some fragmentation-enhanced, and some fragmentation-tolerant, landscape variables appear to affect species composition more than species richness.

The probability of occurrence of mountain lions, bobcats, and coyotes declined in sequence as habitat patches became smaller and more isolated (Fig. 1). Because mountain lions, bobcats, and coyotes generally occurred in fragments above some threshold of size and isolation, local extinctions of their populations in a fragmenting landscape appear deterministic and predictable (Brown 1986). Such thresholds also suggest that, depending on the species and the degree of fragmentation, a single large reserve would have a higher probability of supporting populations of these predators than archipelagos of similar but smaller isolates (Soulé & Simberloff 1986). For example, our models predict that the probability of occurrence of bobcats will be low in 10 1-km^2 isolates but higher in a 10-km^2 reserve, and that the probability of occurrence of mountain lions will be low in 10 10-km^2 isolates but higher in a 100-km^2 reserve (Fig. 1).

Unlike true islands, habitat patches are part of a landscape mosaic, and the presence of a given species in a patch may be a function not only of patch size and isolation, but also of how the species perceives the intervening matrix (Andren 1994; Rosenblatt et al. 1999). In previous studies in this system, fragment age and area were the most important landscape predictors of the distribution and abundance of native plants (Alberts et al. 1993), scrub-breeding birds (Soulé et al. 1988; Crooks et al. 2001), rodents (Bolger et al. 1997), and invertebrates

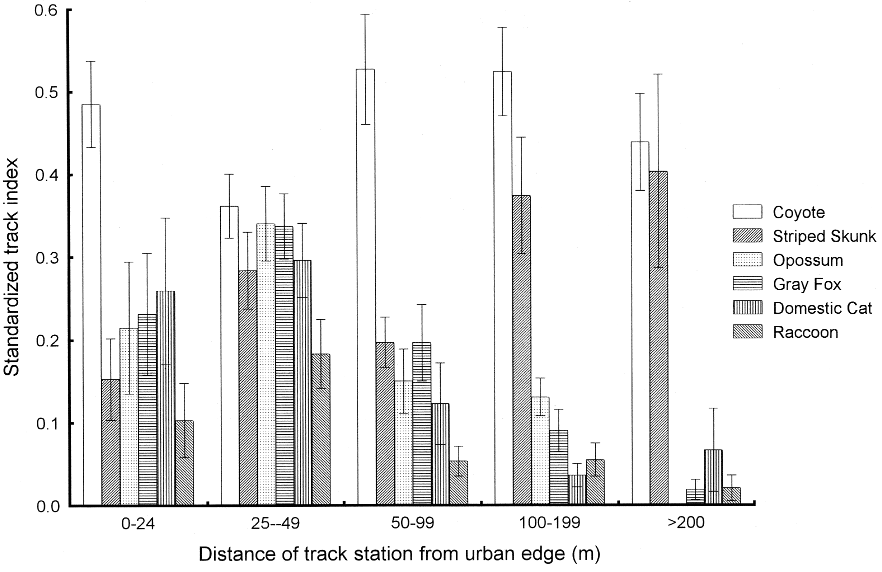

Figure 3. Track indices of carnivore species within urban habitat fragments as a function of the distance of the station from the urban edge. Track indices are standardized for each species.

(Suarez et al. 1998; Bolger et al. 2000). With limited exceptions, isolation effects were absent for these species, likely due to their strict habitat requirements and low dispersal capabilities (Soulé et al. 1992). For these taxa, little to no dispersal across developed areas resulted in complete isolation once fragmentation had occurred, with the fragments operating as true islands immersed within a relatively inhospitable matrix. My results also indicate that fragment isolation was not a strong predictor of the distribution and abundance of human-tolerant mesopredators, although the causal mechanisms differed. Unlike many native scrub-breeding birds, rodents, and invertebrates, mesopredator species such as raccoons, striped skunks, opossums, and domestic cats move through and reside within developed areas and thus perceive the urban matrix as somewhat permeable. High rates of movement through the matrix within which fragments are embedded should also minimize the effects of fragment isolation.

Local Heterogeneity and Carnivore Populations

Within the urban fragments, exotic cover and distance to the urban edge were the strongest local predictors of carnivore distribution and abundance. These two variables were correlated, with more exotic cover and less native shrub cover closer to the urban edge. Previous studies have found that scrub-breeding birds (Soulé et al. 1988), rodents (Bolger et al. 1997), and invertebrates (Suarez et al. 1998; Bolger et al. 2000) require native vegetation to persist in these fragments. Unlike many of these species, however, the mammalian carnivores detected in the habitat fragments are resource generalists that likely benefit from the supplemental food resources

Table 4. Ecological characteristics of mammalian carnivores detected in coastal southern California.[a]

Species	*Weight (kg)*	*Home range (km^2)*	*Density (km^2)*	*Reference*
Mountain lion	69.5 (36.0–103.0)	492 (112–829)	0.027 (0.005–0.048)	Beier & Barrett 1993; Nowak 1999
Coyote	13.5 (7.0–20.0)	5.69 (0.66–11.96)	0.3 (0.2–0.4)	Nowak 1999; Sauvajot et al. 2000
Bobcat	9.7 (4.1–15.3)	2.94 (0.24–5.63)	1.34 (1.15–1.53)	Lembeck 1986; Nowak 1999
Badger	8.0 (4–12)	2.0 (1.6–2.4)	2.70 (0.39–5.0)	Messick 1987; Nowak 1999
Raccoon	7.0 (2.0–12.0)	0.52 (0.39–0.65)	11.2 (2.3–20.0)	Nowak 1999
Gray fox	4.4 (1.8–7.0)	0.69 (0.22–1.87)	5.2 (0.4–10.0)	Nowak 1999; Riley 1999
Domestic cat[b]	3.9 (3.3–4.5)	0.40 (0.001–3.80)	150 (2–500)	Barratt 1997; Nowak 1999
Opossum	3.8 (2.0–5.5)	0.20 (0.05–2.54)	26 (2–116)	Nowak 1999
Striped skunk	1.6 (0.7–2.5)	0.21 (0.11–0.37)	3.3 (1.8–4.8)	Nowak 1999
Spotted skunk	0.6 (0.2–1.0)	0.49 (0.34–0.65)	24.4 (8.8–40)	Crooks & Van Vuren 1995; Kinlaw 1995; Nowak 1999
Long-tailed weasel	0.2 (0.09–0.34)	0.62 (0.04–1.20)	19.4 (0.38–38)	Nowak 1999

[a] *Estimates of body size, home range, and population density vary considerably (Nowak 1999). Values are typical averages and ranges (in parentheses). If no average estimate was provided, median values, calculated from the ranges, are presented. Body-mass estimates were taken from Nowak (1999). Where available, home ranges and population densities were taken from studies conducted in California.*
[b] *Estimates include studies from suburban, urban, rural, and island cat populations.*

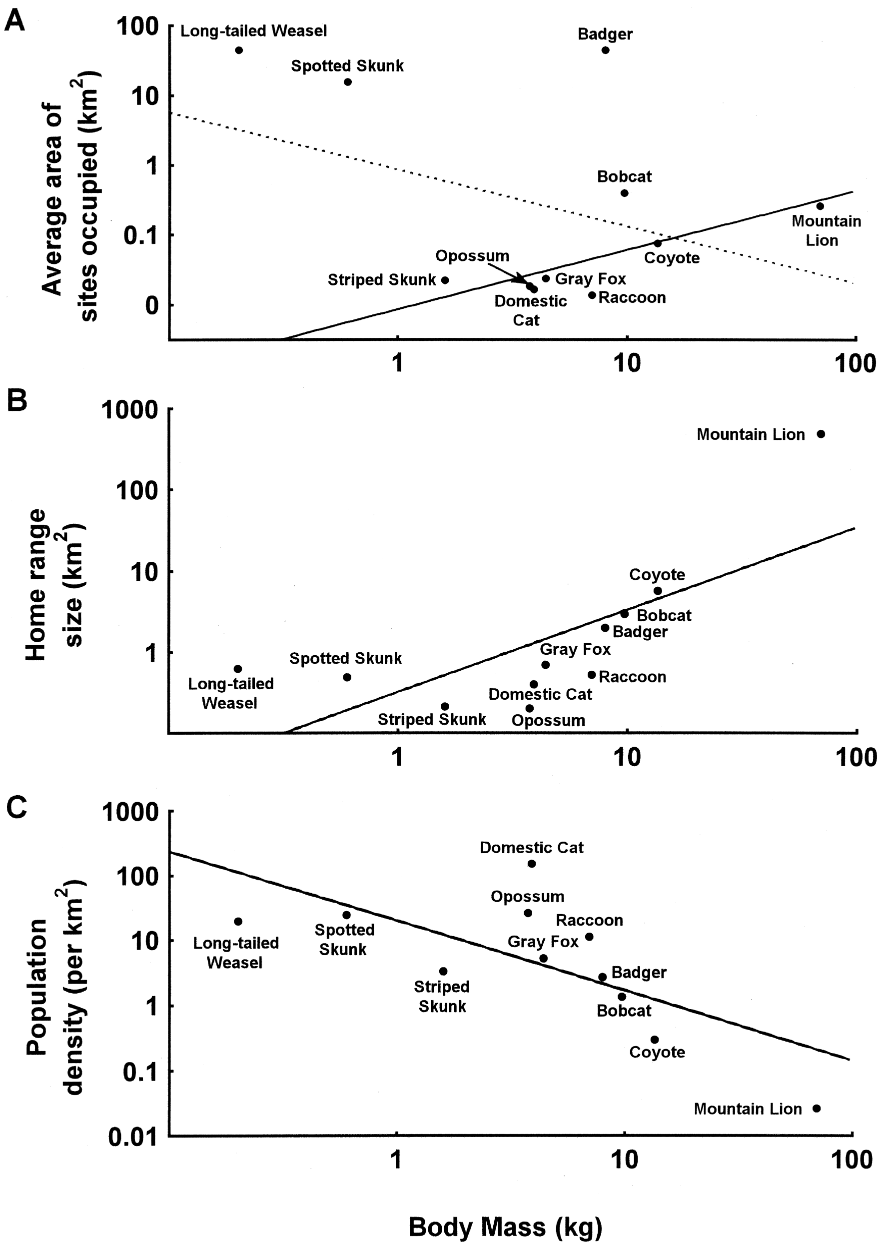

Figure 4. Relationship between log body mass and (a) log average area of sites occupied by mammalian carnivores, weighted by the relative abundance of each species at each site, (b) log home-range size (r = *0.720,* p = *0.012; see Table 4 for values), and (c) log population density* (r = *−0.705,* p = *0.015; see Table 4 for values). Dotted line in (a) is the least-squares regression fit including all species in the analysis* (r = *−0.392,* p = *0.233), and the solid line in (a) is the regression excluding spotted skunks, long-tailed weasels, and badgers* (r = *0.725,* p = *0.042).*

(e.g., garden fruits and vegetables, garbage, direct feeding by humans) associated with residential developments. As a result, the carnivore visitation rate actually increased at sites with more exotic cover and closer to the urban edge, a pattern determined largely by the increased abundance of fragmentation-enhanced mesopredators (gray foxes, opossums, and domestic cats) at edge sites within habitat fragments. Although some carnivores within the habitat fragments seem tolerant of disturbance, these fragments have already lost an entire suite of predator species, including mountain lions, bobcats, spotted skunks, long-tailed weasels, and badgers. Furthermore, the habitat fragments are relatively small (<100 ha), so the most "interior" sites within the fragments are still relatively near (<250 m) urban edges.

Unlike true islands, "edge effects" that emanate from the human-dominated matrix can increase the extinction probability of isolated populations (Murcia 1995; Woodroffe & Ginsberg 1998). Human-tolerant mesopredators in southern California represent such an edge effect. They occur within the developed matrix, are more abundant along the edges of habitat fragments, and are effective predators on birds, bird nests, and other vertebrates in this system and elsewhere (Crooks & Soulé 1999). Several factors likely account for increased numbers and activity of mesopredators in disturbed landscapes. Residential developments represent suitable habitat for some mesopredator species whose distributions are closely associated with human-dominated landscapes (Donovan et al. 1997). In addition to habitat suitability, however, dominance interactions between carnivores affect mesopredator populations. When large, dominant predators disappear in fragmented systems, smaller, subordinant predators can subsequently undergo an ecological release, a pattern termed mesopredator release (Soulé et al. 1988; Crooks & Soulé 1999). In the San Diego habitat fragments, Crooks and Soulé (1999) found that lower visitation rates of coyotes in small, isolated remnants resulted in elevated numbers and activity of urban mesopredators, even after statistically controlling for potential confounding variables such as fragment area, age, and isolation. Mesopredator species therefore appear to be ecologically released by fragmentation not only because they can adapt well to urban environments, but also because such sites may provide refugia from dominant predators.

All Carnivores Are Not Created Equal

Although they are generally considered part of the same ecological guild, I found that carnivores were heterogeneous in their sensitivities to landscape and local fragmentation variables. As predicted, body-size differences partially accounted for this heterogeneity in response. Body mass was positively related to typical home-range sizes (Fig. 4b) and negatively related to typical population densities (Fig. 4c) recorded for these species, patterns consistent with those observed among mammals (Lindstedt et al. 1986). Due to their wide ranges and low densities, larger-bodied carnivores generally required larger areas (Fig. 4a), eventually disappearing in habitat fragments that were not connected by movement corridors. Obvious exceptions to the allometry of body size and fragmentation sensitivity, however, were spotted skunks, long-tailed weasels, and badgers, small- to medium-bodied species that exhibit relatively small home ranges and high population densities but that were detected only in the largest habitat blocks. Unlike the generalist urban mesopredators, these relatively specialized mustelids tend to be primarily carnivorous and somewhat restricted in their habitat preferences (Nowak 1999). Such specializations likely contribute to their patchy distribution in coastal southern California and increase their vulnerability to environmental disturbances. Clearly, in addition to body size, other ecological traits such as diet, resource specialization, social structure, and behavior contribute to species-specific responses to fragmentation effects.

Differential sensitivities to fragmentation can be useful criteria when focal species are chosen for ecological research and conservation planning. Mammalian carnivores can be excellent focal organisms with which to evaluate the degree of functional landscape-level connectivity, because they are area-dependent species that require movement corridors for persistence (Beier 1993; Noss et al. 1996; Soulé & Terborgh 1999). The choice of appropriate carnivore focal species, however, depends on the scale or intensity of fragmentation in an area and the corresponding responses of carnivore populations to fragmentation effects at that scale. As Figs. 1 and 2 make evident, the scale of landscape-level connectivity in southern California varies widely, ranging from small, isolated urban remnants to large, intact habitat blocks.

At one extreme of the connectivity scale are the highly fragmented landscapes of urban coastal southern California (e.g., patch size <1 km^2; Fig. 1a). Coyotes and urban mesopredators can be useful focal species with which to understand the effects of fragmentation at this scale. Fragmentation-enhanced predators such as opossums and domestic cats can function as direct, positive indicators of environmental disturbances associated with urban development, edge effects, and the invasion of exotic predators and competitors into natural systems. Coyotes have also persisted in developed areas in southern California. The remarkable behavioral plasticity of coyotes and their ability to succeed in disturbed areas limits their utility as an indicator of connectivity across much of coastal southern California. Nevertheless, coyote occupancy, residency, and relative abundance declined with fragment area and isolation, to the point of local extinctions of coyote populations in the smallest, most isolated urban remnants. Coyotes can therefore serve as useful indicators of functional connectivity in highly fragmented areas, particularly those sites that have already lost more vulnerable predators such as bobcats and mountain lions (Figs. 1 & 2). Furthermore, the ecologically pivotal role of coyotes (Crooks & Soulé 1999) warrants their inclusion in research and conservation plans, particularly in regions with active predator-control programs.

Mountain lions are situated at the opposite end of the connectivity scale (e.g., patch size >100 km^2; Fig. 1a) and appear extremely sensitive to the loss and fragmentation of habitat. The large body size and solitary behavior of mountain lions translate to large home ranges and low population densities (Table 4). Therefore, many of the isolated habitat remnants in urban southern California are likely too small and too isolated to permanently support any resident lion populations (Figs. 1 & 2) (see also Beier 1993). Consequently, mountain lions or other large, apex predators may not be the most effective indicator species with which to evaluate the degree of functional landscape-level connectivity in moderately to highly fragmented landscapes. The mountain lion's requirement for a large home range and its sensitivity to environmental perturbations, however, can make it a valuable focal species in larger, more intact habitat blocks (Beier 1993).

Finally, bobcats were intermediate in their sensitivity to fragmentation, a degree of sensitivity commensurate to the scale of fragmentation across much of coastal southern California (e.g., 1 km^2 <patch size < 100 km^2; Fig. 1a). Bobcats were less sensitive to disturbance than mountain lions, which seldom occurred in fragmented areas, yet were more sensitive than coyotes and mesopredators, which were detected in even small urban habitat fragments. Bobcats are generally solitary and are strictly carnivorous (Nowak 1999), resulting in low densities and in resource specializations that likely increase their probability of local extinction. Landscape connectivity appears to be the key to the persistence of bobcat populations in developing landscapes. They can persist in fragmented habitats, but, as my results suggest, only in those landscapes with adequate movement linkages to larger natural areas. The status of bobcat populations is therefore a valuable indicator of the degree of functional, landscape-level connectivity across much of the fragmented landscapes of coastal southern California. In other systems, the choice of indicator species will require information on the level of fragmentation and connectivity in that region and how species respond to fragmentation effects at that scale.

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Literature Cited

Alberts, A. C., A. D. Richman, D. Tran, R. Sauvajot, C. McCalvin, and D. T. Bolger. 1993. Effects of habitat fragmentation on native and exotic plants in southern California coastal scrub. Pages 103–110 in J. E. Keeley, editor. Interface between ecology and land development in southern California. Southern California Academy of Sciences, Los Angeles.

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos **71:**355–366.

Barratt, D. G. 1997. Home range size, habitat utilisation and movement patterns of suburban and farm cats *Felis catus.* Ecography **20:** 271–280.

Beier, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. Conservation Biology **7:**94–108.

Beier, P., and R. H. Barrett. 1993. The cougar in the Santa Ana Mountain range, California. Final report. Orange County Mountain Lion Study, University of California, Berkeley.

Belovsky, G. E. 1987. Extinction models and mammalian persistence. Pages 35–58 in M. E. Soulé, editor. Viable populations for conservation. Cambridge University Press, Cambridge, Massachusetts.

Bolger, D. T., A. C. Alberts, R. M. Sauvajot, P. Potenza, C. McCalvin, D. Tran, S. Mazzoni, and M. E. Soulé. 1997. Response of rodents to habitat fragmentation in coastal southern California. Ecological Applications **7:**552–563.

Bolger, D. T., A. V. Suarez, K. R. Crooks, S. A. Morrison, and T. J. Case. 2000. Arthropod diversity in coastal sage scrub fragments: area, age, and edge. Ecological Applications **10:**1230–1248.

Brown, J. H. 1986. Two decades of interaction between the MacArthur-Wilson model and the complexities of mammalian distributions. Biological Journal of the Linnean Society **28:**231–251.

Conner, M. C., R. F. Labisky, and D. R. Progulske. 1983. Scent-station indices as measures of population abundance for bobcats, raccoons, gray foxes, and opossums. Wildlife Society Bulletin **11:**146–152.

Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature **400:**563–566.

Crooks, K. R., and D. Van Vuren. 1995. Resource utilization by two insular endemic carnivores, the island fox and island spotted skunk. Oecologia **104:**301–307.

Crooks, K. R., A. V. Suarez, D. T. Bolger, and M. E. Soulé. 2001. Extinction and recolonization of birds on habitat islands. Conservation Biology **15:**159–172.

Dobson, A. P., J. P. Rodriguez, W. M. Roberts, and D. S. Wilcove. 1997. Geographic distribution of endangered species in the United States. Science **275:**550–553.

Donovan, T. P., W. Jones, E. M. Annand, and F. R. Thompson III. 1997. Variation in local-scale edge effects: mechanisms and landscape context. Ecology **78:**2064–2075.

Hinsley, S. A., P. E. Bellamy, I. Newton, and T. H. Sparks. 1996. Influences of population size and woodland area on bird species distributions in small woods. Oecologia **105:**100–106.

Jameson, E. W., Jr., and H. J. Peeters. 1988. California mammals. University of California Press, Berkeley.

Johst, K., and R. Brandl. 1997. Body size and extinction risk in a stochastic environment. Oikos **78:**612–617.

Kent, M., and P. Coker. 1992. Vegetation description and analysis. CRC Press, Boca Raton, Florida.

Kinlaw, A. 1995. *Spilogale putorius.* Mammalian Species **511:**1–7.

Lembeck, M. 1986. Long term behavior and population dynamics of an unharvested bobcat population in San Diego County. Pages 305–310 in S. D. Miller and D. D. Everett, editors. Cats of the world: biology, conservation, and management. National Wildlife Federation, Washington, D.C.

Lindstedt, S. L., B. J. Miller, and S. W. Buskirk. 1986. Home range, time and body size in mammals. Ecology **67:**413–418.

Linhart, S. B., and F. F. Knowlton. 1975. Determining the relative abundance of coyotes by scent station lines. Wildlife Society Bulletin **3:** 119–124.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

McCaull, J. 1994. The Natural Community Conservation Planning Program and the coastal sage scrub ecosystem of southern California. Pages 281–292 in R. E. Grumbine, editor. Environmental Policy and Biodiversity. Island Press, Washington, D.C.

Mead, R. 1988. The design of experiments: statistical principles for practical applications. Cambridge University Press, Cambridge.

Messick, J. P. 1987. North American badger. Pages 584–597 in M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch, editors. Wild furbearer management and conservation in North America. Ontario Ministry of Natural Resources, Ontario, Canada.

Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology and Evolution **10:**58–62.

Noss, R. F., H. B. Quigley, M. G. Hornocker, T. Merrill, and P. C. Paquet. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. Conservation Biology **10:**949–963.

Nowak, R. M. 1999. Walker's mammals of the world. 6th edition. The Johns Hopkins University Press, Baltimore, Maryland.

Riley, S. P. D. 1999. Spatial organization, food habits and disease ecology of bobcats (*Lynx rufus*) and gray foxes (*Urocyon cinereoargenteus*) in national park areas in urban and rural Marin County, California. Ph.D. dissertation. University of California, Davis.

Rosenblatt, D. L., E. J. Heske, S. L. Nelson, D. M. Barber, M. A. Miller, and B. MacAllister. 1999. Forest fragments in east-central Illinois: islands or habitat fragments for mammals? American Midland Naturalist **141:**115–123.

Sargeant, G. A., D. H. Johnson, and W. E. Berg. 1998. Interpreting carnivore scent-station surveys. Journal of Wildlife Management **62:** 1235–1245.

Sauvajot, R. M., E. C. York, T. K. Fuller, H. S. Kim, D. S. Kamradt, and R. K. Wayne. 2000. Distribution and status of carnivores in the Santa Monica Mountains, California: preliminary results from radiotelemetry and remote camera surveys. Pages 113–123 in J. E. Keeley, M. Baer-Keeley, and C. J. Fotheringham, editors. Open-file report 00-62. U. S. Geological Survey, Sacramento.

Soulé, M. E., and D. Simberloff. 1986. What do genetics and ecology tell us about the design of nature reserves? Biological Conservation **35:**19–40.

Soulé, M. E., and J. Terborgh. 1999. Continental conservation: scientific foundations of regional reserve networks. Island Press, Washington, D.C.

Soulé, M. E., D. T. Bolger, A. C. Alberts, R. Sauvajot, J. Wright, M. Sorice, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. Conservation Biology **2:**75–92.

Soulé, M. E., A. C. Alberts, and D. T. Bolger. 1992. The effects of habitat fragmentation on chaparral plants and vertebrates. Oikos **63:**39–47.

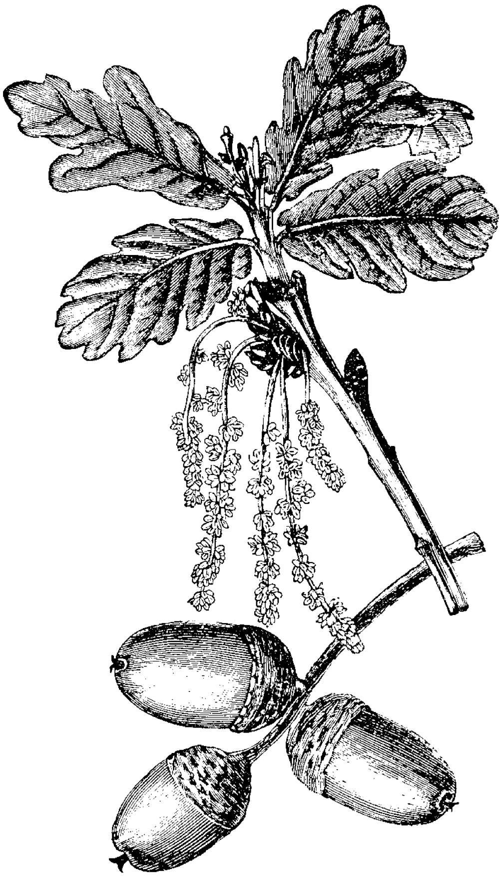
Stuart-Oaten, A. 1995. Rules and judgements in statistics: three examples. Ecology **76:**2001–2009.

Suarez, A. V., D. T. Bolger, and T. J. Case. 1998. The effects of habitat fragmentation and invasion on the native ant community in coastal southern California. Ecology **79:**2041–2056.

Tabachnick, B. G., and L. S. Fidell. 1996. Using multivariate statistics. 3rd edition. HarperCollins College Publishers, New York.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, E. Losos. 1998. Quantifying threats to imperiled species in the United States. Bioscience **48:**607–615.

Woodroffe, R., and J. R. Ginsberg. 1998. Edge effects and the extinction of populations inside protected areas. Science **280:**2126–2128.



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Effects of habitat loss and fragmentation on amphibians: A review and prospectus

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ABSTRACT

Habitat loss and fragmentation are among the largest threats to amphibian populations. However, most studies have not provided clear insights into their population-level implications. There is a critical need to investigate the mechanisms that underlie patterns of distribution and abundance. In order to understand the population- and species-level implications of habitat loss and fragmentation, it is necessary to move from site-specific inferences to assessments of how the influences of multiple factors interact across extensive landscapes to influence population size and population connectivity. The goal of this paper is to summarize the state of knowledge, identify information gaps and suggest research approaches to provide reliable knowledge and effective conservation of amphibians in landscapes experiencing habitat loss and fragmentation. Reliable inferences require attention to species-specific ecological characteristics and their interactions with environmental conditions at a range of spatial scales. Habitat connectivity appears to play a key role in regional viability of amphibian populations. In amphibians, population connectivity is predominantly effected through juvenile dispersal. The preponderance of evidence suggests that the short-term impact of habitat loss and fragmentation increases with dispersal ability. However, species with limited dispersal abilities are likely to be equally imperiled by habitat loss and fragmentation over longer time periods. Rigorous understanding of the effects of habitat loss and fragmentation on amphibians will require species-specific, multi-scale, mechanistic investigations, and will be benefit from integrating large empirical field studies with molecular genetics and simulation modeling. Molecular genetic methods are particularly suited to quantifying the influences of habitat structure across large spatial extents on gene flow and population connectivity. Conservation strategies would benefit by moving from generalizations to species and process specific recommendations and by moving from site-specific actions to implementing conservation plans at multiple scales across broad landscapes.

1. Introduction

1.1. *The extinction crisis and amphibians*

Earth is facing the largest mass extinction in 65 million years (Lawton and May, 1995; Vitousek et al., 1997; Wilson, 1999; Myers and Knoll, 2001; Balmford et al., 2003). Current global extinction rates for animals and plants are estimated to be up to 1000 times higher than the background rate in the fossil record (Wilson, 1999; Baillie et al., 2004). Vertebrate animal taxa are disappearing at disproportionately high rates, and amphibians are the group with the highest proportion of

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species threatened with extinction (Stuart et al., 2004; Beebee and Griffiths, 2005). The 2004 IUCN red list of threatened and endangered species identifies one in three of the world's amphibian species as threatened with extinction (Baillie et al., 2004).

1.2. *Vulnerability of amphibians*

The apparent vulnerability of amphibians (Pechmann et al., 1991; Houlahan et al., 2000; Kiesecker et al., 2001; Baillie et al., 2004) may be due to a complex of factors, including: (1) relatively low vagilities, which amplifies the effects of habitat fragmentation (Sinsch, 1990; Gibbs, 1998; deMaynadier and Hunter, 2000; Bowne and Bowers, 2004), (2) high vulnerability to death when moving across roads and through inhospitable terrain, which depresses population growth rates (Fahrig et al., 1995; Carr and Fahrig, 2001; Carr et al., 2002), (3) often narrow habitat tolerances, which exacerbates the effects of habitat loss, degradation, and edge effects (Findlay and Houlahan, 1997; Semlitsch, 2000; Houlahan and Findlay, 2003), and (4) high vulnerability to pathogens, invasive species, climate change, increased ultraviolate-B exposure and environmental pollution (Pounds et al., 1999; Broomhall et al., 2000; Kiesecker et al., 2001; Blaustein et al., 2000; Hecnar, 1995; Bridges and Semlitsch, 2000; Davidson et al., 2001; Stuart et al., 2004).

1.3. *Importance of habitat loss and fragmentation*

Habitat loss and fragmentation contribute directly to most of these threats (Carr and Fahrig, 2001; Bowne and Bowers, 2004; Houlahan and Findlay, 2003). Recent research has provided information on the relationships between certain amphibians and certain attributes of habitat loss and fragmentation, and has clearly implicated the effects of habitat fragmentation on juvenile dispersal as one of the key issues in the conservation of pond breeding amphibians (Sjögren, 1991; Sinsch, 1992; Sjögren-Gulve, 1994; Vos and Chardon, 1998). However, most studies of the influences of habitat loss, fragmentation, or related mortality risks have not provided clear insights into the population-level implications of these impacts (Carr et al., 2002). There is a clear need for studies that focus on the mechanisms that drive patterns of distribution and abundance (Marsh and Trenham, 2001; Bowne and Bowers, 2004).

1.4. *Moving from sites to landscapes; ponds to populations*

In order to understand the population-level implications of habitat loss and fragmentation, it is necessary to move from site-specific inferences to assessments of how multiple factors interact across large spatial extents to influence population size and population connectivity (Ruggiero et al., 1994; McGarigal and Cushman, 2002; Bowne and Bowers, 2004). Non-spatial studies conducted at local scales do not provide a basis for inferences at the landscape or regional level (McGarigal and Cushman, 2002). There is often a gross mismatch between the scale of ecological research and population-level responses (Kareiva and Anderson, 1988; Ruggiero et al., 1994). For example, correlations between organism abundance and the area of various landcover types within a certain distance of a breeding pond does not provide information necessary to infer how habitat patterns interact with the spatial distribution of breeding ponds to influence distribution and abundance. Landscape-level studies that represent the spatial patterns of the environment in a manner relevant to the organisms of question, and that address species-specific movement and abundance characteristics are essential to extend fine-scale species environment relationships to the population-level (McGarigal and Cushman, 2002).

1.5. *Purpose and goals*

The overall goal of this paper is to summarize the state of knowledge, identify information gaps and suggest approaches to provide reliable knowledge and effective conservation of amphibians in landscapes experiencing habitat loss and fragmentation. The paper is divided into four major components. The first is a review of current knowledge about relationships between habitat loss and fragmentation and pond-breeding amphibian populations at landscape and regional scales. Using this review as context, the second section identifies some important information gaps and research needs. Next, I propose several research approaches that may be effective at filling these information gaps. Then, I suggest several ideas to link research more effectively to conservation, and suggest interim conservation strategies.

2. The state of knowledge

2.1. *Habitat area in uplands*

Relatively few landscape-level studies of amphibian density and movement have been conducted (Houlahan et al., 2000; McGarigal and Cushman, 2002). Most existing studies have focused on relationships between forest cover and species occurrence. These have shown positive relationships between amphibian populations and area of forest in the surrounding landscape (Dupuis and Steventon, 1999; Knutson et al., 1999; Guerry and Hunter, 2002; Houlahan et al., 2000; Trenham and Shaffer, 2005), and negative relationships with urban development (Delis et al., 1996) and roads (Fahrig et al., 1995; Carr et al., 2002). Studies of landscape composition effects have found relationships between forest cover and amphibian presence at spatial scales ranging from 100 m to over 3000 m radii (Hecnar and M'Closkey, 1997; Knutson et al., 1999; Lehtinen et al., 1999; Guerry and Hunter, 2002; Houlahan et al., 2000; Trenham and Shaffer, 2005). Several studies also note a general pattern of increased species richness with increasing forest cover (Gibbs, 1998; Kolozsvary and Swihart, 1999; Houlahan et al., 2000).

Despite these generalizations, reliable inferences about habitat area effects require attention to species-specific ecological characteristics and their interactions with environmental conditions at a range of spatial scales. Species-specific characterization of habitat is essential if scientists are to evaluate the effects of habitat loss on populations. For example, the suggestion that forest cover in the landscape benefits amphibians may not apply to species that are fully aquatic or that depend on nonforested upland habitat. Also, some populations of amphibians have been enhanced by human construction of ponds and wetlands in areas where breeding sites were previously limited, such as arid environments. In addition, the location and slope of critical thresholds in habitat amount are species specific, and related to reproductive potential, dispersal ability, home range size, habitat specificity, and other characteristics (Monkkonen and Reunanen, 1999; Fahrig, 2001). Thus, it is essential to explicitly link the habitat tolerances of a species to the extent and pattern of those habitats in the landscape if one is to produce reliable inferences about relationships between habitat area and species distributions.

2.2. *Habitat isolation*

Several studies have suggested that habitat area is often more important than habitat configuration (Fahrig, 1998, 2003; Cushman and McGarigal, 2004). The evidence for amphibians is equivocal on this question. Guerry and Hunter (2002) found positive associations between nine amphibian species, area of forested habitat and proximity of ponds to forest habitat. Seven of the nine species were associated with forest area. Three of the nine were associated with pond-forest adjacency. This indicates that habitat area and isolation are both important, and that the degree of importance is a species-specific property which likely reflects a combination of life-history and behavioral characteristics.

A growing body of work suggests that roads can have substantial negative effects on amphibian persistence (Vos and Chardon, 1998; Carr and Fahrig, 2001). Habitat fragmentation by roads and other barriers decreases dispersal (Gibbs, 1998; deMaynadier and Hunter, 2000), increases mortality (Fahrig et al., 1995; Carr and Fahrig, 2001) and reduces genetic diversity (Reh and Seitz, 1990). Habitat fragmentation leads to reduced patch size patches, increased patch isolation, and increased risk of demographic, stochastic and genetic events. This increases extinction risk by reducing demographic and genetic input from immigrants and reducing the chance of recolonization after extinction (Lande, 1988; Sjögren-Gulve, 1994).

2.3. *Connectivity: a key to persistence*

A number of researchers have proposed that habitat connectivity is a key to regional viability of amphibian populations (Hecnar and M'Closkey, 1996; Semlitsch et al., 1996; Semlitsch and Bodie, 1998; Skelly et al., 1999; Marsh and Trenham, 2001; Rothermel and Semlitsch, 2002). Amphibians generally have lower rates of movement per generation than invertebrates, mammals or reptiles (Bowne and Bowers, 2004). Low recruitment of dispersing individuals probably plays a major role in decline and extinction of amphibian populations in fragmented landscapes (Sjögren, 1991; Sinsch, 1992; Sjögren-Gulve, 1998; Vos and Chardon, 1998; Bulger et al., 2003). Breeding sites lacking connectivity to suitable terrestrial habitat may be population sinks due to high mortality of juveniles during emigration (Rothermel, 2004). A number of studies have indicated that populations may decline if immigration is prevented (Brown and Kodric-Brown, 1977; Harrison, 1991) and may not be recolonized following a local extinction (Semlitsch and Bodie, 1998). Connectivity seems to be of particular importance as even in unfragmented landscapes, amphibian populations experience relatively frequent local extinction and turnover (Edenhamn, 1996; Hecnar and M'Closkey, 1996; Alford and Richards, 1999; Trenham et al., 2003). Thus, dispersal is critical for recolonization of local populations and maintenance of regional populations (Hecnar and M'Closkey, 1996; Semlitsch et al., 1996; Skelly et al., 1999).

2.4. *Role of juvenile dispersal in population connectivity*

In amphibians, population connectivity is predominantly effected through juvenile dispersal (Madison, 1997; Preisser et al., 2001; Guerry and Hunter, 2002; Rothermel, 2004). Many studies have indicated that post-metamorphic dispersal contributes more to regional persistence than does adult dispersal (Sinsch, 1992, 1997; Sinsch and Seidel, 1995). For example, Preisser et al. (2001) found that adults of a variety of amphibian species move up to 125 m from breeding ponds, while juvenile *Ambystoma* sp. salamanders dispersed up to 670 m, and Wood frog (*Rana sylvatica*) over 1000 m. From this they concluded that juvenile dispersal is essential for landscape connectivity for these species. Other studies have reached similar conclusions based on the relatively small movement distances and philopatry of adults and relatively large dispersal distances of juveniles (Breden, 1987; Berven and Grudzien, 1990).

2.5. *Effects of fragmentation on population connectivity*

There are several important implications of habitat fragmentation on species persistence. First, a number of studies have shown that high levels of post-metamorphic survival are often required to maintain local populations. For example, one study found that survival to first reproduction had to exceed 18% in order to maintain local populations of the California tiger salamander (*Ambysotma californiense*) (Trenham et al., 2000). However, as they report survival to maturity of less than 5%, they conclude their study population is a sink that would be doomed to extinction in the absence of substantial immigration. In addition, a population model developed for marbled salamander (*Ambystoma opacum*) suggested that post-metamorphic survival had to exceed 70% to maintain local populations (Taylor and Scott, 1997). Second, a number of studies have shown substantial reductions in dispersal success and juvenile survival in fragmented landscapes. For example, Rothermel (2004) found an average of only 9% of juvenile spotted salamander (*Ambystoma maculatum*) released 50 m from a forest edge survived their initial migration to forest. Habitat loss and fragmentation can substantially reduce the abilities of juvenile amphibians to disperse across landscapes and the resulting reductions in post-metamorphic survival and population connectivity can threaten viability.

Recently, a number of studies have investigated the relationships between landscape structure and amphibian dispersal with experimental methods. Both spotted salamanders and wood frogs avoid crossing fields, pastures, clearcuts, lawns, and roads (Windmiller, 1996; Gibbs, 1998; deMaynadier and Hunter, 1999; Rothermel and Semlitsch, 2002; Regosin et al., 2003; Marsh et al., 2004). Wood frogs have also been shown to orient toward forest (deMaynadier and Hunter, 1999). Rothermel and Semlitsch (2002) studied the orientation and movement of several amphibian species in open field and forest environments. They found that orientation of spotted salamander and wood frog is biased toward forest. Spotted salamanders moved three times as far into forest as into fields (Rothermel and Semlitsch, 2002). Lower recapture rates in fields reflected high mortality rates due to desiccation and predation. Also, avoidance of open-canopy habitats by juvenile American toads (*Bufo americanus*) indicates that predictions of dispersal behavior based on adult habitat use may be misleading (Rothermel and Semlitsch, 2002). Rothermel (2004) conducted an experimental study of movement of spotted salamanders and American toads in grass fields at distances of 5 or 50 m from a forest edge. Less than 15% of salamanders and toads released 50 m from the forest edge reached forest, suggesting that few juvenile amphibians would be able to migrate greater distances across pastures (Rothermel, 2004). The authors conclude that fields are substantially resistant, and thus forest fragmentation reduces dispersal rates for these species (Rothermel and Semlitsch, 2002; Marsh et al., 2004; Rothermel, 2004).

Recent research has also suggested that the short-term impacts of habitat fragmentation often increase both with population size and dispersal ability, but particularly strongly with increasing dispersal ability (Gibbs, 1998; Newcomb Homan et al., 2004). This pattern is opposite to what many researchers expect on theoretical grounds, namely that species with larger populations and larger dispersal abilities will be less impacted by fragmentation due to their relatively greater abilities to disperse between breeding sites in fragmented landscapes. For example, in a study of five amphibian species across a gradient of habitat loss, Gibbs (1998) found that organisms with low dispersal rates had better persistence in landscapes with low habitat area. This effect has also been seen in comparison of wood frog and spotted salamander habitat occupancy (Newcomb Homan et al., 2004). A possible explanation is that greater dispersal ability results in greater mortality risk in fragmented landscapes. Carr and Fahrig (2001) suggest that highly vagile organisms may be at a disadvantage in landscapes with roads because of increased likelihood of mortality. An example of this may be the response of red-spotted newt (*Notophthalmus viridescens*) in fragmented landscapes (Guerry and Hunter, 2002). Red-spotted newts appear to have high sensitivity to habitat loss and forest fragmentation. In one study, they were the first species to disappear from a fragmented landscape (Gibbs, 1998). The terrestrial stage of red-spotted newts may last seven years (Forester and Lykens, 1991) in which they may travel long distances from the natal pond (Gill, 1978). Declines in fragmented landscapes are probably often related to elevated losses of juveniles in the terrestrial period (Gibbs, 1998). The preponderance of evidence suggests that the short-term impact of habitat loss and fragmentation increases with dispersal ability. In a fragmented landscape individuals of species with large dispersal abilities will generally encounter roads and other anthropogenic barriers at higher rates than less vagile species. This will tend to increase mortality rates for these species. The combined effects of roads and landcover may result in high rates of death among dispersing juveniles, which can imperil local and regional populations by decreasing recruitment (Sinsch, 1992, 1997; Sinsch and Seidel, 1995).

It appears that species with large dispersal abilities and those with relatively small dispersal abilities are both threatened by habitat loss and fragmentation, but in different ways. Those with large dispersal abilities are vulnerable to elevated dispersing mortality, which appears sufficient to lead to local extinctions (Hecnar and M'Closkey, 1996; Semlitsch et al., 1996; Skelly et al., 1999). However, species with limited dispersal abilities are likely to be equally imperiled by habitat loss and fragmentation over longer time periods. Once these local populations are isolated by fragmentation they may be ultimately doomed to extinction. Amphibian populations experience relatively frequent extinction and turnover (Edenhamn, 1996; Hecnar and M'Closkey, 1996; Alford and Richards, 1999; Trenham et al., 2003), thus population connectivity is ultimately important even for populations of species that are not directly impacted by habitat loss or elevated mortality risks in dispersing.

3. Challenges to general knowledge

3.1. *Lack of species-level information*

Despite these generalizations, there are several obstacles that must be overcome before scientists will be able to reliably predict population-level responses of specific species to changes in habitat area or isolation. In most parts of world, there is very limited knowledge of the species–environment relationships of amphibians, their responses to habitat loss and fragmentation and the factors controlling population connectivity (Hazell, 2003). Knowledge is still quite rudimentary about the population-level implications of habitat area, edge, isolation, and road mortality relationships. The precision of knowledge about the habitat relationships, life-history, vagility and behavior of most amphibian species is insufficient. Few studies report population level effects of inter-patch movement and few document movement rates (Bowne and Bowers, 2004). In addition, those studies that do measure movements rarely produce results that can be generally applied, as dispersal data are highly sensitive to sampling scheme and landscape characterization (Carr and Fahrig, 2001). Amphibians exhibit a great range of habitat requirements and dispersal abilities (Stebbins and Cohen, 1995). Little is known about the factors influencing dispersal (Rothermel and Semlitsch, 2002; Rothermel, 2004). Information about the dispersal abilities and relative cost or risk of crossing various landcover types is insufficient for most species to reliably model responses to real landscape mosaics. Additional research is needed to determine appropriate threshold distances and cover-class resistance values for migrating amphibians (Rothermel, 2004). Furthermore, the high variability of population sizes through time confounds efforts to isolate mechanisms through correlative means (Alford and Richards, 1999). The combination of variable population sizes and imprecise knowledge of dispersal parameters and habitat tolerances presents a daunting challenge for researchers attempting to infer population-level impacts of habitat loss and fragmentation on amphibians.

Another obstacle to population-level predictions is that few landscape level studies of habitat fragmentation effects have been conducted. McGarigal and Cushman (2002) reviewed 134 papers on habitat fragmentation published between 1995 and 2000. They identified a paucity of experimental studies at the landscape-level. Most studies were patch-based, and poorly replicated or unreplicated, which greatly limits the inferences that can be reliably drawn. Importantly, they identified amphibians and reptiles as the animal taxa most poorly studied, accounting for only 4% of papers on the effects of habitat fragmentation.

4. Research needs

4.1. *Importance of species-specific, multi-scale, mechanistic investigations*

Survival of amphibian populations in fragmented landscapes depends on the interaction between the pattern of roads, landcover types, the distribution of breeding ponds, the population sizes in those ponds and the dispersal characteristics of the species (Fahrig, 1998; Carr and Fahrig, 2001). For example, Porej et al. (2004) emphasize the importance of considering scaling differences among species and the structure of the landscape mosaic when investigating thresholds and minimum patch sizes. Furthermore Marsh and Trenham (2001) suggest that pond isolation is often better explained by details of the structure of terrestrial habitats than the distribution of breeding habitats in that landscape, and urge researchers to focus on mechanisms underlying patterns of dispersal and abundance. Petranka et al. (2004) found that there is often a lack of demographic independence within clusters of local breeding ponds, and that the degree of spatial synchrony in local populations varied between species and in response to localized disturbances. Predicting such effects would require information about species specific responses to disturbance, population sizes, movement rates and abilities. Both Monkkonen and Reunanen (1999) and Fahrig (2001) predicted that the location and slope of critical thresholds in habitat amount should be species-specific, and based on a variety of traits including reproductive potential, emigration success, home range size, habitat specificity, dispersal ability and other behaviors.

Each species experiences and responds to ecological conditions in its environment uniquely. Thus, reliable understanding of interactions between species and their environments requires careful attention to both scale and the characterization of the environment. First, species-environment relationships may differ greatly among species across scales (Cushman and McGarigal, 2004). The environmental patterns that are important at one scale for a species may not be those that influence it at coarser or finer scales (Grand and Cushman, 2003). Thus, researchers must adopt multi-scale approaches that allow for assessment of the interaction of environmental patterns across scales (Wiens, 1989; Cushman and McGarigal, 2003). Second, the environment is experienced differently among species. Thus, researchers should select and characterize the environmental attributes on a species-specific basis. For amphibians, this often means assessing interrelationships between multiple environmental attributes, across a range of scales, for entire landscapes containing dozens or hundreds of local breeding populations. Only by analyzing species-relevant habitat patterns at scales relevant to the populations of those species will it be possible to obtain reliable inferences about the impacts of habitat loss and fragmentation on amphibian populations (McGarigal and Cushman, 2002).

5. Research approaches

5.1. *Empirical approaches*

There are at least four major ways that one could empirically test relationships between the presence or movement of a particular species and environmental structure at the landscape-level. First, one could conduct large-scale, correlative studies of distribution in relation to habitat composition and configuration at a range of scales (Hecnar and M'Closkey, 1996; Knutson et al., 1999; Kolozsvary and Swihart, 1999; Vallan, 2000; Guerry and Hunter, 2002; Weyrauch and Grubb, 2004). Such studies, if replicated sufficiently at the landscape level, can provide reliable information about relationships between landscape structure and the distribution of specific amphibians. The major challenges to such studies are obtaining sufficient replication at the landscape-level to achieve reasonable statistical power, sampling sufficiently large landscapes to allow adequate consideration of environmental patterns at a range of spatial scales, and representing environmental conditions and landscape structures in manners that are relevant to each species in question (McGarigal and Cushman, 2002). These types of studies are also limited in inference because they do not directly measure biological responses such as mortality, movement and productivity. Presence does not always equate to quality. Patterns of distribution do not necessarily reflect patterns of fitness with respect to environmental gradients and landscape patterns.

Two alternative approaches are mark-recapture and telemetry studies (deMaynadier and Hunter, 1999; Rothermel and Semlitsch, 2002; Rothermel, 2004). By quantifying movement rates, distances and routes of dispersing juveniles through complex environments researchers can describe species-specific responses to environmental conditions. Importantly, these methods are well suited for incorporation in manipulative field experiments in which the area and configuration of habitat are controlled to isolate the effects of habitat loss and fragmentation on organism movement and survival rates. These kinds of studies provide the most reliable inferences about relationships between survival rates, movement and ecological conditions (McGarigal and Cushman, 2002). The challenge in these studies is one of cost and sample sizes. Large-scale manipulative field experiments and mark-recapture metapopulation studies are exceptionally expensive to implement, take a number of years to produce reliable results, and generally do not provide large landscape-level sample sizes due to financial and logistical constraints. Likewise, telemetry studies are often limited by spatial scope, sample size and pseudoreplication (Litvaitis et al., 1994).

A fourth alternative involves using molecular genetic methods to empirically derive rates of gene flow among ponds and effective population sizes (Schwartz et al., 1998;

Manel et al., 2003; Curtis and Taylor, 2004; Funk et al., 2005). Molecular genetic methods offer a particularly attractive approach to quantifying gene flow across heterogeneous landscapes, as the logistical and financial costs of extensive mark-recapture study grids are obviated. The genetic characteristics of subpopulations at each sampled pond can provide both information on its effective population size and the degree to which it differs genetically from other ponds. Such methods allow one to quantify rates of gene flow between ponds, assuming time lags between landscape change and genetic response have been accounted for. This in turn allows researchers to test specific hypotheses about the role of specific landscape features and environmental conditions in affecting population connectivity (Manel et al., 2003).

5.2. *Simulation models*

Simulation models offer a flexible way to investigate the behavior of idealized ecological processes in idealized landscapes. It is important to understand that this idealization in simulation modeling is both a limitation and an asset. It is a limitation in that a simulation is never equivalent to the phenomena being simulated. Decisions are made on which processes to include, at which scales, their relative weights, the functional structure of each and how they interact. Similarly, decisions are made on how to represent the structure and composition of landscapes and how to represent the behavior and ecology of organisms. These decisions fundamentally determine the results, and error in them results inevitably in error in the predictions.

However, the fact that such decisions determine results can also be an advantage. By varying functional parameters, environmental characterization, and organism attributes, scientists can investigate hypotheses about the relative influence of different factors, their interactions, and ranges of organism characteristics, such as gradients of population size or dispersal ability. This provides a means for thorough evaluation of complexes of factors that would be impossible to investigate directly in the field.

5.3. *Integrating simulation models and empirical field studies*

Simulation results are not compelling unless verified by empirical data. Reliable model predictions depend on accurate algorithmic implementation of the process–pattern relationships that dominate the behavior of the phenomena being simulated. Models require extensive empirical understandings for their formulation, and require extensive empirical data for their verification. It can be said that models without data are not compelling, and data without models are not informative.

A powerful research paradigm is based on confronting models with rigorous empirical data to test the applicability and generality of relationships, and account for the influences of spatial patterns, temporal fluctuations and time lags (Kareiva and Anderson, 1988). It is an iterative process, with models proposing relationships, data refuting or supporting models, models being refined as a result and producing new predictions to be empirically tested. Field studies should be designed specifically to provide information needed to parameterize and test simulation models. In this effort, manipulative experiments may provide the best information, given their ability to isolate particular factors. However, the most promising area for integrating models with field data is in the area of landscape genetics (Manel et al., 2003). Simulation models can produce explicit predictions of the level of connectivity among populations across landscapes. Molecular genetics can quantify actual rates and patterns of gene flow. The intersection of these two provides a means to optimize the fit of simulation models to actual patterns of gene flow in complex landscapes. This optimization of the fit of spatial models to patterns of gene flow in real populations provides an unprecedented means to explore and understand the interactions between environmental patterns across a range of spatial scales and the connectivity of populations, which is among the most important questions in conservation biology.

6. Conservation strategies

6.1. *From general to specific*

A number of researchers have proposed generalized conclusions and conservation recommendations based on the observation that forest habitat area, habitat connectivity and road density are related to population persistence and population connectivity. These generalizations include that the effects of adjacent land use on amphibians can extend over large distances (Houlahan and Findlay, 2003), and that the proximity and area of upland/breeding habitat play a key role in determining occupancy (Laan and Verboom, 1990; Pope et al., 2000). It is clearly important to account for impact of uplands surrounding wetlands (Dodd and Cade, 1998; Semlitsch, 1998) as amphibian conservation often requires maintaining relatively large forest areas and relatively low road densities in the regional landscape (Houlahan et al., 2000). However, it is not clear how to translate these general understandings to specific management recommendations for individual species in any given landscape. There are large differences among amphibian species in terms of their habitat requirements and sensitivity to landscape change. Effective conservation requires specific predictions that can be applied to unique situations to produce conservation recommendations tailored to the system, species and situation.

6.2. *Core area conservation*

Several researchers have proposed conservation strategies based on protecting core areas based on limited adult migration and adult philopatry. For example, Bulger et al. (2003) suggested that specific protections for migrating California red-legged frogs (*Rana aurora draytoni*) were usually unwarranted and that protecting breeding sites is critical. Other researchers propose core zone widths based on adult migrations. For example, Semlitsch (1998) and Semlitsch and Bodie (2003) suggest core zones up to 218 meters for pond breeding amphibians and up to 290 meters for amphibians in general. Other researchers stress the importance of forest in core zones for persistence of spotted salamander, marbled salamander, Jefferson's salamander (*Ambystoma jeffersonianum*), and wood frog, based on the fact that they are unlikely to persist and travel long distances in non-forest habitat (Whitford and Vinegar, 1966; Thompson et al., 1980; Douglas and Monroe, 1981; Kleeberger and Werner, 1983; deMaynadier and Hunter, 1998; Rothermel and Semlitsch, 2002). While these core zones have been advocated by some as a guide for setting biologically meaningful buffers for wetlands and riparian zones (Semlitsch and Bodie, 2003), they are insufficient as a basis for a conservation strategy for pond breeding amphibians. Any effective conservation strategy must consider more than critical core habitat for adults (Porej et al., 2004). Juvenile dispersal and habitat connectivity are at least as important (Carr and Fahrig, 2001).

6.3. *Landscape-level, population-based conservation strategies*

Just as it is necessary to move from site-specific to landscape-level analyses to understand the ecological relationships between amphibian populations and their environments, it is also necessary to base conservation planning on landscape-level and population-based approaches. Non-spatial conservation plans implemented at specific sites are unlikely to provide adequate conservation of populations that depend on dispersal across complex landscapes for persistence. Just as there is often a gross mismatch between the scale of ecological research and population-level responses, there is usually the same mismatch between the scale of conservation planning and the scale of population responses.

Effective conservation planning will require vast improvements in our understanding of the factors that influence vital rates, mortality and dispersal in complex landscapes. Given the urgency of the crisis facing amphibian populations (Baillie et al., 2004), it is imperative that conservation planners make the most effective use of the information currently available. This will entail extending information from empirical research on the relationships between population size, reproduction, dispersal, mortality and habitat factors across a range of scales to spatially explicit conservation proposals. These extensions can be made in a variety of ways, including through landscape genetic analysis and spatially explicit simulation models.

7. Summary

- Habitat loss and fragmentation are among the largest threats to amphibian populations.
- The extent, pattern and quality of terrestrial habitat in landscape mosaics are as important for many species as the quality of breeding sites.
- Many species of amphibians appear vulnerable to both the loss and fragmentation of nonbreeding upland habitat.
- Population connectivity appears to be a key to regional viability, and is primarily effected through juvenile dispersal.
- In fragmented landscapes, dispersal survival is often lower than required for population viability.
- The preponderance of evidence suggests that the short term impacts of habitat loss and fragmentation increase with dispersal ability.
- Species with limited dispersal abilities are equally imperiled by habitat loss and fragmentation over longer time periods.
- Combining molecular genetics and spatial modeling of organism movement provides a means to improve understanding of how habitat amounts and configurations influence dispersal, survival and population dynamics.
- Effective conservation of amphibian populations is limited by the lack of species-specific ecological knowledge, and lack of landscape-level studies of the effects of habitat loss and fragmentation on movement, survival rates, and population dynamics.
- Conservation strategies could benefit from taking multi-scale, landscape-level approaches that integrate knowledge of species biology with broad-scale evaluations of the area and accessibility of both breeding and nonbreeding habitat.

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REFERENCES

Alford, R.A., Richards, S.J., 1999. Global amphibian declines: a problem in applied ecology. Annual Review of Ecology and Systematics 30, 133–165.

Baillie, J.E.M., Hilton-Taylor, C., Stuart, S.N., 2004. IUCN Red List of Threatened Species. A Global Species Assessment. IUCN Gland, Switzerland and Cambridge, UK.

Balmford, A., Green, R.E., Jenkins, M., 2003. Measuring the changing state of nature. Trends in Ecology and Evolution 18 (7), 326–330.

Beebee, T.J.C., Griffiths, R.A., 2005. The amphibian decline crisis: a watershed for conservation biology?. Biological Conservation 125, 271–285.

Berven, K.A., Grudzien, T.A., 1990. Dispersal in the wood frog (*Rana sylvatica*): implications for genetic population structure. Evolution 44, 2047–2056.

Blaustein, A.R., Chivers, D.P., Kats, L.B., Kiesecker, J.M., 2000. Effects of ultraviolet radiation on locomotion and orientation in roughskin newts (*Taricha granulosa*). Ethology 106, 227–234.

Bowne, D.R., Bowers, M.A., 2004. Interpatch movements in spatially structured populations: a literature review. Landscape Ecology 19 (1), 1–20.

Breden, F., 1987. The effect of post-metamorphic dispersal on the population genetic structure of fowler's toad, *Bufo woodhousei fowleri*. Copeia 1987, 386–395.

Bridges, C.M., Semlitsch, R.D., 2000. Variation in pesticide tolerance of tadpoles among and within species of Ranidae and patterns of amphibian decline. Conservation Biology 14, 1490–1499.

Broomhall, S.D., Osborne, W.S., Cunningham, R.B., 2000. Comparative effects of ambient ultraviolet-B radiation on two sympatric species of Australian frogs. Conservation Biology 14, 420–427.

Brown, J.H., Kodric-Brown, A., 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58, 445–449.

Bulger, J.B., Scott, N.J., Seymour, R.B., 2003. Terrestrial activity and conservation of adult California red-legged frogs *Rana aurora draytonii* in coastal forests and grasslands. Biological Conservation 110 (1), 85–95.

Carr, L.W., Fahrig, L., 2001. Effect of road traffic on two amphibian species of different vagility. Conservation Biology 15 (4), 1071–1078.

Carr, L.W., Pope, S.E., Fahrig, L., 2002. Impacts of landscape transformation by roads. In: Gutzwiller, K.J. (Ed.), Concepts and Applications of Landscape Ecology in Biological Conservation. Springer-Verlag, New York.

Curtis, J.M.R., Taylor, E.B., 2004. The genetic structure of coastal giant salamander *(Dicamptodon tenebrosus)* in a managed forest. Biological Conservation 115 (1), 45–54.

Cushman, S.A., McGarigal, K., 2003. Hierarchical, multi-scale decomposition of species-environment relationships. Landscape Ecology 17, 637–646.

Cushman, S.A., McGarigal, K., 2004. Hierarchical analysis of forest bird species-environment relationships in the Oregon Coast Range. Ecological Applications 14 (4), 1090–1105.

Davidson, C., Shaffer, H.B., Jennings, M.R., 2001. Declines of the California red-legged frog: climate, UV-B, habitat, and pesticides hypotheses. Ecological Applications 11, 464–479.

Delis, P.R., Mushinsky, H.R., McCoy, E.D., 1996. Decline of some west-central Florida anuran populations in response to habitat degradation. Biodiversity and Conservation 5, 1579–1595.

deMaynadier, P.G., Hunter Jr., M.L., 1998. Effects of silvicultural edges on distribution and abundance of amphibians in Maine. Conservation Biology 12 (2), 340–352.

deMaynadier, P.G., Hunter Jr., M.L., 1999. Forest canopy closure and juvenile emigration by pool-breeding amphibians in Maine. Journal of Wildlife Management 63, 441–450.

deMaynadier, P.G., Hunter Jr., M.L., 2000. Road effects on amphibian movements in a forested landscape. Natural Areas Journal 20, 56–65.

Dodd Jr., C.K., Cade, B.A., 1998. Movement patterns and the conservation of amphibians breeding in small, temporary wetlands. Conservation Biology 12, 331–339.

Douglas, M.E., Monroe, B.L., 1981. A comparative study of topographical orientation in *Ambystoma* (Amphibia:Caudata). Copeia 1981, 460–463.

Dupuis, L.A., Steventon, D., 1999. Riparian management and the tailed frog in northern coastal forests. Forest Ecology and Management 124, 35–43.

Edenhamn, P., 1996. Spatial dynamics of the European tree frog (*Hyla arborea* L.) in a heterogeneous landscape. Dissertation, Swedish University of Agricultural Sciences, Uppsala.

Fahrig, L., 1998. When does fragmentation of breeding habitat affect population survival?. Ecological Modelling 105, 273–292.

Fahrig, L., 2001. How much habitat is enough?. Biological Conservation 100, 65–74.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annual Reviews of Ecology and Systematics 34, 487–515.

Fahrig, L., Pedlar, J.H., Pope, S.E., Taylor, P.D., Wegner, J.F., 1995. Effect of road traffic on amphibian density. Biological Conservation 73, 177–182.

Findlay, C.S., Houlahan, J., 1997. Anthropogenic correlates of species richness in southeastern Ontario wetlands. Conservation Biology 11, 1000–1009.

Forester, D.C., Lykens, D.V., 1991. Age structure in a population of red-spotted newts from the Allegheny plateau of Maryland. Journal of Herpetology 25, 373–376.

Funk, W.C., Blouin, M.C., Cron, P.S., Stephen, Maxell, B.A., Pilliod, D.S., Amish, S., Allendorf, F.W., 2005. Population structure of Columbia spotted frogs *(Rana luteiventris)* is strongly affected by the landscape. Molecular Ecology 14, 483–496.

Gibbs, J.P., 1998. Amphibian movements in response to forest edges, roads, and streambeds in southern New England. Journal of Wildlife Management 62, 584–589.

Gill, D.E., 1978. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridenscens* (Rafinesque). Ecological Monographs 48, 145–166.

Grand, J., Cushman, S.A., 2003. A multiple-scale analysis of species-habitat relationships: breeding birds in a pitch pine-scrub oak *(Pinus rigida-Quercus ilicifolia)* community. Biological Conservation. 112 (3), 307–317.

Guerry, A.D., Hunter Jr., M.L., 2002. Amphibian distributions in a landscape of forests and agriculture: an examination of landscape composition and configuration. Conservation Biology 16, 745–754.

Harrison, S., 1991. Local extinction in a metapopulation context: an empirical evaluation. In: Gilpin, M.E., Hanski, I. (Eds.), Metapopulation Dynamics: Empirical and Theoretical Investigations. Academic Press, London, pp. 73–88.

Hazell, D., 2003. Frog ecology in modified Australian landscapes: a review. Wildlife Research 30 (3), 193–205.

Hecnar, S.J., 1995. Acute and chronic toxicity of ammonium nitrate fertilizer to amphibians from southern Ontario. Environmental Toxicology and Chemistry 14, 2131–2137.

Hecnar, S.J., M'Closkey, R.T., 1996. Regional dynamics and the status of amphibians. Ecology 77, 2091–2097.

Hecnar, S.J., M'Closkey, R.T., 1997. The effects of predatory fish on amphibian species richness and distribution. Biological Conservation 79, 123–131.

Houlahan, J.E., Findlay, C.S., 2003. The effects of adjacent land use on wetland amphibian species richness and community composition. Canadian Journal of Fisheries and Aquatic Sciences 60, 1078–1094.

Houlahan, J.E., Findlay, C.S., Schmidt, B.R., Meyer, A.H., Kuzmin, S.L., 2000. Quantitative evidence for global amphibian population declines. Nature 404, 752–755.

Kareiva, P., Anderson, M., 1988. Spatial aspects of species interactions: the wedding of models and experiments. In: Hastings, A. (Ed.), Community Ecology. Springer-Verlag, New York, pp. 35–50.

Kiesecker, J.M., Blaustein, A.R., Belden, L.K., 2001. Complex causes of amphibian population declines. Nature 410, 681–684.

Kleeberger, S.R., Werner, J.K., 1983. Post-breeding migration and summer movement of *Ambystoma maculatum*. Journal of Herpetology 17, 176–177.

Knutson, M.G., Sauer, J.R., Olsen, D.A., Mossman, M.J., Hemesath, L.M., Lannoo, M.J., 1999. Effects of landscape composition and wetland fragmentation on frog and toad abundance and species richness in Iowa and Wisconsin, USA. Conservation Biology 13, 1437–1446.

Kolozsvary, M.B., Swihart, R.K., 1999. Habitat fragmentation and the distribution of amphibians, patch and landscape correlates in farmland. Canadian Journal of Zoology 77, 1288–1299.

Laan, R., Verboom, B., 1990. Effects of pool size and isolation on amphibian communities. Biological Conservation 54, 251–262.

Lande, R., 1988. Genetics and demography in biological conservation. Science 241, 1455–1460.

Lawton, J.H., May, R.M., 1995. Extinction Rates. Oxford University Press.

Lehtinen, R.M., Galatowitsch, S.M., Tester, J.R., 1999. Consequences of habitat loss and fragmentation for wetland amphibian assemblages. Wetlands 19 (1), 1–12.

Litvaitis, J.A., Titus, K., Anderson, E.M., 1994. Measuring vertebrate use of terrestrial habitats and foods. In: Bookhout, T.A. (Ed.), Research and Management Techniques for Wildlife and Habitats, fifth ed. The Wildlife Society, Bethesda, Maryland, USA, pp. 254–270.

Madison, D.M., 1997. The emigration of radio-implanted Spotted Salamanders, *Ambystoma maculatum*. Journal of Herpetology 31, 542–551.

Manel, S., Schwartz, M.K., Luikart, G., Taberlet, P., 2003. Landscape genetics: combining landscape ecology and population genetics. Trends in Ecology and Evolution 18 (4), 189–197.

Marsh, D.M., Thakur, K.A., Bulka, K.C., Clarke, L.B., 2004. Dispersal and colonization through open fields by a terrestrial, woodland salamander. Ecology 85 (12), 3396–3405.

Marsh, D.M., Trenham, P.C., 2001. Metapopulation dynamics and amphibian conservation. Conservation Biology 15, 40–49.

McGarigal, K., Cushman, S.A., 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. Ecological Applications 12 (2), 335–345.

Monkkonen, M., Reunanen, P., 1999. On critical thresholds in landscape connectivity: a management perspective. Oikos 84, 302–305.

Myers, N., Knoll, A.H., 2001. The biotic crisis and the future of evolution. Proceedings of the National Academy of Science 98 (10), 5389–5392.

Newcomb Homan, R., Windmiller, B.S., Reed, J.M., 2004. Critical thresholds associated with habitat loss for two vernal pool-breeding amphibians. Ecological Applications 14 (5), 1547–1553.

Pechmann, J.H.K., Scott, R.D., Semlitsch, R.D., Caldwell, J.P., Vitt, L.J., Gibbons, J.W., 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. Science 253, 892–985.

Petranka, J.W., Smith, C.K., Scott, A.F., 2004. Identifying the minimal demographic unit for monitoring pond-breeding amphibians. Ecological Applications 14 (4), 1065–1078.

Pope, S.E., Fahrig, L., Merriam, H.G., 2000. Landscape complementation and metapopulation effects on leopard frog populations. Ecology 81, 2498–2508.

Porej, D., Micacchion, M., Hetherington, T.E., 2004. Core terrestrial habitat for conservation of local populations of salamanders and wood frogs in agricultural landscapes. Biological Conservation 120, 399–409.

Pounds, J.A., Fogden, M.P.L., Campbell, J.H., 1999. Biological response to climate change on a tropical mountain. Nature 398, 611–615.

Preisser, E.L., Kefer, J.Y., Lawrence, J.D., 2001. Vernal pool conservation in Connecticut: an assessment and recommendations. Environmental Management 26 (5), 503–513.

Regosin, J.V., Windmiller, B.S., Reed, M.J., 2003. Terrestrial habitat use and winter densities of the wood frog *(Rana sylvatica)*. Journal of Herpetology 37, 390–394.

Reh, W., Seitz, A., 1990. The influence of land use on the genetic structure of populations of the common frog *(Rana temporaria)*. Biological Conservation 54, 239–249.

Rothermel, B.B., 2004. Migratory success of juveniles: a potential constraint on connectivity for pond-breeding amphibians. Ecological Applications 14 (5), 1535–1546.

Rothermel, B.B., Semlitsch, R.D., 2002. An experimental investigation of landscape resistance of forest versus old-field habitats to emigrating juvenile amphibians. Conservation Biology 16, 1324–1332.

Ruggiero, L.F., Hayward, G.D., Squires, J.R., 1994. Viability analysis in biological evaluations: concepts of population viability analysis, biological population, and ecological scale. Conservation Biology 8 (2), 364–372.

Schwartz, M.K., Tallmon, D.A., Luikart, G., 1998. Review of DNA-based census and effective population size estimators. Animal Conservation 1 (4), 293–299.

Semlitsch, R.D., 1998. Critical elements for biologically based recovery plans of aquatic-breeding amphibians. Conservation Biology 16, 619–629.

Semlitsch, R.D., 2000. Principles for management of aquatic-breeding amphibians. Journal of Wildlife Management 64, 615–631.

Semlitsch, R.D., Bodie, J.R., 1998. Are small, isolated wetlands expendable?. Conservation Biology 12 (5), 1129–1133.

Semlitsch, R.D., Bodie, J.R., 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation Biology 17, 1219–1228.

Semlitsch, R.D., Scott, D.E., Pechmann, J.H.K., Gibbons, J.W., 1996. Structure and dynamics of an amphibian community: evidence from a 16-year study of a natural pond. In: Cody, P.M.L., Smallwood, J.A. (Eds.), Long-Term Studies of Vertebrate Communities. Academic Press, San Diego, CA, USA, pp. 217–248.

Sinsch, U., 1990. Migration and orientation in anuran amphibians. Ethology, Ecology and Evolution 2, 65–79.

Sinsch, U., 1992. Structure and dynamics of a natterjack toad metapopulation *(Bufo calamita)*. Oecologia 90, 489–499.

Sinsch, U., 1997. Postmetamorphic dispersal and recruitment of first breeders in a *Bufo calamita* metapopulation. Oecologia 112, 42–47.

Sinsch, U., Seidel, D., 1995. Dynamics of local and temporal breeding assemblages in a *Bufo calamita* metapopulation. Australian Journal of Ecology 20, 351–361.

Sjögren, P., 1991. Extinction and isolation gradients in metapopulations:the case of the pool frog *(Rana lessonae)*. Biological Journal of the Linnean Society 42, 135–148.

Sjögren-Gulve, P., 1994. Distribution and extinction patterns within a northern metapopulation of the pool frog, *Rana lessonae*. Ecology 75, 1357–1367.

Sjögren-Gulve, P., 1998. Spatial movement patterns in frogs:target-oriented dispersal in the pool frog, *Rana lessonae*. Ecoscience 5, 31–38.

Skelly, D.K., Werner, E.E., Cortwright, S.A., 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. Ecology 80, 2326–2337.

Stebbins, R.C., Cohen, N.W., 1995. A Natural History of Amphibians. Princeton University Press, Princeton, NJ, USA. 316 pp.

Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L., Waller, R.W., 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306, 1783–1786.

Taylor, B.E., Scott, D.E., 1997. Effects of larval density dependence on population dynamics of *Ambystoma opacum*. Herpetologica 53, 132–145.

Thompson, E.L., Gates, J.E., Taylor, G.J., 1980. Distribution and breeding habitat selection of Jefferson Salamander *Ambystoma jeffersonianum* in Maryland. Journal of Herpetology 14, 113–120.

Trenham, P.C., Koenig, W.D., Mossman, M.J., Stark, S.L., Jaagger, L.A., 2003. Regional dynamics of wetland-breeding frogs and toads: turnover and synchrony. Ecological Applications 13 (6), 1522–1532.

Trenham, P.C., Shaffer, H.B., 2005. Amphibian upland habitat use and its consequences for population viability. Ecological Applications 15 (4), 1158–1168.

Trenham, P.C., Shaffer, H.B., Koenig, W.D., Stromberg, M.R., 2000. Life history and demographic variation in the California tiger salamander *(Ambystoma californiense)*. Copeia 2000, 365–377.

Vallan, D., 2000. Influence of forest fragmentation on amphibian diversity in the nature reserve of Amohitantely, highland Madagascar. Biological Conservation 96, 31–43.

Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of Earth's ecosystems. Science 277, 494–499.

Vos, C.C., Chardon, J.P., 1998. Effects of habitat fragmentation and road density on the distribution pattern of the moor frog *Rana arvalis*. Journal of Applied Ecology 35, 44–56.

Weyrauch, S.L., Grubb Jr., T.C., 2004. Patch and landscape characteristics associated with the distribution of woodland amphibians in an agricultural fragmented landscape: an information-theoretic approach. Biological Conservation 115, 443–450.

Whitford, W.G., Vinegar, A., 1966. Homing, survivorship, and overwintering of larvae in Spotted salamanders, *Ambystoma maculatum*. Copeia 1966, 515–519.

Wiens, J.A., 1989. Spatial scaling in ecology. Functional Ecology 3, 385–397.

Wilson, E.O., 1999. The Diversity of Life. Longitude, New York, USA.

Windmiller, B.S., 1996. The pond, the forest, and the city: spotted salamander ecology and conservation in human-dominated landscape. Ph.D. Dissertation, Tufts University, Boston, Massachusetts.

21

Biological corridors and connectivity

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> *hring utan ymbbearh, þæt heo þone fyrdhom ðurhfon ne mihte, locene leoðosyrcan laþan fingrum.*
>
> *On his shoulder lay braided breast-mail, barring death, withstanding entrance of edge or blade.*
>
> **Beowulf (Old English epic poem, c. 10th Century)**

Introduction

The ability of individual animals to move across complex landscapes is critical for maintaining regional populations in the short term (Fahrig 2003; Cushman 2006), and for species to shift their geographic range in response to climate change (Heller & Zavaleta 2009). As organisms move through spatially complex landscapes, they respond to multiple biotic and abiotic factors to maximize access to resources and mates while minimizing fitness costs such as mortality risks. Habitat fragmentation decreases dispersal success (Gibbs 1998), increases mortality (Fahrig et al. 1995) and reduces genetic diversity (Reh & Seitz 1990; Wilson & Provan 2003). Local populations may decline if immigration is prevented (Brown & Kodric-Brown 1977; Harrison 1991) and may prevent recolonization following local extinction (Semlitsch & Bodie 1998).

The goal of this chapter is to describe the state of the art in quantitative corridor and connectivity modelling. We will review several critical issues in modelling, and provide expert guidance and examples to help practitioners implement effective programmes to preserve, enhance or create connectivity among wildlife populations. We first

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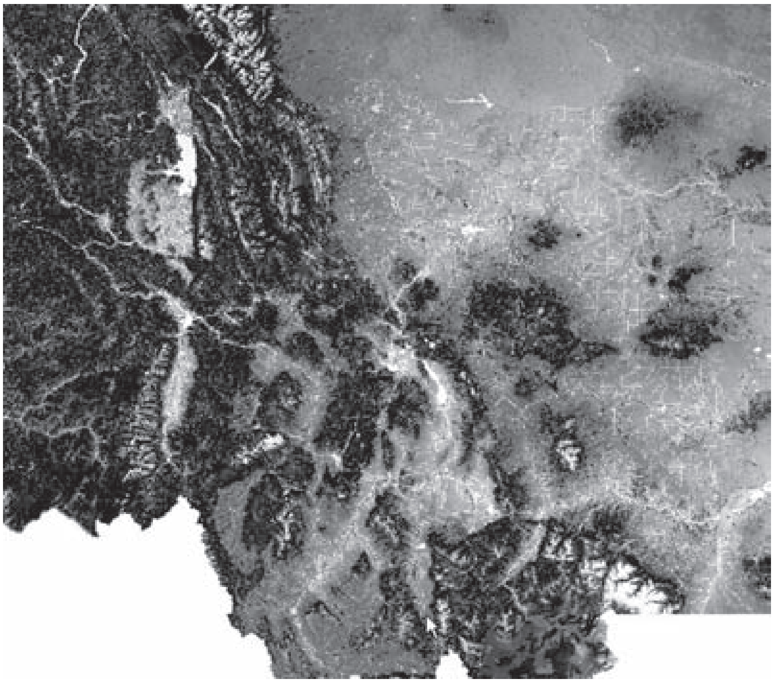


Figure 21.1 Example landscape resistance map for American black bear in an area of the US northern Rocky Mountains encompassing Montana and northern Idaho. Dark areas are low resistance for movement, while light areas are high resistance for movement. The resistance map was developed by Cushman et al. (2006) and validated with independent data by Cushman & Lewis (2010) and in multiple independent study areas by Short Bull et al. (2011).

review the fundamental task of estimating landscape resistance, comparing expert opinion and empirical methods. Next, we describe current methods of predicting connectivity from resistance surfaces. Then we discuss how to develop linkage designs that can maintain connectivity for multiple species, and under changing climate. We conclude with discussion of how effectively to validate connectivity model predictions.

Estimating landscape resistance

Most current methods of predicting population connectivity and mapping areas significant in facilitating animal movements begin with landscape resistance maps (Figure 21.1). Landscape resistance maps depict the cost of movement through any location in the landscape (pixel cell in a raster map) as a function of landscape features of that cell (e.g. high resistance might be assigned to a road or a body of water). In its most basic sense, landscape resistance reflects the local movement cost incurred by an animal. More formally, the resistance reflects the step-wise cost of moving through each cell for least-cost analyses (Singleton et al. 2002) or the relative probability of moving into the cell for circuit theory-based analyses (McRae et al. 2008).

Expert versus empirical estimation

Most published studies using landscape resistance maps have estimated resistance of landscape features to movement based on expert opinion alone (e.g. Compton et al. 2007). However, non-human species perceive landscapes in ways that may not correspond to human assumptions concerning connectivity and habitat quality (With et al. 1997). Using unvalidated expert opinion to develop resistance maps has been a major weakness of most past landscape resistance modelling efforts (Seoane et al. 2005).

Methods for empirically estimating resistance

Habitat quality as surrogate for landscape resistance

Habitat quality can be predicted based on patterns of occupancy in relation to ecological conditions, such as through resource selection functions (e.g. Guerry & Hunter 2002; Weyrauch & Grubb 2004). The simplest way to estimate relationships empirically between population connectivity and environmental conditions is to assume that habitat quality directly equates to population connectivity. Predictions of habitat quality based on patterns of occurrence studies are limited because they do not directly measure biological responses such as mortality, movement and productivity (Cushman 2006). Patterns of species occurrence do not necessarily reflect patterns of fitness with respect to environmental gradients and landscape patterns (Van Horne 1983). More importantly, in the context of connectivity modelling, suitability for occupancy and suitability for dispersal may not be driven by the same factors at the same scales (e.g. Shirk et al. 2010; Wasserman et al. 2010). Habitat selection reflects the behaviour of individual organisms to maximize fitness within home ranges, while population connectivity is driven by dispersal, migration and mating events. These are functionally and biologically different processes. Few studies have formally evaluated the performance of habitat suitability models as surrogates for landscape resistance, but those that have generally have found them to perform poorly (e.g. Shirk et al. 2010; Wasserman et al. 2010). This highlights the importance of not assuming that habitat relationships optimally reflect the landscape features governing population connectivity.

Mark-recapture and experimental movement studies

By quantifying movement rates, distances travelled and routes of animals through complex environments, researchers can quantitatively describe species-specific responses to environmental conditions and landscape structure. For example, a study by Gamble et al. (2007) quantified dispersal in relation to topography and vegetation for several pond-breeding amphibians, demonstrating the value of mark-recapture approaches to evaluating population connectivity. In addition, these methods are well suited for incorporation in manipulative field experiments in which the area and configuration of habitat are controlled to isolate the effects of habitat loss and fragmentation on organism movement and survival rates. For example, Haddad & Baum (1999) used a large-scale experiment to find that three habitat-restricted butterfly species reached higher densities in patches connected by corridors than in similar, isolated patches.

These kinds of studies provide the most reliable inferences about relationships between survival rates, movement and ecological conditions (McGarigal & Cushman 2002). Unfortunately, large-scale manipulative field experiments and mark-recapture meta-population studies are expensive, take several years, and generally suffer from small sample sizes. Another potential limitation is that these studies focus on short-term, fine-scale movement path selection of individual animals, which may not scale up to population-level effects on migration and gene flow.

Telemetry

Advances in wildlife telemetry technology have enabled collection of very accurate and frequent location data for individual animals. Landscape resistance modelling based on telemetry is a powerful technique to address the factors that affect organism movement directly on scales of space and time greater than are possible with mark-recapture and experimental movement studies (e.g. Osborn & Parker 2003; Cushman et al. 2005, 2010a). GPS telemetry data enable direct assessment of the influences of landscape features on movement path selection. For example, Cushman et al. (2010a) modelled the influence of landscape features on elephant movement path selection using telemetry data, showing that elephants (*Loxodonta africana*) select movement paths near water, avoid human settlements and do not cross wildlife cordon fences. Similarly, Cushman & Lewis (2010) used satellite telemetry data to show that American black bears (*Ursus americanus*) choose movement paths that avoid roads and human residences and concentrate activity in forested areas at middle elevations. Directly associating movement paths with landscape features enables the development of species-specific landscape resistance models that are more reliable than those produced by expert opinion.

Landscape genetics

Gene flow among populations is necessary to support the long-term viability of populations, as it maintains local genetic variation and spreads potentially advantageous genes. Thus it is important to infer the functional connectivity among populations and across landscapes (van Dyck & Baguette 2005). The ultimate validation of any method of estimating functional connectivity lies in how well it explains gene flow (Cushman et al. 2006; Shirk et al. 2010; Wasserman et al. 2010; Short Bull et al. 2011). Genetic methods can directly measure dispersal and immigration (Waples 1998; Landguth et al. 2010). Logistical and financial costs associated with tracking individual animals are obviated and because genetic data integrate time and space, slow rates of dispersal through complex landscapes are measurable. Landscape genetic analyses enable direct association of movement cost across resistance surfaces with genetic differentiation, which enables empirical derivation and validation of connectivity maps. For example, Wasserman et al. (2010) used non-invasive monitoring to collect genetic data from several hundred individual American marten (*Martes americana*) across a 4000 square kilometer study area, and were able to use multivariate landscape genetic modelling to identify the landscape features that affect gene flow.

Combining multiple methods to produce robust estimates of resistance

Every method of estimation has its own limitations, so it is valuable to use multiple methods and independent data sets to estimate resistance. The strongest inferences are derived from multiple analyses of different kinds of data that produce a consistent result (Cushman & Lewis 2010). For example, landscape genetics and GPS telemetry are two complementary analyses that can be combined to produce robust estimates of landscape resistance. Using movement data to predict landscape resistance, and comparing that to landscape resistance predicted from landscape genetic analyses of the same species in the same study area, is a useful way to verify the robustness of landscape connectivity hypotheses (e.g. Cushman & Lewis 2010). In addition, such analyses would illuminate the multi-scale drivers of population connectivity, since mating and dispersal movement behaviours are the mechanisms through which gene flow operates in animal populations. At the present time, only a few research programmes have estimated resistance from a combination of approaches (Coulon et al. 2008; Cushman & Lewis 2010; Shanahan et al. 2011; see Box 21.1).

From landscape resistance to population connectivity

While resistance is point specific, connectivity is route specific (Cushman et al. 2008). Therefore, while resistance models can provide the foundation for applied analyses of population connectivity, they do not, in themselves, provide sufficient information to evaluate the existence, strength and location of barriers and movement corridors. Connectivity must be evaluated with respect to the paths, costs and success of moving across a landscape. The resistance model is the

Box 21.1 Combining landscape genetics and telemetry to estimate landscape resistance for American black bear

Cushman et al. (2006) used causal modelling with landscape genetics data to evaluate support for 110 alternative hypotheses describing the effects of landscape variables on population connectivity in an American black bear (*Ursus americanus*) population in northern Idaho, USA. Their analysis rejected hypotheses of isolation by distance and isolation by a geographical barrier, and affirmed a landscape resistance model which predicts that rates of gene flow are related to elevation, forest cover, roads and human development. Cushman & Lewis (2010) used conditional logistic regression to predict landscape resistance based on black bear GPS telemetry data in the same landscape. They used a path-level spatial randomization method to assess the effects of multiple landscape features on movement path selection (e.g. Cushman et al 2010a). The path-level randomization approach provides a robust means to compare the landscape features an animal encounters in its actual path with those that would be encountered in a large sample of available paths of identical length and topology. They found that consistent landscape factors influence genetic differentiation and movement path selection, with strong similarities between the predicted landscape resistance surfaces. Genetic differentiation among individual American black bears is driven by spring movement (mating and dispersal) in relation to residential development, roads, elevation and forest cover. The real value of this study is that it used two independent data sets and different kinds of analyses to validate the results, and it quantified the scale and strength of bear behavioural response to several landscape features. For example, it showed that gene flow is maximum at middle elevations due to impassable snow pack at high elevations in the dispersal season, and concentrated human populations in low-elevation valleys, and that bears strongly avoid roads and human resistances (e.g. near-total avoidance within a 200 m radius buffer around human structures).

foundation for these analyses, but it is explicit consideration of movement paths across the resistance surface that provides the key information for conservation and management.

Identifying corridors using least-cost modelling

In recent years least-cost (LC) modelling (part of graph theory, see below) has become the dominant modelling tool to evaluate functional landscape connectivity, especially in applied studies. This is mainly because:

- it produces an unambiguous corridor or path as an output, whereas most other approaches do not
- it is available in most commercial GIS packages as well as open source software
- LC models generate visually attractive and easy to communicate representations of connectivity (maps) and quantitative metrics of effective distance (cost values) in the same units (meters) as Euclidean distance (Adriaensen et al. 2003; Fagan & Calabrese 2006).

These attributes make LC modelling very well suited for quantitative landscape analyses and for evaluating effects of future scenarios on connectivity.

In LC models the only inputs are the map of sources and targets and the map of resistance values (R; Figure 21.2a). The cost layer is the first and central level of output of a LC analysis (see Figure 21.2a), and provides the functional cost distance values from the designated source to all locations in the geographical extent of the analysis. The least-cost path (Figure 21.2b) is the series of cells in the landscape which results in the minimum cumulative cost value (LC path value) to move from a source cell/cells to the target cell/cells under investigation. The LC path indicates the location of the cheapest route, but gives no information on how cost values are distributed over the landscape. For example, it does not indicate other zones in the landscape resulting in comparable costs (Figure 21.2c) or how wide the LC path zone is (Adriaensen et al. 2003; Pinto & Keitt 2009).

There are several methods available to produce biologically informative measures of landscape connectivity from such cost surfaces. One of these is the combination of several cost

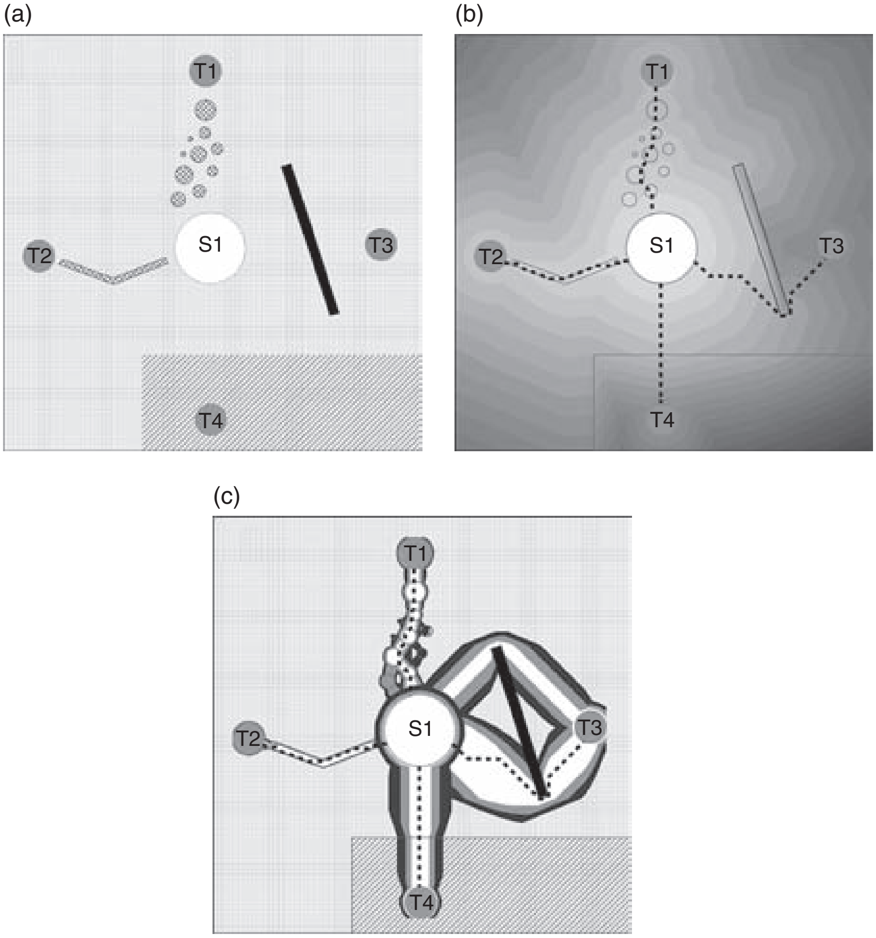


Figure 21.2 Input (a) to output (b-c) in LC modelling using a simple virtual landscape to show the basics of this modelling approach. (a) Landcover map showing a hypothetical landscape (source area S1: forest; target areas T1–4: woodlots; grassland (dotted); intensive cropland (hatched); hedgerow and bushes (cross-hatched); open water (solid black). (b) Cost layer from source area S1 and LC path to 4 target areas (dashed lines). (c) Corridor map showing 1–10% corridor buffers derived from bidirectional cost layers from source area S1. Result of 4 corridor analyses superimposed (targets=T1–4): white, increase in minimum cumulative cost less than 1% of LCP; light grey 1–5%; dark grey 5–10%.

layers into one ‘corridor’ layer (other names: bidirectional cost layer, conditional minimum transit cost [CMTC, Pinto & Keitt 2009]; see Figure 21.2c), in which the value of each cell is the overall cost to reach the target cell T from source cell S, but with the constraint to go through the cell under investigation. The LC path is a special case of this (with all cells having a value equal to the LC path value and thus the minimum present in the corridor layer). The LC path will always be the path of minimal corridor values but elsewhere in the landscape, there could be other zones with nearly equal cost values (see Figure 21.2c). Corridor maps give a more realistic view of the functionally cheapest routes in the landscape from the designated source to the destination (Adriaensen et al. 2003) (Box 21.2). For example, the width of corridors can be determined by taking percent slices of the landscape representing the lowest cumulative resistance (e.g. Singleton et al. 2002; Spencer et al. 2010) or by limiting

Box 21.2 Landscape connectivity in the Taita Hills

The Restoration and Increase of Connectivity among Fragmented Forest Patches in the Taita Hills, South-east Kenya project (CEPF project 1095347968; Adriaensen et al. 2007) included a detailed analysis of functional landscape connectivity in the area. In this project, evidence of the distribution and population status of bird species in the remaining small cloud forest patches on the hill tops (black patches) was successfully combined with output of LC models to support and prioritize habitat restoration actions in plantations with exotic trees (white patches). Forest restoration is now being implemented in a set of five pilot projects.

Least-cost models were used to model the location of exotic tree plantations in relation to modelled connectivity corridors for forest interior birds (dark grey zones), in order to evaluate their potential roles as stepping stones to promote recolonization after rehabilitation of the plantations. In the map shown, corridors between all pairs of remaining forest plots were superimposed (resistance set R1S5 for eco-type 'sensitive interior forest bird', including the critically endangered Taita thrush *Turdus helleri*).

corridors to a maximum cost-weighted cut-off distance above that of the LC path (WHCWG 2010). Regional connectivity assessments can require mapping corridors between hundreds to thousands of core area pairs (e.g. Spencer et al. 2010; WHCWG 2010). The development of GIS tools to automate corridor mapping, including decisions of which pairs

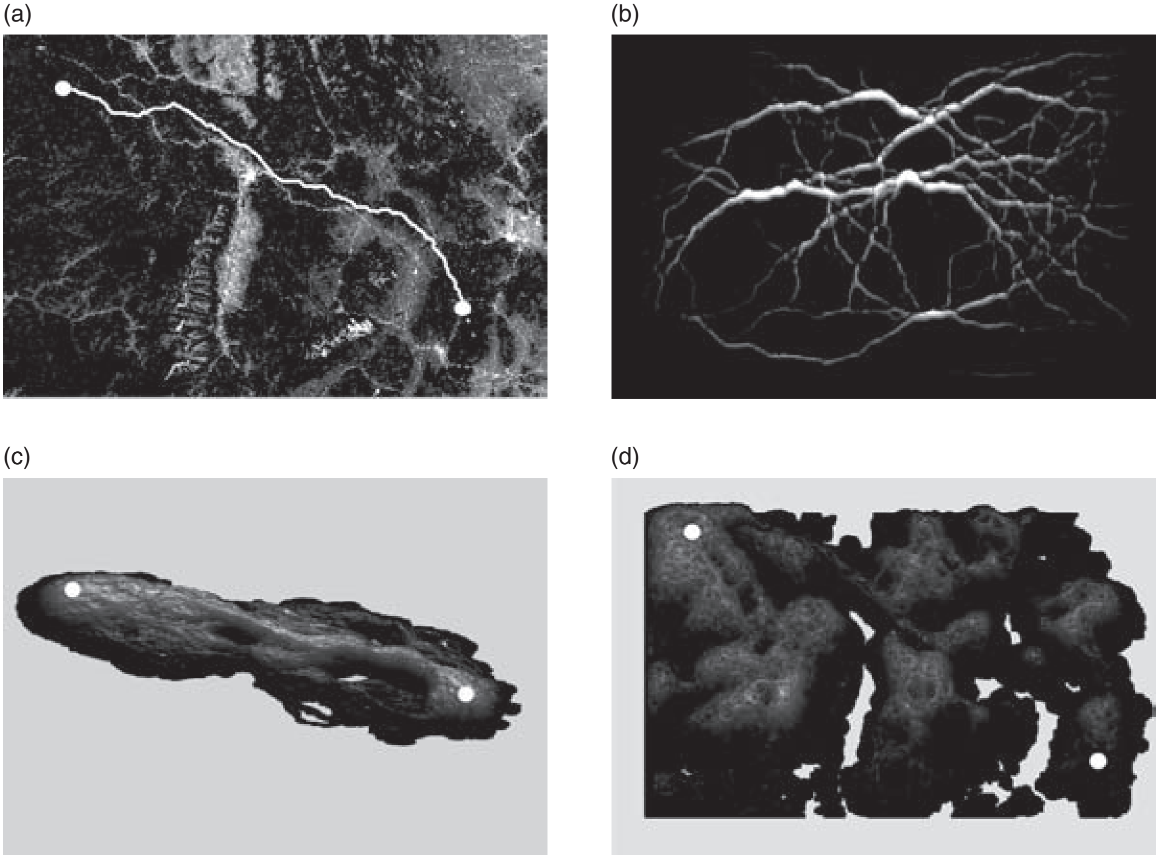


Figure 21.3 Comparison of four connectivity modelling methods applied to a single study area and resistance map. The study area is northern Idaho, USA. The resistance map is shown in panel (a) as a colour scale from blue (low resistance) to red (high resistance), and reflects landscape resistance to black bear gene flow (Cushman et al. 2006). Panel (a) shows a single least-cost path (white line) between two point locations (white dots). Panel (b) shows a factorial least-cost path analysis between several hundred source points. Panel (c) shows the least-cost corridor between the same two source points as in (a). Panel (d) shows the cumulative resistant kernel model of synoptic landscape connectivity.

of core areas to connect (e.g. McRae & Kavanagh 2011), makes this easy.

Factorial least-cost paths

One limitation of traditional LC path and LC corridor analyses is that they are limited to prediction of connectivity between single sources and single destinations (Figure 21.3a). While this may be ideal in the case where one is interested in the lowest cost routes between two focal conservation areas, there are many situations where a more synoptic analysis of connectivity is valuable. For example, it may be that there is a need to calculate corridor connectivity between thousands of sources and a single destination (e.g. Cushman et al. 2010a) or between hundreds of sources and hundreds of destinations distributed across a complex landscape (e.g. Cushman et al. 2008, Cushman et al. 2011; Figure 21.3b). For example, Cushman et al. (2008) used factorial least cost path analysis to predict the most important movement routes for bears between Yellowstone National Park and the Canadian border in the United States Northern Rocky Mountains, showing that there are few major connections and locating several dozen potential barriers. This, in turn, focuses attention on where restoration and mitigation efforts would be most effective. A factorial implementation of least cost paths (e.g. UNICOR; Landguth et al. 2011) permits integration of a vast number of least cost paths to show synoptic connectivity across large and complex landscapes (Figure 21.3b). For example (Cushman et al. 2011) mapped regional corridor networks for several species of conservation concern across a vast area of the United States great plains using UNICOR (Landguth et al. 2011). The analysis identified which species have the most fragmented populations and mapped the most important corridor linkages among population core areas, focusing conservation efforts on the most important locations.

Other ways to analyse connectivity

Ecologists often use the term *graph theory* to refer to a family of analyses in which patches are reduced to nodes at patch centroids, with centroids connected by lines or 'edges' (e.g. Bunn et al. 2000; Urban & Keitt 2001; Minor & Urban 2007). Such graphs underlie many methods in connectivity analysis, including LC corridor modelling. Advances in computing and algorithms borrowed from other disciplines have allowed applications of graph algorithms to continuous landscapes instead of simple networks. Rayfield et al. (2011) review graph-based connectivity measures and provide a framework for classifying them as applications to connectivity conservation.

Circuit theory

Connectivity analyses based on electrical circuit theory use networks of electrical nodes connected by resistors as models for networks of populations, habitat patches or locations on a landscape connected by movement. Because connectivity increases with multiple pathways in electrical networks, distance metrics based on electrical connectivity are applicable to processes (e.g. gene flow; McRae 2006) that respond positively to increasing numbers of pathways. Additionally, previous work has shown that current, voltage and resistance in electrical circuits all have mathematical relationships with random walks (Doyle & Snell 1984; Chandra et al. 1997). Random walks can predict the expected routes that an animal with a preference for low-resistance habitat will take as it moves through a landscape. The precise relationships between circuit theory and random walks mean that circuits can be related to movement ecology and population genetics via random walk and coalescent theories, providing concrete interpretations of connectivity measures (McRae 2006; McRae et al. 2008).

Circuit and LC models represent two extremes in assumptions about movement and connectivity. Least-cost corridors calculate the routes expected to be taken by animals with perfect or near-perfect knowledge of the landscape, whereas current maps generated from circuit models predict movement routes taken by random walkers, with all possible paths contributing to connectivity. Neither will entirely correctly predict movement behaviour of real animals (Spear et al. 2010, and see below) but there are benefits to both models, as we show in the example in Figure 21.4. Least-cost analyses can show what routes/zones would permit the most efficient movement, which can be important for conservation planning; if a large portion of a landscape is likely to be developed, identifying those areas which, if conserved, provide the easiest movement routes will be important. Circuit theory has the advantage of identifying and quantifying 'pinch points' (see Figure 21.4), i.e. constrictions in corridors that, if lost, could sever connectivity entirely. Such areas can be prioritized for early conservation action because options are limited. Circuit algorithms also integrate across all movement pathways to

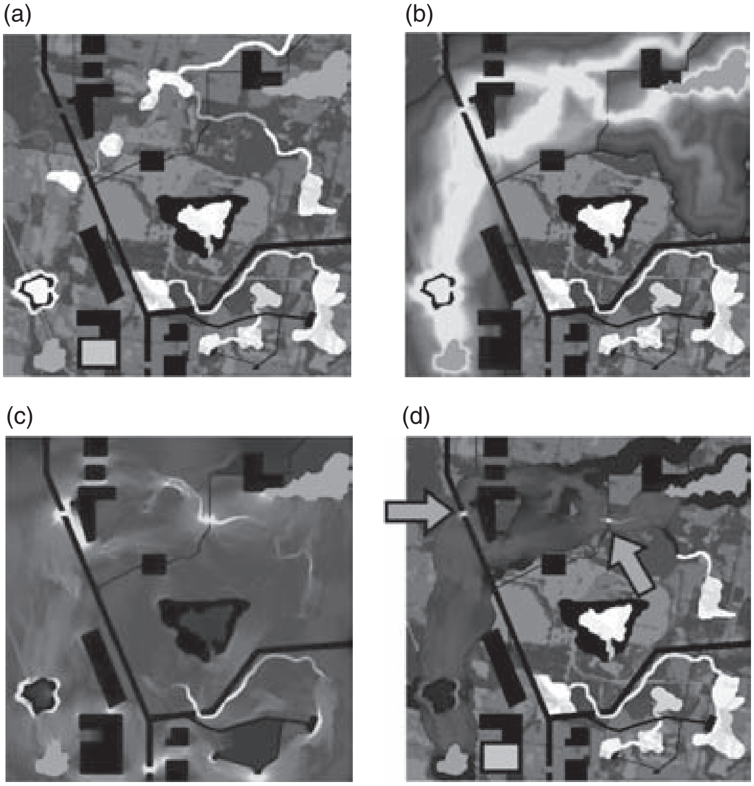


Figure 21.4 Example of how circuit theory can be used to identify and prioritize important areas for connectivity conservation. (a) Simple landscape, with two patches to be connected (green) separated by a matrix with varying resistance to dispersal (low resistance in white, higher resistance in darker shades, and complete barriers in black). (b) Least-cost corridor between the patches (lowest resistance routes in yellow, highest in blue). (c) Current flow between the same two habitat patches derived using Circuitscape (McRae & Shah 2009), with highest current densities shown in yellow (from McRae et al. 2008). Circuit analyses complement least-cost path results by identifying important alternative pathways and 'pinch points', where loss of a small area could disproportionately compromise connectivity. (d) A promising application is restricting circuit analyses to least-cost corridor slices to take advantage of the strengths of both approaches (from McRae & Kavanagh 2011). This hybrid approach shows both the most efficient movement pathways and critical 'pinch points' within them,which glow yellow. These could be prioritized over areas that contribute little to connectivity, such as the corridor at the top right of the map that has been coloured dark blue because it does not provide connectivity between the patches.

provide measures of redundancy, i.e. availability of alternative pathways for movement (see Figure 21.4). New applications allow identification of barriers that have a strong effect on connectivity, which can be useful for highlighting opportunities to restore connectivity, e.g. through re-establishment of natural vegetation or installation of highway crossing structures (McRae, unpublished data).

Centrality analyses

A promising graph-theoretic approach to connectivity modelling is centrality analysis, which ranks the importance of habitat patches or corridors in providing movement across an entire network, i.e. as 'gatekeepers' of flow across a landscape (Carroll et al. 2011). Centrality analyses can be based in LC path, circuit theory or other connectivity analysis methods. The difference is that, instead of mapping corridors or current flow between single pairs of core areas, they add up results from connectivity analyses between all pairs of nodes (sites or cells) on a landscape. Centrality analyses can be applied to raster GIS data or networks to identify core areas, linkages or grid cells that are particularly important for overall connectivity. Because centrality metrics can incorporate connectivity between all pairs of nodes on a landscape, they can eliminate the need to identify specific pairs of habitat patches to connect. For example, betweenness centrality (Freeman et al. 1991) identifies the shortest paths connecting all pairs of nodes in a network, and sums the number of such shortest paths involving each intervening node. This procedure identifies areas lying on a large proportion of the shortest paths in a network, the loss of which can disproportionately disrupt connectivity across the network as a whole. The Connectivity Analysis Toolkit (Carroll 2010) specializes in centrality analysis, and supports metrics based on betweenness, current flow (Newman 2005), maximum flow (Freeman et al. 1991) and minimum-cost flow (Ahuja et al. 1993). It also allows time-series analyses of connectivity across landscapes where habitats shift through time (Phillips et al. 2008).

Resistant kernels

The resistant kernel approach to connectivity modelling is based on least-cost dispersal from some defined set of sources. The model calculates the expected density of dispersing individuals in each pixel around the source, given the dispersal ability of the species, the nature of the dispersal function and the resistance of the landscape (Compton et al. 2007; Cushman et al. 2010b). Once the expected density around each source cell is calculated, the kernels surrounding all sources are summed to give the total expected density at each pixel (see Figure 21.3d). The results of the model are surfaces of expected density of dispersing organisms at any location in the landscape. For example, Cushman et al. (2010b) used resistant kernel modelling to evaluate the interactive effects of roads and human land use change on population connectivity for a large number of pond-breeding species in Massachusetts (USA). The resistant kernel approach quantified expected density of dispersers in the upland environment as functions of breeding population size, dispersal ability and quantified the relative impacts of roads and land use on population connectivity (Figure 21.5).

The resistant kernel approach to modelling landscape connectivity has a number of advantages as a robust approach to assessing current population connectivity (Compton et al. 2007; Cushman et al. 2010b, 2011). First, unlike most approaches to mapping corridors , it is spatially synoptic and provides prediction and mapping of expected migration rates for every pixel in the whole study area, rather than only for a few selected 'linkage zones' (e.g. Compton et al. 2007). Second, scale dependency of dispersal ability can be directly included to assess how species of different vagilities will be affected by landscape change and fragmentation under a range of scenarios (e.g. Cushman et al. 2010b). Third, it is computationally efficient, enabling simulation and mapping at a fine spatial scale across large geographical extents (e.g. Cushman et al. 2010b, 2011).

Individual-based movement models

Individual-based (IB) models explicitly simulate the processes acting on the individual to predict movement. IB models predict movement paths of simulated dispersers based on parameters such as energetic cost of movement in different patch types, turning angles within patches and at patch transitions, movement speeds, duration of movement events, mortality risks in different patch types, and likelihoods of movements between patch types. Thus, IB models usually incorporate much more detail and thus greater realism than other

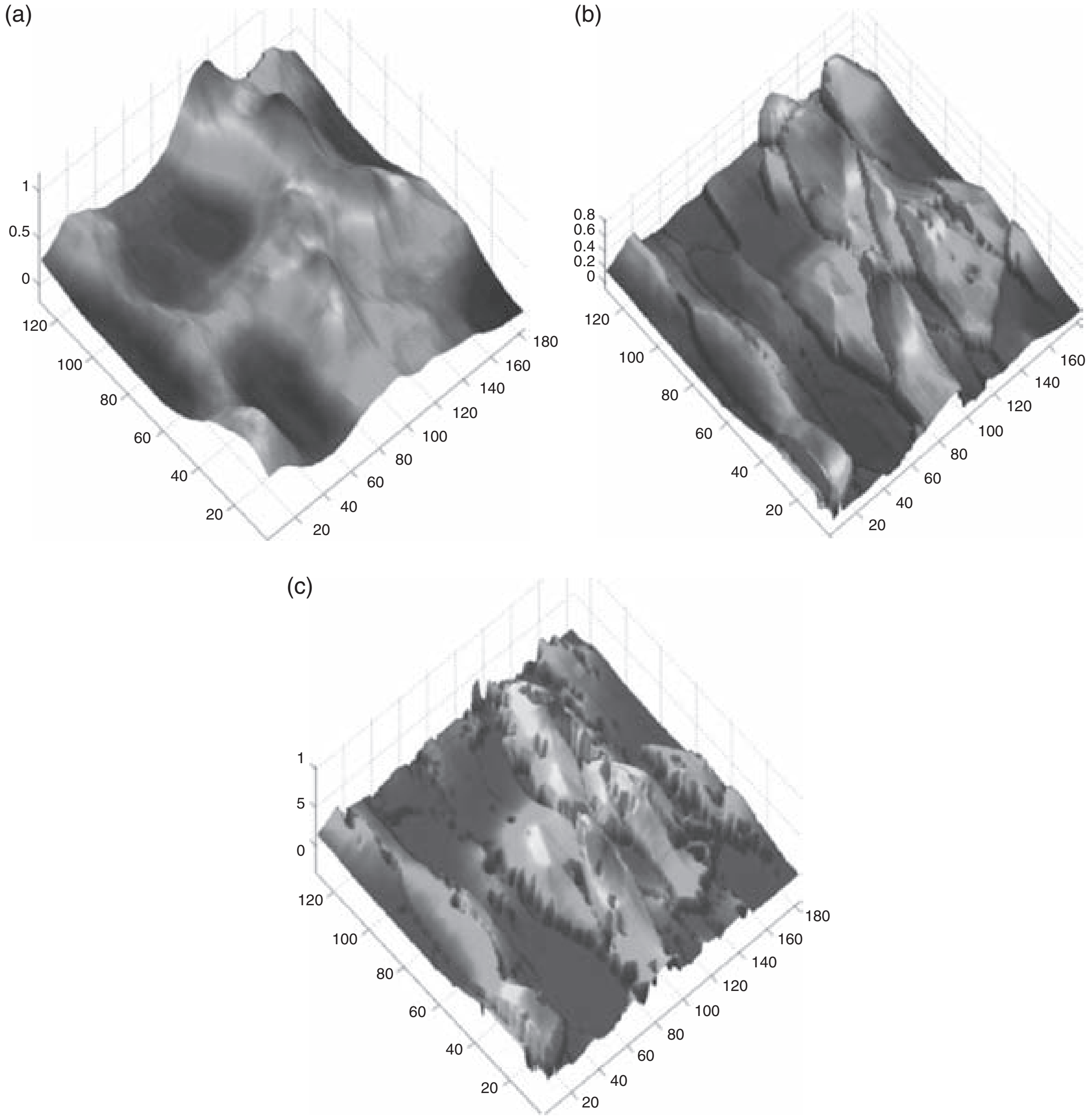


Figure 21.5 Example of resistant kernel results from Cushman et al. (2010b) showing predicted density of dispersing individuals in upland habitat under three hypotheses: (a) connectivity is unaffected by land use and roads and only a function of distance, (b) connectivity is reduced by roads but not by differences in land cover and land use, (c) connectivity is affected by roads and land use/land cover.

connectivity models, such as demographic and dispersal data, in addition to landscape characteristics.

There are three broad categories of models that simulate individual movement (raster based, vector based and network based), which differ according to whether the landscape is represented as fields, features or graphs. Conceived as fields, a landscape is a continuous surface defined by one or more variables (layers) that can be measured at any point within the field. Fields usually model continuous data such as elevation, or temperature gradients, but can also represent categorical data such as habitat classification. If movement through the landscape is dependent on the variables of the field, then raster-based movement rules are most appropriate. Features are discrete entities that occupy positions in space, such as lines (rivers, roads, hedgerows) and polygons (lakes, woodland). The interiors of polygons are considered to be homogeneous. Movement between features is usually simulated using vector-based models. Finally, graphs represent the positional relationship between discrete elements in a landscape; a graph consists of a set of nodes that may represent continuous or categorical data, and a set of edges, which are dimensionless but describe how the nodes are connected to one another. Edges may be temporally referenced, indicating changes in graph connectivity over time. Network-based models are used to simulate IB movement in graphs. Examples of all three of these categories are discussed below.

Movement rules and models

Regardless of whether movement models are raster, vector or network based, they encode a series of rules that predict how the dispersal behaviour of individual animals is expected to interact with the spatial pattern of landscape structure (King & With 2002). Variations in patch quality, boundaries between patches, the nature of the mosaic, and overall landscape connectivity all affect the permeability of the landscape to dispersing individuals (Wiens 1997). The limited empirical information on the behavioural responses of animals to landscape structure (Turner et al. 1995; Lima & Zollner 1996) means that model parameters are usually based on observed habitat preference, dispersal rates in different patches, and how the energetic costs of crossing a landscape affect distance moved as well as direction taken. For example, the rules employed by Boone & Hunter (1996) simulated IB searching behaviour in grizzly bears by encoding permeability into the cells of habitat patches. Highly permeable habitat patches produced straight paths and long distance movements whereas patches of low permeability caused convoluted paths and short displacement.

Raster-based models

Raster- or grid-based representations of the landscape permit the greatest flexibility with which movement interacts with the landscape, and are appropriate where the dispersal matrix is heterogeneous (Wiegand et al. 1999). The landscape is represented as a series of tessellated shapes, usually square grid cells, and the model animal moves through each cell based on movement rules.

An advantage of this approach to modelling is the inclusion of a clear relationship between a cell and its neighbours, facilitating the description of local interactions by state transition rules. Each cell stores its own state variables that influence the decisions made by individuals through the landscape it represents. However, there are three principal disadvantages to raster-based models.

- The resolution of the grid is limited by memory capacity and simulation speed, and raster-based models have a tendency to be computationally demanding.
- The fixed spatial structure implies a fixed relationship between the spatial scale in the simulation and the scale of individual movements of the organism investigated.
- The geometry chosen to represent landscape in raster-based models (i.e. square grid, hexagonal grid, Dirichlet tessellation, etc.) can substantially affect the simulated behaviour of the individual dispersers even if the rules for movement and settlement are the same between different geometries (Holland et al. 2007).

Vector-based models

Vector-based models simulate organisms dispersing through continuous or homogeneous landscapes. If the motivations for these movements are random or quasi-random search patterns, they can be simulated using correlated random walk algorithms (Kareiva & Shigesada 1983). Alternatively, if individual movements are targeted searches for resources with a particular spatial or temporal distribution, movement decisions will be informed by the underlying landscape structure. Finally, if motivation for movement is prompted by the desire to avoid or join conspecifics, it will result in density-dependent movement rules. Where motivations for movement are known and appropriate, IB models benefit from vector-based dispersal simulations, which are less computationally demanding than the raster-based alternative.

Network-based models

Network-based models differ from the other types in that they do not include a continuous representation of the landscape. Rather, connectivity between locations is represented by an edge between nodes. Network-based models usually specify an *a priori* representation of patch size, patch adjacency and other criteria (e.g. Lookingbill et al. 2010). Edges are formed when movement is possible between nodes. Dispersal corridors can be represented as nodes as well as edges in network visualizations of a landscape used as analytic connectivity models (McRae et al. 2008). They calculate walks through the network that minimize total weight, suggesting optimal pathways for dispersal. In IB models, network-based landscapes are utilized probabilistically (Lookingbill et al. 2010; Morzillo et al. 2011), and may result in biologically plausible but analytically suboptimal solutions. Graph-theoretic approaches to network analysis can be applied to the utilized networks of IB models to identify the nodes and edges that maintain cohesion of the network. For example, Gurnell et al. (2006) identified routes of entry for invasive grey squirrels into potential conservation areas for the endangered red squirrel in northern England through network analysis.

Corridors based on shifting climate envelopes

This approach produces ’temporal corridors’ that track how a species’ climatic envelope (suitable temperature and moisture regimes) might move across a landscape under climate change scenarios. Like some types of individual-based models, this approach avoids the concept of resistance that is central to most previous approaches. The heart of this approach is either a dispersal chain model (Williams et al. 2005) or a network flow model (Phillips et al. 2008), either of which identifies cells with suitable climate envelopes that are spatially contiguous for long enough to allow the species to establish new populations in cells as they become suitable. Although dispersal chain and network flow models are conceptually sound, they depend completely on the outputs of three other models, namely models of future emissions of greenhouse gasses, models of future climate resulting from how the atmosphere and oceans respond to these emissions, and climate envelope models for the focal species. Unfortunately, each of these latter three models is plagued with massive uncertainty (summarized in Beier & Brost 2010). In the future, ensemble modelling (building many alternative corridors based on various combinations of emission scenarios, circulation models and climate envelope models) might identify corridors robust across the range of assumptions in the ensemble.

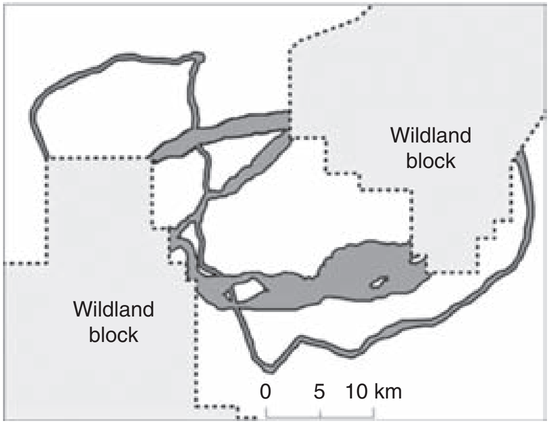
Beyond single species

From optimal corridors for single species to linkage designs for multiple species

Up to this point, we have described methods of mapping an optimal corridor, or areas important for connectivity, for a single species. Beier et al. (2008) proposed the term *linkages* to denote lands intended to support movement of

Box 21.3 Example of optimizing multispecies linkage

A hypothetical linkage design including optimal corridors for eight focal species, expanded to include patches of modelled breeding habitat for an additional five focal species for which corridor models were not appropriate, and a narrow riparian strand for fishes. Each strand needs to be >1 km wide in order to create large interior spaces free of edge effects, support meta-populations of species needing multiple generations to achieve gene flow through the corridor, and support ecological processes more complex than animal movement.



multiple focal species and ecosystem processes. To design linkages, conservation planners can select a suite of representative focal species suitable to serve as a collective umbrella for the entire biota. For instance, each of 27 linkage plans in California and Arizona (Beier et al. 2006, 2007) was designed to meet the needs of 10–30 focal mammals, reptiles, fishes, amphibians, plants and invertebrates. Focal species included species requiring dispersal for meta-population persistence, species with short or habitat-restricted dispersal movements, species tied to an important ecological process (e.g. predation, pollination, fire regime), and species reluctant to traverse barriers in the planning area. Although large carnivores are appropriate focal species and flagships (Servheen et al. 2001; Singleton et al. 2002), most of them are highly mobile habitat generalists and thus inadequate umbrellas for other species (Beier et al. 2009; Minor & Lookingbill 2010).

A simple unweighted union of single-species corridors is an obvious way to produce a linkage design to promote the goal of 'no species left behind' (Beier et al. 2006, 2007; Adriaensen et al. 2007; Cushman et al. 2011) (Box 21.3). But corridor models are not appropriate for some focal species, such as many flying animals, that do not move across the landscape in pixel-to-pixel fashion. To support movement of these species, Beier et al. (2008) recommend draping maps of known or modelled breeding habitat over the union of corridors, and enlarging the union to include patches that would decrease the inter-patch distances that dispersers would need to cross. The linkage design should be further expanded to include major riverine connections, which provide natural corridors for aquatic and some upland organisms, and promote other ecological processes and flows such as movement of sediment, water and nutrients.

Coarse-filter linkage designs for climate change

Climate change poses a challenge to all types of conservation planning, including linkage design. As climate changes, existing land covers in some planning areas will not merely shift but will disappear as plant associations reassemble (Hunter et al. 1988; Lovejoy & Hannah 2005). Linkage designs should be robust to such changes, and should allow species to shift their ranges into and out of the planning area. To address this, one could attempt to model corridors for the shifting climate envelopes of all species (above). A simpler alternative is to design linkages with a coarse-filter approach based on the abiotic drivers of land cover and species distributions (Hunter et al. 1988; Anderson & Ferree 2010). This idea is grounded in the foundational ecological concept (Jenny 1941; Amundson & Jenny 1997) that biodiversity at any point in time is determined by the interaction of the recent species pool with climate, soils and topography.

Beier & Brost (2010) and Brost & Beier (2012) developed multivariate procedures to identify *land facets*, defined as recurring landscape units with uniform topographic and soil attributes, from readily available digital maps of elevation and soils. They used multivariate dissimilarity as a measure of pixel resistance for each land facet type. Finally, they used least-cost modelling to design land facet corridors, and joined these corridors into a linkage design. Other coarse-filter approaches are feasible. For instance, Rouget et al. (2006) suggest that species will shift their ranges by sequentially colonizing areas that lie along the most gentle and monotonic temperature gradients. Assuming these gradients in temperature are conserved in a changing climate, it may be possible to identify corridors along today's most gentle and monotonic temperature gradients, without the need for uncertain models of future climate.

Linkage designs should be produced by a combination of coarse-filter and focal species approaches. In each of three landscapes, Beier & Brost (in preparation) developed two linkages designs – one based on land facets and the other on focal species. The land facet linkage designs included optimal corridors for 25 of 28 focal species, whereas the focal species designs encompassed optimal corridors for 21 of 32 land facets. Neither approach on its own was likely to meet all conservation goals.

Validation of predicted corridors

Corridors resulting from models have sometimes been criticized because they lack supporting movement data (Simberloff et al. 1992; Rosenberg et al. 1997) and because they may contain errors in model parameters or incorrect assumptions (Spear et al. 2010). Therefore, additional vetting of modelled corridors in the field is strongly recommended.

Many field studies have evaluated the efficacy of existing corridors, such as corridors that follow linear features like fencerows or rivers (Hill 1995; Castellón & Sieving 2006), or that were constructed as part of experimental landscapes (Berggren et al. 2002; Haddad et al. 2003). There have also been tests of species' response to conservation action in established corridors (Duke at al. 2001; Shepherd & Whittington 2006). But field testing of modelled corridors, like the ones described in this chapter, have been scarce.

Modelled corridors may cover large spatial extents and span multiple land ownerships and management types, or even national borders, making the collection of field data logistically complex and resource intensive. If corridors are modelled for dispersal movement, capturing infrequent dispersal events is akin to finding a needle in a haystack, so collecting sufficient data to reliably test predicted corridors can be difficult. Finally, modelled corridors can only be truly validated if movement through the corridor is documented along with the outcome for which the corridor was intended, whether that be by successful migration to summer or winter ranges, successful recolonization of habitat patches, safe passage across a road, demographic rescue, or successful breeding and gene flow.

Even if all aspects of linkage cannot be validated, a partial field study will add confidence and transparency to a corridor project. For example, Clevenger et al. (2002) developed two habitat models for black bears, one based on expert opinion and the other based on data from the literature. They identified road crossing zones from these models, and using data on crossings by real bears, they tested if the predicted linkages were used more than would be expected by chance. They found that the linkage models based on data from the literature outperformed the expert opinion models. The authors indicated that the expert opinion models may not have performed as well due to an overestimation of the importance of riparian habitat.

As an additional example of empirical field validation of corridors, Quinby (2006) used existing data from the annual breeding bird survey to test the utility of a proposed corridor. More bird species were found inside the corridor than outside it, confirming its validity. Chardon et al. (2003) used presence/absence data on the speckled wood butterfly from two different landscapes to compare the explanatory power of Euclidean distance and effective-distance connectivity models. They found that cost-distance was better able to predict connectivity than Euclidean distance. Zeller et al. (2011) used interviews with local residents to collect detection/non-detection data on jaguars and seven prey species in a grid-based design. The data were analysed by a site-occupancy model to determine probability of habitat use inside and outside the modelled corridor. It was found that probabilities of habitat use were mostly higher outside the modelled corridor, a conclusion which prompted a redesign of the final corridor.

The fact that there have been few studies to validate corridor models calls for more attention to this topic. Corridor validation techniques not only need to be improved upon, they need to be accessible to researchers and land managers working at different scales and on various species. Bridging the gap between corridor identification and corridor implementation will increasingly depend upon these validation studies, since land managers do not want to be left to implement a corridor of questionable efficacy, or be blamed for creating a sub-par corridor while more appropriate lands are unprotected from development and fragmentation (Hess & Fischer 2001; Morrison & Boyce 2008).

Conclusions

Population connectivity is critical for maintaining viable regional populations in the short term and to enable species to shift their geographic range in response to future climate change and other pressures such as land use change. In this chapter, we described the state of the art in quantitative corridor and connectivity modelling approaches. The first step in most quantitative connectivity analyses is to estimate and map landscape resistance. Traditional expert opinion is less useful for developing landscape resistance maps now that new and effective approaches using empirical data provide a much more reliable and robust means to map landscape resistance. There are a number of ways to predict or describe connectivity from resistance surfaces. Least-cost paths, least-cost corridors, circuit theory, centrality analyses, and resistant kernels are all powerful approaches suitable for different objectives. The efficient application of corridor analyses to future applied conservation problems must develop corridor designs to maintain connectivity for multiple species, and under changing climate. Finally, empirical validation of predicted corridors and linkages is essential to demonstrate their functionality and guide improvement of future corridor designs.

References

Adriaensen, F., Chardon, J.P., de Blust, G., *et al.* (2003) The application of 'least-cost' modelling as a functional landscape model. *Landscape and Urban Planning*, **64**, 233–247.

Adriaensen, F., Githiru, M., Mwang'ombe, J., Matthysen, E. & Lens, L. (2007) *Restoration and*

Increase of Connectivity among Fragmented Forest Patches in the Taita Hills, Southeast Kenya. Part II technical report, CEPF project 1095347968, University of Gent, Gent, Belgium.

Ahuja, R.K., Magnanti, T.L. & Orlin, J.B. (1993) *Network Flows: Theory, Algorithms, and Applications*. Prentice Hall, Englewood Cliffs, NJ.

Amundson, R. & Jenny, H. (1997) On a state factor model of ecosystems. *BioScience*, **47**, 536–543.

Anderson M.G. & Ferree, C.E. (2010) Conserving the stage: climate change and the geophysical underpinnings of species diversity. *PLoS ONE*, **5**(7), e11554.

Beier, P. & Brost, B. (2010) Use of land facets to plan for climate change: conserving the arenas, not the actors. *Conservation Biology*, **24**, 701–710.

Beier, P., Penrod, K., Luke, C., Spencer, W. & Cabanero, C. (2006) South Coast missing linkages: restoring connectivity to wildlands in the largest metropolitan area in the USA. In: *Connectivity Conservation* (eds K.R. Crooks & M.A. Sanjayan), pp.555–586. Cambridge University Press, Cambridge.

Beier, P., Majka, D. & Bayless, T. (2007) *Linkage Designs for Arizona's Missing Linkages*. Arizona Game and Fish Department, Phoenix. www.corridordesign.org/arizona/

Beier, P., Majka, D.R. & Spencer, W.D. (2008) Forks in the road: choices in procedures for designing wildland linkages. *Conservation Biology*, **22**, 836–851.

Beier, P., Majka, D.R. & Newell, S.L. (2009) Uncertainty analysis of least-cost modeling for designing wildlife linkages. *Ecological Applications*, **19**, 2067–2077.

Berggren, A., Birath, B. & Kindvall, O. (2002) Effect of corridors and habitat edges on dispersal behavior, movement rates, and movement angles in Roesel's bush-cricket (*Metrioptera roeseli*). *Conservation Biology*, **16**, 1562–1569.

Boone, R.B. & Hunter, M.L. (1996) Using diffusion models to simulate the effects of land use on grizzly bear dispersal in the Rocky Mountains. *Landscape Ecology*, **11**, 51–64.

Brost, B. & Beier, P. (2012) Use of land facets to design linkages for climate change. *Ecological Applications*, **22(**1), 87–103.

Brost, B.M. & Beier, P. (in press) Comparing linkage designs based on land facets to linkage designs based on focal species. *Journal of Applied Ecology*.

Brown, J.H. & Kodric-Brown, A. (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, **58**, 445–449.

Bunn, A.G., Urban, D.L. & Keitt, T. (2000) Landscape connectivity: a conservation application of graph theory. *Journal of Environmental Management*, **59**(4), 265–278.

Carroll, C. (2010) *Connectivity Analysis Toolkit (CAT) Manual*. Klamath Center for Conservation Research. www.connectivitytools.org

Carroll, C., McRae, B.H. & Brookes, A. (2011) Use of linkage mapping and centrality analysis across habitat gradients to conserve connectivity of Gray Wolf populations in Western North America. *Conservation Biology*, **26**(1), 78–87.

Castellón, T.D. & Sieving, K.E. (2006) An experimental test of matrix permeability and corridor use by an endemic understory bird. *Conservation Biology*, **20**: 135–145.

Chandra, A.K., Raghavan, P., Ruzzo, W.L., Smolensky, R. & Tiwari, P. (1997) The electrical resistance of a graph captures its commute and cover times. *Computational Complexity*, **6**(4), 312–340.

Chardon, J.P., Adriaensen, F. & Matthysen, E. (2003) Incorporating landscape elements into a connectivity measure: a case study for the Speckled Wood Butterfly (*Pararge aegeria* L.). *Landscape Ecology*, **18**, 561–573.

Clevenger, A.P., Wierzchowski, J., Chruszcz, B. & Gunson, K. (2002) GIS-generated, expert-based models for identifying wildlife habitat linkages and planning mitigation passages. *Conservation Biology*, **16**, 503–514.

Compton, B., McGarigal, K., Cushman, S.A. & Gamble, L. (2007) A resistant kernel model of connectivity for vernal pool breeding amphibians. *Conservation Biology*, **21**, 788–799.

Coulon, A., Morellet, N., Goulard, M., Cargnelutti, B., Angibault, J.-M. & Hewston, A.J. (2008) Inferring the effects of landscape structure on roe deer (Capreolus capreolus) movements using a step selection function. *Landscape Ecology*, **23**, 603–614.

Cushman, S.A. (2006) Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biological Conservation*, **128**, 231–240.

Cushman, S.A. & Lewis, J. (2010) Movement behavior explains genetic differentiation in American black bear. *Landscape Ecology*, **25**, 1613–1625.

Cushman, S.A., Chase, M. & Griffin, C. (2005) Elephants in space and time. *Oikos*, **109**, 331–341.

Cushman, S.A., Schwartz, M.K., Hayden, J. & McKelvey, K. (2006) Gene flow in complex landscapes: confronting models with data. *American Naturalist*, **168**, 486–499.

Cushman, S.A., McKelvey, K. & Schwartz, M.K. (2008) Using empirically derived source-destination models to map regional conservation corridors. *Conservation Biology*, **23**, 368–376.

Cushman, S.A., Chase, M.J. & Griffin, C. (2010a) Mapping landscape resistance to identify corridors and barriers for elephant movement in southern Africa. In: *Spatial Complexity, Informatics and Wildlife Conservation* (eds S.A. Cushman & F. Huettman), pp.349–368. Springer, Tokyo.

Cushman, S.A., Compton, B.W. & McGarigal, K. (2010b) Habitat fragmentation effects depend on complex interactions between population size and dispersal ability: Modeling influences of roads, agriculture and residential development across a range of lifehistory characteristics. In: *Spatial Complexity, Informatics and Wildlife Conservation* (eds S.A. Cushman & F. Huettman), pp.369–387. Springer, Tokyo.

Cushman, S.A., Landguth, E.L. & Flather, C.H. (2011) *Climate Change and Connectivity: Assessing Landscape and Species Vulnerability*. Final Report to USFWS Great Plains Landscape Conservation Co-operative.

Doyle, P.G. & Snell, J.L. (1984) *Random Walks and Electric Networks*. Mathematical Association of America, Washington, D.C.

Duke, D.L., Hebblewhite, M., Paquet, P.C., Callaghan, C. & Percy, M. (2001) Restoration of a large carnivore corridor in Banff National Park, Alberta. In: *Large Mammal Restoration: Ecological and Sociological Challenges in the 21st Century* (eds D.S. Maehr, R.F. Noss & J.F. Larkin), pp.261–275. Island Press, Washington, D.C.

Fagan, W.F. & J.M. Calabrese. (2006) Quantifying connectivity: balancing metric performance with data requirements. In: *Connectivity Conservation* (eds K.R. Crooks & M.A. Sanjayan), pp.297–317. Cambridge University Press, Cambridge.

Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution and Systematics*, **34**, 487–515.

Fahrig, L., Pedlar, J.H., Pope, S.E., Taylor, P.D. & Wegner, J.F. (1995) Effect of road traffic on amphibian density. *Biological Conservation*, **73**, 177–182.

Freeman, L.C., Borgatti S.P. & White, D.R. (1991) Centrality in valued graphs: a measure of betweenness based on network flow. *Social Networks*, **13**, 141–154.

Gamble, L.R., McGarigal, K. & Compton, BW. (2007) Fidelity and dispersal in the pond-breeding amphibian, *Ambystoma opacum*: implications for spatio-temporal population dynamics and conservation. *Biological Conservation*, **139**, 247–257.

Gibbs, J.P. (1998) Amphibian movements in response to forest edges, roads, and streambeds in southern New England. *Journal of Wildlife Management*, **62**, 584–589.

Guerry, A.D. & Hunter, M.L. Jr (2002) Amphibian distributions in a landscape of forests and agriculture: an examination of landscape composition and configuration. *Conservation Biology*, **16**, 745–754.

Gurnell, J., Rushton, S.P., Lurz, P.W., *et al*. (2006) Squirrel poxvirus: landscape scale strategies for managing disease threat. *Biological Conservation*, **131**, 287–295.

Haddad, N.M & Baum, K.A. (1999) An experimental test of corridor effects on butterfly densities. *Ecological Applications*, **9**, 623–633.

Haddad, N.M., Bowne, D.R., Cunningham, A., *et al*. (2003) Corridor use by diverse taxa. *Ecology*, **84**, 609–615.

Harrison, S. (1991) Local extinction in a meta population context: an empirical evaluation. In: *Metapopulation Dynamics: Empirical and Theoretical Investigations*. (eds M.E. Gilpin & I. Hanski), pp. 73–88. Academic Press, London.

Heller, N.E. & Zavaleta, E.A. (2009) Biodiversity management in the face of climate change: a review of 22 years of recommendations. *Biological Conservation*, **142**, 14–32.

Hess, G.R. & Fischer, R.A. (2001) Communicating clearly about conservation corridors. *Landscape and Urban Planning*, **55**, 195–208.

Hill, C.J. (1995) Linear strips of rainforest vegetation as potential dispersal corridors for rainforest insects. *Conservation Biology*, **9**, 1559–1566.

Holland, E.P., Aegerter, J.N., Dytham, C. & Smith, G.C. (2007) Landscape as a model: the importance of geometry. *PLoS Computational Biology*, **3**, 1979–1992.

Hunter, M.L. Jr, Jacobson, G.L. Jr & Webb, T. III (1988) Paleoecology and the coarse-filter approach to maintaining biological diversity. *Conservation Biology*, **2**, 375–385.

Jenny, H. (1941) *Factors of Soil Formation: A System of Quantitative Pedology*. McGraw-Hill, New York.

Kareiva, P.M. & Shigesada, N. (1983) Analyzing insect movement as a correlated random walk. *Oecologia*, **56**, 234–238.

King, A.W. & With, K.A. (2002) Dispersal success on spatially structured landscapes: when do spatial pattern and dispersal behavior really matter? *Ecological Modelling*, **147**, 23–39.

Landguth, E.L., Cushman, S.A., Murphy, M.A. & Luikart, G. (2010) Relationships between migration rates and landscape resistance assessed using individual-based simulations. *Molecular Ecology Resources*, **10**, 854–862.

Landguth, E.L., Hand, B.K., Glassy, J., Cushmann, S.A. & Sawaya, M. (2011) UNICOR: a species connectivity and corridor network simulator. *Ecography*, **35**, 9–14.

Lima, S.L. & Zollner, P.A. (1996) Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution*, **11**, 131–135.

Lookingbill, T.R., Gardner, R.H., Ferrari, J.R. & Keller, C.E. (2010) Combining a dispersal model with network theory to assess habitat connectivity. *Ecological Applications*, **20**, 427–441.

Lovejoy, T.E. & Hannah, L. (eds) (2005) *Climate Change and Biodiversity*. Yale University Press, New Haven, CT.

McGarigal, K. & Cushman, S.A. (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecological Applications*, **12**(2), 335–345.

McRae, B.H. (2006) Isolation by resistance. *Evolution*, **60**, 1551–1561.

McRae, B.H. & Kavanagh, D.M. (2011) *Linkage Mapper Connectivity Analysis Software*. The Nature Conservancy, Seattle, WA. www.waconnected.org/habitat-connectivity-mapping-tools.php

McRae, B.H. & Shah, V.B. (2009) *Circuitscape User Guide*. University of California, Santa Barbara, CA. www.circuitscape.org

McRae, B.H., Dickson, B.G., Keitt, T.H. & Shah, V.B. (2008) Using circuit theory to model connectivity in ecology and conservation. *Ecology*, **10**, 2712–2724.

Minor, E.S. & Lookingbill, T.R. (2010) Network analysis of protected-area connectivity for mammals in the United States. *Conservation Biology*, **24**(6), 1549–1558.

Minor, E.S. & Urban, D.L. (2007) Graph theory as a proxy for spatially explicit population models in conservation planning. *Ecological Applications*, **17**, 1771–1782.

Morrison, S.A. & Boyce, W.M. (2009) Conserving connectivity: some lessons from Mountain Lions in Southern California. *Conservation Biology*, **23**(2), 275–285.

Morzillo, A.T., Ferrari, J.R. & Liu, J.G. (2011) An integration of habitat evaluation, individual based modeling, and graph theory for a potential black bear population recovery in southeastern Texas, USA. *Landscape Ecology*, **26**, 69–81.

Newman, M.E. (2005) A measure of betweenness centrality based on random walks. *Social Networks*, **27**, 39–54.

Osborn, F.V. & Parker, G.E. (2003) Linking two elephant refuges with a corridor in the communal lands of Zimbabwe. *African Journal of Ecology*, **41**, 68–74.

Phillips, S.J., Williams, P., Midgley, G. & Archer, A. (2008) Optimizing dispersal corridors for the Cape Proteaceae using network flow. *Ecological Applications*, **18**, 1200–1211.

Pinto N. & Keitt, T.H. (2009) Beyond the least-cost path: evaluating corridor redundancy using a graph theoretic approach. *Landscape Ecology*, **24**, 253–266.

Quinby, P.A. (2006) Evaluating regional wildlife corridor mapping: a cast study of breeding birds in Northern New York State. *Adirondack Journal of Environmental Studies*, **13**, 27–33.

Rayfield, B., Fortin, M.J. & Fall, A. (2011) Connectivity for conservation: a framework to classify network measures. *Ecology*, **92**, 847–858.

Reh, W. & Seitz, A. (1990) The influence of land use on the genetic structure of populations of the common frog (Rana temporaria). *Biological Conservation*, **54**, 239–249.

Rosenberg, D.K., Noon, B.R. & Meslow, E.C. (1997) Biological corridors: form, function, and efficacy. *BioScience*, **47**, 677–687.

Rouget, M., Cowling, R.M., Lombard, A.T., Knight, A.T. & Kerley, G.I. (2006) Designing large-scale conservation corridors for pattern and process. *Conservation Biology*, **20**, 549–561.

Semlitsch, R.D., Bodie, J.R. (2003) Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. *Conservation Biology*, **17**, 1219–1228.

Seoane, J., Bustamante, J. & Diaz-Delgado, R. (2005) Effect of expert opinion on the predictive ability of environmental models of bird distribution. *Conservation Biology*, **19**, 512–522.

Servheen, C., Walker, J.S. & Sandstrom, P. (2001) Identification and management of linkage zones for grizzly bears between the large blocks of public land in the northern Rocky Mountains. In: *Proceedings of the 2001 International Conference on Ecology and Transportation* (eds C.L. Irwin, P. Garrett & K.P. McDermott), pp. 161–179. Center for Transportation and the Environment, North Carolina State University, Raleigh, NC.

Shanahan, D.F., Possingham, H.P. & Riginos, C. (2011) Models based on individual-level movement predict spatial patterns of genetic relatedness for two Australian forest birds. *Landscape Ecology*, **26**, 137–148.

Shepherd, B. & Whittington, J. (2006) Response of wolves to corridor restoration and human use management. *Ecology and Society*, **11**. www.ecologyandsociety.org/vol11/iss2/art1

Shirk, A., Wallin, D.O., Cushman, S.A., Rice, R.C. & Warheit, C. (2010) Inferring landscape effects on gene flow: a new multi-scale model selection framework. *Molecular Ecology*, **19**, 3603–3619.

Short Bull, R.A., Cushman, S.A., Mace, R., *et al.* (2011) Why replication is important in landscape genetics: American black bear in the Rocky Mountains. *Molecular Ecology*, **20**(6), 1092–1107.

Simberloff, D., Farr, J.A., Cox, J. & Mehlman, D.W. (1992) Movement corridors: conservation bargains or poor investments? *Conservation Biology*, **6**, 493–504.

Singleton, P.H., Gaines, W. & Lehmkuhl, J.F. (2002) *Landscape Permeability for Large Carnivores in Washington: A Geographic Information System Weighted-Distance and Least-Cost Corridor Assessment*. USDA Forest Service Research Paper, PNW-RP 549. Pacific Northwest Field Station, OR.

Spear, S.F., Balkenhol, N., Fortin, M.J., McRae, B.H. & Scribner, K. (2010) Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. *Molecular Ecology*, **19**, 3576–3591.

Spencer, W.D., Beier, P., Penrod, K. (2010) *California Essential Habitat Connectivity Project: A Strategy for Conserving a Connected California*. Report prepared for California Department of Transportation and California Department of Fish and Game. www.dfg.ca.gov/habcon/connectivity

Turner, M.G., Arthaud, G.J., Engstrom, R.T., *et al.* (1995) Usefulness of spatially explicit population models in land management. *Ecological Applications*, **5**, 12–16.

Urban, D. & Keitt, T. (2001) Landscape connectivity: a graph-theoretic perspective. *Ecology*, **82**, 1205–1218.

Van Dyck, H. & Baguette, M. (2005) Dispersal in fragmented landscapes: routine or special movements? *Basic and Applied Ecology*, **6**, 535–545.

Van Horne, B. (1983) Density as a misleading indicator of habitat quality. *Journal of Wildlife Management*, **47**, 893–901.

Waples, R.S. (1998) Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. *Journal of Heredity*, **89**, 438–450.

Wasserman, T.N., Cushman, S.A., Schwartz, M.K. & Wallin, D.O. (2010) Spatial scaling and multi-model inference in landscape genetics: *Martes americana* in northern Idaho. *Landscape Ecology*, **25**, 1601–1612.

Weyrauch, S.L. & Grubb, T.C. (2004) Patch and landscape characteristics associated with the distribution of woodland amphibians in an agricultural fragmented landscape: an information-theoretic approach. *Biological Conservation*, **115**(3), 443–450.

WHCWG (2010) *Washington Connected Landscapes Project: Statewide Analysis*. Washington Wildlife Habitat Connectivity Working Group, Washington Departments of Fish and Wildlife, and Transportation, Olympia, WA. www.waconnected.org

Wiegand, T., Moloney, K.A., Naves, J. & Knauer, F. (1999) Finding the missing link between landscape structure and population dynamics: a spatially explicit perspective. *American Naturalist*, **154**, 605–627.

Wiens, J.A. (1997) Metapopulation dynamics and landscape ecology. In: *Metapopulation Dynamics, Ecology, Genetics, and Evolution* (eds I. Hanski & M. Gilpin), pp.43–62. Academic Press, London.

Williams, P., Hannah, L., Andelman, S., *et al.* (2005) Planning for climate change: identifying minimum-dispersal corridors for the Cape Proteaceae. *Conservation Biology*, **19**, 1063–1074.

Wilson, P.J. & Provan, J. (2003) Effect of habitat fragmentation on levels and patterns of genetic diversity in natural populations of peat moss Polytrichum commone. *Proceedings of the Royal Society Series B: Biological Sciences*, **270**, 881–886.

With, K.A., Gardner, R.H. & Turner, M.G. (1997) Landscape connectivity and population distributions in heterogeneous environments. *Oikos*, **78**, 151–169.

Zeller, K.A., Nijhawan, S., Salom-Pérez, R., Potosme, S.H. & Hines, J.E. (2011) Integrating occupancy modeling and interview data for corridor identification: a case study for jaguars in Nicaragua. *Biological Conservation*, **144**, 892–901.

PLANT ECOLOGY

Ongoing accumulation of plant diversity through habitat connectivity in an 18-year experiment

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Deleterious effects of habitat fragmentation and benefits of connecting fragments could be significantly underestimated because changes in colonization and extinction rates that drive changes in biodiversity can take decades to accrue. In a large and well-replicated habitat fragmentation experiment, we find that annual colonization rates for 239 plant species in connected fragments are 5% higher and annual extinction rates 2% lower than in unconnected fragments. This has resulted in a steady, nonasymptotic increase in diversity, with nearly 14% more species in connected fragments after almost two decades. Our results show that the full biodiversity value of connectivity is much greater than previously estimated, cannot be effectively evaluated at short time scales, and can be maximized by connecting habitat sooner rather than later.

Habitat loss and fragmentation are leading threats to biodiversity in ecosystems across the globe (*1*–*4*). In a world replete with small, isolated fragments, where 70% of the world's forest area is within just 1 km of an edge, biodiversity loss is mounting (*1*). Increasing habitat connectivity is a key conservation strategy to minimize biodiversity losses by facilitating dispersal and rescuing declining populations from extinction (*5*). However, it is not known if restoring connectivity among habitat fragments will increase biodiversity by promoting the colonization of new species.

A well-established body of ecological theory predicts the importance of connectivity for biodiversity. Metapopulation theory (*6*, *7*) illustrates how increasing connectivity is predicted to lead to greater regional population persistence by promoting colonization of new habitats, increasing recolonization of habitats where extinction has occurred (recolonization rescue), and buffering existing populations against extinction via increased immigration (demographic rescue). Metacommunity theory (*8*, *9*) and island biogeography theory (*10*) integrate these population-level effects of connectivity to yield predictions regarding biodiversity. These developments provide strong theoretical reasons to expect that modifying connectivity can increase biodiversity by increasing colonization and decreasing extinction, but they also caution that nonintuitive effects (e.g., synchronization of population dynamics or modification of interactions) are possible (*8*, *11*).

Despite the presumed importance of connectivity for community diversity in both basic and applied ecology (*12*, *13*), empirical evidence for predictions from theory has been mixed (*14*–*16*). A primary challenge in evaluating these predictions in empirical systems is that ecological processes vary greatly in space and time: The dynamic nature of colonization and extinction processes necessitates well-replicated, large-scale, and long-term studies to draw meaningful inference about the ultimate role of connectivity in affecting diversity. For example, changes in biodiversity due to either lost or restored connectivity do not occur instantaneously. In fragmented habitats, species can continue to persist for years before eventually going extinct (*17*), resulting in an "extinction debt" paid over decades or even centuries (*18*, *19*). Similarly, "colonization credits" can accrue when habitat connectivity is restored among species-impoverished habitats, catalyzing the potential for biodiversity gains (*20*–*23*). Species may not colonize immediately because of low dispersal rates, which are difficult to measure, making the extent of colonization credits unknown (*20*, *23*). This lack of information is important because colonization credits could forestall or even reverse extinction debt.

We tested the long-term effects of habitat connectivity on plant colonization and extinction dynamics and their resulting impacts on species richness over nearly two decades in a habitat fragmentation experiment at the Savannah River Site in South Carolina, USA. This experiment manipulates connectivity through the creation of habitat corridors—thin strips of habitat that connect otherwise isolated habitat fragments (*24*). Ten experimental landscapes each contain four 1.375-ha fragments of equal area that are either unconnected or connected to a central 1-ha fragment by a 150 m–by–25 m corridor (Fig. 1). Fragments and corridors are being restored to longleaf pine savanna, a threatened ecosystem within a global biodiversity hotspot (*25*), and are surrounded by dense pine plantations that limit herbaceous plant growth. For 18 years, we censused occupancy of all plant species as communities assembled after each restored fragment's creation. Connected and unconnected fragments were randomly assigned and did not differ in species richness at the start of the experiment [fig. S1; see also supplementary materials and methods (*26*)].

Habitat connectivity has increased rates of colonization and decreased rates of extinction. As communities assembled, connectivity increased the average annual species colonization rate by 5% and decreased the average annual extinction rate by 2% beyond expected successional dynamics (Fig. 2A and fig. S2). These apparently small differences in annual rates are persistent and have compounded over time, generating large increases in species richness in fragments connected by corridors, magnifying colonization credits (Fig. 2B and fig. S3). These impacts occur across 239 plant species with diverse life histories, including species of conservation and restoration concern from the longleaf pine ecosystem (fig. S6) and species that vary in their dispersal ability (fig. S7).

Higher colonization rates and lower extinction rates have shortened the average time for a species to colonize a fragment (Fig. 3) and have driven a large increase in plant species richness (Fig. 2B and figs. S3 and S5). Corridor-connected fragments now support, on average, 24 additional plant species compared with unconnected fragments (200 versus 176 in connected versus unconnected fragments, respectively; fig. S3), an increase of 14%. Notably, connectivity's effects on species richness continue to accumulate; our best-fit models of species richness differences over time show no asymptote. Moreover, connectivity's impacts on colonization and extinction rates remain consistent across the 18 years of this study (Fig. 2 and figs. S4 and S5) (*26*).

Our results underscore that typical experiments of 1 to 5 years in duration (*1*, *27*) likely underestimate the impact of long-term connectivity restoration on community diversity. Connectivity's impacts are not fully realized until the ongoing, lagged assembly processes and responses equilibrate. Theory from spatial ecology and community assembly predicts that connectivity's effect on diversity will eventually reach an asymptote because of local ecological processes constraining species richness (e.g., competition) and because local communities draw from a finite number of species in the region (*10*, *28*). Long-term empirical investigations of how landscape configuration alters colonization

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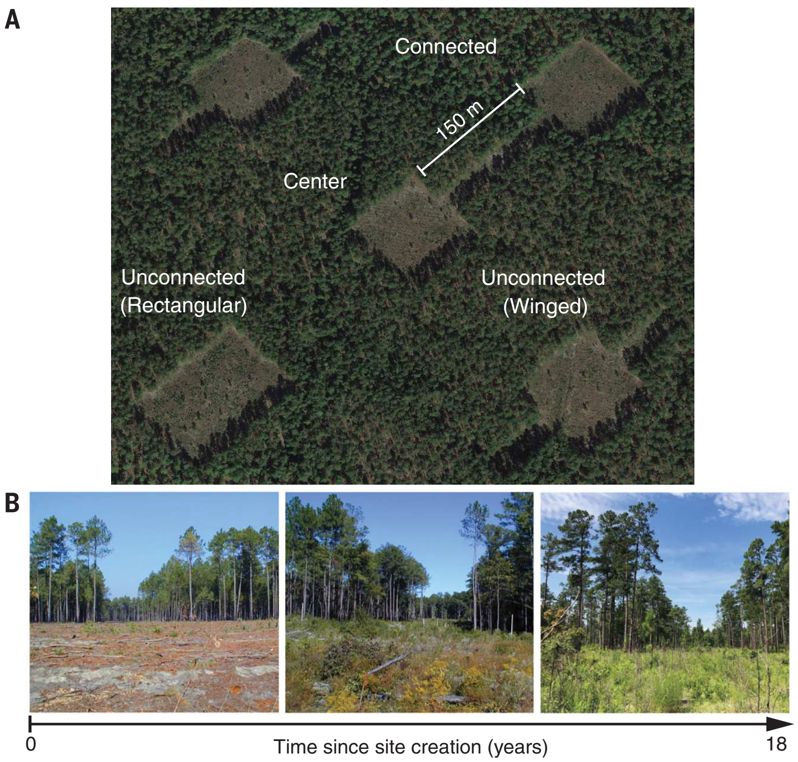

Fig. 1. A long-term habitat connectivity experiment. (**A**) One of 10 experimental landscapes (*N* = 10), each containing a center fragment that is connected or unconnected (winged and rectangular) to peripheral fragments of open longleaf pine savanna surrounded by dense pine plantations [additional details in (*26*)]. [Credit: Google Earth 2019] (**B**) Plant communities within fragments have assembled over nearly two decades and are being restored to native longleaf pine savanna using frequent, low-intensity fires that mimic the historic fire regime. See (*26*) for further information on the study design. [Credits (left to right): M. A. Burt, N. M. Haddad, and E. I. Damschen]

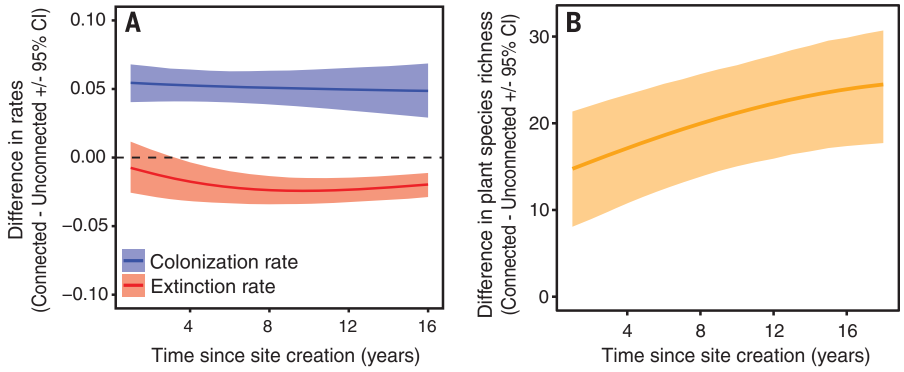

Fig. 2. Connectivity reduces extinction and increases colonization rates over two decades, resulting in accruals of species in connected fragments. (**A**) Average colonization rates are 5% greater and extinction rates are 2% lower for species in connected fragments than rates for those in unconnected fragments. These rates are constant over time. The net accrual of colonization credits increases biodiversity in connected fragments. (**B**) Plant species richness in connected fragments has increased at a greater rate than in unconnected fragments. Shown is the difference in estimated species richness over time, illustrating greater increases in richness in connected versus unconnected fragments. This rate increase has been consistent for nearly two decades and has resulted in connected fragments having 24 more plant species than unconnected fragments (fig. S3). A linear model (on the logit scale) is the best fit for the difference in species richness between connected and unconnected fragments over time (*26*). Shaded regions represent 95% confidence intervals.

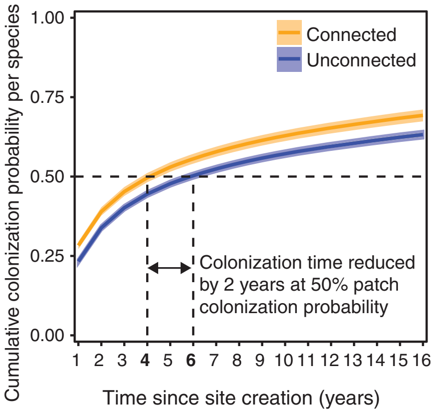

Fig. 3. Connectivity reduces colonization timing, resulting in colonization credits. The average cumulative probability of each individual species colonizing connected fragments is 1 to 6 years earlier than in unconnected fragments, resulting in reduced colonization lags and increased colonization credits. For example, the point at which a single species has a 50% likelihood of colonizing a habitat fragment (dotted lines) occurs a full 2 years earlier in connected versus unconnected fragments. Shaded regions represent 95% confidence intervals.

and extinction rates are critical for determining and predicting human-induced changes to the environment; communities will almost never exhibit instantaneous responses or equilibrial dynamics (*29*).

We show that connectivity directly alters colonization and extinction dynamics among fragments, providing mechanisms for observed landscape-level biodiversity patterns (*30*). Our results contrast with hypotheses that attribute biodiversity change to habitat area alone and those that do not attempt to isolate underlying mechanisms (*14*). In our study system, connectivity leads to wholesale temporal shifts in community assembly, driven by lags in colonization that generate colonization credits, regardless of whether an equilibrium is achieved. Connecting fragments with corridors results in a 1- to 6-year reduction in the time it takes an individual species to colonize new habitat fragments, relative to the time needed for colonization of unconnected fragments (Fig. 3). For example, the 50% likelihood of a single species colonizing a fragment (dotted lines in Fig. 3) occurs a full 2 years earlier in connected fragments than for that same species in unconnected fragments (Fig. 3). These temporal shifts in the speed of colonization (Fig. 3 and fig. S8) have unexplored and potentially important ramifications for time-dependent ecological processes (e.g., priority effects). Although less explored, our results also suggest that corridor-mediated changes in the movement of individuals and alleles may affect evolutionary processes by altering effective population size and gene flow (*31*). Our results raise the need for theory to better integrate temporal duration in conservation and management.

Conservation strategies to mitigate biodiversity losses due to habitat fragmentation and loss are urgently needed, and habitat corridors feature prominently in global conservation plans (*4*). Our study shows that efforts to increase connectivity will pay off over the long term. Conservation plans that ignore connectivity, such as plans that focus solely on habitat area, will leave unrealized the substantial, complementary, and persistent gains in biodiversity attributable specifically to landscape connectivity (*30*, *32*).

REFERENCES AND NOTES

1. N. M. Haddad *et al*., *Sci. Adv.* **1**, e1500052 (2015).
2. M. Pfeifer *et al*., *Nature* **551**, 187–191 (2017).
3. T. Newbold *et al*., *Nature* **520**, 45–50 (2015).
4. IPBES, "The IPBES assessment report on land degradation and restoration" [Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), 2018].
5. J. H. Brown, A. Kodric-Brown, *Ecology* **58**, 445–449 (1977).
6. R. Levins, *Bull. Entomol. Soc. Am.* **15**, 237–240 (1969).
7. I. Hanski, *Metapopulation Ecology* (Oxford Univ. Press, 1999).
8. M. Holyoak, M. A. Leibold, R. D. Holt, *Metacommunities: Spatial Dynamics and Ecological Communities* (Univ. of Chicago Press, 2005).
9. M. A. Leibold, J. M. Chase, *Metacommunity Ecology* (Princeton Univ. Press, 2018), vol. 59.
10. R. H. MacArthur, E. O. Wilson, *The Theory of Island Biogeography* (Princeton Univ. Press, 1967).
11. D. J. Earn, S. A. Levin, P. Rohani, *Science* **290**, 1360–1364 (2000).
12. E. O. Wilson, E. O. Willis, in *Ecology and Evolution of Communities*, M. L. Cody, J. M. Diamond, Eds. (Belknap Press, 1975), vol. 522, pp. 522–534.
13. R. K. Didham, V. Kapos, R. M. Ewers, *Oikos* **121**, 161–170 (2012).
14. L. Fahrig, *Annu. Rev. Ecol. Evol. Syst.* **48**, 1–23 (2017).
15. J. Aström, T. Pärt, *Ecology* **94**, 72–82 (2013).
16. N. M. Haddad *et al*., *Ecography* **40**, 48–55 (2017).
17. M. L. Rosenzweig, *Science* **284**, 276–277 (1999).
18. D. Tilman, R. M. May, C. L. Lehman, M. A. Nowak, *Nature* **371**, 65–66 (1994).
19. M. Kuussaari *et al*., *Trends Ecol. Evol.* **24**, 564–571 (2009).
20. S. T. Jackson, D. F. Sax, *Trends Ecol. Evol.* **25**, 153–160 (2010).
21. T. Naaf, J. Kolk, *Biol. Conserv.* **182**, 155–163 (2015).
22. J. Kolk, T. Naaf, M. Wulf, *Biol. Conserv.* **26**, 735–755 (2017).
23. I. Hanski, *Ann. Zool. Fenn.* **37**, 271–280 (2000).
24. K. R. Crooks, M. Sanjayan, Eds., *Connectivity Conservation: Maintaining Connections for Nature* (Cambridge Univ. Press, 2006).
25. R. F. Noss *et al*., *Divers. Distrib.* **21**, 236–244 (2014).
26. See supplementary materials.
27. E. I. Damschen, N. M. Haddad, J. L. Orrock, J. J. Tewksbury, D. J. Levey, *Science* **313**, 1284–1286 (2006).
28. H. V. Cornell, S. P. Harrison, *Annu. Rev. Ecol. Evol. Syst.* **45**, 45–67 (2014).
29. A. J. Miller-Rushing *et al*., *Biol. Conserv.* **232**, 271–273 (2019).
30. N. M. Haddad, R. D. Holt, R. J. Fletcher Jr., M. Loreau, J. Clobert, *Ecography* **40**, 1–8 (2017).
31. T. Lenormand, *Trends Ecol. Evol.* **17**, 183–189 (2002).
32. R. J. Fletcher Jr. *et al*., *Biol. Conserv.* **226**, 9–15 (2018).
33. E. I. Damschen *et al*., SRS Corridor Experiment Annual Plant Occurrence Dataset, South Carolina, USA, 2000 - current, Environmental Data Initiative (2019); https://doi.org/10.6073/pasta/ea07f86ced76a28f8cb843f517959e0b.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Supplementary Results
Figs. S1 to S8
Table S1
References (*34*–*61*)
Supplementary Code

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Science

Ongoing accumulation of plant diversity through habitat connectivity in an 18-year experiment

Ellen I. Damschen, Lars A. Brudvig, Melissa A. Burt, Robert J. Fletcher Jr., Nick M. Haddad, Douglas J. Levey, John L. Orrock, Julian Resasco and Joshua J. Tewksbury

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Habitat connectivity enhances diversity

Fragmentation of ecosystems leads to loss of biodiversity in the remaining habitat patches, but retaining connecting corridors can reduce these losses. Using long-term data from a large, replicated experiment, Damschen *et al.* show quantitatively how these losses are reduced. In their pine savanna system, corridors reduced the likelihood of plant extinction in patches by about 2% per year and increased the likelihood of patch colonization by about 5% per year. These benefits continued to accrue over the course of the 18-year experiment. By the end of monitoring, connected patches had 14% more species than unconnected patches. Restoring habitat connectivity may thus be a powerful technique for conserving biodiversity, and investment in connections can be expected to magnify conservation benefit.

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Supplementary Materials for

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This PDF file includes:

- Materials and Methods
- Supplementary Results
- Figs. S1 to S8
- Table S1
- Caption for Supplementary Code
- References

Other Supplementary Material for this manuscript includes the following:
(available at science.sciencemag.org/content/365/6460/1478/suppl/DC1)

- Supplementary Code (.pdf)

Materials and Methods

Landscape experiment

In 2000, we initiated a landscape experiment to test whether habitat corridors promote connectivity and impact community diversity. The experiment is at the Savannah River Site, a National Environmental Research Park in Aiken and Barnwell Counties, South Carolina, USA. Established by the U.S. Department of Energy, the site is managed by the US Forest Service under agreement with the Department of Energy.

The experiment consists of 10 replicate landscapes (experimental blocks), each comprised of five open-habitat fragments created by clearing mature pine plantation forest and restoring fragments to native longleaf pine savanna. There is a strong contrast between the open fragments and the surrounding closed-canopy pine plantation matrix. Eight landscapes were created prior to the 2000 growing season (i.e., before April) and two additional landscapes were created prior to the 2007 growing season. Two of the original eight landscapes were discontinued following the 2007 growing season due to management constraints and one was destroyed by a wind event following the 2015 growing season. The remaining five landscapes initiated in 2000 and the two landscapes initiated in 2007 continue through the end of this study. When examining patterns over time, landscapes are evaluated based on the number of years since that landscape was created. All available replicate landscapes (blocks) are used for each time point in this study. This staggered initiation of replicate landscapes also provides a benefit by separating connectivity effects due to time since replicate initiation from annual effects attributable to specific years.

Each landscape contains a center fragment (100 × 100 m, 1 ha) surrounded by four peripheral fragments that are each 150 m from the center fragment (Fig. 1). The center fragment is connected to one peripheral fragment by a 150 × 25 m corridor and the other three peripheral fragments are isolated from the center fragment by dense, mature loblolly (*Pinus taeda*) or longleaf pine (*Pinus palustris*) plantation forest. Unconnected fragments are equal in area to the connected peripheral fragment plus its corridor (1.375 ha) and are either rectangular (100 × 137.5 m) or winged. Winged fragments have two 75 × 25 m projections, each with the dimensions of half of a corridor, extending from each side of a 100 × 100 m fragment (Fig. 1). The identity of peripheral fragments (connected, rectangle, winged) was randomly assigned within each landscape, with one duplicate winged or rectangle fragment in each landscape. This study design allows us to separate influences of corridors mediated through connectivity from those mediated through differences in edge-to-area ratio. Specifically, impacts of connectivity are assessed by comparing response variables in winged and connected fragments (comparable edge-to-area ratio, different connectivity). Impacts of edge-to-area ratio are assessed by comparing the same variables in winged and rectangle fragments (comparable connectivity, different edge-to-area ratio). Because analyses used in this study showed no differences among unconnected fragment types (Table S1), response variables were averaged for those fragment types. The center fragment is not included in analyses comparing fragment types, therefore comparisons are always made for fragments of equal area. This approach is directly comparable to an earlier analysis of species richness in these fragments (*27*).

Through periodic prescribed fire and removal of establishing hardwood trees, we have restored fragments to their historical ecosystem type: open-canopy longleaf pine savanna. We used standard management practices in this ecosystem (*34*) and applied them consistently across experimental treatments (i.e., we managed all fragment types in the same way). Prescribed fires are implemented and controlled by our partners at the USDA Forest Service-Savannah River consistent with the historic fire regime and with fire management in longleaf pine savanna conservation today (*35*). Low-intensity surface fires are ignited every two to three years during the dormant season (November - April) and are allowed to burn across large burn areas that include all experimental fragments for a given experimental landscape (block). Longleaf pine savanna species are fire-adapted and many species readily re-sprout after fire. Thus, ecological communities in our experimental landscapes recover quickly following fire, yet fire results in both mortality of resident species and recruitment opportunities for new species (*36*). Consistent with restoration practices in this ecosystem (*34*), we have also reduced woody encroachment in our fragments by cutting hardwood tree species with brush saws every three-to-four years and applying targeted herbicide to cut stumps and/or the base of individual stems. These management practices allow the fragments to undergo succession toward mature longleaf pine savanna, characterized by low density overstory longleaf pine trees and an understory dominated by highly diverse perennial herbs and grasses (*36*), while maintaining the contrast between our experimental fragments and surrounding matrix over the duration of the study.

Data collection

To quantify plant species richness and rates of extinction and colonization within our fragments, we annually survey each fragment for all plant species occurrences. We conduct surveys between May 15 and July 15, when most species in our system are visually identifiable. Here, we include data from 2001 through 2018 (except 2004 when active management prevented sampling). The goal of each survey is to census all species in each fragment by systematically walking the area of each fragment in a set pattern around permanent 3m-tall poles placed in a 12.5m grid. This grid consists of 88 small (12.5 × 12.5 m) sampling units in each fragment. For each census, we record all species in the first sampling unit and then record only new species in subsequent sampling units. This method allows us to consistently cover the entire area of each fragment and compile a list of all vascular plant species observed in each fragment as well as the order in which they were detected across the 88 sampling units. Over the entire 18-year time series, we have kept the number of observers to a minimum – three (Damschen, Brudvig, and Burt). These observers standardize sampling effort and taxonomic identification rules prior to each annual survey. Resulting estimates of species richness for each fragment are from equal areas (1.375 ha). Taxonomy follows (*38*) and (*39*). In rare cases where identification is not possible at the species level (2% of taxa), we combine species to the genus level.

We assigned each plant species one of three primary dispersal modes: wind, animal, or gravity. We chose these modes because they capture distinctive classes of seed movement. We determined dispersal modes by first searching the Kew Garden Seed Information Database (*40*). If species were not in that database, we searched the primary literature with ISI Web of Science for papers that described dispersal for the species and/or genus. In some cases, we also searched reliable plant natural history websites to cross-reference obtained information. All designations were independently reviewed by two plant ecologists within our plant ecology research team (E. Damschen, L. Brudvig, M. Burt, C. Warneke, Q. Sorenson). Any conflicting or missing designations were discussed and decided by this entire team and decided on based on morphological and field observations (11% of species). Wind dispersal included both wind and tumbling dispersal mechanisms. Animal dispersal included endozoochory and epizoochory by birds and mammals and myrmecochory by ants. Gravity dispersal included ballistic dispersal mechanisms and species lacking apparent morphology to assist dispersal.

We also determined whether each species was associated with longleaf pine savannas (i.e., “longleaf pine species”). We were interested in assessing the responses of these species because they are of particular conservation and restoration concern and could respond more strongly to the contrasting habitat differences between the fragments and matrix in our experimental landscapes. We classified species as longleaf pine indicator species if they met one or both of the following criteria: 1) designation as longleaf pine upland species in published species lists for the Savannah River Site (*41*, *42*), or 2) designation as “indicator species” in previous analyses of longleaf pine savanna plant communities at the Savannah River Site (*43*).

Because soil moisture is an important determinant of plant diversity in longleaf pine savannas (*44*, *45*), we quantified soil water holding capacity. We used the same methods as Damschen et al. (*27*) by collecting 96-136, 10-cm deep × 2.5-cm diameter soil cores, evenly distributed across each fragment. We then determined soil water holding capacity as (wet mass - dry mass)/dry mass for each sample (*46*) and used the average of all samples from a fragment in our analyses.

All data are available from the Environmental Data Initiative and Data One (*33*).

Analyses

We modeled changes in plant communities using multi-species occupancy models and their extensions to capture both changes in species richness and colonization-extinction dynamics (*47, 48*). Occupancy modeling provides two major benefits. First, it can account for species-specific imperfect detection (observation errors). Second, it estimates species directly rather than modeling summary statistics of communities (e.g., species richness), such that species identity is honored and tracked in the modeling process. The latter benefit also allows for understanding how species-specific characteristics (e.g., dispersal mode) may impact communities while also providing a means to derive community-level parameters (e.g., species richness). This general approach uses a hierarchical framework. To ensure that results were robust to the modeling framework we used, we used a negative binomial regression to contrast results to those from modeling species richness without accounting for imperfect detection.

As part of our occupancy modeling, we estimated imperfect detection using detection histories for each species in each fragment for each year. We used spatial replicates based on the long-term sampling design to create those detection histories. For each fragment, we pooled 88 samples that covered the entire fragment into $J = 8$ replicates. This sampling strategy is best viewed as a ‘removal’ design (*49*), where once a species is detected, it is no longer tracked in fragment *i*. For example, a detection history for species *k* at fragment *i* in year *t* could be [0 0 0 0 1 NA NA NA], where NA refers to no data, given the ‘removal’ design. For most analyses, we focus on comparing communities in connected (corridor) versus unconnected (rectangular and winged) fragments and did not include the center fragment in modeling (but see below for interpreting if colonization of corridor fragments arose from center fragments).

We first modeled the entire plant community ($K = 309$ species) to estimate potential effects of corridors over time on species richness. To model species richness over time, we used an ‘implicit dynamics’ formulation of the multi-species occupancy model (*50*). In this context, we modeled the probability of occurrence ψ for species *k* in time *t* at fragment *i* as:

$$z_{k,i,t} \sim \text{Bernoulli}(\psi_{k,i,t}) \tag{1}$$

where *z* is the latent occupancy state (0,1). We modeled ψ as:

$$logit(\psi_{k,i,t}) = \alpha_{trt,k} + \beta_{trt,k} time_t \tag{2}$$

such that each species k had a different, treatment-specific intercept and slope over time (i.e., an interaction of treatment*species*time). Note that in this model, we initially considered site as a random effect to account for within-site repeated measures over time, which provided similar results. We removed this effect in the final model to simplify model structure given the large number of latent parameters (e.g,. species-specific effects).

Our observation model was described as:

$$y_{k,i,t,j} \sim \text{Bernoulli}\big(z_{k,i,t}p_k\big) \tag{3}$$

Where $y_{k,i,t,j}$ is the detection of species k in fragment i at year t for replicate observation j and p_k is the probability of detection of species k, conditional on presence. We allowed detection to vary by species.

This model formulation assumes a linear effect of time since corridor creation (on the logit scale) on species-specific occurrence; however, this effect can appear non-linear on the probability (and species richness) scale, as in logistic regression. We also considered two types of non-linear functions (considering the log of time or adding a quadratic term of time), neither of which were supported by the data based on the Deviance Information Criterion, DIC (lower values indicate better fit; linear time: 93634; log time: 93840; quadratic time: 94352). We also initially considered the potential effects of soil moisture in this model, but found no support for its effect based on DIC (soils ignored: 93634; soils included: 99562). Thus, we did not include soil moisture in final models. We contrasted these results to modeling raw species richness with non-linear effects over time using a negative binomial regression, finding similar support for a linear effect of time and qualitatively similar patterns of changes in species richness as found in the multi-species occupancy model (Figs. S4, S5).

For a subset of the community (i.e., those species with > 10 detections over time; K = 239 species of the possible 309 species), we explicitly modeled colonization-extinction dynamics. While the entire community could be modeled to interpret colonization-extinction dynamics, little information is available for rare species to interpret treatment effects and how they change over time. Thus, such an approach would make the implicit assumption that rare species, which contribute a comparatively small amount of data on extinction and colonization, respond similarly to treatments as more common species, such that rare species dynamics do not have a large impact on conclusions (*48*). Because of this effect, we use the 239 species subset of more common species to make conclusions on colonization-extinction dynamics. We note, however, that modeling colonization-extinction dynamics of all species showed similar patterns.

We followed methods of Dorazio et al. (*48*), who extended the multi-species occupancy framework for capturing colonization-extinction dynamics. The dynamics of species occurrence can be described and estimated with time-series data by assuming a first-order Markov process, where $z_{k,i}$ at time t is contingent on $z_{k,i}$ at time t - 1, as well as local colonization, γ, and local extinction, ε, processes. If we define ϕ= 1 - ε, then:

$$z_{k,i,t} = \text{Bernoulli}\big(z_{k,i,t-1}\phi_{k,i,t-1} + \left(1 - z_{k,i,t-1}\right)\gamma_{k,i,t-1}\big)\ . \tag{4}$$

This framework requires estimating occupancy at time 1, and then colonization-extinction dynamics in subsequent time steps. We also considered an alternative parameterization that accounts for potential rescue effects ("pseudo-rescue effects" sensu Hanski 1999) replacing $\phi_{k,i,t-1}$ in equation 4 as (*51*):

$$\phi^*_{k,i,t-1} = \Big(1 - \big(1 - \phi_{k,i,t-1}\big)\Big)\left(1 - \gamma_{k,i,t-1}\right). \tag{5}$$

To further interpret support of rescue effects, we contrasted similar models as described in equations 4-5 but fit to single species (i.e., 'dynamic occupancy models'; *52*). We also note that rescue effects are also often interpreted as occurring when connectivity (e.g., corridors) decrease local extinction rates, although it can be unclear if such patterns are driven by rescue effect mechanisms (*53*).

We allowed for ψ to vary by species (we also initially considered that ψ could vary by treatment; however, there was no support for this added complexity so we do not consider it further, See Fig. S1). We also allowed for γ and ε to vary by treatment over time for each species as:

$$logit(\gamma_{k,i,t}) = \alpha_{trt,k} + \beta_{trt,k} time_t \tag{6}$$

$$logit(\phi_{k,i,t}) = \alpha_{trt,k} + \beta_{trt,k} time_t \tag{7}$$

From this model, we then summarized the average ε and γ across species and associated 95% credible intervals for each treatment over time based on the species-specific posterior distributions of model parameters. We averaged unconnected treatments (winged, rectangular) because the rates of change for these treatments were similar (Table S1).

To determine if the results are consistent for species of conservation and restoration concern and to determine whether movement ability of species influences our results, we also summarize colonization-extinction dynamics on two types of species traits: 1) longleaf indicator status; and 2) dispersal mode (see Data Collection for descriptions of these characteristics).

To better interpret if colonization was driven by corridors, we re-ran the colonization-extinction model (using equation 4) and included the center fragment (Fig. 1) into the model. Based on this model, we determined if connected fragments tended to be colonized sooner than unconnected fragments for species that occurred (i.e., $z_{k,i,t} = 1$) in center fragments prior to other fragments within each landscape.

We assumed vague priors for all parameters ($N \sim (0, 100)$), and used uniform hyperpriors for standard deviation parameters ($U \sim (0, 10)$). We ran all models in jags using the jagsUI package to call jags from R. We ran four chains for 37,500 Markov chain Monte Carlo (MCMC) iterations and thinned chains by 50 after a burn-in of 15000 and an adaptation phase of 15000, ultimately saving 3000 samples from the posteriors. We assessed model convergence using the Gelman-Rubin statistic R-hat, assuming that an R-hat > 1.05 indicated convergence problems (*50, 54*).

Supplementary Text

Supplementary Results

Plant species in may have arrived in fragments through three different pathways. First, seeds could have arrived in the area where we created our experimental fragments before our experiment was created and remained in the soil seed bank. In our study system, the soil seed bank is dominated by annual herbs and graminoids, a small subset of the total species in our study system, and whose composition did not differ by fragment type at the start of our study (*27*). Second, plants were present in the pine plantation understory before our experiment was created, and some regrew after forest harvest. Our assignment of treatments to fragments was randomized and we have previously confirmed that species richness and composition did not differ by fragment type at the start of our study (*27*) (Figure S1). Third, species may arrive from the regional species pool into one of the fragments within an experimental landscape. The increased colonization rates and decreased extinction rates in connected fragments suggests that species are more likely to move to a connected fragment than unconnected fragments. Based on temporal changes in $z_{k,i,t}$ from the colonization-extinction model that include all five fragments in each experimental landscape, we found species that first arrived in the center fragment of an experimental landscape (block) were more likely to next colonize a connected fragment than an unconnected fragment (Fig. S8). Our analysis of the order of colonization events showed that connected fragments were colonized sooner than unconnected fragments in 60% of the species (out of 120 species for which this situation occurred), but the distribution was highly skewed (Fig. S8), providing evidence of corridors facilitating colonization of species from center fragments. This evidence is bolstered by studies of individual species' movement in our experiment that overwhelmingly show increased rates of movement between connected fragments when compared to unconnected fragments (*55*).

It is also possible that rescue effects – instances where immigration prevents extinction (*5*) – are responsible for the lower extinction rates in connected fragments. When we evaluated the potential for rescue effects for the entire community, the model parameterization that included rescue effects (Eq. 5) did not fit the data as well as when no rescue effects were assumed (based on DIC: assuming rescue effect, DIC = 194,151.7, assuming no rescue effect, DIC = 192,533.7). Thus, there was no strong support for rescue effects at the community level. When evaluating whether models that included rescue effects were important for individual species, there was support for rescue effects for 54% of the 239 species based on DIC (i.e., lower DIC for the rescue effects parameterization than assuming no rescue effects). This support did not explain variation in species responses to corridors (i.e., variation in DIC did not correlate with corridor effect sizes based on treatment parameters in Eq. 6-7; $r < |0.07|$). Thus, we focused on the non-rescue effect model parameterization above for all general results in the main text. However, it is important to note that while rescue effects do not generally explain the community-level patterns we report, they can and do occur for some species.

Finally, once species arrive within fragments, connectivity may alter species interactions in ways that minimize species extinctions or promote colonization. For example, we have documented higher pollination rates in connected than unconnected fragments (*56*, *57*), which may increase seed set and population size, thereby lowering the likelihood of extinction. Additionally, changes in seed predation caused by connectivity may create competition-free microsites that facilitate colonization (*58*). Corridors also increase the temperature at which prescribed fires burn, opening microsites for plant colonization and reducing dominance by woody species, which can increase persistence of subordinate herbs (*59*). Populations may also benefit from corridors by increasing gene flow and reducing impacts of inbreeding depression (*60*). Gene flow takes place through seed dispersal and pollination, both of which are facilitated by corridors in our study system (*56*, *57*, *61*).

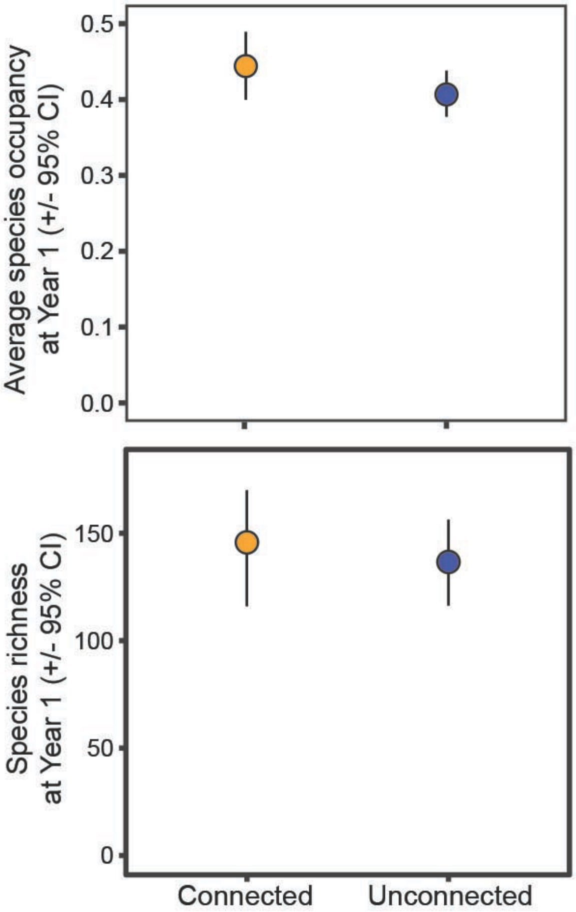

Fig. S1. Starting conditions did not vary by treatment. Initial probability of **(A)** species occurrence and **(B)** species richness did not differ by fragment type.

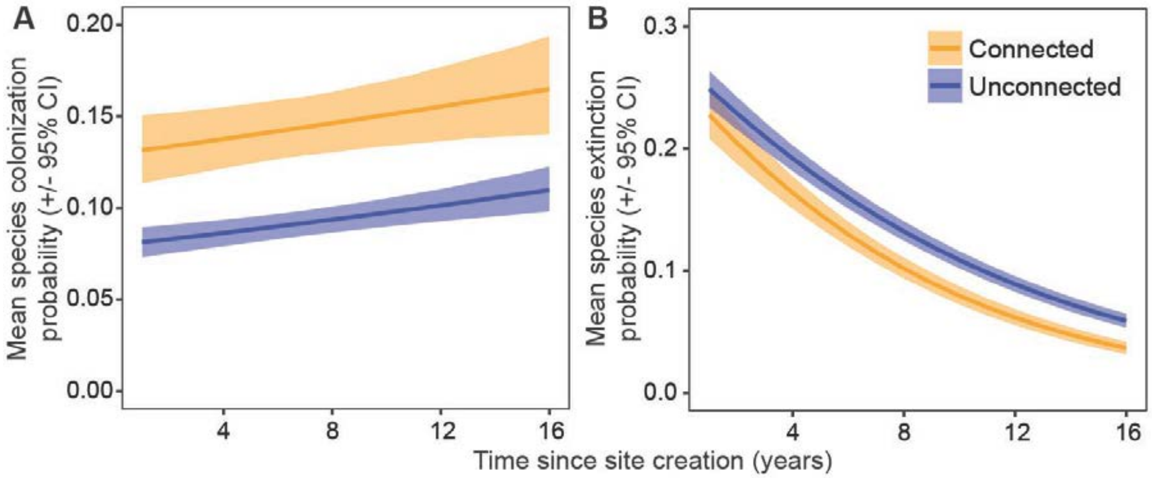

Fig. S2. (A) Colonization and (B) extinction rates over time for connected and unconnected fragments. The difference in these rates were used to produce Fig. 2A.

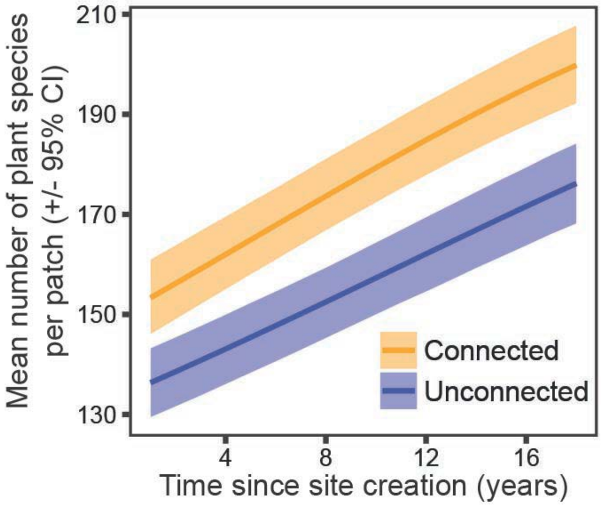

Fig. S3. Estimated species richness over time in connected and unconnected fragments. In the last time point (Year 18), on average there are 24 more species in connected than unconnected fragments (200 vs 176 species, respectively). The difference in these rates were used to produce Fig. 2B.

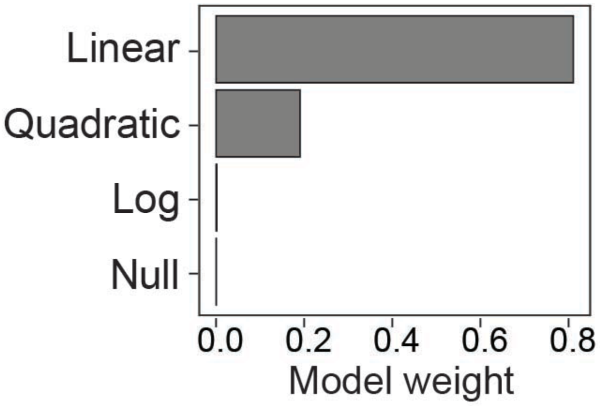

Fig. S4. A linear model is the best fit for the difference in species richness between connected and unconnected fragments over time. Model weights represent AIC model weights taken from negative binomial regressions that included the main and interactive effects of treatment and time since site creation (treated as either a linear, log-linear, or quadratic effect of time, in contrast to no effect of time represented as ‘Null’. Higher model weight signifies greater support for a model relative to the other models considered, with a value of 1 indicating full support. Consequently, these weights suggest overwhelming support of a linear effect of treatments over time relative to potential non-linear (log time, quadratic time) effects of time.

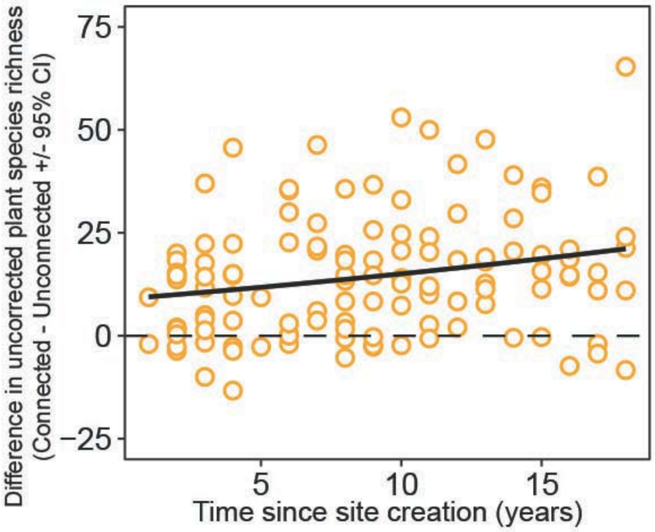

Fig. S5. The linear increase over time is evident in the difference in uncorrected, raw plant species richness over time between connected and unconnected fragments. Predicted line comes from the linear model (Fig. S4).

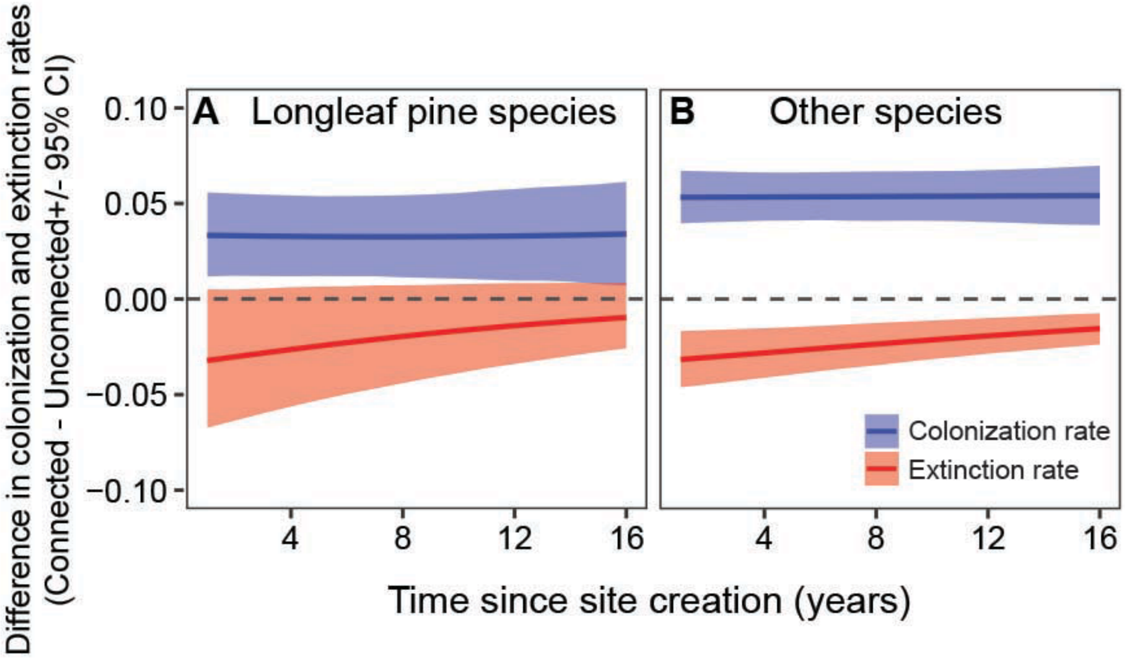

Fig. S6. Plant species (A) associated with longleaf pine habitat and (B) other species respond similarly to connectivity over time, although uncertainty is greater for species associated with longleaf pine habitat due to a smaller number of species**.** The difference between connected and unconnected fragments for colonization and extinction probabilities is shown for both groups.

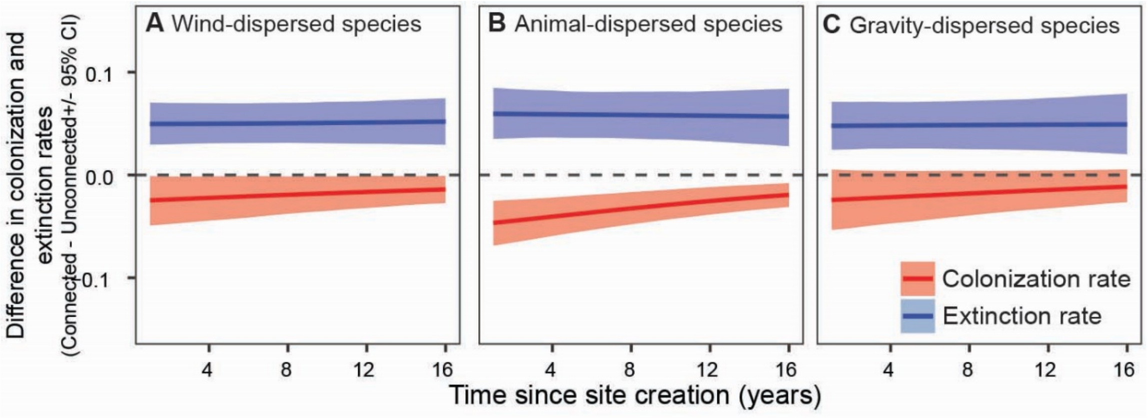

Fig. S7. Plant species respond similarly to connectivity over time across seed dispersal modes. The difference between connected and unconnected fragments for colonization and extinction probabilities of **(A)** wind-dispersed, **(B)** animal-dispersed, and **(C)** gravity-dispersed plant species over time.

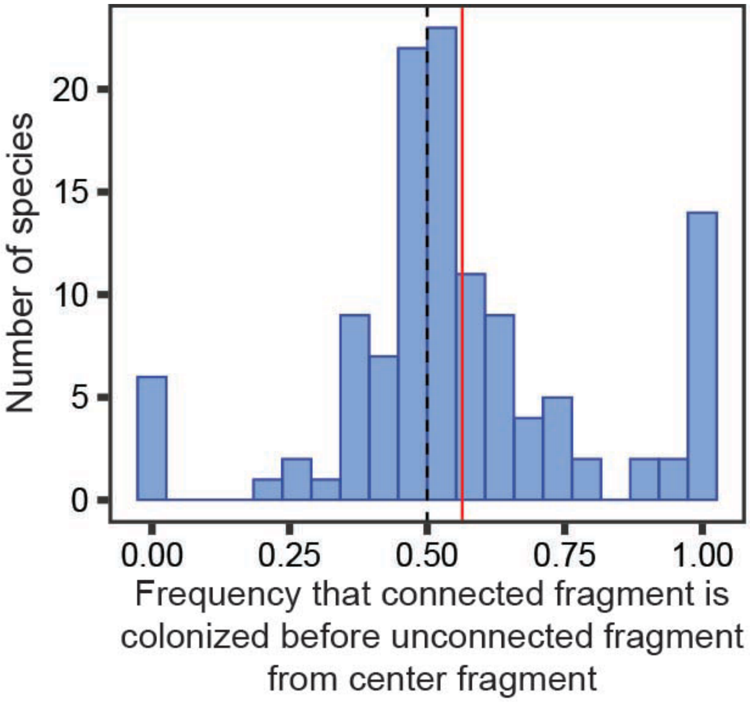

Fig. S8. Colonization events from the center fragment reach connected fragments sooner than unconnected fragments. When species arrived for the first time in an experimental block in the center fragment, connected fragments were colonized sooner than unconnected fragments for 60% of the species (out of 120 species for which this situation occurred; mean frequency = 0.56). The distribution was highly skewed providing some evidence of corridors facilitating colonization of species from center fragments.

Table S1. Summary of parameter estimates (on the logit scale) from multi-species occupancy model used to derive species richness over time. We show average estimates across species because this model estimates a parameter for each species (K = 309) regarding species detectability, treatment intercepts and rates of change over time. Estimates are provided for connected, unconnected rectangular, and unconnected winged fragments. LCL and UCL are lower and upper confidence limits, respectively.

Parameter	Estimate	95% LCL	95% UCL
Species mean detectability	-2.123	-2.466	-1.773
Species mean occupancy			
Connected intercept	0.447	0.294	0.607
Rectangular intercept	-0.220	-0.379	-0.065
Winged intercept	0.251	0.098	0.407
Connected time effect	0.672	0.574	0.768
Rectangular time effect	0.491	0.404	0.578
Winged time effect	0.553	0.467	0.672

Supplementary Code. The code used to estimate occupancy, species richness, and colonization-extinction dynamics over time is provided as a separate supplementary file.

References and Notes

1. N. M. Haddad, L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, J. O. Sexton, M. P. Austin, C. D. Collins, W. M. Cook, E. I. Damschen, R. M. Ewers, B. L. Foster, C. N. Jenkins, A. J. King, W. F. Laurance, D. J. Levey, C. R. Margules, B. A. Melbourne, A. O. Nicholls, J. L. Orrock, D.-X. Song, J. R. Townshend, Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* **1**, e1500052 (2015). doi:10.1126/sciadv.1500052 Medline

2. M. Pfeifer, V. Lefebvre, C. A. Peres, C. Banks-Leite, O. R. Wearn, C. J. Marsh, S. H. M. Butchart, V. Arroyo-Rodríguez, J. Barlow, A. Cerezo, L. Cisneros, N. D'Cruze, D. Faria, A. Hadley, S. M. Harris, B. T. Klingbeil, U. Kormann, L. Lens, G. F. Medina-Rangel, J. C. Morante-Filho, P. Olivier, S. L. Peters, A. Pidgeon, D. B. Ribeiro, C. Scherber, L. Schneider-Maunoury, M. Struebig, N. Urbina-Cardona, J. I. Watling, M. R. Willig, E. M. Wood, R. M. Ewers, Creation of forest edges has a global impact on forest vertebrates. *Nature* **551**, 187–191 (2017). doi:10.1038/nature24457 Medline

3. T. Newbold, L. N. Hudson, S. L. L. Hill, S. Contu, I. Lysenko, R. A. Senior, L. Börger, D. J. Bennett, A. Choimes, B. Collen, J. Day, A. De Palma, S. Díaz, S. Echeverria-Londoño, M. J. Edgar, A. Feldman, M. Garon, M. L. K. Harrison, T. Alhusseini, D. J. Ingram, Y. Itescu, J. Kattge, V. Kemp, L. Kirkpatrick, M. Kleyer, D. L. P. Correia, C. D. Martin, S. Meiri, M. Novosolov, Y. Pan, H. R. P. Phillips, D. W. Purves, A. Robinson, J. Simpson, S. L. Tuck, E. Weiher, H. J. White, R. M. Ewers, G. M. Mace, J. P. W. Scharlemann, A. Purvis, Global effects of land use on local terrestrial biodiversity. *Nature* **520**, 45–50 (2015). doi:10.1038/nature14324 Medline

4. IPBES, "The IPBES assessment report on land degradation and restoration" [Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), 2018].

5. J. H. Brown, A. Kodric-Brown, Turnover Rates in Insular Biogeography: Effect of Immigration on Extinction. *Ecology* **58**, 445–449 (1977). doi:10.2307/1935620

6. R. Levins, Some Demographic and Genetic Consequences of Environmental Heterogeneity for Biological Control. *Bull. Entomol. Soc. Am.* **15**, 237–240 (1969). doi:10.1093/besa/15.3.237

7. I. Hanski, *Metapopulation Ecology* (Oxford Univ. Press, 1999).

8. M. Holyoak, M. A. Leibold, R. D. Holt, *Metacommunities: Spatial Dynamics and Ecological Communities* (Univ. of Chicago Press, 2005).

9. M. A. Leibold, J. M. Chase, *Metacommunity Ecology* (Princeton Univ. Press, 2018), vol. 59.

10. R. H. MacArthur, E. O. Wilson, *The Theory of Island Biogeography* (Princeton Univ. Press, 1967).

11. D. J. Earn, S. A. Levin, P. Rohani, Coherence and conservation. *Science* **290**, 1360–1364 (2000). doi:10.1126/science.290.5495.1360 Medline

12. E. O. Wilson, E. O. Willis, in *Ecology and Evolution of Communities*, M. L. Cody, J. M. Diamond, Eds. (Belknap Press, 1975), vol. 522, pp. 522–534.

13. R. K. Didham, V. Kapos, R. M. Ewers, Rethinking the conceptual foundations of habitat fragmentation research. *Oikos* **121**, 161–170 (2012). doi:10.1111/j.1600-0706.2011.20273.x

14. L. Fahrig, Ecological Responses to Habitat Fragmentation Per Se. *Annu. Rev. Ecol. Evol. Syst.* **48**, 1–23 (2017). doi:10.1146/annurev-ecolsys-110316-022612

15. J. Aström, T. Pärt, Negative and matrix-dependent effects of dispersal corridors in an experimental metacommunity. *Ecology* **94**, 72–82 (2013). doi:10.1890/11-1795.1 Medline

16. N. M. Haddad, A. Gonzalez, L. A. Brudvig, M. A. Burt, D. J. Levey, E. I. Damschen, Experimental evidence does not support the Habitat Amount Hypothesis. *Ecography* **40**, 48–55 (2017). doi:10.1111/ecog.02535

17. M. L. Rosenzweig, Heeding the Warning in Biodiversity's Basic Law. *Science* **284**, 276–277 (1999). doi:10.1126/science.284.5412.276

18. D. Tilman, R. M. May, C. L. Lehman, M. A. Nowak, Habitat destruction and the extinction debt. *Nature* **371**, 65–66 (1994). doi:10.1038/371065a0

19. M. Kuussaari, R. Bommarco, R. K. Heikkinen, A. Helm, J. Krauss, R. Lindborg, E. Öckinger, M. Pärtel, J. Pino, F. Rodà, C. Stefanescu, T. Teder, M. Zobel, I. Steffan-Dewenter, Extinction debt: A challenge for biodiversity conservation. *Trends Ecol. Evol.* **24**, 564–571 (2009). doi:10.1016/j.tree.2009.04.011 Medline

20. S. T. Jackson, D. F. Sax, Balancing biodiversity in a changing environment: Extinction debt, immigration credit and species turnover. *Trends Ecol. Evol.* **25**, 153–160 (2010). doi:10.1016/j.tree.2009.10.001 Medline

21. T. Naaf, J. Kolk, Colonization credit of post-agricultural forest patches in NE Germany remains 130–230 years after reforestation. *Biol. Conserv.* **182**, 155–163 (2015). doi:10.1016/j.biocon.2014.12.002

22. J. Kolk, T. Naaf, M. Wulf, Paying the colonization credit: Converging plant species richness in ancient and post-agricultural forests in NE Germany over five decades. *Biol. Conserv.* **26**, 735–755 (2017).

23. I. Hanski, Extinction debt and species credit in boreal forests: Modelling the consequences of different approaches to biodiversity conservation. *Ann. Zool. Fenn.* **37**, 271–280 (2000).

24. K. R. Crooks, M. Sanjayan, Eds., *Connectivity Conservation: Maintaining Connections for Nature* (Cambridge Univ. Press, 2006).

25. R. F. Noss, W. J. Platt, B. A. Sorrie, A. S. Weakley, D. B. Means, J. Costanza, R. K. Peet, How global biodiversity hotspots may go unrecognized: Lessons from the North American Coastal Plain. *Divers. Distrib.* **21**, 236–244 (2014). doi:10.1111/ddi.12278

26. See supplementary materials.

27. E. I. Damschen, N. M. Haddad, J. L. Orrock, J. J. Tewksbury, D. J. Levey, Corridors increase plant species richness at large scales. *Science* **313**, 1284–1286 (2006). doi:10.1126/science.1130098 Medline

28. H. V. Cornell, S. P. Harrison, What Are Species Pools and When Are They Important? *Annu. Rev. Ecol. Evol. Syst.* **45**, 45–67 (2014). doi:10.1146/annurev-ecolsys-120213-091759

29. A. J. Miller-Rushing, R. B. Primack, V. Devictor, R. T. Corlett, G. S. Cumming, R. Loyola, B. Maas, L. Pejchar, How does habitat fragmentation affect biodiversity? A controversial question at the core of conservation biology. *Biol. Conserv.* **232**, 271–273 (2019). doi:10.1016/j.biocon.2018.12.029

30. N. M. Haddad, R. D. Holt, R. J. Fletcher Jr., M. Loreau, J. Clobert, Connecting models, data, and concepts to understand fragmentation's ecosystem-wide effects. *Ecography* **40**, 1–8 (2017). doi:10.1111/ecog.02974

31. T. Lenormand, Gene flow and the limits to natural selection. *Trends Ecol. Evol.* **17**, 183–189 (2002). doi:10.1016/S0169-5347(02)02497-7

32. R. J. Fletcher Jr., R. K. Didham, C. Banks-Leite, J. Barlow, R. M. Ewers, J. Rosindell, R. D. Holt, A. Gonzalez, R. Pardini, E. I. Damschen, F. P. L. Melo, L. Ries, J. A. Prevedello, T. Tscharntke, W. F. Laurance, T. Lovejoy, N. M. Haddad, Is habitat fragmentation good for biodiversity? *Biol. Conserv.* **226**, 9–15 (2018). doi:10.1016/j.biocon.2018.07.022

33. E. I. Damschen, L. A. Brudvig, M. A. Burt, R. J. Fletcher, N. M. Haddad, D. J. Levey, J. L. Orrock, J. Resasco, J. J. Tewksbury, SRS Corridor Experiment Annual Plant Occurrence Dataset, South Carolina, USA, 2000 - current, Environmental Data Initiative (2019); https://doi.org/10.6073/pasta/ea07f86ced76a28f8cb843f517959e0b..

34. J. L. Walker, A. M. Silletti, in *The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration*, S. Jose, E. J. Jokela, D. L. Miller, Eds. (Springer, 2006), pp. 9–42.

35. C. Frost, in *The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration*, S. Jose, E. J. Jokela, D. L. Miller, Eds. (Springer, 2006), pp. 9–48.

36. J. A. Myers, K. E. Harms, Seed arrival and ecological filters interact to assemble high-diversity plant communities. *Ecology* **92**, 676–686 (2011). doi:10.1890/10-1001.1 Medline

37. R. F. Noss, *Forgotten Grasslands of the South: Natural History and Conservation* (Island Press, 2013).

38. A. E. Radford, H. E. Ahles, C. R. Bell, *Guide to the Vascular Flora of the Carolinas* (Univ. of North Carolina Press, 1964).

39. A. S. Weakley, *Flora of the Carolinas, Virginia, Georgia and Surrounding Areas* (Univ. of North Carolina Press, 2006).

40. Royal Botanic Gardens Kew, Seed Information Database, Version 7.1 (2017); http://data.kew.org/sid/.

41. S. W. Workman, K. W. McLeod, "Vegetation of the Savannah River Site: Major community types" (Savannah River Site National Environmental Research Park Program, 1990); www.osti.gov/biblio/6877070.

42. J. C. Kilgo, J. I. Blake, Eds., *Ecology and Management of a Forested Landscape: Fifty Years on the Savannah River Site* (Island Press, 2005).

43. N. E. Turley, J. L. Orrock, J. A. Ledvina, L. A. Brudvig, Dispersal and establishment limitation slows plant community recovery in post-agricultural longleaf pine savannas. *J. Appl. Ecol.* **54**, 1100–1109 (2017). doi:10.1111/1365-2664.12903

44. L. K. Kirkman, R. J. Mitchell, R. C. Helton, M. B. Drew, Productivity and species richness across an environmental gradient in a fire-dependent ecosystem. *Am. J. Bot.* **88**, 2119–2128 (2001). doi:10.2307/3558437 Medline

45. J. W. Veldman, L. A. Brudvig, E. I. Damschen, J. L. Orrock, W. B. Mattingly, J. L. Walker, Fire frequency, agricultural history and the multivariate control of pine savanna understorey plant diversity. *J. Veg. Sci.* **25**, 1438–1449 (2014). doi:10.1111/jvs.12195

46. L. A. Brudvig, E. I. Damschen, Land-use history, historical connectivity, and land management interact to determine longleaf pine woodland understory richness and composition. *Ecography* **34**, 257–266 (2011). doi:10.1111/j.1600-0587.2010.06381.x

47. R. M. Dorazio, J. A. Royle, B. Söderström, A. Glimskär, Estimating species richness and accumulation by modeling species occurrence and detectability. *Ecology* **87**, 842–854 (2006). doi:10.1890/0012-9658(2006)87[842:ESRAAB]2.0.CO;2 Medline

48. R. M. Dorazio, M. Kéry, J. A. Royle, M. Plattner, Models for inference in dynamic metacommunity systems. *Ecology* **91**, 2466–2475 (2010). doi:10.1890/09-1033.1 Medline

49. C. T. Rota, R. J. Fletcher Jr., R. M. Dorazio, M. G. Betts, Occupancy estimation and the closure assumption. *J. Appl. Ecol.* **46**, 1173–1181 (2009). doi:10.1111/j.1365-2664.2009.01734.x

50. M. Kery, J. A. Royle, *Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS* (Academic Press, 2015).

51. R. B. Chandler, E. Muths, B. H. Sigafus, C. R. Schwalbe, C. J. Jarchow, B. R. Hossack, Spatial occupancy models for predicting metapopulation dynamics and viability following reintroduction. *J. Appl. Ecol.* **52**, 1325–1333 (2015). doi:10.1111/1365-2664.12481

52. D. I. MacKenzie, J. D. Nichols, J. E. Hines, M. G. Knutson, A. B. Franklin, Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* **84**, 2200–2207 (2003). doi:10.1890/02-3090

53. M. Clinchy, D. T. Haydon, A. T. Smith, Pattern does not equal process: What does patch occupancy really tell us about metapopulation dynamics? *Am. Nat.* **159**, 351–362 (2002). doi:10.1086/338990 Medline

54. A. Gelman, D. B. Rubin, Inference from Iterative Simulation Using Multiple Sequences. *Stat. Sci.* **7**, 457–472 (1992). doi:10.1214/ss/1177011136

55. N. M. Haddad, L. A. Brudvig, E. I. Damschen, D. M. Evans, B. L. Johnson, D. J. Levey, J. L. Orrock, J. Resasco, L. L. Sullivan, J. J. Tewksbury, S. A. Wagner, A. J. Weldon, Potential negative ecological effects of corridors. *Conserv. Biol.* **28**, 1178–1187 (2014). doi:10.1111/cobi.12323 Medline

56. J. J. Tewksbury, D. J. Levey, N. M. Haddad, S. Sargent, J. L. Orrock, A. Weldon, B. J. Danielson, J. Brinkerhoff, E. I. Damschen, P. Townsend, Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proc. Natl. Acad. Sci. U.S.A.* **99**, 12923–12926 (2002). doi:10.1073/pnas.202242699 Medline

57. P. A. Townsend, D. J. Levey, An experimental test of whether habitat corridors affect pollen transfer. *Ecology* **86**, 466–475 (2005). doi:10.1890/03-0607

58. J. L. Orrock, E. I. Damschen, Corridors cause differential seed predation. *Ecol. Appl.* **15**, 793–798 (2005). doi:10.1890/04-1129

59. L. A. Brudvig, S. A. Wagner, E. I. Damschen, Corridors promote fire via connectivity and edge effects. *Ecol. Appl.* **22**, 937–946 (2012). doi:10.1890/11-1026.1 Medline

60. J. A. Hilty, W. Z. Lidicker Jr., A. M. Merenlender, *Corridor Ecology* (Island Press, 2006).

61. D. J. Levey, B. M. Bolker, J. J. Tewksbury, S. Sargent, N. M. Haddad, Effects of landscape corridors on seed dispersal by birds. *Science* **309**, 146–148 (2005). doi:10.1126/science.1111479 Medline

The New York Times

CALIFORNIA TODAY

California Today: The Increasing Strain on State Firefighters

By Jose A. Del Real and Inyoung Kang

July 30, 2018

Good morning.

(Want to get California Today by email? Here's the sign-up.*)*

Firefighters are working 24- to 36-hour shifts to put out several large fires across the state, often with little rest between assignments. For many, the strain of this recent spate of blazes has been compounded with a wildfire season that has become year-round and more intense.

"There used to be a rhythm to this, and you could at least count on that rhythm," said Brian Rice, who retired from fighting fires in 2011 and is now president of California Professional Firefighters, a statewide union.

Since 2012, there has not been a month without a wildfire, according to state emergency management officials. The intensity of the fires has appeared to increase as well; the fires in 2017 were among the most destructive in California's history, leaving 46 people dead and causing nearly $12 billion in damage.

Mike Daw, the executive director of the Firefighters Burn Institute, which works with injured firefighters through the U.C. Davis Burn Unit in Sacramento, said that firefighters often do not report injuries that might sideline them. Those injuries are often exacerbated over time, especially because mutual assistance programs in California mean that firefighters can end up battling fires all over the state.

"Firefighters are a unique culture," he said. "They're putting themselves in danger, and a lot of times they feel like they can endure more than a normal human being can."

Michael Feyh, a captain with the Sacramento Fire Department, said that fatigue and sleep deprivation are significant problems for firefighters and can leave them particularly vulnerable in already dangerous situations.

And the emotional trauma after injuries or high-stakes events, he said, is often not discussed enough.

“It’s not just burns, its all the things that come with the trauma — what people see throughout their careers,” he said. “It’s hard to get guys to come forward and accept that they could be getting some help and get counseling.”

Mr. Feyh knows the risks firsthand. In 2010, he sustained second- and third-degree burns on 10 percent to 15 percent of his body, largely around his face, while responding to a report of a gas leak. The house exploded, sending him flying 20 feet and leading to the burns as well as orthopedic injuries that took about a year to heal.

“And it’s not just the individual, either; we go to work and our families always have in the back of their minds that something can happen,” Mr. Feyh said. “My wife had her worst nightmare come true.”

Ashley Iverson lost her husband, Cory, in December while he was fighting the Thomas Fire in Ventura County. Mr. Iverson, a fire apparatus engineer with CalFire, had already worked a 24-hour shift but was helping put out spot fires when he became trapped in a gulch. The fire reached him before he could escape.

Thousands honored his sacrifice at a funeral in San Diego, his hometown, just days before Christmas. Ms. Iverson was four months pregnant at the time, and today is caring for their two daughters. Sometimes she is overcome by pain, she said. “How can I raise my kids without my best friend? Why don’t they get to have him in their lives?”

Ms. Iverson hopes to turn her husband’s tragic death into something positive. She is laying the groundwork for a foundation in his name that will advocate expanding mental health awareness among fire responders and firefighters. She said she finds comfort in knowing that he had dedicated himself to helping people.

“After it happened, I took a breath. O.K., the worst has happened. Now what? Where do we go from here?” Ms. Iverson said. “A lot of widows, their life is over. I feel like Cory has given me legs. I’m just so damn proud of him and everything he did.”

California Online

(Please note: We regularly highlight articles on news sites that have limited access for nonsubscribers.)

A fire truck on Highway 299 as the Carr Fire continued to burn near Whiskeytown on Sunday. Josh Edelson/Agence France-Presse — Getty Images

- The death toll in the **Carr Fire** rose to six as firefighters continued to battle the blaze over the weekend. A woman and her two young great-grandchildren were among the dead in Redding. [The New York Times]

- Urban sprawl and climate change are making areas **increasingly vulnerable to wildfires**, experts say. [The Associated Press]

- In the face of sharp opposition and questions about how to pay for it, construction of California's **high-speed rail line** is roaring ahead. [The New York Times]

- A ballot initiative aimed to address **prohibitive housing costs** could divide California Democrats. [Politico]

- California students are flocking to **universities in Arizona**. [Sacramento Bee]

- L.A. paid tribute to the restaurant critic Jonathan Gold over the weekend with a **"City of Gold."** [Los Angeles Times]

- President Trump has joined anxious Republicans in pouring millions into **close House races** in California. [San Francisco Chronicle]

- "If we want to understand a world where Russia and China are ramping up their **spy games** against the United States, then we need to pay attention to what's happening in San Francisco." [Politico]

- **A Silicon Valley life cycle:** The chief executive of Social Finance was ousted last year after questions about sexual misconduct. Months later, two venture capitalists who were on his board have invested $17 million in his new start-up. [The New York Times]

- **Maternal death rates** are rising in the U.S., but California is bucking the trend. [NPR]

Beautycon is at the forefront of a trend known as experiential retail that combines marketing, entertainment and shopping. Anna Beeke for The New York Times

- Sephora meets Coachella: Our Styles reporter went to the L.A. Convention Center for **Beautycon**, an event that is equal parts competitive shopping scene, feel-good festival and marketing bonanza. (Here's what she learned.) [The New York Times]

- With so many players who can play multiple positions, the **Dodgers** are making it work, our baseball columnist writes. [The New York Times]

- **In memoriam:** Bill Loud, the patriarch in "An American Family" on PBS, which shocked viewers with its depiction of domestic dramas in Santa Barbara. He was 97. [The New York Times]

This undeveloped property in Los Angeles, promoted as the Mountain of Beverly Hills, has 360-degree views. You can spot many of the city's major landmarks in the distance, from Century City to downtown. Beth Coller for The New York Times

- Would you pay **$1 billion** for this view? A Beverly Hills property is being pitched as L.A.'s most expensive residence ever. [The New York Times]

Coming Up This Week

- The 2018 International Surf Festival kicks off **Wednesday**, with events in Torrance Beach, Manhattan Beach, Hermosa Beach and Redondo Beach.
- The Del Norte County Fair runs from **Thursday to Sunday**.

And Finally …

Indian Rock Park offers easy bouldering and rewarding vistas at the top.
Jason Henry for The New York Times

A lot has changed in Berkeley since the heyday of the Free Speech Movement in the 1960s.

But the college town has made “an extraordinary effort to stay true to its freethinking, iconoclastic roots,” our Frugal Traveler columnist writes.

He wandered the area sampling cheap eats, nearby parks and the music shops off Telegraph Avenue. And he confirmed what a generation before him knew: This funky trifecta of great food, live music and outdoor activities makes Berkeley ideal for a quick — and frugal — Bay Area getaway.

California Today goes live at 6 a.m. Pacific time weekdays. Tell us what you want to see: CAtoday@nytimes.com.

California Today is edited by Julie Bloom, who grew up in Los Angeles and graduated from U.C. Berkeley.

READ 20 COMMENTS

PLoS one

A Rapid, Strong, and Convergent Genetic Response to Urban Habitat Fragmentation in Four Divergent and Widespread Vertebrates

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Abstract

Background: Urbanization is a major cause of habitat fragmentation worldwide. Ecological and conservation theory predicts many potential impacts of habitat fragmentation on natural populations, including genetic impacts. Habitat fragmentation by urbanization causes populations of animals and plants to be isolated in patches of suitable habitat that are surrounded by non-native vegetation or severely altered vegetation, asphalt, concrete, and human structures. This can lead to genetic divergence between patches and in turn to decreased genetic diversity within patches through genetic drift and inbreeding.

Methodology/Principal Findings: We examined population genetic patterns using microsatellites in four common vertebrate species, three lizards and one bird, in highly fragmented urban southern California. Despite significant phylogenetic, ecological, and mobility differences between these species, all four showed similar and significant reductions in gene flow over relatively short geographic and temporal scales. For all four species, the greatest genetic divergence was found where development was oldest and most intensive. All four animals also showed significant reduction in gene flow associated with intervening roads and freeways, the degree of patch isolation, and the time since isolation.

Conclusions/Significance: Despite wide acceptance of the idea in principle, evidence of significant population genetic changes associated with fragmentation at small spatial and temporal scales has been rare, even in smaller terrestrial vertebrates, and especially for birds. Given the striking pattern of similar and rapid effects across four common and widespread species, including a volant bird, intense urbanization may represent the most severe form of fragmentation, with minimal effective movement through the urban matrix.

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Introduction

Habitat loss and the resulting fragmentation can have many impacts on wildlife populations. However, the effects of fragmentation may vary based on many factors including the size, configuration, and age of habitat patches, the vagility of the species in question, and the characteristics of the matrix between patches. Urban development may represent a particularly intense form of fragmentation for many animals. Species that are particularly sensitive to urban development may be quickly lost from urban areas [1,2,3]. For species that remain widely distributed across fragmented landscapes, connectivity and gene flow between populations may be reduced, leading to longer-term problems such as inbreeding, loss of genetic diversity, and even local extinction [4,5,6,7]. If local extinction occurs, then more isolated patches will be harder to re-colonize [4]. In addition, the loss of genetic diversity within isolated patches can lead to a decrease in a species' ability to adapt to environmental change [8,9].

An increasing number of studies of the genetic effects of fragmentation have occurred in the past decade or so, although 30–40% of these have not shown significant effects and many are in non-urban landscapes such as fragmented forests [10]. Urbanization is a common cause of fragmentation, and conservation efforts point to the extreme land use changes associated with urbanization as one of the largest threats to biodiversity [11]. However, to date, fine-scale (within 5–10 km) genetic effects of urban fragmentation have been documented for few species [12,13,14,15,16,17], and many studies find little effect [18,19,20]. Moreover, studies of the genetic effects of fragmentation are overwhelmingly on a single species, and we know of no studies where genetic patterns were compared in the same urban landscape for species from different broad taxa, such as reptiles (Class *Reptilia*) and birds (Class *Aves*), and with radically different means of locomotion, such as flying and crawling.

We investigated the genetic effects of urban fragmentation on three lizards, the side-blotched lizard (*Uta stansburiana*), western skink (*Plestiodon skiltonianus*) and western fence lizard (*Sceloporus occidentalis*), and one bird, the wrentit (*Chamaea fasciata*) in Santa Monica Mountains National Recreation Area (SMMNRA), a national park near Los Angeles. The three lizard species have widespread distributions in California [21], are small in size, are still relatively common and widespread in natural habitat throughout the area [22], and have low dispersal capabilities [23,24,25,26,27]. Side-blotched lizards and fence lizards are both in the family *Iguanidae*, but side-blotched lizards are considerably smaller and prefer more open habitat. Western skinks are in a distantly-related different family (*Scincidae*) and locally prefer grassland habitat, although all three species are broadly sympatric in the region.

Wrentits are small birds (approximately 15 g) with a distribution that is limited to the west coast of North America and follows the scrub and chaparral habitat that they prefer[28]. Wrentits are monogamous, hold small (1–2.5 acres), year-round multi-purpose territories [28], and have short dispersal distances [29]. Wrentits are obviously very different phylogenetically and ecologically from the lizards and also have the ability to fly, which could potentially increase their movement across the landscape. A bird isolated in a habitat fragment could presumably simply fly over urban areas to disperse to other suitable habitats, thereby preventing genetic divergence between patches. However, because wrentits have short dispersal distances, small territories, and relatively specific habitat requirements, it is possible that wrentits could be affected by habitat fragmentation.

The landscape of southern California continues to be rapidly altered by urbanization and the resulting habitat loss and fragmentation, even though it is part of the California Floristic Province and is one of Conservation International's world biodiversity hotspots ([30,31], www.biodiversityhotspots.org). Because it is in the Los Angeles area, SMMNRA is under intense development pressure and urbanization might increase to as much as 47% of the area by 2050, whereas only 11% was urbanized in 2000 [32]. Given the low vagility of these four focal species, it is possible that movement out of suitable habitat across a highly urbanized landscape is rare. This isolation could increase the genetic divergence between populations living in fragments and also decrease genetic variability within fragments. If urbanization is not an impenetrable barrier to movement, migration between patches by individuals could mitigate negative genetic effects [4,33,34]. Understanding plant and animal responses to habitat destruction and fragmentation will be important for maintenance of this important biodiversity hotspot, especially in the face of unknown consequences of global climate change.

Results

We attempted to genotype approximately 20 individuals from each species for each sample site (Fig. 1a, Table 1), although for some locations fewer than 20 were captured. Microsatellite loci in lizards did not significantly deviate from HWE, however three loci in wrentits did (Ase48, Ase64, Ase50). We didn't find an excess of homozygotes, which could indicate the presence of null alleles, at any of the three loci; so analyses were done using all loci. All microsatellite loci were in linkage equilibrium for all 4 species, except that in western skinks 2 pairs of loci were significantly linked ($p = 0.05$; Eufa1×Elo34, Elo34×Eufa27).

Genetic Divergence

Pairwise F_{ST} values indicated many significant genetic differences between patches for all four species (84% of comparisons were significant for side-blotched lizards, 89% for fence lizards, 87% for skinks, and 71% for wrentits; Table S1). Average pairwise F_{ST} between patches was highest in the wrentit at 0.095 (range 0.012–0.299). Among lizards, the level of differentiation was highest for side-blotched lizards, with an average pairwise F_{ST} of 0.073 (range −0.006–0.200), and very similar for western skinks (mean $F_{ST} = 0.040$, range 0.003–0.104) and western fence lizards (mean $F_{ST} = 0.040$, range 0.003–0.095). As a baseline comparison from continuous habitat, when we computed genetic distances between the sampling arrays within large and core patches and between several other sites outside of our urban study area (but within the park, see Methods), we found lower average F_{ST} for all three lizard species (side-blotched lizards, 0.02; western fence lizard, 0.016; western skinks, 0.013), and fewer significant pairwise F_{ST} (side-blotched lizards, 12.5%; western fence lizards, 16.7%; western skinks, 30%; Table S2). For wrentits, genetic samples were also collected from two coastal canyons outside of our study area, and the F_{ST} between these two sites was non-significant ($F_{ST} = 0.026$). Significant genetic distances between patches could also be caused by isolation by geographic distance. We found no significant correlations between genetic distance (F_{ST}) and geographic distance in any of the four species, suggesting no pattern of isolation by distance (Table 2). However, partial Mantel tests showed that genetic distances for all four species were significantly correlated with highway presence, roads presence, and time since isolation (patch age) when geographic distance was held constant (Table 2).

Alleles in Space allows for visualization of genetic divergence over geographic space. We found that the largest area of genetic divergence for all four species was located in the area surrounding and including Highway 23 (Fig. 1b). There was also an area of higher divergence in the eastern part of the study area for two of the four species (wrentits, Fig. 1c; and western skinks, Fig. 1e).

Genetic clustering analysis revealed that the most likely number of genetic groups for all four species was between three and five (Table S3, Fig. 2). For wrentits (Fig. 2a) there were three most likely clusters, with the main genetic break again located across the developed areas surrounding and including Highway 23. For side-blotched lizards (Fig. 2b) and skinks (Fig. 2d) the most likely number of clusters was five, and for western fence lizards (Fig. 2c) it was four.

Genetic Diversity

Mean heterozygosity (H_e) and the mean number of effective alleles (N_A) were not significantly lower in smaller patches for any of the four species (Table S4). However, relatedness was higher in small patches for all three lizard species (side-blotched lizard difference = 0.03, $t = 4.1$, $p = 0.003$, d.f. = 6.2; fence lizard difference = 0.02, $t = 4.5$, $p = 0.001$, d.f. = 7; skink difference = 0.02, $t = 2.25$, $p = 0.03$, d.f. = 6). Rarefaction analysis indicated that the number of loci used produced consistent average relatedness results for all species and that the addition of the last locus added a 0.5% (fence lizards), 0.8% (side-blotched lizards), 1.4% (western skinks), and 0.1% (wrentits) change in relatedness estimates.

We tested the relationship between genetic diversity and the degree of isolation of each habitat patch and found that for wrentits, H_e was lower in more isolated patches ($R^2 = 0.498$, $p = 0.051$,

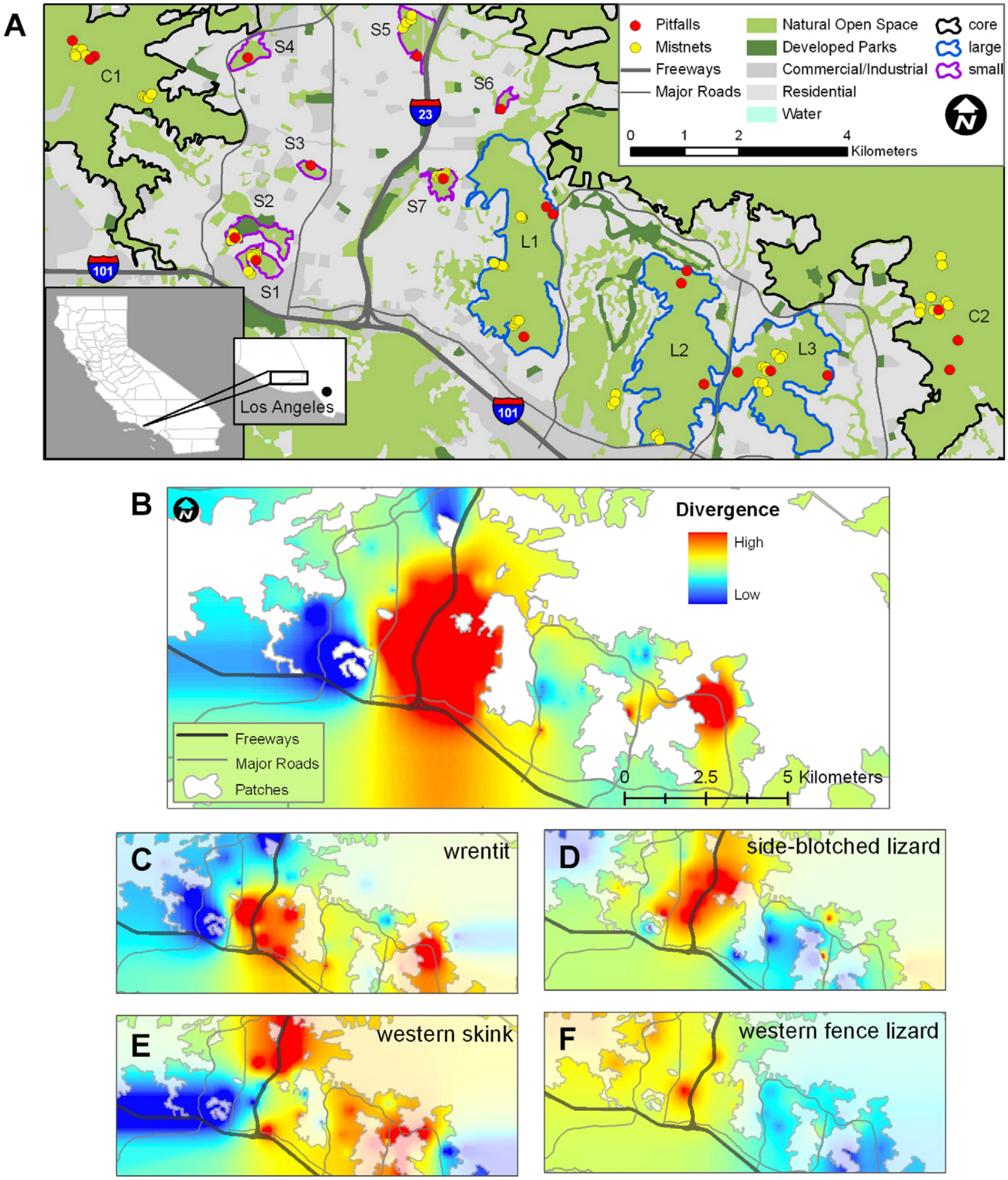

Figure 1. Study area and genetic divergence. A. Sampling sites (mist-net and pitfall locations), roads, and habitat patches (S = small, L = large, C = core) within the study area (Sample sizes are shown in Table 1). B. Mean genetic divergence mapped on the Simi Hills landscape for all four species, and separately for C. wrentits, D. side-blotched lizards, E. western skinks, and F. western fence lizards.
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d.f. = 7), as was N_A ($R^2 = 0.55$, $p = 0.035$, d.f. = 7; Fig. 3a). Relatedness was higher in more isolated patches for all three lizard species (side-blotched lizard $R^2 = 0.4$, $p = 0.03$, d.f. = 10; fence lizards $R^2 = 0.52$, $p = 0.002$, d.f. = 8; western skink $R^2 = 0.33$, $p = 0.05$, d.f. = 9; Fig. 3b). There were no correlations between genetic diversity and patch age for any of the four species (Table S5).

Table 1. Patch metrics (area, isolation, and age) and the number of samples genotyped by species.

Patch metrics					Number of samples genotyped			
Patch type	Sample site/patch	Area (ha)	Isolation (PROX)[a]	Age (years)[b]	Wrentit	Side-blotched lizard	Western fence lizard	Western skink
Small	S1	267.2	119.3	13	0	14	14	16
	S2	376.6	115.4	13	3	15	18	17
	S3	104.8	52.8	33	0	18	0	18
	S4	254.8	6404.8	23	0	17	0	0
	S5	450.2	195.9	33	5	14	18	5
	S6	78.2	747.4	13	0	17	0	20
	S7	206.5	133.1	43	8	15	16	10
Large	L1	4445.4	18428.1	28	7	0	18	28
	L2	3905.7	1598.1	23	8	22	17	29
	L3	3276.1	30121.0	18	12	18	17	18
Core	C1	25453.6	6368.9	23	11	7	15	0
	C2	121014.2	10718.8	13	15	24	14	18

[a] Patch isolation values (PROX) decrease with increasing isolation of patches.

[b] Patch age was calculated as the number of years since the patch was 100% isolated from other open natural space.

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Discussion

Loss of genetic connectivity

Using three different methods, traditional pair-wise genetic distance analysis (F_{ST}; Table S1), landscape genetic analysis (Fig. 1b), and Bayesian genetic clustering (Fig. 2), we found significant genetic differences between sample locations in all four species. Moreover, the three methods showed strikingly similar and strong genetic effects of fragmentation. All four species exhibited the largest genetic divergence over the oldest (based on building dates, see Methods) and widest expanse of urban areas surrounding and including Highway 23 (Fig. 1b).

Pairwise F_{ST} between habitat patches showed that the genetic divergence was significant, especially given the short amount of time that the habitat fragments have been isolated from each other and from core areas. For all four species, average F_{ST} values within continuous habitat were 2.5 to 3.6 times lower than in fragmented habitat, and the majority of comparisons were non-significant (Table S2). This suggests that microsatellite allele frequencies within and between habitat patches are changing on a very short time scale. Several other reptile and amphibian studies have found similar genetic divergences on similar time scales. For example, genetic divergence between fragmented populations of two gecko species in Australia was higher than divergence between samples in un-fragmented landscapes [35]. In that study, forested habitat patches were fragmented beginning around 1900 by wheat fields, which can be dry and barren during the non-growing season. In our study, however, the intervening landscape is concrete, asphalt, buildings, or urban yard landscaping, and although fragmentation began in the 1940s, many patches were only 50–75% isolated until 1980, making the isolation more recent. The long-lived tuatara (*Sphenodon punctatus*) was shown to have small yet significant genetic structuring (overall $R_{ST} = 0.012$) over less than 500 meters on a recently fragmented island [18]. Overall divergence was driven by one remnant forest fragment which was most isolated by island topography. Therefore, it was unclear that human activity, in this case pasture cleared for livestock grazing, was the cause of the genetic divergence. The eastern red-backed salamander (*Plethodon cinereus*), an even smaller and less mobile animal then the lizards we investigated, had pairwise F_{ST} between patches similar in value to the lizards in our study [14]. In that study, habitat fragmentation was also caused by 20th Century urbanization.

For birds, few studies have shown large pairwise F_{ST} between patches on such a small scale. For example, a study of the

Table 2. Mantel and partial Mantel tests with genetic distance and landscape features.

Mantel Tests	Wrentit		Side-blotched lizard		Western skink		Western fence lizard	
	r	*p*	r	*p*	r	*p*	r	*p*
F_{ST} and GD[a]	−0.015	0.500	−0.011	0.509	0.178	0.162	0.042	0.408
Partial test, HWY[b]	0.430	0.001	0.259	0.027	0.442	0.007	0.255	0.049
Partial test, RDS[b]	0.425	0.031	0.314	0.015	0.495	0.012	0.399	0.016
Partial test, AGE[b]	0.458	0.009	0.393	0.033	0.466	0.045	0.760	0.002

[a] Mantel test correlations between genetic distance (F_{ST}) and geographic distance (GD).

[b] Partial Mantel tests for partial correlations between the presence of Highway 23 only (HWY), the presence of major roads including Highway 23 (RDS), and the age of isolation between patches (patch age; AGE) while controlling for geographic distance.

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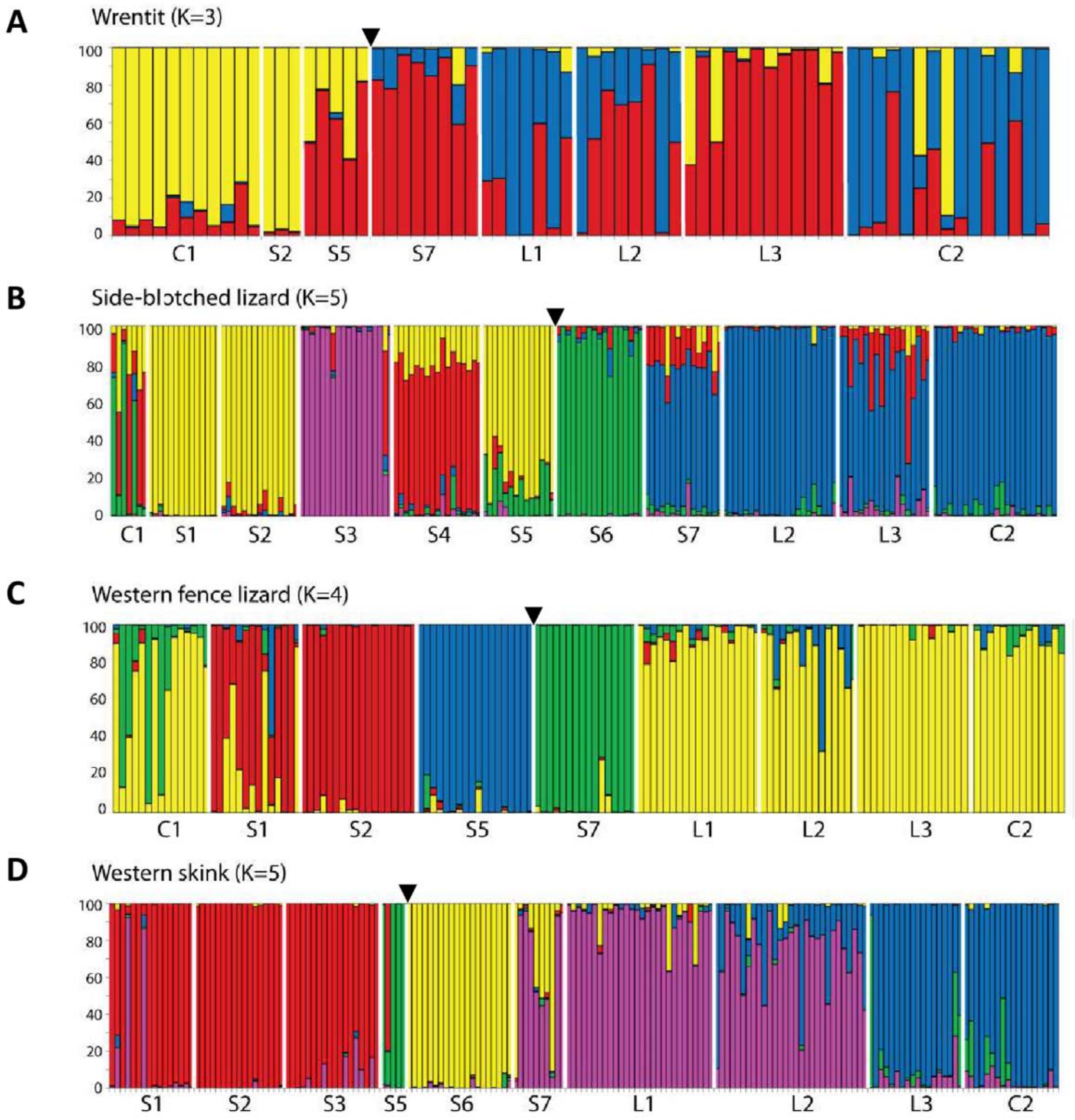

Figure 2. Genetic clustering analysis reveals the most likely K. Each column represents one individual and colors correspond to the percentage of assignment to each cluster. Patch names (Fig. 1a) are on the X-axis organized from west (left) to east (right). A black triangle indicates the location of the 23 freeway.
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capercaillie (*Tetrao urogallus*) in the Black Forest in Germany showed significant pairwise F_{ST} between sites, ranging from 0.007 to 0.036 [36]. In their study area, which was approximately 10 times the size of ours, suitable forest habitat was fragmented by other forest types and grassland, as opposed to by residential and commercial development. A study [37] of white-ruffed manikins (*Corapipo altera*) showed similar results to the capercaillie. There was some genetic structuring shown between remnant forest fragments, however all significant pairwise F_{ST} could be attributed to one forest fragment. In addition, pairwise F_{ST} between forest fragments ranged from 0.001 to 0.029 for manikins, whereas in our study the pairwise F_{ST} were approximately 10 times higher. Finally, a study of great tits (*Parus major*) in forest parks within the city of Barcelona found many significant pairwise F_{ST} between parks (average 0.067), but the parks actually had higher genetic diversity than the surrounding forest, and there was significant gene flow both between parks and from the parks to the forest [38]. Overall, there are few comparable studies of avian fine-scale genetic structure, particularly in urban landscapes, but wrentits in southern California appear to have the highest amount of genetic structure documented to date.

The Bayesian clustering analysis confirmed the loss of genetic connectivity for each species in our study area. Similar analyses in other bird studies have consistently shown that one genetic cluster is most likely [36,37,39,40], with only the great tit study finding two clusters [38]. For the lizards, in many of the small patches most or all individuals were given close to 100% assignment to that patch (e.g. S3 for side-blotched lizards, S5 and S7 for fence lizards, and S6 for skinks; Figure 2), which suggests a remarkable amount of genetic isolation within patches over relatively short geographic and temporal scales (Table S6). The short dispersal distances for all four species suggest that gene flow even within the natural landscape may be limited (for lizards, we did find a few significant F_{ST} values between sampling sites within continuous habitat), and therefore may be extremely restricted in a fragmented landscape.

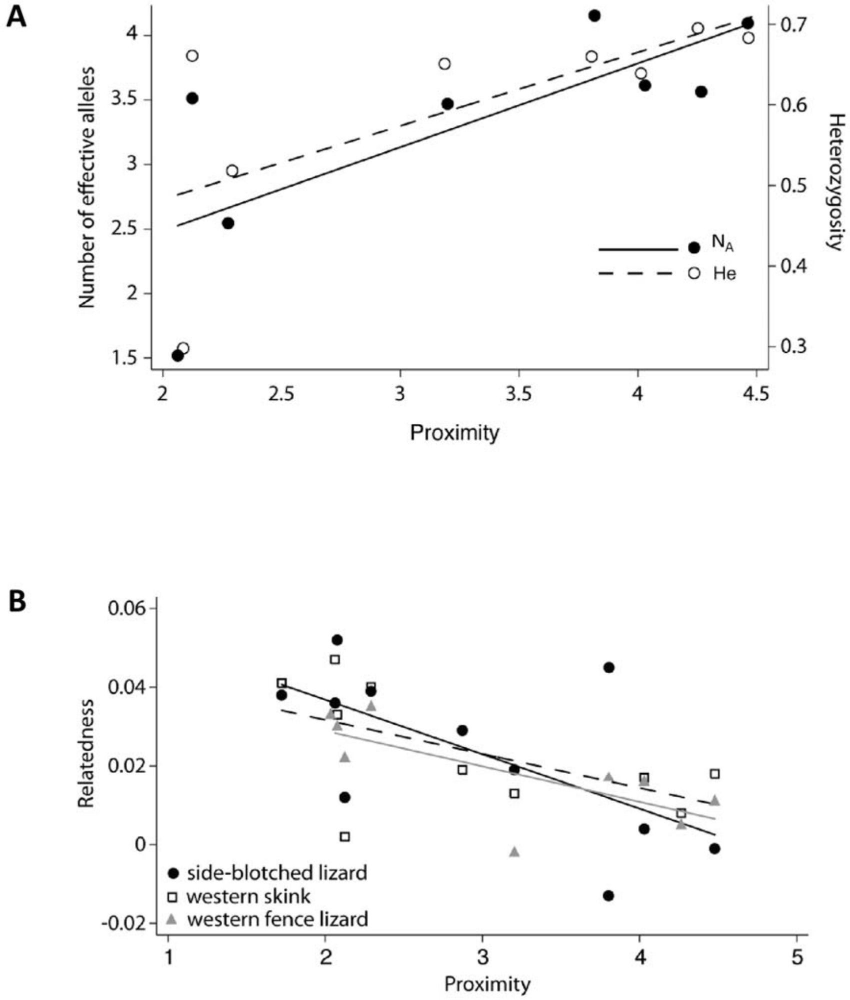

Figure 3. Relationship between genetic diversity (heterozygosity, number of effective alleles, and relatedness) and patch proximity[a] (log transformed). A. wrentits (H_e: $R^2 = 0.698$, $p = 0.051$, d.f. = 7; N_A: $R^2 = 0.55$, $p = 0.035$, d.f. = 7) and B. three lizard species (R_{LR}: side-blotched lizard $R^2 = 0.4$, $p = 0.03$, d.f. = 10; western skink $R^2 = 0.33$, $p = 0.05$, d.f. = 9; western fence lizard $R^2 = 0.52$, $p = 0.002$, d.f. = 8). [a] Patch proximity is the inverse of patch isolation.
doi:10.1371/journal.pone.0012767.g003

In one of the few other studies using Bayesian genetic clustering analysis, red-backed salamanders (*Plethodon cinereus*) were found to have two genetic clusters on either side of a large highway running through the urbanized study area [41]. Our genetic clustering results suggest that the intense fragmentation from urbanization may be a particularly strong barrier to animal movement and gene flow for all four species.

Along with significant divergence between patches, we also found significant correlations between specific causes (roads) and measures (patch age) of fragmentation and genetic divergence in all four species (Table 2). Further, our landscape genetic results revealed that the areas surrounding and including Highway 23 in the city of Thousand Oaks, which are the oldest and most densely urbanized, consistently had the highest peaks of differentiation, again for all four species (Fig. 1b). The concordance of these results for all four species is remarkable given their differences in mobility, ecology, and taxonomy. A second area of high genetic divergence in the eastern portion of our study area, also characterized by a major road surrounded by a wide swath of residential development, was shared by two species, wrentits and skinks. Other species have also shown fine-scale genetic changes related to roads and fragmentation in this region. Coyotes and bobcats exhibited significant genetic differentiation across Highway 101, the largest highway in the study area [42]. It is unknown if the species in our study would cross such a large barrier, but with short dispersal distances and small home range sizes, those events would likely be rare. Similarly, in smaller and less mobile species, a loss of genetic connectivity and diversity was found in two Jerusalem crickets (*Stenopelmatus 'santa monica'* and *Stenopelmatus 'mahogani'*) across the same region [16,43]. Genetic divergence in Jerusalem crickets was significantly associated with urban development and the presence of highways within the Simi Hills.

The significant genetic divergence and loss of genetic diversity over short geographic and temporal scales in these four vertebrates suggest that the urban matrix is relatively impenetrable for these animals. Anecdotal observations suggest that *S. occidentalis*, but not *P. skiltonianus* or *U. stansburiana*, will move through or persist in the residential areas of the urban matrix (RNF personal observation). However, reliable data on the urban movement and habitat use of these species does not exist. In fact, knowledge about use of the urban matrix by native animal species is extremely limited in general, but would be very valuable for understanding the conservation and management implications of urbanization. Urbanized areas may be dangerous places for these small vertebrates. Residential neighborhoods often introduce predators such as domestic cats, which may regularly prey on native vertebrates [44]. Of course residential areas also include roads, which lizards and birds may actively avoid, or which may be a significant source of mortality [45,46,47].

Loss of genetic diversity

When the landscape is fragmented and gene flow is restricted, as we have shown for these four species, genetic diversity may be reduced in populations within smaller or more isolated habitat patches. Although we found no relationships between patch age and genetic diversity, we found significant relationships between genetic diversity measures and patch size or isolation for all four species. All three lizards had increased relatedness in smaller patches and with increasing patch isolation (Fig. 3b). Other reptile species have shown increased relatedness within habitat patches that were fragmented by agriculture [48,49,50]. In wrentits, although we did not find increased within-patch relatedness, we found lowered heterozygosity (H_e) and fewer alleles (N_A) in smaller patches (Fig. 3a). Decreased gene flow can result in decreased H_e and N_A in small patches as alleles are lost over the generations. This effect tends to be gradual and may not threaten populations in the short term, however, inbreeding within habitat patches tends to happen quickly and can lead to inbreeding depression [51]. Lizard relatedness values suggest that inbreeding is occurring within smaller and more isolated patches. The difference between taxa may be attributed to the increased effective isolation of lizards on suitable habitat patches as a result of more restricted dispersal ability compared to wrentits. Our results suggest that populations within smaller and more isolated patches may have an increased risk of harmful genetic effects and, over the long-term, even extirpation. In fact, the absence of individuals from certain study patches (e.g. skinks and fence lizards absent from S4; Table 1) suggests that populations that were presumably present at the time of patch isolation may have been extirpated.

In a relatively short time, we have documented significant genetic divergence between isolated patches and decreased genetic diversity in all four species. However, although time since isolation (patch age) was strongly correlated with genetic divergence between patches, the effects on genetic diversity in these animals were significantly related to patch size and degree of patch isolation, but not to patch age. This would suggest that the habitat is still relatively suitable in habitat fragments, resulting in relatively stable populations that are not going through bottlenecks, such that more time since isolation is not as important a factor. But patches that are smaller from the outset simply cannot support as large a population, and therefore are more subject to the deleterious effects of genetic drift, specifically the loss of genetic diversity. Patches that are more isolated may in turn be less likely to receive new dispersers, i.e. they would benefit less from the "rescue effect" that could offset reductions in genetic diversity [52]. Presumably patches that were both small and isolated would suffer the most ill effects.

Conservation implications

The extreme urbanization within the Simi Hills area has had a significant effect on lizard and bird population genetics. Unlike some other studies of landscape level genetic changes where a species' habitat is naturally patchy, this study examined genetic responses to species living in habitat that was likely once relatively continuous [42]. While these species are still widely distributed and relatively abundant throughout the study area, genetic effects of fragmentation have been manifested in a relatively short period of 40 years or less. This may be the most profound and potentially disturbing result of our study: the vulnerability even of species that are perceived to be common and thereby likely less affected by habitat fragmentation. This may be particularly true for low-vagility organisms, and for those with more specific habitat requirements. As a chaparral and coastal sage scrub requiring species, wrentits are likely rare in developed areas and have been shown to go extinct in habitat patches as urbanization progresses [2,53,54].

For rarer species in the region, such as horned lizards (*Phrynosoma coronatum*) and whiptail lizards (*Aspidoscelis tigris*), whose distributions have already been reduced by urban development [55], the genetic effects of fragmentation may be even more profound. Many endangered species in southern California are declining because of habitat loss, and many of these species also have low dispersal abilities along with more specific habitat requirements (e.g. light-footed clapper rail, *Rallus longirostris obsoletus*; Belding's savannah sparrow, *Passerculus sandwichensis beldingi*; red-legged frog, *Rana draytonii*; least bell's vireo, *Vireo bellii pusillus*). It is also unknown how stressors, such as increasing local or global temperature and urbanization, might affect species in southern California. A recent study of *Sceloporus* lizards in Mexico found that 12% of local populations have gone extinct since 1975 [56]. Sites where these common lizards were extirpated were too hot for too many hours of the day, presumably due to increasing global temperatures, which caused lizards to seek refuge from the heat instead of spending time foraging. In addition, our results have implications for endangered species such as the California gnatcatcher, where lack of differentiation at certain loci (e.g. mtDNA; [57]) may not reflect important genetic differentiation detectable with other markers such as microsatellites.

Materials and Methods

Study Area

Southern California is characterized by a Mediterranean climate with cool, wet winters and hot, dry summers. Vegetation consisted of coastal sage scrub, chaparral, riparian habitat, and oak woodlands. Our study site is within SMMNRA, the USA's largest urban national park (154,095 acres or 623.6 km^2; www.nps.gov/samo/parkmgmt/statistics.htm), which is located in Los Angeles and Ventura counties, California, USA (Fig. 1a). Approximately half of the land within the park boundary is privately owned, although some public acquisitions continue. Habitat patches within our study area were within 12.5 kilometers (km) of each other but were separated by roads of all sizes, housing, and commercial development (Fig. 1a). Most building started in the middle of the 20th Century, and none of the habitat patches have been completely isolated for longer than 43 years (Table 1; [58]). Two major freeways (101 and 23) and many busy four-lane roads run through the study area (Fig. 1a). The peak average daily traffic in this area is approximately 180,000 cars per day for the 101 Freeway and 90,000 cars per day for Highway 23 (Caltrans, www.ca.dot.gov). Both freeways are mostly surrounded by commercial and residential development. Within the study area there are large core areas of relatively undisturbed habitat, although some low-impact human recreation does occur. Within the urban mosaic, habitat patches were surrounded by high- or low-density housing, highways and other roads, golf courses and other landscaped areas.

We collected samples from habitat fragments which we characterized as "small" (75–450 ha) or "large" (3200–4400 ha) and from larger areas of continuous habitat which we called "core" areas (Fig. 1a). There were 7 small patches (S1-S7), 3 large patches (L1-L3) and 2 core areas (C1 and C2). Patch area (m^2) and degree of isolation (PROX) were calculated using FRAGSTATS [59]. PROX is the sum of patch area divided by the nearest edge-to-edge distance squared between all of the patches within a defined search radius and the focal patch. PROX approaches 0 if the patch has no neighbors within the search radius (a 20 km radius encompassed our entire study site) specified in FRAGSTATS, therefore patches with smaller PROX numbers are more isolated. Building dates for roads, housing developments, and commercial areas were used to calculate the ages (in years) at which patches were 100% isolated up to the time of trapping for this study (patch age; Table 1). Patches were considered 100% isolated when they were completely surrounded on all edges by either commercial buildings, housing, or roads or a combination of these. We also made a matrix of patch ages (for pair wise comparisons) by calculating the number of years that each patch was separated from each other patch.

Field sampling

To capture lizards we used arrays of pitfall traps and drift fencing. All samples for this study were collected between October 2000 and September 2005. Each array had seven 19-liter buckets buried in the ground with the lip of the bucket flush with the ground to act as a pitfall trap [55,60]. Buckets were arranged in a "Y" configuration and buried approximately 7.5 m apart. Between the buckets, short drift fencing (0.5 m tall) consisting of erosion cloth acted to intercept reptiles moving through the habitat and directed them towards the buckets. Shade and moisture were provided for each bucket to maximize the chance of survival for reptiles, amphibians, or small mammals that were trapped. Pitfall traps were checked daily for a week at one-month intervals [22]. Each reptile was identified to species and snout to vent length was measured in mm. Each individual was assigned a unique number, was permanently marked by toe clipping [61,62] and a small sample from the tip of the tail was taken. Toes and tail tips were stored in 70% ethanol at 4°C or −80°C depending on storage space.

To capture birds, we used mist-nets. Trapping occurred from August 2004 to May 2006. Generally, we would open mist-nets (9–12 m long, 30 cm mesh) at sunrise and close them as the temperature increased to a potentially unsafe level in mid-morning. We targeted wrentits by playing male territorial songs with portable speakers placed at the base of the net. Once a bird was caught in the net, it was immediately removed and a U.S. Fish and Wildlife Service band was placed on its leg. We also took measurements of culmen length (mm), culmen width (mm), unflattened wing chord length (cm), tail length (cm), tarsus length (cm) and mass (g). Culmen length was taken from the anterior end of the nares to the tip of the beak using calipers. For genetic samples, we punctured the brachial vein on the wing of each bird with a small gauge needle and collected the blood that pooled there with a small capillary tube. Bleeding usually stopped after 10 seconds which yielded approximately 100 µl of blood. Blood was then placed in avian blood buffer [63].

All samples used in this study came from animals that were captured, handled, and released according to relevant national and international scientific guidelines. We used common field and handling methods that minimize stress and long-term effects of capture. We also researched methods alternative to toe-clipping of reptiles and determined that there were no less harmful yet permanent ways of marking individuals [62]. We obtained approval for our animal capture protocol from the UCLA Office of the Protection of Animals (OPRS).

We extracted genomic DNA with the Qiagen DNA mini kit (Qiagen Inc.). DNA samples were stored in TE buffer (10 mM Tris-Cl pH 8.0, 1 mM EDTA pH 8.0) at −20°C. We used six to eight microsatellite markers for each species (Table S6, J. Archie, Pers. Comm.; [64,65,66,67]). We used flourescently-labeled forward microsatellite primers when available. Alternatively, we used a three-primer genotyping protocol, where the forward microsatellite primer had an M13 sequence attached to the 5′ end (5′-GTAAAACGACGGCCAG-3′) and a third primer with the complementary M13 sequence was dye-labeled [68,69]. The forward, reverse and M13-dye primers were then used in a three-primer PCR protocol using Multiplex Mix (Qiagen Inc.) and 0.01% Bovine Serum Albumin (BSA) to generate microsatellite alleles which are flourescently labeled. Genotypes were run on an ABI 3700 sequencer and alleles were visualized using GENEMAPPER (Applied Biosystems, Inc.).

Genetic Analysis

We used the computer program CONVERT to translate our microsatellite genotype files into the correct input format for various analysis programs [70]. We used FSTAT 2.9.3 [71] to test for deviations from Hardy-Weinberg equilibrium (HWE) within samples using 1000 permutations. We also used FSTAT to test for linkage disequilibrium (LD) between loci. P-values were adjusted for multiple tests using a sequential Bonferonni correction [72]. For HWE and LD, all samples for each species were assumed to be a single population.

Genetic divergence. We used the program ARLEQUIN to estimate pair-wise F_{ST} values between patches using the infinite-allele model and 1000 permutations for significance [73,74]. We also calculated pair-wise F_{ST} between arrays within large and core patches with ARLEQUIN to show genetic divergence between sampling sites that were located within a patch of continuous habitat. For this calculation we also included some sampling sites from core areas of continuous habitat that were outside of the Simi Hills (our study area), but within SMMNRA, with an average of 4.28 km (range 1.8–6.6 km) separating these sites.

To examine patterns of sample clustering based on genetic similarity, we used the program STRUCTURE v. 2.3.1 [75]. We chose the LOCPRIOR model [76], assumed populations were not admixed and that allele frequencies were correlated between populations, and ran 100,000 MCMC chains with a 10,000 burn-in. We ran seven runs each of $K = 1$ to $K =$ number of sample sites (Fig. 1a) for each species. We compiled results from our STRUCTURE runs with the program STRUCTURE HARVESTER (Dent Earl, http://taylor0.biology.ucla.edu/struct_harvest/). To determine the most likely K, we calculated the posterior probabilities of the mean of seven runs at each K (Table S3; [75]).

Isolation by distance, as revealed by a correlation between pairwise genetic and geographic (Euclidean) distances using a Mantel test, was performed using IBDWS 3.14 [77]. IBDWS uses a Reduced Major Axis (RMA) regression to estimate the slope and intercept of the isolation by distance relationship.

To test for the effect of major roads, highways, and patch age on genetic divergence, we performed partial Mantel tests [78] in IBDWS 3.14. Partial Mantel tests determined correlations of roads presence (RDS), highway presence (HWY), and patch age of isolation (AGE) on a genetic divergence matrix, while holding geographic distance constant. Tests were performed separately, one for each of these three variables, and all animals that were captured within a patch were used to calculate a patch average genetic divergence (F_{ST}; as calculated in ARLEQUIN, see above). The presence of major roads and the presence of Highway 23 were used separately in the analysis because the highway in our study area is larger and has more traffic than other roads. Also, several habitat fragments are only separated by major roads. Age of isolation was chosen because this measure incorporates not only when roads and freeways were built, but also when residential and commercial developments were erected.

We mapped genetic distance on the landscape using Alleles in Space (AIS) and the landscape shape interpolation [79]. We used a Delaunay triangulation-based connectivity network to identify midpoints between our sample sites, then the raw genetic distance (D_{ij}) at each midpoint was calculated [79]. This genetic distance measure is similar to Nei's standard genetic distance (D_s; [80]), where D_{ij} is 0 if individuals are completely genetically identical, and D_{ij} is 1 if individuals are completely genetically dissimilar. We did not calculate the residual genetic distance, because we did not find a significant isolation by distance effect in the Simi Hills samples for any species (see Results). By this method, a landscape of genetic distances between sampling sites are expressed as "surface heights" and are displayed as a 3-dimensional graph. To better visualize the AIS height output, we imported the output file into ArcGIS 9.3 (ESRI Corporation, Redlands, CA) and created a 2-dimensional color hot-spot map overlaid on the geographic study area. Colors correspond to "heights" of genetic distance between points (e. g. Fig. 1b).

Genetic diversity. We used the program GENALEX [81] to calculate the genetic diversity indices of within-patch expected heterozygosity (H_e), observed heterozygosity (H_o), number of effective alleles (N_A), and relatedness (R_{LR}) [82]. We used the Lynch & Ritland (1999) estimator of relatedness because it has been shown to perform well in simulations for a wide range of marker data and population structure [83]. We performed a rarefaction analysis using the web-based program RERAT [84] which uses multiple simulations to determine the change in relatedness values as additional microsatellite loci are added. In RERAT, we performed 100 simulations and used the Lynch and Ritland (1999) relatedness analysis for each of the four species. For lizards, cores and large patches had three pitfall trap arrays while small patches had one (Fig. 1a). To reduce bias because of array clustering, we calculated pair wise relatedness of all individuals caught in the same array, and then used the mean of those within-array measures to calculate within patch relatedness.

We used the program STATA 9 (StataCorp, College Station, TX) to transform variables until they approached normal distributions and then to examine the relationship between the indices of genetic diversity and the size, degree of isolation, and age of the habitat patches. We used unpaired t-tests (with unequal variance when necessary) and Bonferroni corrections to compare genetic diversity measures between small and large/core habitat patches. Degrees of freedom for t-tests were calculated using the Satterthwaite (1946) method [85]. We lumped large patches and core areas for this analysis because, for these small species, population size is likely equivalently large in the large patches and the core areas, and because the numbers of sites were relatively small for core areas ($n = 2$) and large patches ($n = 3$). To test for a relationship between patch isolation and genetic diversity, we used linear regression to examine the relationship of the genetic diversity indices with the size, pair wise age of isolation, and proximity (PROX) of the habitat patches, where the degree of isolation of a patch is the inverse of proximity. Spearman's rank correlations were used to test for significant associations between patch age and genetic diversity.

Supporting Information

Table S1 F_{ST} between sample sites for 4 species. Significant pairwise F_{ST} values are in bold (see Fig. 1a for sample site locations).

Found at: doi:10.1371/journal.pone.0012767.s001 (0.22 MB DOC)

Table S2 Pairwise F_{ST} and the number of significant comparisons between patches in and continuous habitat.

Found at: doi:10.1371/journal.pone.0012767.s002 (0.05 MB DOC)

Table S3 Estimated posterior probabilities for K. Most likely number of genetic clusters (K) identified with the program Structure is shown in bold.

Found at: doi:10.1371/journal.pone.0012767.s003 (0.07 MB DOC)

Table S4 Mean genetic diversity measurements within patches (number of effective alleles, N_A; relatedness, R_{LR}; heterozygosity, H_e).

Found at: doi:10.1371/journal.pone.0012767.s004 (0.12 MB DOC)

Table S5 Spearman's Rho correlation coefficients. The number of individuals genotyped (N), the number of alleles (A), expected (H_e) and observed (H_o) heterozygosity.

Found at: doi:10.1371/journal.pone.0012767.s005 (0.04 MB DOC)

Table S6 Microsatellite primers used for each species. The number of individuals genotyped (N), the number of alleles (A), expected (H_e) and observed (H_o) heterozygosity.

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Author Contributions

Conceived and designed the experiments: KSD SPDR RNF. Performed the experiments: KSD. Analyzed the data: KSD. Contributed reagents/materials/analysis tools: KSD SPDR. Wrote the paper: KSD SPDR.

References

1. Crooks KR, Suarez AV, Bolger DT, Soule ME (2001) Extinction and colonization of birds on habitat islands. Conservation Biology 15: 159–172.
2. Soule ME, Bolger DT, Alberts AC, Wright J, Sorice M, et al. (1988) Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. Conservation Biology 2: 75–92.
3. Case TJ, Fisher RN (2001) Measuring and predicting species presence: coastal sage scrub case study. In: Hunsaker M, Goodchild M, Friedl M, Case TJ, eds. Uncertainty in spatial data for ecology. Berlin: Springer-Verlag Press. pp 47–71.
4. Frankham R (2006) Genetics and landscape connectivity. In: Crooks KR, Sanjayan M, eds. Connectivity Conservation. Cambridge: Cambridge University Press. pp 72–96.
5. Reed DH (2004) Extinction risk in fragmented habitats. Animal Conservation 7: 181–191.

6. Reed DH, Briscoe DA, Frankham R (2002) Inbreeding and extinction: The effect of environmental stress and lineage. Conservation Genetics 3: 301–307.
7. Reed DH, Lowe EH, Briscoe DA, Frankham R (2003) Inbreeding and extinction: Effects of rate of inbreeding. Conservation Genetics 4: 405–410.
8. Lande R (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist 142: 911–927.
9. Reed DH, Frankham R (2003) Correlation between fitness and genetic diversity. Conservation Biology 17: 230–237.
10. Keyghobadi N (2007) The genetic implications of habitat fragmentation for animals. Canadian Journal of Zoology 85: 1049–1064.
11. Miller JR, Hobbs RJ (2002) Conservation where people live and work. Conservation Biology 16: 330–337.
12. Keller I, Largiader CR (2003) Recent habitat fragmentation caused by major roads leads to reduction of gene flow and loss of genetic variability in ground beetles. Proceedings of the Royal Society of London Series B-Biological Sciences 270: 417–423.
13. Keller I, Nentwig W, Largiader CR (2004) Recent habitat fragmentation due to roads can lead to significant genetic differentiation in an abundant flightless ground beetle. Molecular Ecology 13: 2983–2994.
14. Noel S, Ouellet M, Galois P, Lapointe FJ (2007) Impact of urban fragmentation on the genetic structure of the eastern red-backed salamander. Conservation Genetics 8: 599–606.
15. Redeker S, Andersen LW, Pertoldi C, Madsen AB, Jensen TS, et al. (2006) Genetic structure, habitat fragmentation and bottlenecks in Danish bank voles (*Clethrionomys glareolus*). Mammalian Biology 71: 144–158.
16. Vandergast AG, Lewallen EA, Deas J, Bohonak AJ, Weissman DB, et al. (2009) Loss of genetic connectivity and diversity in urban microreserves in a southern California endemic Jerusalem cricket (Orthoptera: Stenopelmatidae: *Stenopelmatus n. sp "santa monica"*). Journal of Insect Conservation 13: 329–345.
17. Magle SB, Ruell EW, Antolin MF, Crooks KR (2010) Population genetic structure of black-tailed prairie dogs, a highly interactive species, in fragmented urban habitat. Journal of Mammology 91: 326–335.
18. Moore JA, Miller HC, Daugherty CH, Nelson NJ (2008) Fine-scale genetic structure of a long-lived reptile reflects recent habitat modification. Molecular Ecology 17: 4630–4641.
19. Sumner J, Jessop T, Paetkau D, Moritz C (2004) Limited effect of anthropogenic habitat fragmentation on molecular diversity in a rain forest skink, *Gnypetoscincus queenslandiae*. Molecular Ecology 13: 259–269.
20. Richmond JQ, Reid DT, Ashton KG, Zamudio KR (2008) Delayed genetic effects of habitat fragmentation on the ecologically specialized Florida sand skink (*Plestiodon reynoldsi*). Conservation Genetics 10: 1291–1297.
21. Stebbins RC (1954) Amphibians and Reptiles of Western North America. New YorkNY: Mc-Graw-Hill Book Company Inc. 536 p.
22. Busteed GT (2003) Effects of habitat fragmentation on reptiles and amphibians in coastal sage scrub and grassland communities. NorthridgeCA: California State University, Northridge 59 p.
23. Doughty P, Sinervo B (1994) The Effects of habitat, time of hatching, and body-size on the dispersal of hatchling *Uta stansburiana*. Journal of Herpetology 28: 485–490.
24. Doughty P, Sinervo B, Burghardt GM (1994) Sex-biased dispersal in a polygynous lizard, *Uta stansburiana*. Animal Behaviour 47: 227–229.
25. Fitch HS, Von Achen PL (1977) Spatial relationships and seasonality in the skinks *Eumeces fasciatus* and *Scincella laterale* in northeastern Kansas USA. Herpetologica 33: 303–313.
26. Massot M, Huey RB, Tsuji J, van Berkum FH (2003) Genetic, prenatal, and postnatal correlates of dispersal in hatchling fence lizards (*Sceloporus occidentalis*). Behavioral Ecology 14: 650–655.
27. Sinervo B, Calsbeek R, Comendant T, Both C, Adamopoulou C, et al. (2006) Genetic and maternal determinants of effective dispersal: The effect of sire genotype and size at birth in side-blotched lizards. American Naturalist 168: 88–99.
28. Geupel GR, Ballard G, eds;Wrentit (*Chamaea fasciata*). Ithaca: Cornell Lab of Ornithology. Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/654 doi:10.2173/bna.654.
29. Baker M, Nur N, Geupel GR (1995) Correcting biased estimates of dispersal and survival due to limited study area - theory and an application using wrentits. Condor 97: 663–674.
30. Cincotta RP, Wisnewski J, Engelman R (2000) Human population in the biodiversity hotspots. Nature 404: 990–992.
31. Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403: 853–858.
32. Syphard AD, Clarke KC, Franklin J (2005) Using a cellular automaton model to forecast the effects of urban growth on habitat pattern in southern California. Ecological Complexity 2: 185–203.
33. Brown JH, Kodric-Brown A (1977) Turnover rates in insular biogeography effect of immigration on extinction. Ecology 58: 445–449.
34. Hanski I (1999) Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. Oikos 87: 209–219.
35. Hoehn M, Sarre SD, Henle K (2007) The tales of two geckos: does dispersal prevent extinction in recently fragmented populations? Molecular Ecology 16: 3299–3312.
36. Segelbacher G, Manel S, Tomiuk J (2008) Temporal and spatial analyses disclose consequences of habitat fragmentation on the genetic diversity in capercaillie (*Tetrao urogallus*). Molecular Ecology 17: 2356–2367.
37. Barnett JR, Ruiz-Gutierrez V, Coulon A, Lovette IJ (2008) Weak genetic structuring indicates ongoing gene flow across White-ruffed Manakin (*Corapipo altera*) populations in a highly fragmented Costa Rica landscape. Conservation Genetics 9: 1403–1412.
38. Bjorklund M, Ruiz I, Senar JC (2010) Genetic differentiation in the urban habitat: the great tits (*Parus major*) of the parks of Barcelona city. Biological Journal of the Linnean Society 99: 9–19.
39. Mylecraine KA, Bulgin NL, Gibbs HL, Vickery PD, Perkins DW (2008) Limited genetic structure and evidence for dispersal among populations of the endangered Florida grasshopper sparrow, *Ammodramus savannarum floridanus*. Conservation Genetics 9: 1633–1638.
40. Veit ML, Robertson RJ, Hamel PB, Friesen VL (2005) Population genetic structure and dispersal across a fragmented landscape in cerulean warblers (*Dendroica cerulea*). Conservation Genetics 6: 159–174.
41. Marsh DM, Page RB, Hanlon TJ, Corritone R, Little EC, et al. (2008) Effects of roads on patterns of genetic differentiation in red-backed salamanders, *Plethodon cinereus*. Conservation Genetics 9: 603–613.
42. Riley SPD, Pollinger JP, Sauvajot RM, York EC, Bromley C, et al. (2006) A southern California freeway is a physical and social barrier to gene flow in carnivores. Molecular Ecology 15: 1733–1741.
43. Vandergast AG, Bohonak AJ, Weissman DB, Fisher RN (2007) Understanding the genetic effects of recent habitat fragmentation in the context of evolutionary history: phylogeography and landscape genetics of a southern California endemic Jerusalem cricket (Orthoptera : Stenopelmatidae : *Stenopelmatus*). Molecular Ecology 16: 977–992.
44. Chace JF, Walsh JJ (2006) Urban effects on native avifauna: a review. Landscape and Urban Planning 74: 46–69.
45. Forman RTT, Alexander LE (1998) Roads and their major ecological effects. Annual Review of Ecology and Systematics 29: 207–231.
46. Shepard DB, Kuhns AR, Dreslik MJ, Phillips CA (2008) Roads as barriers to animal movement in fragmented landscapes. Animal Conservation 11: 288–296.
47. Koenig J, Shine R, Shea G (2001) The ecology of an Australian reptile icon: how do blue-tongued lizards (*Tiliqua scincoides*) survive in suburbia? Wildlife Research 28: 215–227.
48. Stow AJ, Sunnucks P (2004) High mate and site fidelity in Cunningham's skinks (*Egernia cunninghami*) in natural and fragmented habitat. Molecular Ecology 13: 419–430.
49. Stow AJ, Sunnucks P (2004) Inbreeding avoidance in Cunningham's skinks (*Egernia cunninghami*) in natural and fragmented habitat. Molecular Ecology 13: 443–447.
50. Sumner J (2005) Decreased relatedness between male prickly forest skinks (*Gnypetoscincus queenslandiae*) in habitat fragments. Conservation Genetics 6: 333–340.
51. Keller LF, Waller DM (2002) Inbreeding effects in wild populations. Trends in Ecology & Evolution 17: 230–241.
52. Hanski I (1991) Single-species metapopulation dynamics - concepts, models and observations. Biological Journal of the Linnean Society 42: 17–38.
53. Bolger DT, Alberts AC, Soule ME (1991) Occurrence patterns of bird species in habitat fragments - sampling, extinction, and nested species subsets. American Naturalist 137: 155–166.
54. Crooks KR, Suarez AV, Bolger DT (2004) Avian assemblages along a gradient of urbanization in a highly fragmented landscape. Biological Conservation 115: 451–462.
55. Fisher RN, Suarez AV, Case TJ (2002) Spatial patterns in the abundance of the coastal horned lizard. Conservation Biology 16: 205–215.
56. Sinervo B, Méndez-de-la-Cruz F, Miles DB, Heulin B, Bastiaans E, et al. (2010) Erosion of lizard diversity by climate change and altered thermal niches. Science 328: 894–899.
57. Zink RM, Barrowclough GF, Atwood JL, Blackwell-Rago RC (2000) Genetics, taxonomy, and conservation of the threatened California gnatcatcher. Conservation Biology 14: 1394–1405.
58. Southern California Association of Governments Existing Land Use Database (2005) Land use data for the counties of Imperial, Los Angeles, Orange, Riverside, San Bernardino and Ventura.
59. McGarigal K, Cushman SA, Neel MC, Ene E (2002) FRAGSTATS: Spatial pattern analysis program for categorical maps. ;Computer software program produced by the authors at the University of Massachusetts, Amherst.
60. Campbell HW, Christman SP (1982) Field techniques for herpetofaunal community analysis. In: Scott, NJ, ed. Herpetofaunal Communities, Wildlife Research Report 13. Washington DC: USDI Fish and Wildlife Service. pp 193–200.
61. Donnelly MA, Guyer C, Juterbock JE, Alford RA (1994) Techniques for marking amphibians. In: Heyer WR, Donnelly MA, McDiarmid RW, Hayek LC, Foster MS, eds. Measuring and monitoring biological diversity, standard methods for amphibians. Washington DC: Smithsonian Institution Press. pp 277–284.
62. Langkilde T, Shine R (2006) How much stress do researchers inflict on their study animals? A case study using a scincid lizard, *Eulamprus heatwolei*. The Journal of Experimental Biology 209: 1035–1043.
63. Seutin G, White BN, Boag PT (1991) Preservation of avian blood and tissue samples for DNA analyses. Canadian Journal of Zoology 69: 82–90.

64. Coughlan JP, Kitson L, Dillane E, Davenport J, Cross TF (2004) Characterization of six microsatellite loci in the Bermuda skink (*Eumeces longirostris*). Molecular Ecology Notes 4: 678–679.
65. Howes BJ, Lee-Yaw A, Robertson AV, Bogart JP, Lougheed SC (2004) Microsatellite loci from the five-lined skink (*Eumeces fasciatus*). Molecular Ecology Notes 4: 237–238.
66. Richardson DS, Jury FL, Dawson DA, Salgueiro P, Komdeur J, et al. (2000) Fifty Seychelles warbler (*Acrocephalus sechellensis*) microsatellite loci polymorphic in Sylviidae species and their cross-species amplification in other passerine birds. Molecular Ecology 9: 2226–2231.
67. Zamudio KR, Sinervo E (2000) Polygyny, mate-guarding, and posthumous fertilization as alternative male mating strategies. Proceedings of the National Academy of Sciences of the United States of America 97: 14427–14432.
68. Boutin-Ganache I, Raposo M, Raymond M, Deschepper CF (2001) M13-tailed primers improve the readability and usability of microsatellite analyses performed with two different allele-sizing methods. Biotechniques 31: 24–27.
69. Schuelke M (2000) An economic method for the fluorescent labeling of PCR fragments. Nature Biotechnology 18: 233–234.
70. Glaubitz JC (2004) CONVERT: A user-friendly program to reformat diploid genotypic data for commonly used population genetic software packages. Molecular Ecology Notes 4: 309–310.
71. Goudet J (2002) FSTAT: a software to estimate and test gene diversities and differentiation statistics from codominant markers (version 2.9.3.2). Available from http://www2.unil.ch/popgen/softwares/fstat.htm.
72. Rice WR (1989) Analyzing tables of statistical tests. Evolution 43: 223–225.
73. Schneider S, Roessli D, Excoffier L (2000) Arlequin ver. 2.000. A software for population genetics data analysis. Geneva, Switzerland: Genetics and Biometry Laboratory.
74. Weir BS, Cockerham CC (1984) Estimating F-statistics for the analysis of population structure. Evolution 38: 1358–1370.
75. Pritchard JK, Stefens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155: 945–959.
76. Hubisz MJ, Falush D, Stephens M, Pritchard JK (2009) Inferring weak population structure with the assistance of sample group location. Molecular Ecology Resources 9: 1322–1332.
77. Jensen JL, Bohonak AJ, Kelley ST (2005) Isolation by distance, web service. BMC Genetics 6: 13.
78. Legendre P, Legendre L (1998) Numerical Ecology. New York: Elsevier. 853 p.
79. Miller MP (2005) Alleles In Space (AIS): Computer software for the joint analysis of inter-individual spatial and genetic information. Journal of Heredity 96: 722–724.
80. Nei M, Tajima F, Tateno Y (1983) Accuracy of estimated phylogenetic trees from molecular data .2. Gene-frequency data. Journal of Molecular Evolution 19: 153–170.
81. Peakall R, Smouse PE (2006) GENALEX 6: Genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes 6: 288–295.
82. Lynch M, Ritland K (1999) Estimation of pairwise relatedness with molecular markers. Genetics 152: 1753–1766.
83. Thomas SC (2005) The estimation of genetic relationships using molecular markers and their efficiency in estimating heritability in natural populations. Philosophical Transactions of the Royal Society Series B 360: 1457–1467.
84. Schwacke L, Schwacke J, Rosel P (2005) RERAT: relatedness estimation and rarefaction analysis tool, URL http://people.musc.edu/~schwaclh.
85. Satterthwaite FE (1946) An approximate distribution of estimates of variance components. Biometrics Bulletin 2: 110–114.

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The relationship of respiratory and cardiovascular hospital admissions to the southern California wildfires of 2003

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Abstract

Objective—There is limited information on the public health impact of wildfires. The relationship of cardiorespiratory hospital admissions (n = 40 856) to wildfire-related particulate matter ($PM_{2.5}$) during catastrophic wildfires in southern California in October 2003 was evaluated.

Methods—Zip code level $PM_{2.5}$ concentrations were estimated using spatial interpolations from measured $PM_{2.5}$, light extinction, meteorological conditions, and smoke information from MODIS satellite images at 250 m resolution. Generalised estimating equations for Poisson data were used to assess the relationship between daily admissions and $PM_{2.5}$, adjusted for weather, fungal spores (associated with asthma), weekend, zip code-level population and sociodemographics.

Results—Associations of 2-day average $PM_{2.5}$ with respiratory admissions were stronger during than before or after the fires. Average increases of 70 $\mu g/m^3$ $PM_{2.5}$ during heavy smoke conditions compared with $PM_{2.5}$ in the pre-wildfire period were associated with 34% increases in asthma admissions. The strongest wildfire-related $PM_{2.5}$ associations were for people ages 65– 99 years (10.1% increase per 10 $\mu g/m^3$ $PM_{2.5}$, 95% CI 3.0% to 17.8%) and ages 0–4 years (8.3%, 95% CI 2.2% to 14.9%) followed by ages 20–64 years (4.1%, 95% CI 20.5% to 9.0%). There were no

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$PM_{2.5}$–asthma associations in children ages 5–18 years, although their admission rates significantly increased after the fires. Per 10 μg/m^3 wildfire-related $PM_{2.5}$, acute bronchitis admissions across all ages increased by 9.6% (95% CI 1.8% to 17.9%), chronic obstructive pulmonary disease admissions for ages 20–64 years by 6.9% (95% CI 0.9% to 13.1%), and pneumonia admissions for ages 5–18 years by 6.4% (95% CI 21.0% to 14.2%). Acute bronchitis and pneumonia admissions also increased after the fires. There was limited evidence of a small impact of wildfire-related $PM_{2.5}$ on cardiovascular admissions.

Conclusions—Wildfire-related $PM_{2.5}$ led to increased respiratory hospital admissions, especially asthma, suggesting that better preventive measures are required to reduce morbidity among vulnerable populations.

The numbers of wildfires and their duration in the USA have increased over the past two decades due to warmer temperatures, earlier snowmelts and less rainfall, all of which are expected to worsen because of global warming.[1] These phenomena will likely impact public health. However, although the adverse effects of urban fine particulate air pollution ($PM_{2.5}$ or particles with an aerodynamic diameter of <2.5 μm) on cardiovascular and respiratory health have been well documented,[2] far fewer studies have evaluated the impacts of wildfire-generated $PM_{2.5}$. $PM_{2.5}$ is the air pollutant with the greatest increase in concentrations during fire events,[3] followed by particulate matter with an aerodynamic diameter of <10 μm (PM_{10}).[4] Studies that have evaluated the impacts of wildfire PM on hospital admissions, emergency department visits or clinic visits found associations with respiratory outcomes.[5–11] There is little research on the impact of wildfire smoke on cardiovascular outcomes; two studies have found no significant associations.[89] There have been conflicting reports on wildfire smoke and total mortality.[1213] Several other studies have found adverse impacts of wildfire smoke on respiratory symptoms, medication use and lung function.[1014–16]

We present here the largest study to date evaluating the relationships of hospital admissions for cardiorespiratory outcomes to wildfire-associated $PM_{2.5}$ using data from the catastrophic wildfires that struck southern California in the autumn of 2003. We linked $PM_{2.5}$ concentrations estimated at the zip code level[17] to a population-based dataset of hospital admissions using spatial time series analyses of data before, during and after the fires. Strong, dry winds from inland deserts fanned flames from nine distinct fires, which burned nearly three quarters of a million acres and destroyed approximately 5000 residences and outbuildings. The wildfires generated large amounts of dense smoke that covered much of urban southern California (2003 population of 20.5 million).[18] $PM_{2.5}$ and PM_{10} concentrations far exceeded US federal regulatory standards.[317] The goal of the present study is to assess the impact of this large wildfire event on serious morbidity.

METHODS

Hospital admission data

Hospital admission data for children and adults were obtained from the California State Office of Statewide Health Planning and Development (OSHPD). Specifically, we analysed 40 856 hospital admissions from the period before the wildfire episode (1–20 October), the episode period across southern California (21–30 October) and the period following the episode (31 October–15 November), for individuals who lived in affected counties and were diagnosed with the respiratory and cardiovascular illnesses listed in table 1. Other variables from OSHPD included in analyses were age, sex, race, ethnicity, five-digit zip code and admission date. Patient zip code data from OSHPD were geocoded to zip code centroids and linked to air monitoring data and U.S. Census 2000 sociodemographic data. Institutional Review Board approvals were obtained from the California State Health and Human Services Agency, Committee for the Protection of Human Subjects, and from the University of California, Irvine Office of Research Administration.

Analyses were stratified by age groups: paediatric (0–4 and 5– 19 years), adult (20–64 years) and elderly (65–99 years), except for chronic obstructive pulmonary disease (COPD, 20–64 and 65–99 years) and cardiovascular outcomes (45–99 years). Census demographic characteristics were missing for 474 admissions due to unmatched zip codes. We also analysed associations for asthma by gender because of differences in the age-dependent prevalence of asthma.

Exposures

We estimated daily PM_{10} and $PM_{2.5}$ concentrations at a zip code level from 1 October through 15 November 2003. These data are presented in more detail in our previous publication.[17] To our knowledge, this was the first study that systematically examined and estimated daily particle concentrations at such a fine spatial resolution over a relatively large study domain for this type of application. Spatially-resolved particle mass data are superior to using only the nearest available monitoring station data because they are expected to better represent personal exposures. We used available air pollution data from governmental network sites to build prediction models. Missing gravimetric PM concentrations from every 3rd or 6th day measurements or due to the incapacitation of monitors by the fires were estimated based on (1) temporal profiles of continuous hourly PM data at co-located or closely located sites and (2) light extinction from visibility data, meteorological conditions and smoke information extracted from moderate resolution imaging spectroradiometer (MODIS) satellite images at a 250 m resolution. Moderately strong prediction equations were developed for gravimetric PM mass at monitoring stations. Light extinction coefficient and MODIS satellite smoke data were the most important predictors of those measurements. Measured $PM_{2.5}$ was more accurately predicted in regression models compared with PM_{10} (R^2 0.78 vs 0.65, respectively). Therefore, the present analysis focuses only on $PM_{2.5}$.

Spatial interpolations of $PM_{2.5}$ concentrations were performed using inverse distance weighting, kriging or cokriging methods for the non-fire periods. Since the fire and smoke created highly heterogeneous pollution surfaces, typical inverse distance weighting and kriging were not suitable during the wildfire period. Therefore, polygons were created based on satellite images to represent each smoke-covered area under different smoke densities. $PM_{2.5}$ concentrations in each smoke-polygon were assigned separately, using measured or estimated concentrations from the predictive models (as described above). For each non-fire and fire day, the spatial $PM_{2.5}$ surfaces and zip code boundary map were overlaid and corresponding $PM_{2.5}$ concentrations were assigned to each zip code centroid (fig 1).

Measurements of daily airborne fungal spores (see online supplement) were carried out in another ongoing study in Riverside County.[19] Pollen concentrations were low and therefore were not included in the analysis. We assumed that Riverside ambient fungal data reflected region-wide trends.

Analysis

Outcomes were the total number of admissions for a diagnostic group within each zip code on each day of the study period. We hypothesised that associations between the wildfires and hospital admission rates would primarily be attributable to an increase in daily zip code-specific levels of $PM_{2.5}$ resulting from the fires. However, it is difficult to separate wildfire-generated PM from other PM sources in this heavily urbanised region. To this end, we constructed a wildfire indicator representing prewildfire, wildfire and post-wildfire periods, and tested the interaction between $PM_{2.5}$ and this indicator. We considered product terms to be significant at the $p<0.1$ level. Because dates of the wildfires varied throughout southern California, dates for the wildfire period indicator were defined to be county-specific based on MODIS satellite images of smoke covering any part of the county's urban areas (table 2).

The choice of adjustment covariates was motivated by biological plausibility that the covariate might confound the relationship between wildfire-related $PM_{2.5}$ and hospital admissions or an a priori belief that the variable could affect both $PM_{2.5}$ and admissions. Meteorological covariates from the National Climatic Data Center (http://www.ncdc.noaa.gov/oa/ncdc.html) included relative humidity, temperature and surface pressure gradient. So-called Santa Ana winds coming off the inland desert regions to the east (a large negative pressure gradient) are a strong determinant of wildfire events. There are few data on the effects of Santa Ana winds on asthma or other outcomes, but it is anticipated that hot dry desert winds associated with this weather pattern bring with them high concentrations of bioaerosols. Therefore, for asthma admissions, we also included fungal spores as a covariate. Deuteromycetes (eg, *Alternaria*) tend to increase during hot, dry windy periods.[20]

In addition, we decided a priori that spatial heterogeneity in census demographic factors at the aggregate zip code level (age, gender, race and income distributions) could confound associations. The distributions of each of these potential confounders were obtained at the zip code level from the 2000 U.S. Census (percentage of non-Caucasians, percentage of females, median household income and age distributions). Income was recoded into discrete variables by quartile. To control for zip code population age distribution, we first calculated the percentage of individuals in a zip code younger than 20 years and older than 65 years. Each zip code was then classified into one of four age categories by cross-classification of young (proportion of individuals <20 years old higher than the median proportion across all zip codes) and old (proportion of individuals>65 years old higher than the median proportion across all zip codes).

We also tested various functions of time including weekend versus weekday, day of the week and a smooth of time. In order to investigate residual confounding by date, we allowed for a flexible functional form (via smoothing splines, with degrees of freedom ranging from 1 to 10) (see online supplement). Controlling for day-of-week trend or the flexible time-adjusted models showed the $PM_{2.5}$ associations were robust with respect to these adjustments. We also tested various forms of temperature and relative humidity, including raw continuous scales, smoothed and categorical forms. Those models exhibiting the best fit with the fewest assumptions for functional form included weekend versus weekday, and temperature and relative humidity categorised into quartiles. The full set of adjustment covariates included these variables plus local pressure gradient, fungal spores (for asthma), county, and zip code-level distributions of median household income, age, gender and race. Effects of covariates on point estimates of $PM_{2.5}$ were small.

Generalised estimating equations for Poisson data[21] were used to estimate the marginal association of daily hospital admission rates with daily $PM_{2.5}$ levels and presence of the wildfires. Log-transformed zip code-specific population estimates were used as the offset (denominator) term in all models. Age-specific population estimates were used as an offset term in the analysis of age group-specific outcomes. In order to obtain asymptotically valid inferences, covariate estimation was carried out using an independence working correlation structure in combination with empirical variance estimates clustering on zip code.[2223] We note that the use of an independence working correlation structure was motivated by the desire to obtain consistent parameter estimates in the presence of time-varying covariates.[24]

Multiple lag models were considered to investigate associations between $PM_{2.5}$ and hospital admission rates, including a 7-day polynomial distributed lag,[25] and stratified analyses considering different lag associations. We found the 2-day moving average of $PM_{2.5}$ (average of today and yesterday) provided the best fitting model that adequately captured the association between $PM_{2.5}$ and admissions.

RESULTS

PM exposures

During the wildfires, smoke events dramatically increased local PM concentrations and created highly heterogeneous pollution surfaces.[17] For reference, the US National Ambient Air Quality Standard for 24 h average $PM_{2.5}$ is 35 μg/m^3. The highest 24 h concentrations were ≥240 μg/m^3 at two sites in San Diego County. Table 2 contains county-level descriptive statistics for $PM_{2.5}$. As expected, average $PM_{2.5}$ concentrations during the wildfire period increased in all counties. Average PM levels during the period following the fires were observed to be lower in all counties relative to the period prior to the fires. This is because of the onshore flow that brought in the cool and moist clean air from the Pacific Ocean that helped end the wildfires.

Spatial time series analysis of hospital admissions

$PM_{2.5}$ associations: interactions with wildfire period—We found that associations of 2-day lagged average of $PM_{2.5}$ with admissions for most respiratory outcomes were stronger during as compared with before or after the wildfires in models including a product term of wildfire period and $PM_{2.5}$, but the interaction was $p<0.1$ primarily for asthma.

Table 3 shows estimates for the relative change in rates for admissions in relation to a 10 μg/m^3 increase in $PM_{2.5}$. The table includes results for age and sex (asthma only) subgroups for the entire monitored period, and for wildfire periods. In product term models of $PM_{2.5}$ by wildfire period, $PM_{2.5}$ during the wildfire period was associated with combined respiratory admissions. Asthma admissions across all ages increased by 4.8% (95% CI 2.1% to 7.6%) in relation to $PM_{2.5}$ during the wildfire period, but there was no $PM_{2.5}$ association before or after the fires. The strongest wildfire-related $PM_{2.5}$ associations with asthma admissions were for the elderly, ages 65–99 years (10.1% increase), and children ages 0–4 years (8.3%), followed by adults ages 20–64 years (4.1%). There were no $PM_{2.5}$ associations in school aged children. Among women ages 20– 64 years, the strongest asthma and $PM_{2.5}$ association was during the wildfires, but for men those ages it was after the wildfires. Among women ages 65–99, the strongest $PM_{2.5}$ association was after the wildfires, but for men those ages it was during the wildfires. Fungal spores were also significantly associated with asthma admissions in the adjusted model that included $PM_{2.5}$ (see online supplement).

The wildfires led to notably higher particle concentrations, so that a 10 $\mu g/m^3$ increase in $PM_{2.5}$ used for effect estimates in table 3 represents only a small part of that increase. The overall population-weighted concentrations of predicted 24 h $PM_{2.5}$ at the zip code level were 90 $\mu g/m^3$ and 75 $\mu g/m^3$, under heavy and light smoke conditions, respectively, in contrast to concentrations of 20 $\mu g/m^3$ during the non-fire period.[17] Therefore, we rescaled effect estimates to represent the wildfire-related increases in $PM_{2.5}$. A 55 $\mu g/m^3$ increase in $PM_{2.5}$ during light smoke and a 70 $\mu g/m^3$ increase in $PM_{2.5}$ during heavy smoke conditions are predicted to lead to an adjusted 26% and 34% increase in asthma admissions for all ages, respectively.

For combined ages, acute bronchitis admissions increased more in relation to 10 $\mu g/m^3$ $PM_{2.5}$ during the wildfires (9.6%), but there was no association before or after the fires. In subgroup analyses, this association was still evident in children ages 0–4 years and the elderly.

COPD admissions for people ages 20–64 years significantly increased by 6.8% from 10 $\mu g/m^3$ $PM_{2.5}$ during the wildfires, but there was no association before or after the fires. The COPD increase with $PM_{2.5}$ during the fires was smaller for subjects ages 65–99 years (3.1%).

$PM_{2.5}$ was also associated with increased overall pneumonia admissions, both before (4.5%) and during the fires (2.8%). This was consistent across ages, except children ages 5–19 years showed an association only during the wildfires. There were no associations of $PM_{2.5}$ with admissions for upper respiratory infections (not shown).

There was a small relative increase in admission rates for total cardiovascular outcomes in people ages 45–99 years in relation to $PM_{2.5}$ during the fires. There were suggestions of a small increase in admissions for congestive heart failure in relation to $PM_{2.5}$ during the wildfires ($p<0.1$ compared with the pre-wildfire period), and an even smaller increase in admissions for ischaemic heart disease, but for both outcomes, the 95% confidence intervals crossed 1.0. $PM_{2.5}$ was inversely associated with cardiac dysrhythmia admissions across all periods. Admissions for cerebrovascular disease and stroke were positively associated with $PM_{2.5}$ (1.9%) across all periods.

Associations with wildfire period—In this analysis of the wildfire indicator variable, the prewildfire period is the referent time. Models were adjusted for the same covariates as $PM_{2.5}$ models, and are shown unadjusted and adjusted for $PM_{2.5}$ (table 4). Generally, there was little change in point estimates adjusting for $PM_{2.5}$. There were significantly increased risks for all respiratory hospital admissions after the fires compared with the pre-fire period. Admissions increased for all ages by 17% ($p<0.001$), and in age groups 5–19 years by 37% ($p<0.008$) and 65–99 years by 15% ($p<0.004$). Unexpected decreased risks of respiratory admissions were found during the fires compared with the pre-fire period in 0–4 year olds and elderly adults.

The period following the fires was associated with a 26% increase in the rate of asthma admissions for all ages. Asthma admissions were also increased during the fires among those aged 5–19 years (25%) and 20–64 years (27%), but associations for both groups were stronger after the fires (56% and 36%, respectively).

Increased risk of asthma admissions for the period during the wildfires was stronger in females ages 5–19 years (49%, $p<0.02$) than males (11%, $p = 0.5$) and in females ages 20–64 years (41%, $p<0.001$) than males (27.6%, $p = 0.7$) (not shown). Increased risk of asthma admissions for the period after the wildfires was also stronger in females ages 5–19 years (81%, $p<0.01$) than males (39%, $p<0.11$) and in females ages 20–64 years (47%, $p<0.02$) than males (12%, $p = 0.7$).

Admissions for acute bronchitis and bronchiolitis for combined ages were increased by 48% after the fires. The association for the post-fire period was seen in both ages 0–4 years (51%) and ages 20–64 years (137%). Pneumonia admissions for ages 0– 4, 20–64 and 65–99 years were 46%, 30% and 27% higher during the period after the fires, respectively.

There was a 6.1% increased risk of combined cardiovascular admissions ($p<0.05$), and an 11.3% increased risk of congestive heart failure admissions after the fires ($p<0.06$). However, risk of cardiovascular admissions was lower during the fires by 4.4%. A relative increase in cerebrovascular disease and stroke admissions during the wildfires may have been attributable to a cross-period effect of $PM_{2.5}$ (table 3) because this period association was confounded in the model adjusting for $PM_{2.5}$.

DISCUSSION

This is the first study to systematically examine and estimate the impacts on hospital admissions from wildfire-related $PM_{2.5}$ at such a fine spatial resolution (zip codes) over a large urban region. During the wildfire period, smoke events dramatically increased $PM_{2.5}$ compared to the preceding non-fire period. The wildfires and associated $PM_{2.5}$ were significantly associated with hospital admissions for respiratory illnesses, especially asthma, but also acute bronchitis and COPD. The impact on cardiovascular admissions was weaker.

Although product terms between $PM_{2.5}$ and the wildfire period indicator were not significant at the $p<0.1$ level in many models, we still observed a trend of stronger associations for $PM_{2.5}$ with respiratory admissions during the wildfire period. Some models showed increased admissions in relation to $PM_{2.5}$ before the wildfires, possibly due to the relatively high concentration of urban PM seen during this hot period (table 2). Some models also showed increased admissions in relation to $PM_{2.5}$ after the wildfires, despite much lower $PM_{2.5}$ concentrations. This may have been attributable to notable increases in respiratory admissions seen then, possibly due to a delayed impact of wildfire smoke.

Models with the wildfire period indicator support this possibility and suggest that some effects of wildfires are not entirely explained by $PM_{2.5}$ exposures. Results yielded inconsistencies for respiratory and cardiovascular admissions when comparing product term models for $PM_{2.5}$ by period to models using the period indicator alone. There were nominal associations of daily $PM_{2.5}$ during the wildfires with cardiovascular admissions, but the period indicator showed associations only after the wildfires. Non-asthma respiratory admission rates were also most strongly increased after the wildfires ended compared with the pre-fire period, while the $PM_{2.5}$ association was generally strongest during the wildfires. We also found the period following the wildfires was significantly associated with higher overall asthma admission rates. These associations were stronger among females. Asthma admissions were increased during the fires as well, but evident only among females ages 5–19 and ages 20–64. Possible reasons for stronger associations among females include the differential impact of hormones and the menstrual cycle, airway function and structure, atopy and perception of symptoms.[26]

Although there was no association of asthma admissions with $PM_{2.5}$ in young people ages 5–19 years, the periods during and after the wildfires were significantly associated with increased admissions in this group. We speculate this may be attributable to unmeasured volatile (non-particulate) toxic air pollutants, including those associated with the more than 5000 buildings that burned. Alternatively, factors associated with the fires, such as psychosocial stress, could have led to effects that were independent of $PM_{2.5}$.

Associations with the post-wildfire period and wildfire-related $PM_{2.5}$ were also found for acute bronchitis and bronchiolitis, and pneumonia. This is the first report of wildfire associations with admissions for acute bronchitis and bronchiolitis, and pneumonia.

We also found a significantly increased risk of admissions for total cardiovascular outcomes and congestive heart failure after the fires. It is possible that systemic inflammation increases more strongly in relation to sustained multiday exposures to air pollutants than with acute single day exposures, as recently shown in our panel study of subjects with coronary artery disease.[27] Analyses of the London ‘‘killer smog’’ of 1952,[28] and recent analyses of particulate air pollution in Dublin, Ireland,[29] suggest that there may be delayed effects for weeks to months. The post-fire increases in cardiorespiratory admissions may be attributed to the following:

1. People may delay deciding to go to hospital until symptoms become too severe[30];
2. Cumulative biological effects of wildfire PM may culminate in severe symptoms many days after the initial cardiorespiratory impact. For example, most subjects with asthma show a progressive clinical and functional deterioration that takes place over hours to weeks[31];

3. Sustained effects of wildfire PM may lead to susceptibility to, or increased severity of, later respiratory infections, possibly through alterations in immune function or respiratory clearance mechanisms.

The strongest evidence for delayed effects in our study was the post-fire increase in asthma admissions combined with the association between asthma admission and $PM_{2.5}$ during the wildfires. However, given past annual trends (see online supplement), it is possible that asthma admissions following the wildfire period would have increased at this time of year anyway. This also applies to the post-fire increases in admissions for acute bronchitis and bronchiolitis, and pneumonia. Other limitations are that the period analysis does not have the temporal resolution of the daily time series analysis of $PM_{2.5}$. Therefore, differences in results of these analyses could result due to imprecision in the estimate for the non-quantitative indicator variable. Furthermore, power may be limited for specific outcomes subdivided by gender and age, which would apply to several nominally significant associations we found.

Our results for respiratory admissions are consistent with two other studies of the 2003 southern California wildfires using other less severe outcomes and focusing on particular regions, including emergency department visits in San Diego county[1132] and respiratory symptoms in 16 towns in southern California.[16] Kunzli et al[16] reported results for school children in an ongoing cohort study who were potentially affected by the wildfires. They found parental self-reports of the smell of fire smoke indoors were associated with reported asthma attacks, wheezing, cough, bronchitis, colds, upper respiratory symptoms, medication usage and physician visits. Authors also analysed the impacts of between-community differences in PM_{10} using data from our study.[17] Changes in PM_{10} were associated with upper respiratory symptoms, cough and unspecified medication use.

Several investigations of wildfires have identified people with asthma as an especially sensitive subpopulation, using analyses of emergency department visits in California mountain counties during wildfires in 1987,[6] emergency department visits in eight Florida hospitals during wildfires in 1998,[5] and hospital admissions during the 1997 Indonesian wildfires.[9] A report from Australia examining smoke from bushfires and asthma emergency department visits found no association.[33]

Other time series studies have shown associations of asthma hospital admissions with urban air pollution.[34] However, the period of observation in our investigation is far shorter than most time series investigations, and thus statistical power is lower. Despite this, we found strong associations between $PM_{2.5}$ and hospital admissions. We attribute this to the large increase in wildfire-related PM, and the spatial time series approach, which likely reduced exposure error compared with the typical use of widely-dispersed regional PM data. Nevertheless, we are still limited by aggregate (not personal) exposure data.

This is the first report of associations of wildfire-related $PM_{2.5}$ with admissions for acute bronchitis and bronchiolitis, and for pneumonia. Our results showing increased COPD admissions in relation to $PM_{2.5}$ during the wildfires are consistent with a study of increased COPD hospital admissions during the 1997 Indonesian wildfires,[9] increased COPD emergency department visits during the 1987 wildfires in California mountain counties,[6] and respiratory symptoms in a panel of 21 patients with COPD associated with a forest fire near Denver, Colorado in June 2002.[35]

Total cardiovascular and congestive heart failure admissions increased only in the period following the wildfires. However, there was a small relative increase in admission rates for total cardiovascular outcomes in relation to $PM_{2.5}$ during the fires.

Cerebrovascular disease and stroke were significantly increased in relation to $PM_{2.5}$ across the entire study period. Unexpected findings were the inverse associations for cardiac dysrhythmias and $PM_{2.5}$ across the whole period. While urban particles generally have been associated with a variety of adverse cardiovascular outcomes,[2] including stroke,[36] there is little research investigating the effects of smoke from wildfires or wood combustion on circulatory disease.[4] Our results can only be compared to null associations for cardiovascular hospital admissions during the 1997 Indonesian wildfires.[9] Moore et al[8] found that, although there was an excess of respiratory complaints, physician visits for cardiovascular illnesses in regions of British Columbia, Canada were not associated with wildfires.

The mechanisms explaining our findings for wildfire smoke are likely somewhat similar to those found for pollutant components from fossil fuel combustion. Evidence is mounting that urban air pollution triggers oxidative stress and inflammation.[2] A study of people exposed to forest fire smoke in Indonesia in 1997 showed increased circulating levels of interleukin-1b and interleukin-6 during the smoke period.[37] An experimental study of subjects exposed to clean air versus wood smoke in a chamber showed increased airway inflammatory responses (exhaled alveolar NO) and evidence of increased oxidative stress (malonadehyde in breath condensates).[38] An in vitro study using mouse alveolar macrophages tested the effects of size-segregated PM from transported wildfire smoke collected in Helsinki, Finland.[39] Investigators showed that although the transported particles induced less cytokine production per unit mass compared with urban particles, they found enhanced inflammatory and cytotoxic activities per cubic meter of air due to the increased particulate mass concentration in the accumulation mode size range (0.1–2.5 mm in diameter). This might explain our finding of a larger asthma association per 10 $\mu g/m^3$ $PM_{2.5}$ during the wildfires as compared with the pre-wildfire period as simply due to the considerably higher concentrations rather than higher toxicity of wildfire smoke.

It is also possible that unmeasured volatile and semivolatile organic compound components are important in the effects of wildfire smoke, but such data are rarely available. In the present study, these include toxic gases emitted from synthetic materials in the approximately 5000 residences and outbuildings that burned.

Conclusions

We conclude the catastrophic wildfires that struck southern California in October of 2003 led to significantly increased hospital admissions for respiratory illnesses, especially asthma. Southern California experienced a second similar wildfire disaster in October 2007, yielding the two largest wildfire disasters in California's history within this recent 4-year period. A concern is that growing impacts of global warming on wildfire risk will continue to impact public health in similar regions across the globe.[1]

Given there were significant morbidity impacts associated with wildfire-related $PM_{2.5}$, we recommend that in addition to advisories to avoid outdoor activities that increase exposure during wildfires, preventive measures need to be taken where possible to reduce exacerbations of asthma. This may include the early use of anti-inflammatory medications at the first sign of increasing asthma symptoms. All of the health impacts identified in this study occurred in the face of numerous advisories by public health agencies and the media to avoid outdoor activities and to use air conditioning. Additional preventive measures in susceptible people including those with persistent asthma, such as the use of indoor air filters,[1040] should be considered and then systematically evaluated in future wildfires.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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REFERENCES

1. Westerling AL, Hidalgo HG, Cayan DR, et al. Warming and earlier spring increase western U.S. forest wildfire activity. Science. 2006; 313:940–3. [PubMed: 16825536]
2. Pope CA 3rd, Dockery DW. Health effects of fine particulate air pollution: lines that connect. J Air Waste Manag Assoc. 2006; 56:709–42. [PubMed: 16805397]
3. Phuleria H, Fine PM, Zhu Y, et al. Air quality impacts of the October 2003 Southern California wildfires. J Geophys Res. 2005; 110:D07S20.
4. Naeher LP, Brauer M, Lipsett M, et al. Wood smoke health effects: a review. Inhal Toxicol. 2007; 19:67–106. [PubMed: 17127644]
5. Centers for Disease Control and Prevention (CDC). Surveillance of morbidity during wildfires--Central Florida, 1998. MMWR Morb Mortal Wkly Rep. 1999; 48:78–9. [PubMed: 10023629]
6. Duclos P, Sanderson LM, Lipsett M. The 1987 forest fire disaster in California: assessment of emergency room visits. Arch Environ Health. 1990; 45:53–8. [PubMed: 2180383]
7. Emmanuel SC. Impact to lung health of haze from forest fires: the Singapore experience. Respirology. 2000; 5:175–82. [PubMed: 10894108]
8. Moore D, Copes R, Fisk R, et al. Population health effects of air quality changes due to forest fires in British Columbia in 2003: estimates from physician-visit billing data. Can J Public Health. 2006; 97:105–8. [PubMed: 16619995]
9. Mott JA, Mannino DM, Alverson CJ, et al. Cardiorespiratory hospitalizations associated with smoke exposure during the 1997, Southeast Asian forest fires. Int J Hyg Environ Health. 2005; 208:75–85. [PubMed: 15881981]
10. Mott JA, Meyer P, Mannino D, et al. Wildland forest fire smoke: health effects and intervention evaluation, Hoopa, California, 1999. West J Med. 2002; 176:157–62. [PubMed: 12016236]
11. Viswanathan S, Eris L, Diunugala N, et al. An analysis of effects of San Diego wildfire on ambient air quality. J Air Waste Manag Assoc. 2006; 56:56–67. [PubMed: 16499147]

12. Sastry N. Forest fires, air pollution, and mortality in Southeast Asia. Demography. 2002; 39:1–23. [PubMed: 11852832]
13. Vedal S, Dutton SJ. Wildfire air pollution and daily mortality in a large urban area. Environ Res. 2006; 102:29–35. [PubMed: 16716288]
14. Frankenberg E, McKee D, Thomas D. Health consequences of forest fires in Indonesia. Demography. 2005; 42:109–29. [PubMed: 15782898]
15. Kunii O, Kanagawa S, Yajima I, et al. The 1997 haze disaster in Indonesia: its air quality and health effects. Arch Environ Health. 2002; 57:16–22. [PubMed: 12071356]
16. Kunzli N, Avol E, Wu J, et al. Health effects of the 2003 Southern California wildfires on children. Am J Respir Crit Care Med. 2006; 174:1221–8. [PubMed: 16946126]
17. Wu J, Winer A, Delfino R. Exposure assessment of particulate matter air pollution before, during, and after the 2003 southern California wildfires. Atmos Environ. 2006; 40:3333–8.
18. State of California. California county population estimates and components of change by year. California Department of Finance; Sacramento, CA: Jul 1. 2000–2006 2006
19. Delfino RJ, Zeiger RS, Seltzer JM, et al. The effect of outdoor fungal spore concentrations on asthma severity. Environ Health Perspect. 1997; 105:622–35. [PubMed: 9288497]
20. Weber RW. Meteorologic variables in aerobiology. Immunol Allergy Clin North Am. 2003; 23:411–22. [PubMed: 14524383]
21. Zeger SL, Liang KY. Longitudinal data analysis for discrete and continuous outcomes. Biometrics. 1986; 42:121–30. [PubMed: 3719049]
22. Huber, PJ. The behavior of maximum likelihood estimates under nonstandard conditions.. In: Le Cam, LM.; Neyman, J., editors. Proceedings of the Fifth Berkeley Symposium on Mathematical Statistics and Probability. Vol. 1. University of California Press; Berkeley, CA: 1967. p. 221-3.
23. White H. A heteroskedasticity-consistent covariance matrix estimator and a direct test for heteroskedasticity. Econometrica. 1980; 48:817–30.
24. Pepe MS, Anderson GL. A cautionary note on inference for marginal regression models with longitudinal data and general correlated response data. Communications in Statistics - Simululation and Computation. 1994; 23:939–51.
25. Schwartz J. The distributed lag between air pollution and daily deaths. Epidemiology. 2000; 11:320–6. [PubMed: 10784251]
26. Becklake MR, Kauffmann F. Gender differences in airway behaviour over the human life span. Thorax. 1999; 54:1119–38. [PubMed: 10567633]
27. Delfino RJ, Staimer N, Tjoa T, et al. Circulating biomarkers of inflammation, antioxidant activity, and platelet activation are associated with urban air pollution in elderly subjects with a history of coronary artery disease. Environ Health Perspect. 2008; 116:898–906. [PubMed: 18629312]
28. Bell ML, Davis DL. Reassessment of the lethal London fog of 1952: novel indicators of acute and chronic consequences of acute exposure to air pollution. Environ Health Perspect. 2001; 109(Suppl 3):389–94. [PubMed: 11427388]
29. Goodman PG, Dockery DW, Clancy L. Cause-specific mortality and the extended effects of particulate pollution and temperature exposure. Environ Health Perspect. 2004; 112:179–85. [PubMed: 14754572]
30. Janson S, Becker G. Reasons for delay in seeking treatment for acute asthma: the patient's perspective. J Asthma. 1998; 35:427–35. [PubMed: 9734350]
31. Rodrigo GJ, Rodrigo C, Hall JB. Acute asthma in adults: a review. Chest. 2004; 125:1081–1102. [PubMed: 15006973]
32. Johnson JM, Hicks L, McClean C, et al. Leveraging syndromic surveillance during the San Diego wildfires, 2003. MMWR Morb Mortal Wkly Rep. 2005; 54(Suppl):190.
33. Smith MA, Jalaludin B, Byles JE, et al. Asthma presentations to emergency departments in western Sydney during the January 1994 bushfires. Int J Epidemiol. 1996; 25:1227–36. [PubMed: 9027529]
34. Sheppard L, Levy D, Norris G, et al. Effects of ambient air pollution on nonelderly asthma hospital admissions in Seattle, Washington, 1987–1994. Epidemiology. 1999; 10:23–30. [PubMed: 9888276]

35. Sutherland ER, Make BJ, Vedal S, et al. Wildfire smoke and respiratory symptoms in patients with chronic obstructive pulmonary disease. J Allergy Clin Immunol. 2005; 115:420–2. [PubMed: 15696107]
36. Wellenius GA, Schwartz J, Mittleman MA. Air pollution and hospital admissions for ischemic and hemorrhagic stroke among Medicare beneficiaries. Stroke. 2005; 36:2549–53. [PubMed: 16254223]
37. van Eeden SF, Tan WC, Suwa T, et al. Cytokines involved in the systemic inflammatory response induced by exposure to particulate matter air pollutants (PM_{10}). Am J Respir Crit Care Med. 2001; 164:826–30. [PubMed: 11549540]
38. Barregard L, Sällsten G, Andersson L, et al. Experimental exposure to wood smoke: effects on airway inflammation and oxidative stress. Occup Environ Med. 2008; 65:319–24. [PubMed: 17704195]
39. Jalava PI, Salonen RO, Halinen AI, et al. In vitro inflammatory and cytotoxic effects of size-segregated particulate samples collected during long-range transport of wildfire smoke to Helsinki. Toxicol Appl Pharmacol. 2006; 215:341–53. [PubMed: 16678872]
40. Henderson DE, Milford JB, Miller SL. Prescribed burns and wildfires in Colorado: impacts of mitigation measures on indoor air particulate matter. J Air Waste Manag Assoc. 2005; 55:1516–26. [PubMed: 16295277]

Main messages

- ▶ Wildfire-related $PM_{2.5}$ led to significantly increased asthma, bronchitis and COPD hospital admissions.
- ▶ Sensitive subgroups included young children and the elderly.

Policy implications

▶ In addition to advisories to avoid outdoor activities that increase exposure during wildfires, preventive measures need to be taken where possible to reduce exacerbations of asthma

▶ Preventive measures may include advisories for the early use of anti-inflammatory medications at the first sign of increasing asthma symptoms.

▶ The health impacts of wildfires reported here are anticipated to increase worldwide due to global warming, which has broad policy implications.

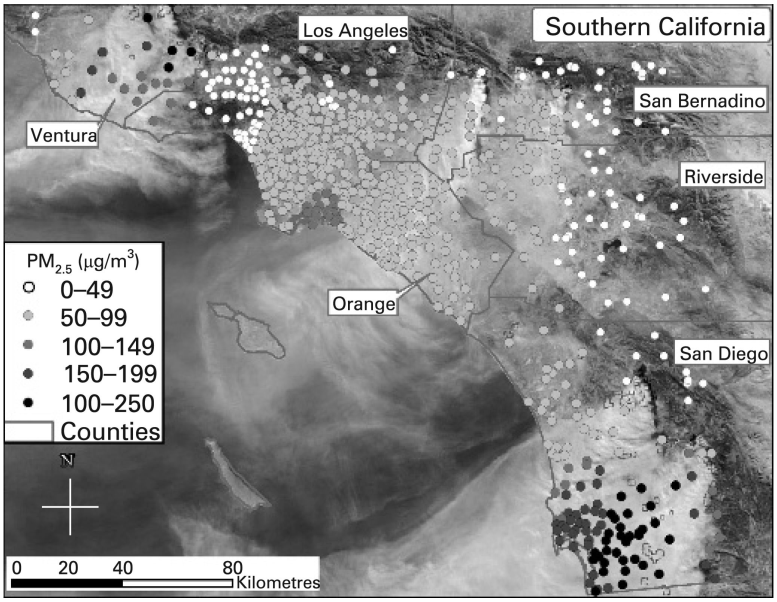

Figure 1.
Interpolated $PM_{2.5}$ concentrations (μg/m^3) at zip code centroids on 27 October 2003.

Table 1

Number of hospital admission by diagnostic[*] and age groups

Diagnosis	Total events	Events with U.S. Census 2000 defined population[†]
All respiratory[‡]		
Ages 0–4	2158	2143
Ages 5–19	1216	1205
Ages 20–64	8480	8314
Ages 65–99	9456	9357
Total	21 310	21 019
Asthma (ICD-9 493), primary		
Ages 0–4	606	600
Ages 5–19	739	733
Ages 20–64	1165	1151
Ages 65–99	543	538
Total	3053	3022
Acute bronchitis and bronchiolitis (ICD-9 466)		
Ages 0–4	354	353
Ages 5–19	23	23
Ages 20–64	108	106
Ages 65–99	137	136
Total	622	618
Chronic obstructive pulmonary disease (ICD-9 491, 492 and 496)		
Ages 20–64	927	910
Ages 65–99	1973	1950
Total	2900	2860
Pneumonia (ICD-9 480-87)		
Ages 0–4	542	537
Ages 5–19	298	293
Ages 20–64	1721	1686
Ages 65–99	3957	3924
Total	6518	6440
Upper respiratory infections (ICD-9 460–65)		
Ages 0–4	522	518
Ages 5–19	77	77
Ages 20–64	108	104
Ages 65–99	47	47
Total	754	746
All cardiovascular[§]		
Ages 45–99	27 486	27 170
Ages 65–99	19 380	19 197
Ischaemic heart disease (ICD-9 410–414)		

Diagnosis	**Total events**	**Events with U.S. Census 2000 defined population**[†]
Ages 45–99	10 448	10 319
Ages 65–99	6491	6430
Cardiac dysrhythmias (ICD-9 426, 427)		
Ages 45–99	4051	4004
Ages 65–99	3048	3018
Congestive heart failure (ICD-9 402, 428)		
Ages 45–99	6202	6144
Ages 65–99	4750	4712
Cerebrovascular disease and stroke (ICD-9 430–438)		
Ages 45–99	5973	5908
Ages 65–99	4465	4422

[*] Principal cause of admission was coded by version 9 of the International Classification of Diseases (ICD-9)

[†] population with available covariates for census population and census distribution of demographic characteristics used in the multivariate analysis. This excludes subjects aged ≥100 years (48 (0.23%) respiratory and 51 (0.18%) cardiovascular admissions) because 2000 census age categories needed in the analysis stopped at 99 years

[‡] includes all listed specific respiratory ICD-9 plus 7463 additional admissions for the following ICD-9 codes: 277 (cystic fibrosis), 490 (bronchitis NOS), 494 (bronchiectasis), 495 (extrinsic allergic alveolitis), 506 and 508 (other acute/subacute respiratory conditions due to fumes/vapours, or external agents, not separately analysed because n = 44), 786 (symptoms involving the respiratory system/other chest symptoms).

[§] includes all listed specific cardiovascular ICD-9 codes plus 812 additional admissions for ICD-9 codes 440–459 (diseases of the peripheral circulation).

Table 2

County-level mean particulate matter (PM2.5) levels,* Southern California, 1 October–15 November 2003

Daily PM$_{25}$ levels (mg/m^3)	**County**					
	Los Angeles	**Orange**	**Riverside**	**San Bernardino**	**San Diego**	**Ventura**
Before fires						
Dates	01/10–23/10	01/10–23/10	01/10–20/10	01/10–20/10	01/10–24/10	01/10–22/10
Concentration (SD)	27.2 (12.4)	23.3 (9.6)	32.7 (14.7)	35.7 (16.6)	18.5 (6.7)	18.4 (8.3)
During fires						
Dates	24/10–29/10	24/10–28/10	21/10–29/10	21/10–30/10	25/10–30/10	23/10–30/10
Concentration (SD)	54.1 (21)	64.3 (26.5)	42.1 (25.5)	45.3 (28.7)	76.1 (66.6)	50.1 (50.5)
After fires						
Dates	30/10–15/11	29/10–15/11	30/10–15/11	31/10–15/11	31/10–15/11	31/10–15/11
Concentration (SD)	15.9 (5.5)	15.5 (10.2)	16.9 (8.6)	18.4 (8.3)	14.2 (7.2)	12.9 (4.3)

*PM25 concentrations are calculated with equal weighting per zip code.

Table 3

Relative rate of asthma admissions in relation to a 10 μmg/m^3 increase in 2-day moving average particulate matter (PM$_{2.5}$)

Hospital admissions outcome	All periods RR (95% CI)*	Pre-wildfire period RR (95% CI)	Wildfire period RR (95% CI)	p Value†	Post-wildfire period RR (95% CI)	p Value
All respiratory						
All ages	1.009 (0.999 to 1.018)	1.022 (1.004 to 1.040)	1.028 (1.014 to 1.041)	0.639	0.999 (0.968 to 1.031)	0.198
Ages 0–4	0.994 (0.967 to 1.021)	0.982 (0.921 to 1.046)	1.045 (1.010 to 1.082)	0.103	0.894 (0.807 to 0.991)	0.126
Ages 5–19	1.014 (0.983 to 1.046)	1.026 (0.946 to 1.113)	1.027 (0.984 to 1.076)	0.990	0.958 (0.852 to 1.077)	0.354
Ages 20–64	1.015 (1.002 to 1.029)	1.036 (1.007 to 1.066)	1.024 (1.005 to 1.044)	0.534	1.007 (0.960 to 1.056)	0.315
Ages 65–99	1.009 (0.996 to 1.022)	1.022 (0.994 to 1.050)	1.030 (1.011 to 1.049)	0.649	1.024 (0.976 to 1.074)	0.932
Asthma						
All ages						
Males and females	1.022 (1.001 to 1.042)	0.998 (0.949 to 1.050)	1.048 (1.021 to 1.076)	0.097	0.986 (0.910 to 1.068)	0.792
Males	1.010 (0.980 to 1.040)	1.021 (0.944 to 1.106)	1.031 (0.990 to 1.073)	0.848	1.063 (0.948 to 1.192)	0.553
Females	1.029 (1.001 to 1.058)	0.979 (0.913 to 1.050)	1.059 (1.022 to 1.097)	0.056	0.928 (0.829 to 1.037)	0.412
Ages 0–4						
Males and females	0.996 (0.947 to 1.048)	0.924 (0.824 to 1.035)	1.083 (1.021 to 1.149)	0.017	0.924 (0.767 to 1.113)	0.999
Males	1.018 (0.963 to 1.076)	0.942 (0.815 to 1.089)	1.086 (1.016 to 1.162)	0.101	1.057 (0.839 to 1.332)	0.380
Females	0.937 (0.845 to 1.040)	0.880 (0.706 to 1.099)	1.073 (0.965 to 1.194)	0.116	0.699 (0.515 to 0.949)	0.214
Ages 5–19						
Males and females	1.006 (0.966 to 1.048)	1.045 (0.936 to 1.167)	0.999 (0.935 to 1.068)	0.492	0.918 (0.788 to 1.069)	0.198
Males	0.991 (0.935 to 1.051)	1.034 (0.892 to 1.198)	0.969 (0.883 to 1.064)	0.462	0.979 (0.806 to 1.189)	0.671
Females	1.026 (0.964 to 1.092)	1.065 (0.901 to 1.260)	1.033 (0.943 to 1.132)	0.768	0.831 (0.640 to 1.079)	0.136
Ages 20–64						
Males and females	1.043 (1.012 to 1.076)	1.037 (0.957 to 1.123)	1.041 (0.995 to 1.090)	0.931	1.000 (0.882 to 1.132)	0.624
Males	1.013 (0.954 to 1.077)	1.159 (0.996 to 1.349)	0.939 (0.837 to 1.053)	0.026	1.275 (1.020 to 1.595)	0.486
Females	1.052 (1.015 to 1.090)	0.995 (0.904 to 1.096)	1.064 (1.014 to 1.116)	0.247	0.908 (0.780 to 1.056)	0.310
Ages 65–99						
Males and females	1.027 (0.974 to 1.082)	0.951 (0.849 to 1.064)	1.101 (1.030 to 1.178)	0.032	1.168 (0.967 to 1.412)	0.072
Males	1.046 (0.957 to 1.142)	0.948 (0.804 to 1.116)	1.185 (1.077 to 1.305)	0.029	0.902 (0.629 to 1.294)	0.804

Hospital admissions outcome	**All periods RR (95% CI)**[*]	**Pre-wildfire period RR (95% CI)**	**Wildfire period RR (95% CI)**	**p Value**[†]	**Post-wildfire period RR (95% CI)**	**p Value**
Females	1.018 (0.958 to 1.081)	0.947 (0.813 to 1.102)	1.065 (0.977 to 1.162)	0.195	1.263 (1.024 to 1.557)	0.032
Acute bronchitis and bronchiolitis						
All ages	1.044 (0.990 to 1.102)	1.001 (0.890 to 1.126)	1.096 (1.018 to 1.179)	0.223	1.031 (0.870 to 1.222)	0.779
Ages 0–4	1.017 (0.949 to 1.089)	0.987 (0.847 to 1.149)	1.092 (0.997 to 1.195)	0.276	0.910 (0.700 to 1.183)	0.588
Ages 5–19	No convergence					
Ages 20–64	1.039 (0.912 to 1.183)	1.001 (0.792 to 1.266)	1.044 (0.872 to 1.252)	0.778	1.259 (0.921 to 1.722)	0.275
Ages 65–99	1.134 (1.039 to 1.238)	1.073 (0.764 to 1.505)	1.143 (1.032 to 1.265)	0.730	1.190 (0.865 to 1.638)	0.652
Chronic obstructive pulmonary disease						
Ages 20–99	1.018 (0.994 to 1.042)	1.007 (0.958 to 1.058)	1.038 (1.004 to 1.075)	0.320	1.024 (0.943 to 1.112)	0.728
Ages 20–64	1.022 (0.980 to 1.066)	0.995 (0.916 to 1.081)	1.068 (1.009 to 1.131)	0.161	1.015 (0.893 to 1.153)	0.781
Ages 65–99	1.019 (0.992 to 1.048)	1.014 (0.955 to 1.077)	1.031 (0.990 to 1.074)	0.660	1.023 (0.928 to 1.128)	0.878
Pneumonia						
All ages	1.009 (0.994 to 1.024)	1.045 (1.012 to 1.078)	1.028 (1.007 to 1.050)	0.420	0.980 (0.927 to 1.035)	0.045
Ages 0–4	0.995 (0.944 to 1.049)	1.048 (0.931 to 1.180)	1.018 (0.948 to 1.092)	0.691	0.823 (0.649 to 1.044)	0.089
Ages 5–19	1.030 (0.966 to 1.098)	1.017 (0.882 to 1.172)	1.064 (0.990 to 1.142)	0.586	1.017 (0.767 to 1.349)	0.998
Ages 20–64	1.008 (0.982 to 1.035)	1.041 (0.982 to 1.104)	1.032 (0.994 to 1.072)	0.823	1.013 (0.913 to 1.124)	0.633
Ages 65–99	1.011 (0.993 to 1.030)	1.050 (1.006 to 1.097)	1.029 (1.002 to 1.057)	0.445	0.985 (0.920 to 1.055)	0.127
All cardiovascular	0.996 (0.989 to 1.003)	0.992 (0.976 to 1.009)	1.008 (0.999 to 1.018)	0.104	0.991 (0.964 to 1.019)	0.955
Ischaemic heart disease	0.991 (0.980 to 1.003)	0.990 (0.963 to 1.017)	1.007 (0.990 to 1.024)	0.313	0.989 (0.950 to 1.030)	0.976
Congestive heart failure	0.989 (0.974 to 1.004)	0.978 (0.942 to 1.015)	1.016 (0.993 to 1.039)	0.096	0.969 (0.914 to 1.027)	0.791
Cardiac dysrhythmia	0.980 (0.962 to 0.998)	0.979 (0.935 to 1.025)	0.989 (0.961 to 1.017)	0.721	0.976 (0.912 to 1.044)	0.934
Cerebrovascular disease and stroke	1.019 (1.004 to 1.035)	1.015 (0.980 to 1.052)	1.016 (0.997 to 1.036)	0.971	1.044 (0.987 to 1.104)	0.379

[*] Rate ratio and 95% confidence interval per 10 µg/m^3 increase in 2-day moving average PM$_{2.5}$, adjusted for fungal spore counts (asthma only), race, gender, county, median income, weekend, relative humidity, temperature, age and pressure gradient. RR×100 is the percentage increase in hospital admissions. Estimates for the three strata are derived from the product term models, while estimates for the full period are from a model without interaction terms

[†] the product term p value for the difference with the pre-fire period.

Table 4

Relative rate of respiratory admissions in relation to wildfire period

Hospital admissions outcome	n*	Pre-wildfire period (referent)	Wildfire period RR (95% CI)†		Post-wildfire period RR (95% CI)	
			Unadjusted for $PM_{2.5}$	Adjusted for $PM_{2.5}$	Unadjusted for $PM_{2.5}$	Adjusted for $PM_{2.5}$
All respiratory						
All ages	21 019	1.00	0.961 (0.916 to 1.008)	0.903 (0.850 to 0.960)	1.143 (1.072 to 1.219)	1.173 (1.097 to 1.253)
Ages 0–4	2143	1.00	0.865 (0.757 to 0.989)	0.842 (0.717 to 0.988)	1.152 (0.957 to 1.388)	1.162 (0.954 to 1.415)
Ages 5–19	1205	1.00	1.098 (0.910 to 1.324)	1.087 (0.863 to 1.370)	1.373 (1.089 to 1.732)	1.467 (1.142 to 1.883)
Ages 20–64	8314	1.00	0.991 (0.922 to 1.066)	0.923 (0.843 to 1.012)	1.074 (0.971 to 1.188)	1.104 (0.992 to 1.228)
Ages 65–99	9357	1.00	0.932 (0.867 to 1.003)	0.874 (0.795 to 0.959)	1.147 (1.045 to 1.259)	1.193 (1.084 to 1.313)
Asthma						
All ages	3022	1.00	1.088 (0.965 to 1.227)	0.992 (0.856 to 1.149)	1.264 (1.085 to 1.473)	1.336 (1.134 to 1.573)
Ages 0–4	600	1.00	0.806 (0.632 to 1.029)	0.714 (0.515 to 0.990)	1.092 (0.759 to 1.572)	1.133 (0.777 to 1.654)
Ages 5–19	733	1.00	1.254 (0.999 to 1.575)	1.282 (0.958 to 1.716)	1.564 (1.160 to 2.109)	1.629 (1.184 to 2.243)
Ages 20–64	1151	1.00	1.273 (1.067 to 1.518)	1.221 (0.979 to 1.524)	1.362 (1.043 to 1.779)	1.486 (1.111 to 1.987)
Ages 65–99	538	1.00	0.869 (0.657 to 1.151)	0.645 (0.450 to 0.925)	0.924 (0.606 to 1.408)	1.005 (0.650 to 1.552)
Acute bronchitis/bronchiolitis						
All ages	618	1.00	1.143 (0.878 to 1.490)	0.959 (0.696 to 1.321)	1.482 (1.042 to 2.109)	1.580 (1.089 to 2.291)
Ages 0–4	353	1.00	1.128 (0.819 to 1.555)	0.899 (0.607 to 1.333)	1.520 (0.947 to 2.440)	1.547 (0.954 to 2.507)
Ages 5–19	23	1.00				
Ages 20–64	106	1.00	1.350 (0.688 to 2.648)	1.320 (0.608 to 2.863)	2.454 (1.068 to 5.640)	2.515 (1.055 to 5.998)
Ages 65–99	136	1.00	1.166 (0.643 to 2.115)	0.934 (0.422 to 2.066)	0.911 (0.428 to 1.942)	0.997 (0.439 to 2.262)
Chronic obstructive pulmonary disease						
Ages 20–99	2860	1.00	0.988 (0.875 to 1.115)	0.913 (0.779 to 1.069)	1.043 (0.885 to 1.228)	1.064 (0.897 to 1.262)
Ages 20–64	910	1.00	0.967 (0.779 to 1.201)	0.873 (0.660 to 1.156)	1.175 (0.862 to 1.601)	1.311 (0.954 to 1.802)
Ages 65–99	1950	1.00	1.002 (0.869 to 1.156)	0.926 (0.767 to 1.117)	0.985 (0.811 to 1.196)	0.981 (0.798 to 1.206)
Pneumonia						
All ages	6440	1.00	0.943 (0.868 to 1.025)	0.888 (0.799 to 0.986)	1.294 (1.158 to 1.446)	1.318 (1.174 to 1.479)
Ages 0–4	537	1.00	0.938 (0.705 to 1.247)	0.951 (0.678 to 1.333)	1.458 (0.974 to 2.182)	1.374 (0.885 to 2.133)
Ages 5–19	293	1.00	0.891 (0.604 to 1.312)	0.830 (0.541 to 1.272)	0.960 (0.588 to 1.569)	0.969 (0.578 to 1.624)

Hospital admissions outcome	n[*]	Pre-wildfire period (referent)	Wildfire period RR (95% CI)[†]		Post-wildfire period RR (95% CI)	
			Unadjusted for $PM_{2.5}$	Adjusted for $PM_{2.5}$	Unadjusted for $PM_{2.5}$	Adjusted for $PM_{2.5}$
Ages 20–64	1686	1.00	0.927 (0.795 to 1.081)	0.837 (0.690 to 1.016)	1.314 (1.064 to 1.622)	1.300 (1.047 to 1.615)
Ages 65–99	3924	1.00	0.959 (0.861 to 1.068)	0.899 (0.782 to 1.033)	1.277 (1.102 to 1.481)	1.331 (1.142 to 1.552)
			Unadjusted for $PM_{2.5}$	Adjusted for $PM_{2.5}$	Unadjusted for $PM_{2.5}$	Adjusted for $PM_{2.5}$
All cardiovascular[‡]	27 170	1.00	0.958 (0.920 to 0.997)	0.947 (0.902 to 0.994)	1.061 (1.006 to 1.119)	1.053 (0.994 to 1.114)
Ischaemic heart disease	10319	1.00	0.913 (0.852 to 0.978)	0.905 (0.832 to 0.985)	1.029 (0.943 to 1.123)	1.029 (0.936 to 1.131)
Congestive heart failure	6144	1.00	0.891 (0.817 to 0.972)	0.911 (0.819 to 1.014)	1.113 (0.997 to 1.242)	1.105 (0.982 to 1.244)
Cardiac dysrhythmia	4004	1.00	0.968 (0.874 to 1.072)	0.964 (0.851 to 1.093)	1.089 (0.949 to 1.251)	1.057 (0.914 to 1.223)
Cerebrovascular disease and stroke	5908	1.00	1.066 (0.981 to 1.159)	1.017 (0.922 to 1.123)	1.013 (0.907 to 1.132)	1.013 (0.902 to 1.138)

[*] Number of hospital admissions for zip codes with defined populations

[†] adjusted for race, gender, county, median income, weekend, relative humidity, temperature, age and pressure gradient

[‡] cardiovascular admissions were for subjects ages 45-99 years. $PM_{2.5}$, particulate matter.

Relationship between habitat and genetics in a wide-ranging large carnivore

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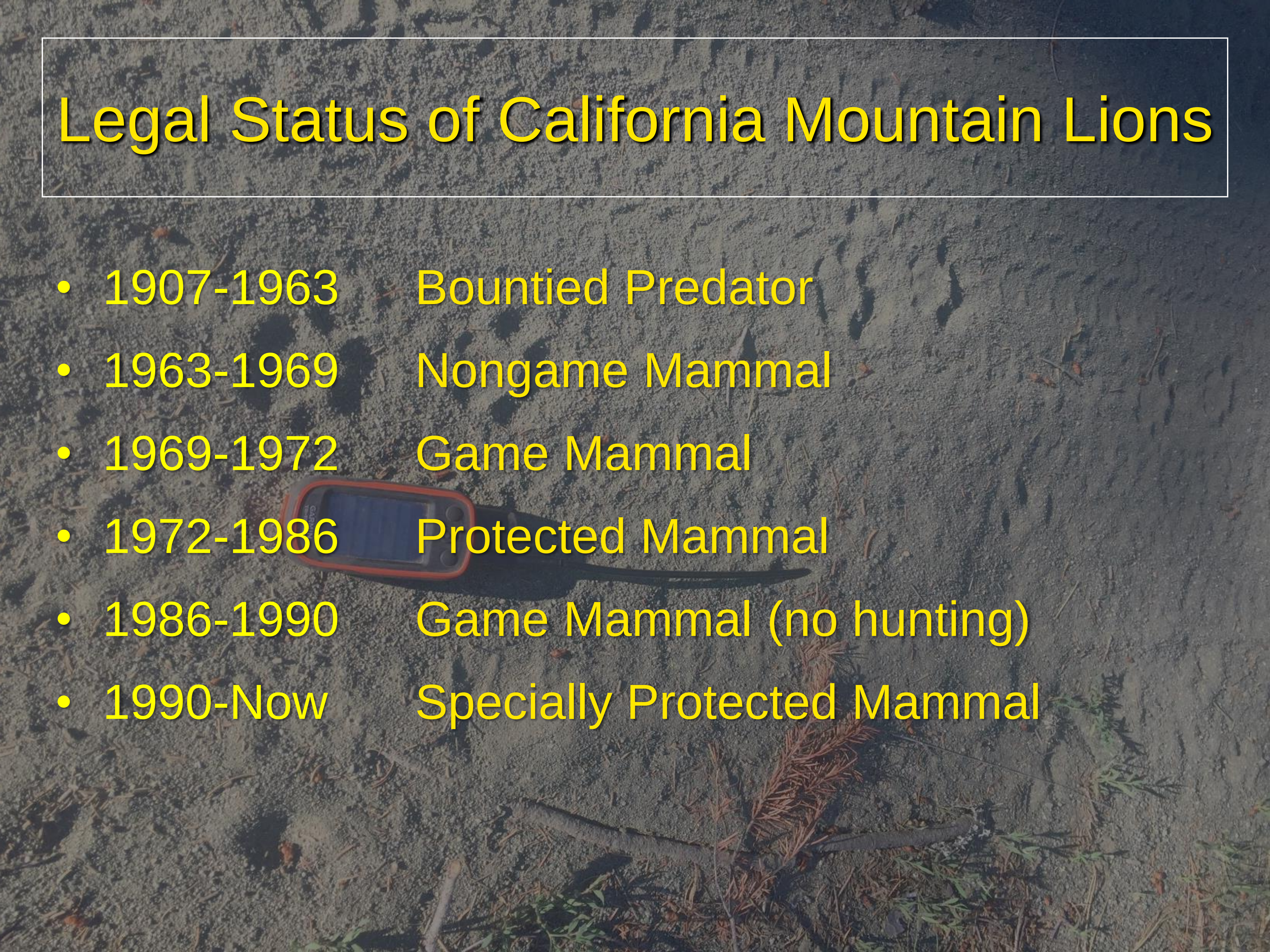


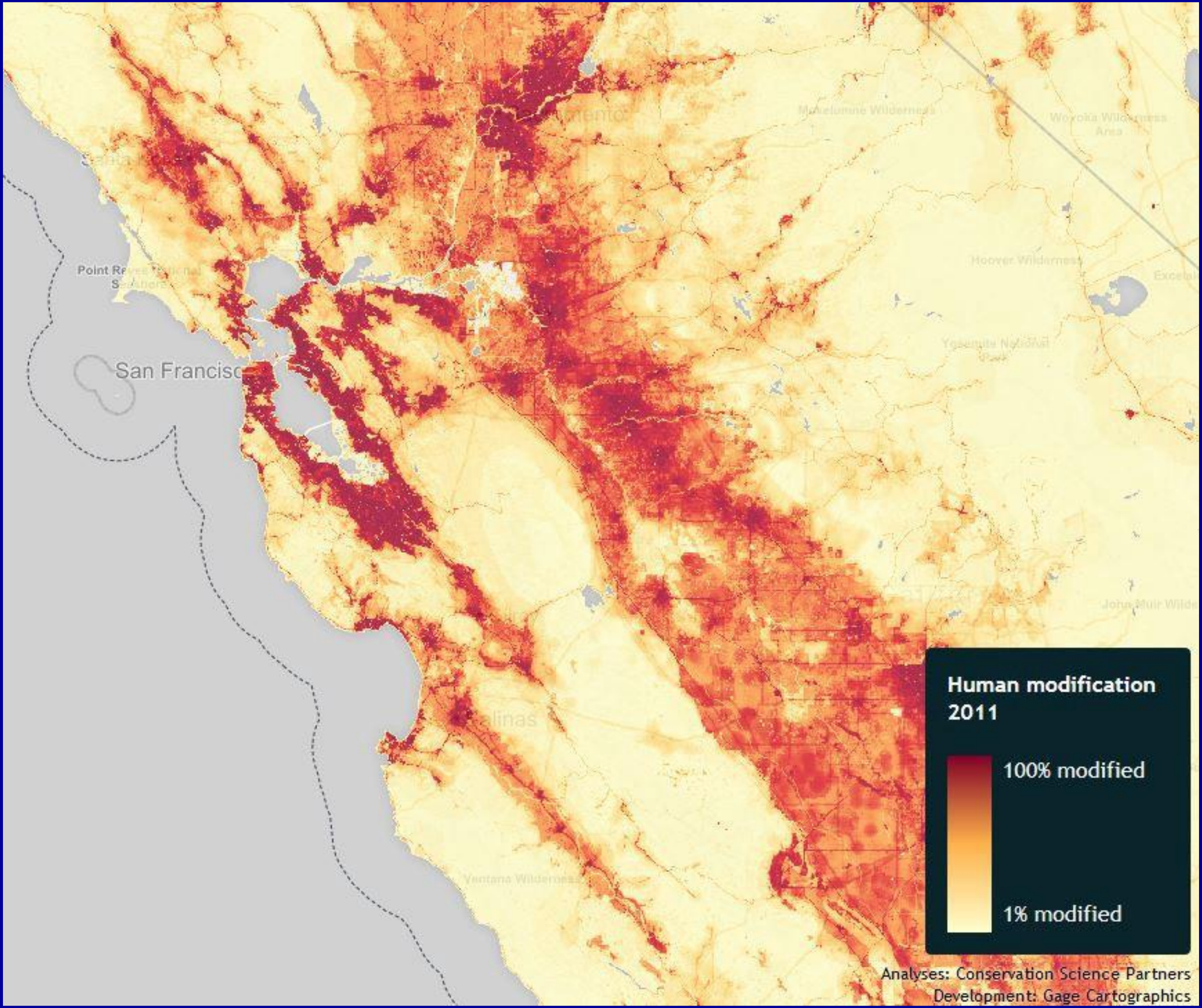
Legal Status of California Mountain Lions

1907-1963	Bountied Predator
1963-1969	Nongame Mammal
1969-1972	Game Mammal
1972-1986	Protected Mammal
1986-1990	Game Mammal (no hunting)
1990-Now	Specially Protected Mammal

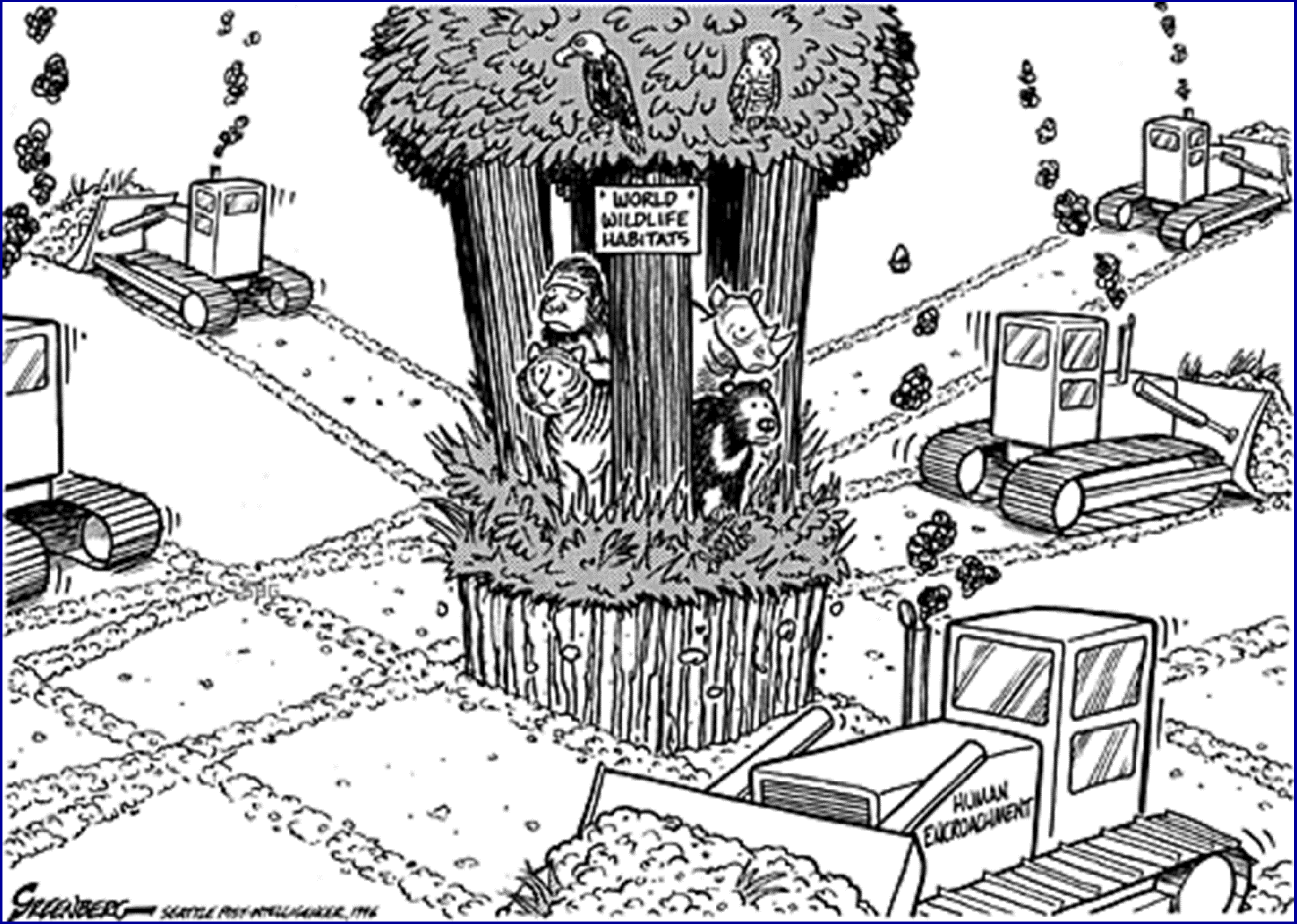
Human population growth

Year	Population	% Growth
1900	1,485,053	22.4%
1910	2,377,549	60.1%
1920	3,426,861	44.1%
1930	5,677,251	65.7%
1940	6,907,387	21.7%
1950	10,586,223	53.3%
1960	15,717,204	48.5%
1970	19,953,134	27.0%
1980	23,667,902	18.6%
1990	29,760,021	25.7%
2000	33,871,648	13.8%
2010	37,253,956	10.0%

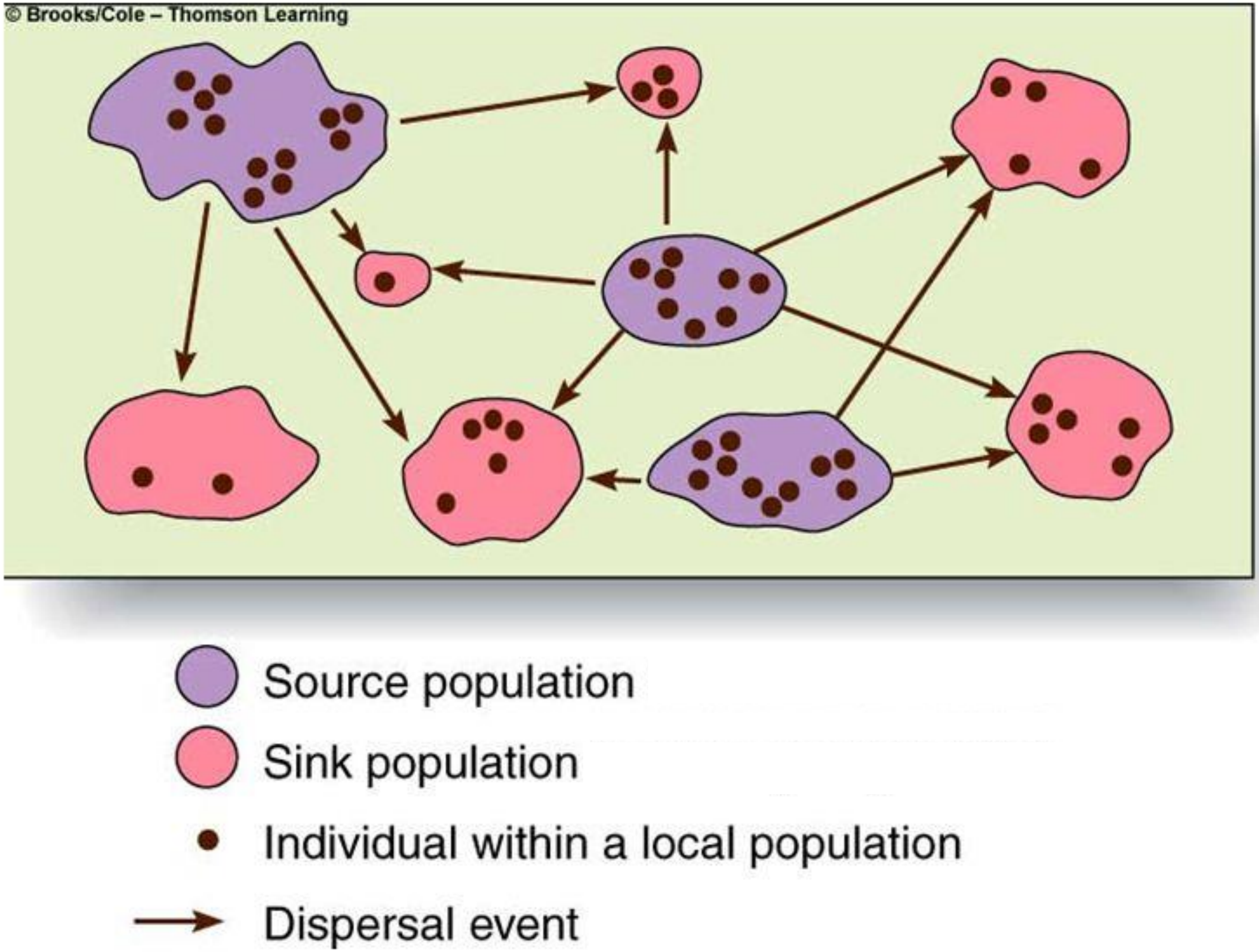
*U.S. Census Bureau



Analyses: Conservation Science Partners
Development: Gage Cartographics


WORLD WILDLIFE HABITATS
HUMAN ENCROACHMENT
GREENBERG SEATTLE POST-INTELLIGENCER, 1996

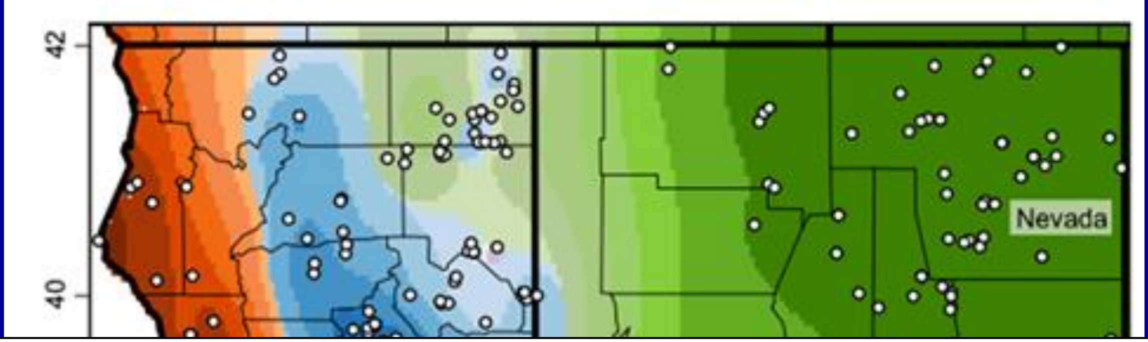
Ernest et al. 2014

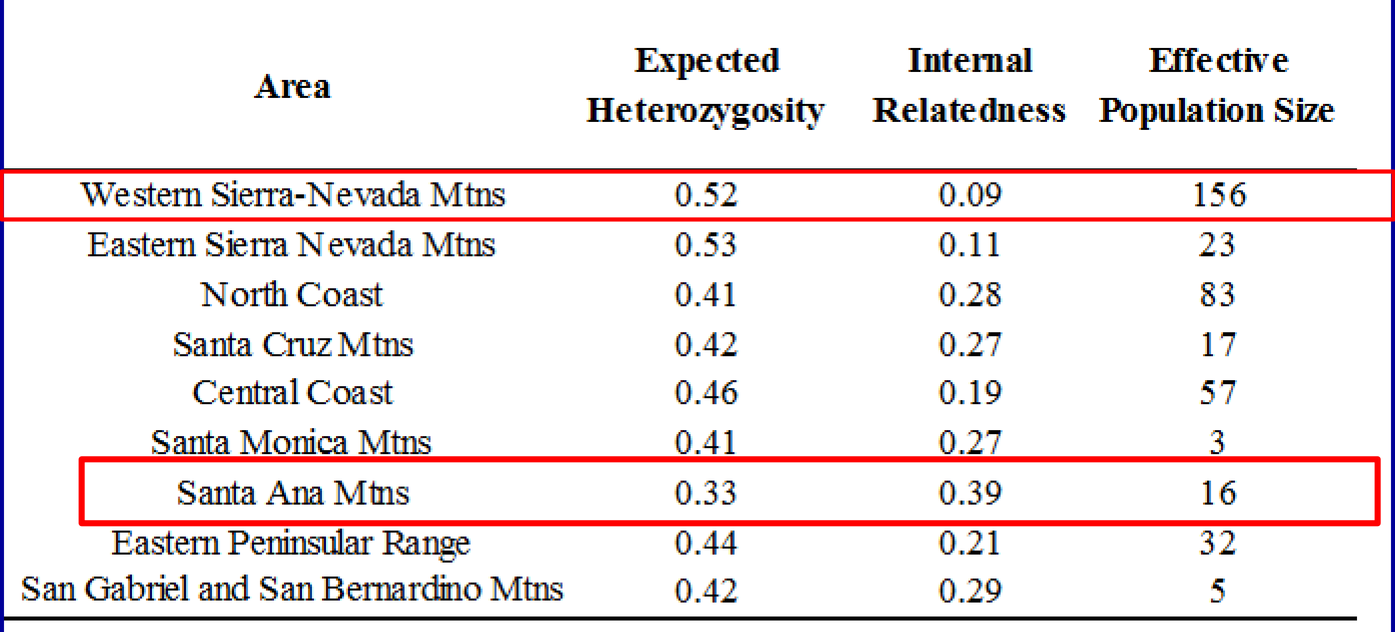


Source population
Sink population
Individual within a local population
Dispersal event

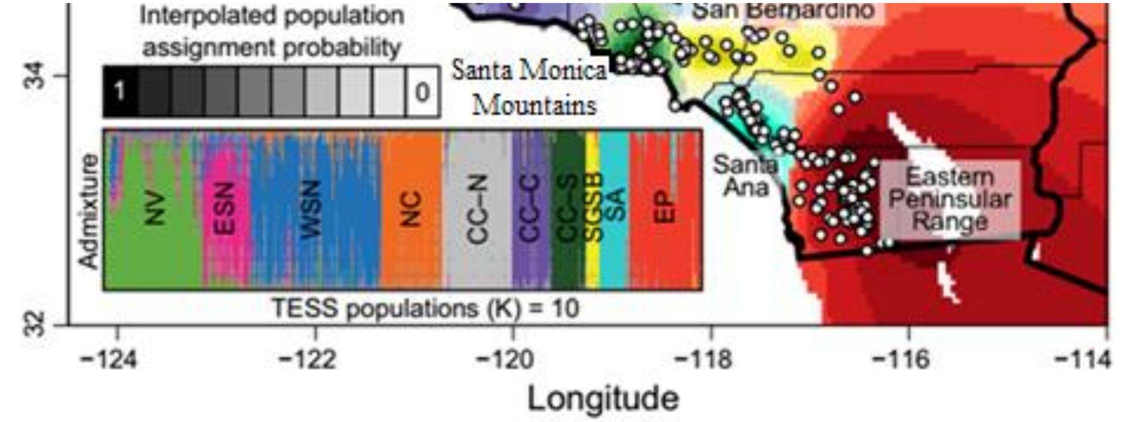
Overarching goals

- Habitat vs genetics
- Protected habitat vs unprotected habitat





Area	Expected Heterozygosity	Internal Relatedness	Effective Population Size
Western Sierra-Nevada Mtns	0.52	0.09	156
Eastern Sierra Nevada Mtns	0.53	0.11	23
North Coast	0.41	0.28	83
Santa Cruz Mtns	0.42	0.27	17
Central Coast	0.46	0.19	57
Santa Monica Mtns	0.41	0.27	3
Santa Ana Mtns	0.33	0.39	16
Eastern Peninsular Range	0.44	0.21	32
San Gabriel and San Bernardino Mtns	0.42	0.29	5



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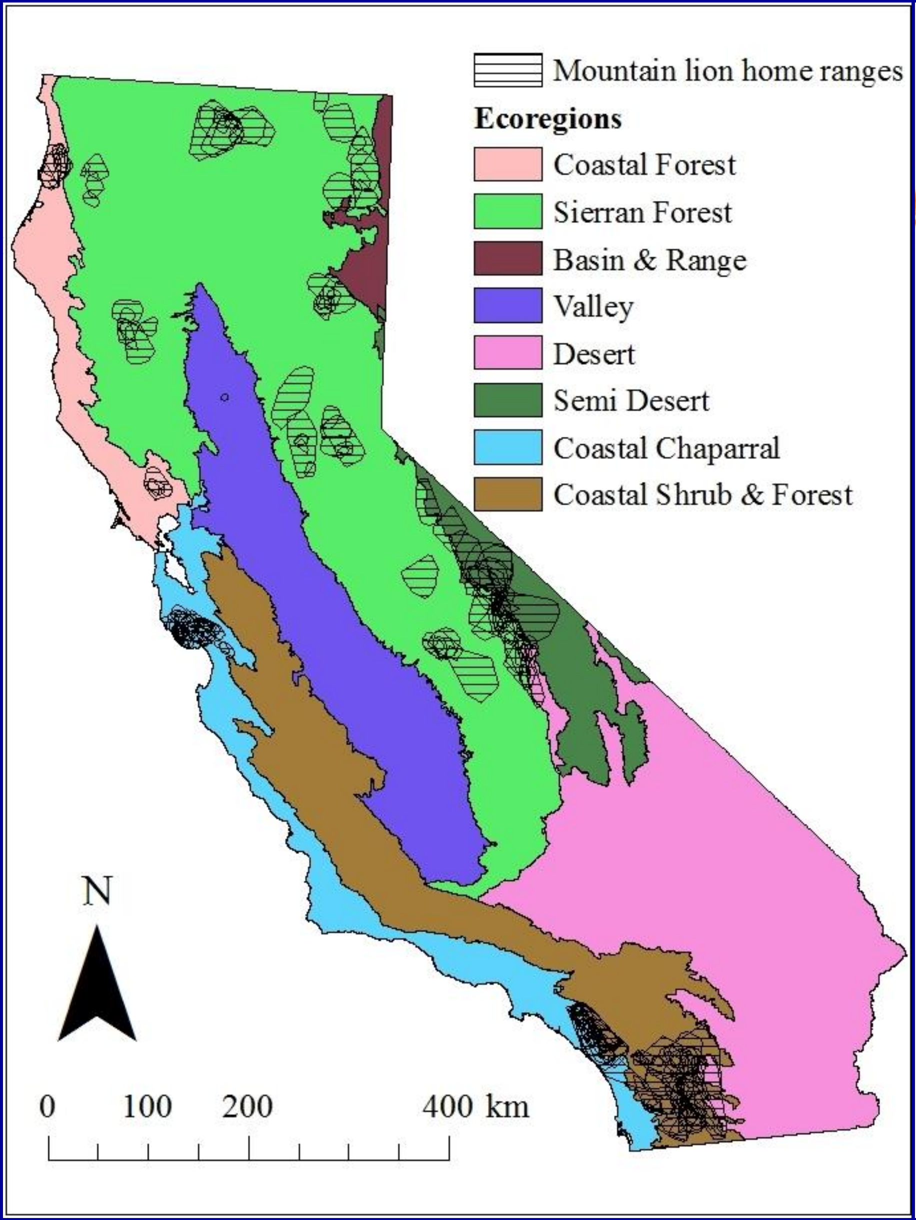
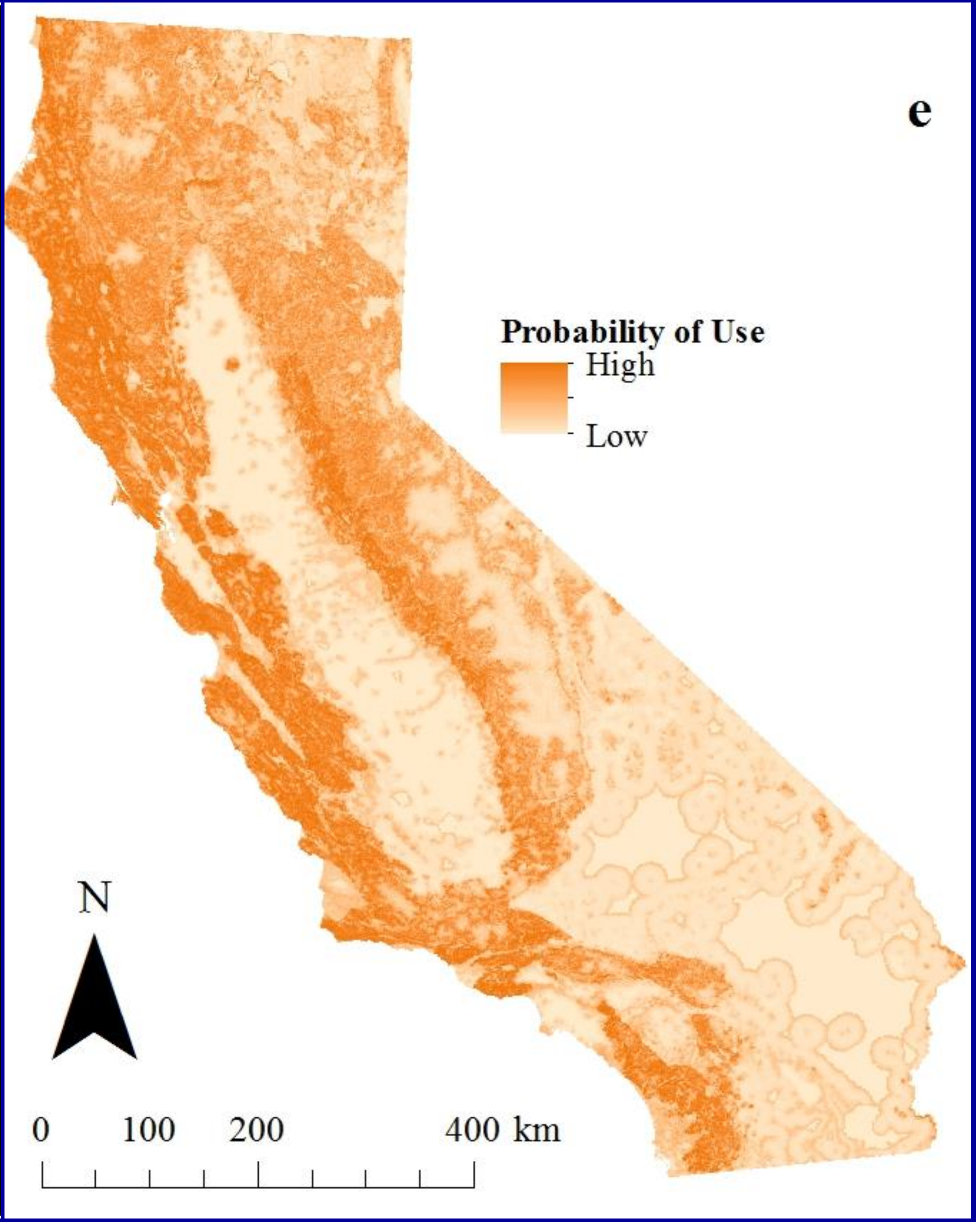

Mountain lion home ranges
Ecoregions
Coastal Forest
Sierran Forest
Basin & Range
Valley
Desert
Semi Desert
Coastal Chaparral
Coastal Shrub & Forest
N
0 100 200 400 km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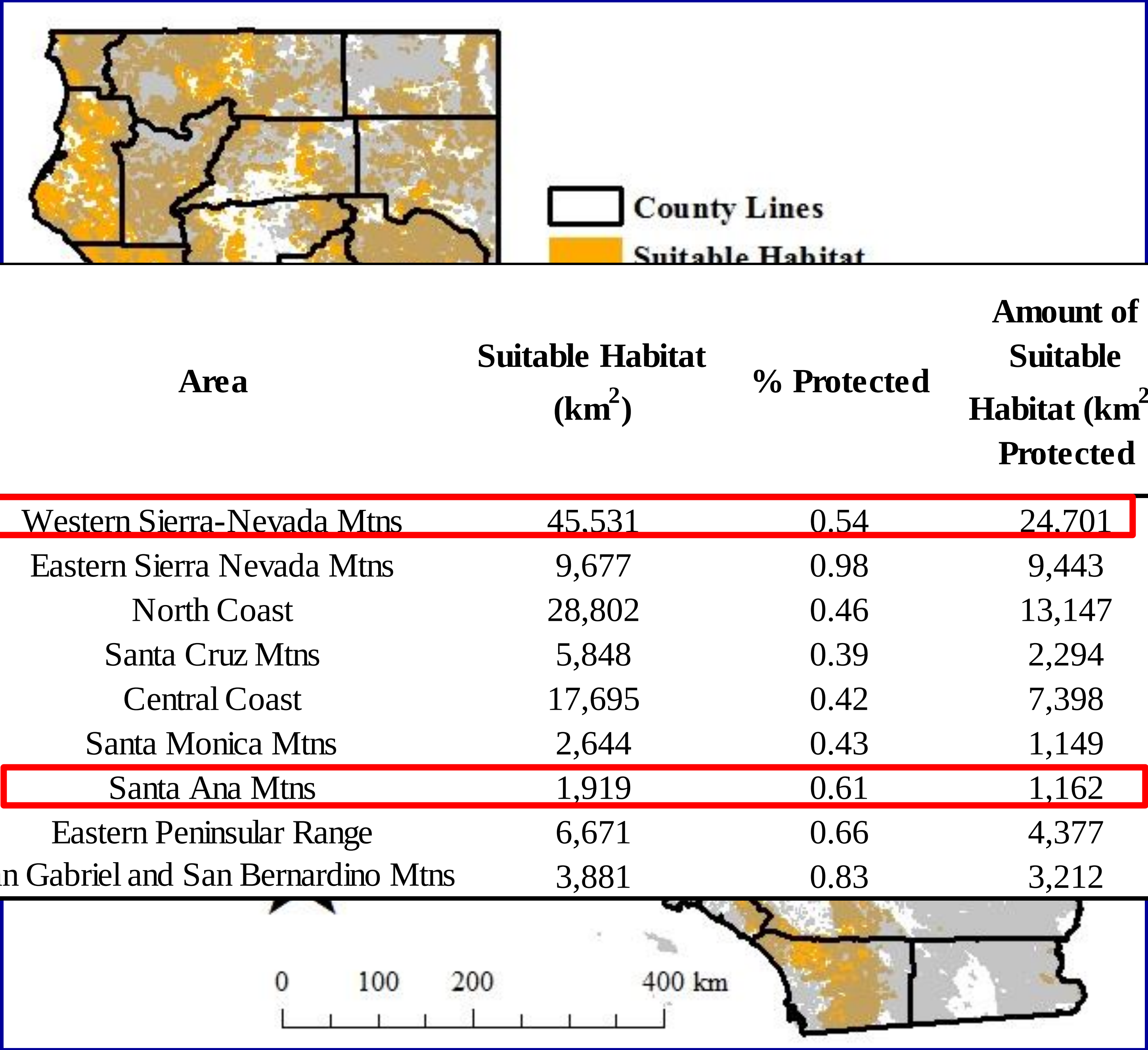


Area	Suitable Habitat (km^2)	% Protected	Amount of Suitable Habitat (km^2) Protected
Western Sierra-Nevada Mtns	45,531	0.54	24,701
Eastern Sierra Nevada Mtns	9,677	0.98	9,443
North Coast	28,802	0.46	13,147
Santa Cruz Mtns	5,848	0.39	2,294
Central Coast	17,695	0.42	7,398
Santa Monica Mtns	2,644	0.43	1,149
Santa Ana Mtns	1,919	0.61	1,162
Eastern Peninsular Range	6,671	0.66	4,377
San Gabriel and San Bernardino Mtns	3,881	0.83	3,212

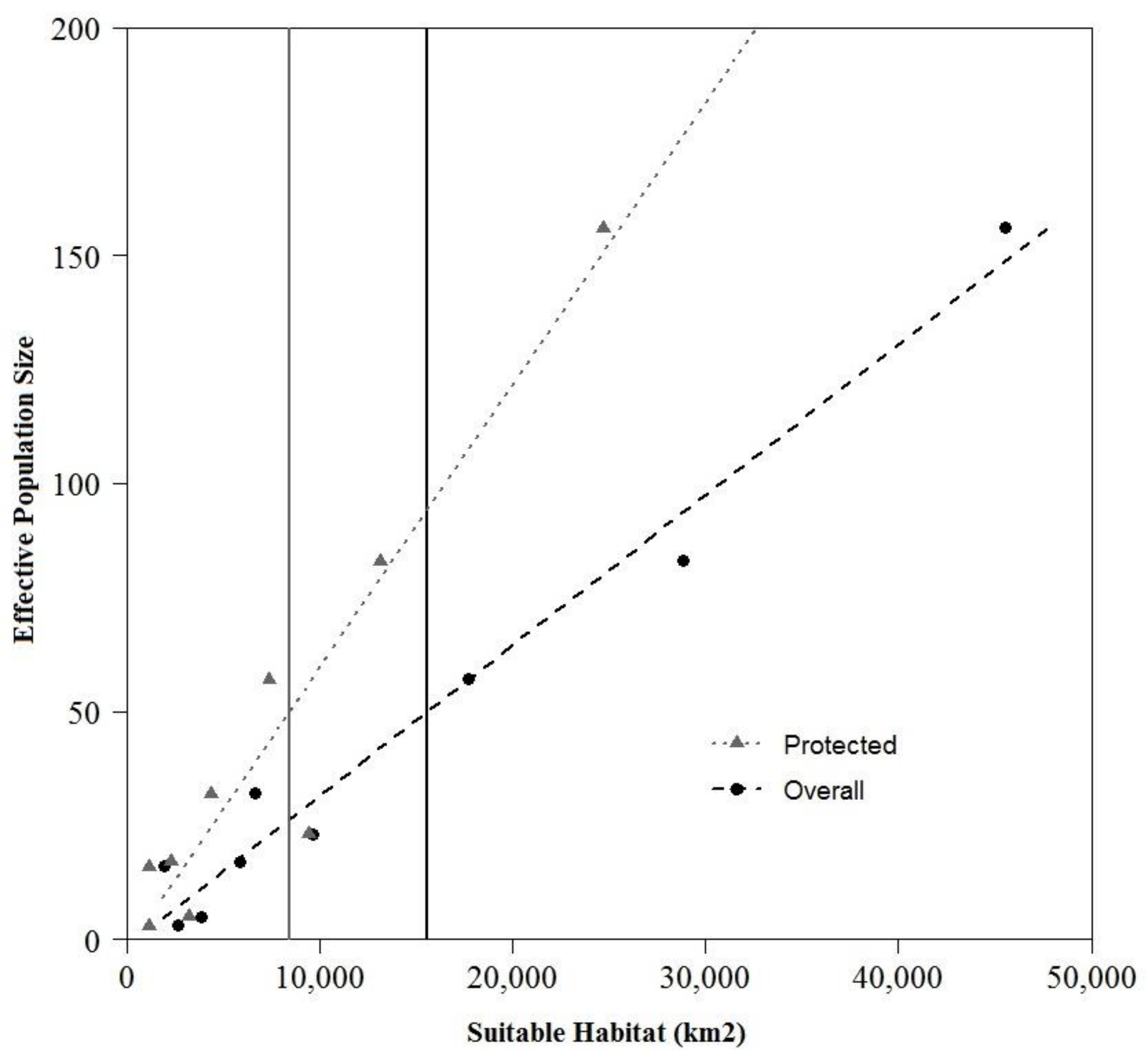
Analyses

- Analyses
  - Effect. Pop. Size ~ Overall suitable habitat
  - Effect. Pop. Size ~ Protected suitable habitat
  - Minimum Threshold – Effect. Pop. Size n = 50

Results

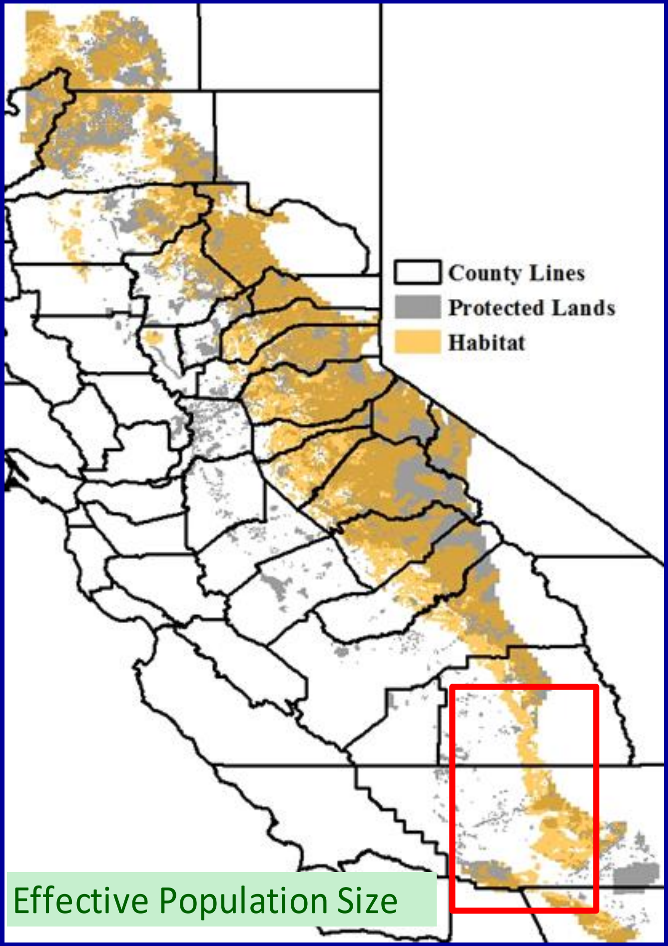
	Effective Population Size	
	Overall	Protected
R^2 value	0.97	0.91
***p* value**	<0.001	<0.001
Minimum Threshold (km2)	15,600	8,450

Area
Western Sierra-Nevada Mtns
Eastern Sierra Nevada Mtns
North Coast
Santa Cruz Mtns
Central Coast
Santa Monica Mtns
Santa Ana Mtns
Eastern Peninsular Range
San Gabriel and San Bernardino Mtns



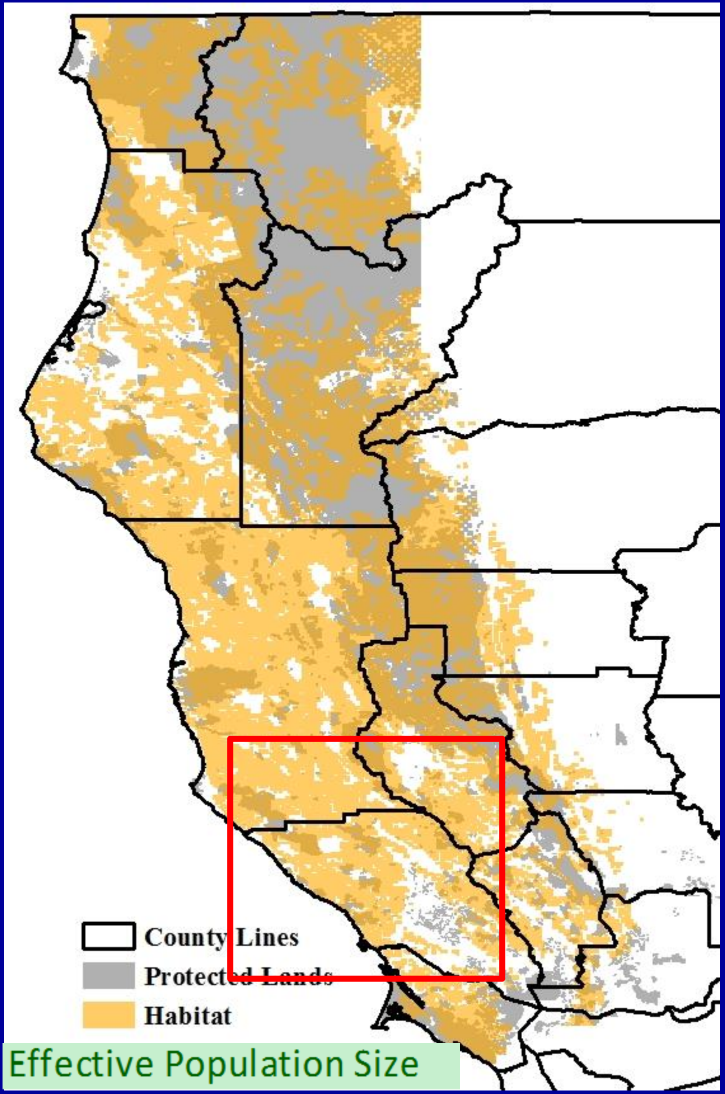
Western Sierra

- No current concerns
- Important source for entire state & beyond
- Important to maintain habitat in southern extent



North Coast

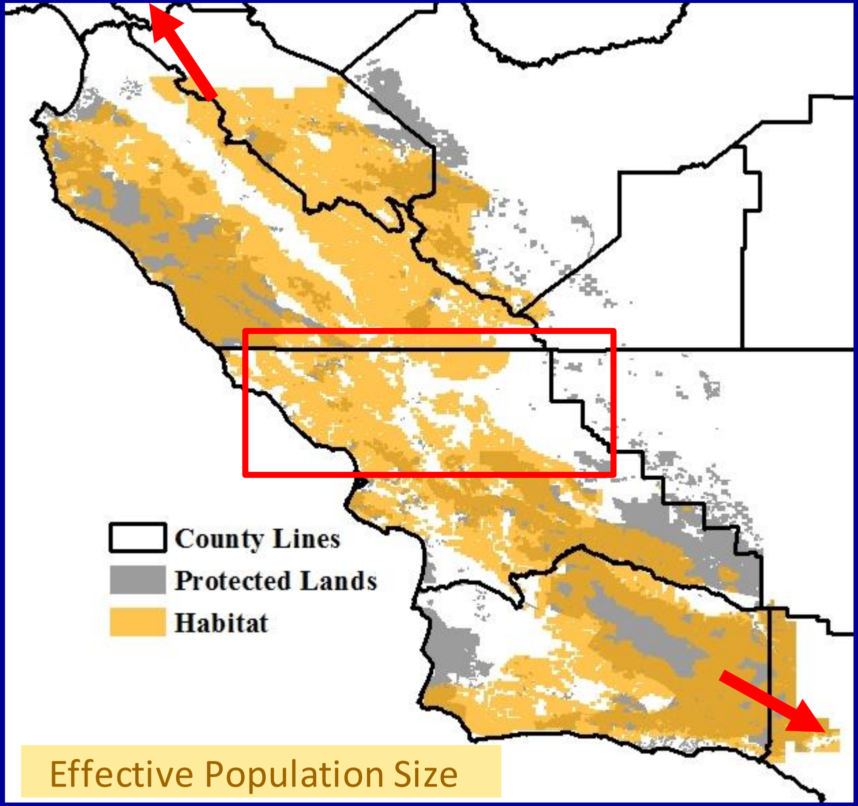
- No current concerns
- Southern extent a possible concern due to ‘habitat peninsula’ and little protected habitat



Effective Population Size

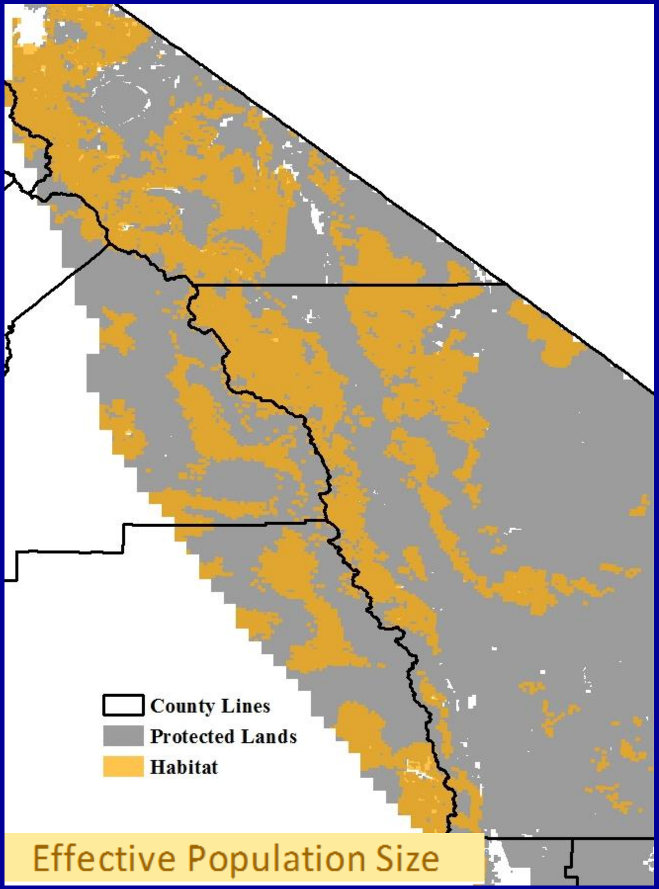
Central Coast

- No current concerns
- Increase protected habitat
- Central section is vulnerable
- Improve connectivity to smaller adjacent areas



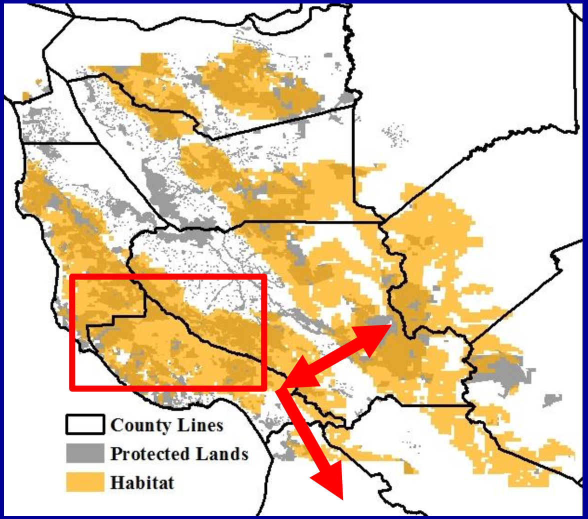
Eastern Sierra

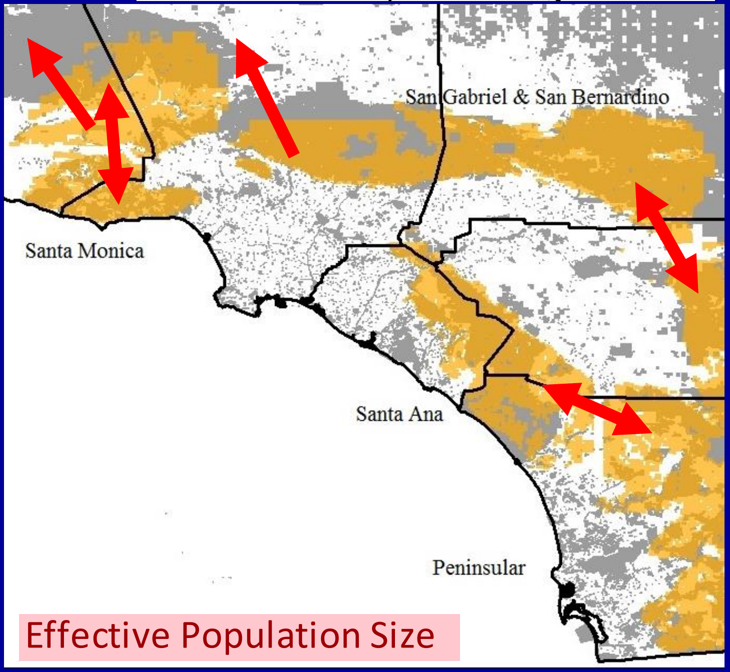
- Currently no concerns despite lower amount of habitat
- All habitat protected
- Maintenance of metapopulation dynamics likely promote persistence



Santa Cruz & SoCal

- Current habitat/genetic concerns
- Internal habitat & connectivity at risk
- External connectivity limited
- Long-term viability of these areas a concern unless habitat protection & connectivity improved



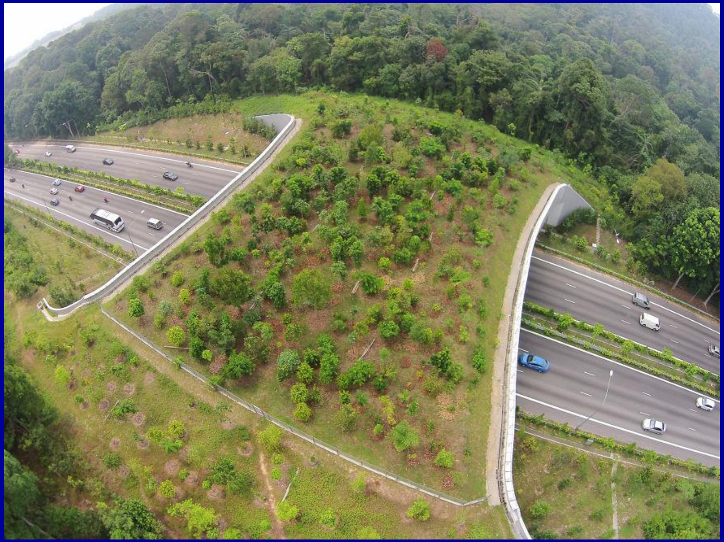


Summary

- Habitat predictor of genetic integrity
- Suitable habitat isn’t as good as protected suitable habitat
- Regional habitat/genetic concerns in CA
- Improved habitat connectivity & protection = restored metapopulation dynamics = increased genetic integrity
- Ensuring habitat requirements for lions to persist ensures persistence of many other species (and ecological processes) too

Path Forward?

- Conservation easements
- Open spaces
- Wildlife passage



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INFLUENCE OF VEGETATION, TOPOGRAPHY, AND ROADS ON COUGAR MOVEMENT IN SOUTHERN CALIFORNIA

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Abstract: Models of individual movement can help conserve wide-ranging carnivores on increasingly human-altered landscapes, and cannot be constructed solely by analyzing the daytime resting locations typically collected in carnivore studies. We examined the movements of 10 female and 7 male cougars (*Puma concolor*) at 15-min intervals during 44 nocturnal or diel periods of hunting or traveling in the Santa Ana Mountain Range of southern California, USA, between 1988 and 1992. Cougars tended to move in a meandering path (mean turning angle ~54°), and distance moved (mean and mode ~300 m) was not correlated with turning angle. Cougars used a broader range of habitats for nocturnal or diel movements than for previously described daybed locations for this same population. Riparian vegetation ranked highest in a compositional analysis of vegetation types selected during movement; grassland, woodland and urbanized sites were least selected. During periods of stasis (we presume many of these were stalking locations), patterns of selection were less marked. Cougars spent a disproportionate amount of time in highly ranked vegetation types, and traveled slowest through riparian habitats and fastest through human-dominated areas. Our results suggest that travel speed may provide an efficient index of habitat selection in concert with other types of analysis. Hunting or traveling individuals consistently used travel paths that were less rugged than their general surroundings. Traveling cougars avoided 2-lane paved roads, but dirt roads may have facilitated movement. Maintenance and restoration of corridors between large wildlands is essential to conserving cougars in southern California. Our results indicate that riparian vegetation, and other vegetation types that provide horizontal cover, are desirable features in such corridors, that dirt roads should not impede cougar use of corridors, and that corridors should lie along routes with relatively gentle topography. Our results suggest that cougars do not key in on highway-crossing structures in a way that creates a prey trap. Our empirical frequency distributions of distances and turning angles, along with cougar responses to vegetation, topography, and roads can help parameterize an individually-based movement model for cougars in human-altered landscapes.

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Key words: California, compositional analysis, cougar, habitat selection, movement, prey trap, *Puma concolor*, riparian, roads, scale, topography, travel speed, urbanized, vegetation.

Least-cost path analysis (Bunn et al. 2000, Paquet et al. 2001) and individual-based movement models (DeAngelis and Gross 1992, Bergman et al. 2000) for wide-ranging animals depend crucially on an understanding of how individuals move. These models, especially those built for terrestrial carnivores, can be used as tools for conservation planning and to assess, maintain, or improve habitat connectivity in human-dominated landscapes (Minta et al. 1999, Schadt et al. 2002). Animal movement probably depends on patterns of resource use relative to availability across multiple scales (Senft et al. 1987, Wiens 1989, Turchin 1998, Pace 2001), natural impediments in the landscape (With 1994), the animal's knowledge of its environment (including locations of conspecifics and primary prey), and human-induced habitat fragmentation and loss (Crooks 2002). A first step to modeling movement behavior is to study fine-scale movements and patterns of selection exhibited by individual animals (Wiens et al. 1993). If the broad-scale distribution patterns of individuals are the aggregate of fine-scaled movement behaviors (Turchin 1991, With 1994), then these behaviors may provide a mechanistic link to many ecological processes (Wiens et al. 1993).

Despite the increased use of wide-ranging nocturnal carnivores in conservation planning, little research has described their fine-scale movement patterns or factors influencing those movements. For instance, most studies of movement patterns of western cougars have described these patterns over weeks or months, based on ≤1 location per day, usually during daylight hours (Hemker et al. 1984, Anderson et al. 1992, Beier 1995, Ruth et al. 1998, Sweanor et al. 2000). Beier et al. (1995) described patterns in the distances cougars moved per 15-min interval as a function of time

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of day, sex, gross behavior state (e.g., hunting, feeding on previously-killed deer, raising cubs), but did not characterize cougar movements as a function of vegetation, topography, or other features in the animal's vicinity.

Cougar aversion to paved roads has been documented previously (Van Dyke et al. 1986, Belden and Hagedorn 1993, Sweanor et al. 2000, Dickson and Beier 2002), but all of these studies analyzed diurnal locations, presumably daybed locations in most cases, and no study has compared the observed number of paved road crossings with the number of crossings expected if cougars were indifferent to crossing. There has been increasing concern that highway crossing structures such as underpasses and culverts could funnel prey into areas where predators would exploit high prey density, creating a prey trap (Norman et al. 1998, Little et al. 2002), but there are no data supporting or refuting this possibility for cougars.

We attempted to address some of these information gaps by examining a subset of data collected and previously analyzed by Beier et al. (1995). Because cougar movement depends not only on habitat type and arrangement, but also on nonhabitat factors (e.g., location of a previously killed carcass, interactions with conspecifics), we attempted to isolate habitat factors by studying cougar movements during those periods when the focal animal was apparently not feeding on deer or interacting with other cougars. We studied animals during diel or nocturnal monitoring sessions to include periods of greatest daily movement. We also chose a time scale (movement during 15-min intervals) that minimized the risk that habitats traversed differed from those intersected by a line segment between consecutive locations, and we buffered these line segments to reflect the resolution of our measurements. Finally, we speculated that travel speed in a habitat might be a useful index of habitat selection. We reasoned that cougars would travel most quickly through habitats in which they are most uncomfortable (or that they perceive as less-profitable places to spend their time). If our data confirmed this pattern, travel speed could be used as a complement to more complex approaches such as compositional analysis.

Our objectives were to: (1) describe the travel path characteristics of individual cougars monitored during nocturnal or diel periods; (2) compare the vegetation, topography, and road density on paths used by and available to cougars during individual movement sessions; (3) investigate whether travel speed is correlated with habitat selection patterns; (4) identify landscape features that facilitated or inhibited cougar movements, with particular attention to cougar movements near 2-lane paved roads; and (5) describe the extent to which cougars might linger at road crossing structures to ambush prey.

STUDY AREA

The Santa Ana Mountain Range (SAMR) encompassed approximately 2,060 km^2 of nonurban wildlands and included portions of Orange (38% of study area), Riverside (28%), and San Diego (34%) counties; over 1 million people lived in the cities and communities surrounding the SAMR (Beier 1993). Our study area boundaries were delineated where the core of the study area met a major freeway or where human dwellings exceeded 4 residences per ha. The Cleveland National Forest, Camp Pendleton Marine Corps Base, Fallbrook Naval Weapons Station, Caspers Regional Park and several smaller reserves (Padley 1990, Beier and Barrett 1993) comprised most of the protected cougar habitat in the area. Beier (1993, 1995) and Dickson (2001) provide maps of the study area.

Plant communities on the study area included chaparral, oak woodlands (*Quercus engelmannii* and *Q. agrifolia*), coastal scrub, annual grasses, and coniferous forests at higher elevations (Barbour and Major 1995). Citrus and avocado orchards and other nonnative vegetation types occurred in parts of the area. Although human influence on the SAMR was widespread and included cattle grazing, agriculture, military training facilities, and public recreation areas, much of the study area remained undeveloped. Maximum average daily temperature was 24°C and mean annual precipitation was 33 cm in lower elevations (Santa Ana Fire Station, Santa Ana, California, USA, 1948–2000), with somewhat cooler and more mesic conditions at higher elevations. Precipitation in the form of fog drip was common throughout the year and light snow accumulation was possible in winter at the higher elevations (Barbour and Major 1995). Elevations within the study area ranged from sea level at the coast to 1,717 m on Santiago Peak. The topography was rugged. Although perennial streamflow was intermittent, springs, seeps, and other water sources were widely available throughout the study area (Beier and Barrett 1993).

Other carnivores common to the SAMR included coyotes (*Canis latrans*), gray foxes (*Urocyon* *cinereoargenteus*), bobcats (*Lynx rufus*), raccoons (*Procyon lotor*), and striped skunks (*Mephitis mephitis*). Mule deer (*Odocoileus hemionus*) were common throughout the study area and were the most important prey species for this cougar population (Beier and Barrett 1993). Smaller prey included opossum (*Didelphis virginiana*), raccoon, and coyote (Beier and Barrett 1993).

METHODS

Radiotelemetry

Between May 1988 and December 1992, we captured, radiocollared, and monitored movements of cougars during distinct periods that ran from 1 hr before sunset until 1 hr after sunrise (nocturnal sessions) or for 24 hr (diel sessions, which always started and ended in the afternoon). During each session, we determined the location of a focal animal every 15 min using radiotelemetry. We obtained radiotelemetry locations from the ground using standard triangulation techniques (Mech 1983) conducted by a single observer using a vehicle. We attempted to track the focal animal at a distance >100 m to minimize influencing its movement and <500 m away to obtain accurate locations. To determine a single location, we took bearings within a span of 2–6 min. Because only a single observer was used and no network of precisely located receiving stations was available, we cannot compute meaningful error polygons (White and Garrott 1990). We minimized location errors by using only azimuths that differed by 60–120° and by getting close to the animal (White and Garrott 1990). We determined 85% and 96% of all locations from within 500 m and 1 km of the focal animal, respectively. We recorded these locations to the nearest 50 m of easting and northing; thus, movements ≤50 m in 15 min we typically recorded as stasis. We recorded each radiolocation as a Universal Transverse Mercator (UTM) point on a 1:24,000 U.S. Geological Survey (USGS) topographic map and then exported all points into a vector-based Geographic Information System (GIS; ArcView® 3.2a; Environmental Systems Research Institute, Redlands, California, USA).

By back-tracking movements with hounds on the day after a monitoring session to look for kills, tracks, and feces, and using other knowledge (such as vocalizations), Beier et al. (1995) classified the animal's behavior in each session into 1 of several categories. For this analysis, we used only sessions on adults (≥2 years old) and juveniles independent of their mother, excluding sessions involving copulation, raising cubs, feeding on a previously killed large mammal, or killing a large mammal. We assume that the focal animal was hunting or traveling during these sessions; cougars in these sessions traveled much farther, and for a much larger fraction of the night, than cougars in other behavior categories (Beier et al. 1995). We chose sessions with this pattern because it was the most common movement pattern and because this choice minimized the risk that cougar response to vegetation, topography, and roads would be obscured by other factors (presence of a kill, cub, or mate).

Analysis of Movement and Selection

Within the GIS, we developed an ArcView® extension (CGRMVMNT) using an object-oriented programming language (AVENUE; Environmental Systems Research Institute). Using this extension, we calculated whether the animal was moving or static during each 15-min period (interval, hereafter), the straight-line distance and rate of movement between consecutive locations, proportion of a movement segment (the straight line connecting consecutive locations) intersecting each vegetation type, deviation angles for consecutive movement segments, and the maximum slope encountered during a movement segment. Additionally, we used the CGRMVMNT extension to calculate the proportion of vegetation types and the maximum slope available to an individual (see below). Our approach assumed a constant rate of movement during a movement interval, and attributed that rate to movement in each vegetation type traversed during the interval.

We use the term "habitat composition" to refer to a vector of proportions of vegetation types used by or available to an animal and where total habitat composition adds up to 100%. To account for error in assigning an individual radio-location to a single vegetation type, which can seriously bias analyses of selection (Rettie and McLoughlin 1999), we assumed that a cougar used all types within a 100-m radius of a linear movement segment or a static location in proportion to the area of that type within the buffered region (Fig. 1). We chose a 100-m radius buffer partly to encompass triangulation error in estimating animal locations (Beier et al. 1995) and to encompass errors inherent in the digital coverages used to analyze selection. Additionally, this buffer allows our analysis to detect the potential importance of habitat mosaics in the selection process (see Rettie and McLoughlin 1999).

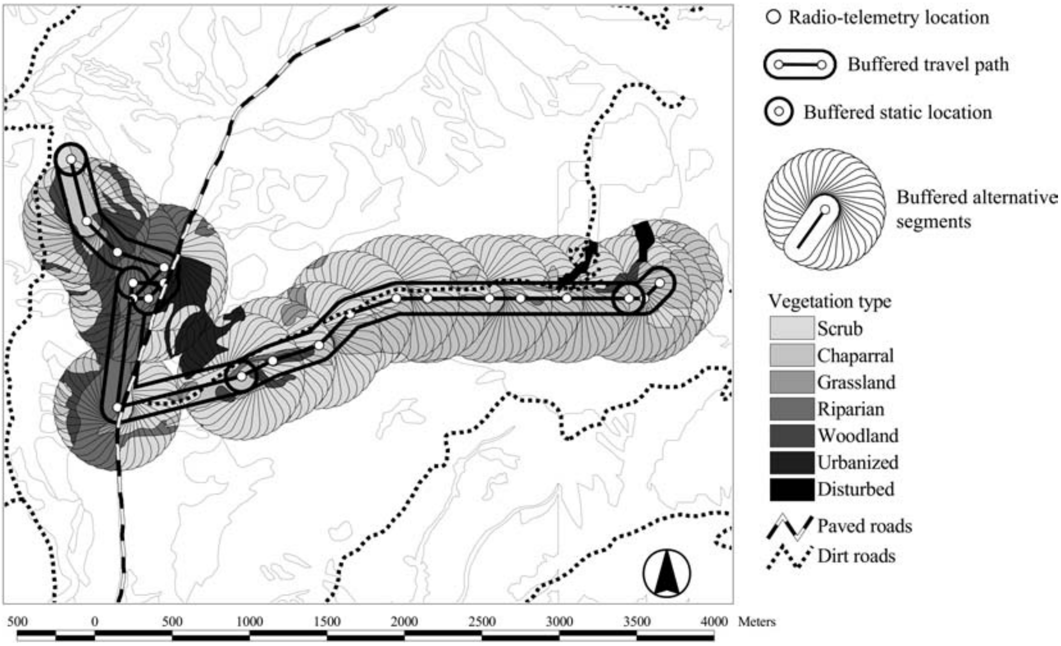

Fig. 1. Travel path through 7 vegetation types for female cougar F2 (session #100) monitored in the Santa Ana Mountain Range of southern California, USA, 1988–1992. This session began at 1800 hr, 6 Jul 1990 (eastern-most location) and ended at 0630 hr, 7 Jul 1990 (western-most location). Buffered static locations, travel path, and alternative segments generated by the CGRMVMNT extension are shown.

To evaluate selection for all movements during an individual session, we compared the average habitat composition of the buffered movement segments (used) to the average habitat composition of systematically assigned buffered movement segments (available). To estimate availability at each movement segment, we calculated the average proportion of each vegetation type captured within 35 alternative travel path segments (also buffered at 100 m) generated at 10° increments around the starting point of each movement segment and equal in length to the mean of all movement segments during that nocturnal or diel monitoring session (Fig. 1). To evaluate selection during static intervals within a session, we compared the average habitat composition of buffered radio-locations to the average habitat compositions of buffered movement segments during that session. For an individual monitored for >1 session, we first calculated used and available habitat compositions within a session, and then averaged across sessions so that each animal contributed only 1 composition to any inferential statistical analysis.

We used compositional analysis (Aitchison 1986, Aebischer and Robertson 1992, Aebischer et al. 1993) to rank cougar selection of habitats, with separate analyses for intervals of movement and stasis. Compositional analysis correctly uses the individual animal and not the radio-location as the sampling unit, thereby avoiding statistical problems arising from non-independence of proportions within a habitat composition (Aebischer et al. 1993). When cougar use of habitats was significantly nonrandom ($-N \ln \Lambda$ = test statistic, $\alpha < 0.05$), we used paired *t*-tests to compare mean utilization between all pairs of vegetation types ($\alpha < 0.05$). For each compositional analysis, we included only those habitat classes (e.g., vegetation types) available to all cougars, and included only those individual cougars using the same habitat classes. Because Aebischer et al. (1993) recommend a sample size ≥10 for compositional analyses, we pooled males and females together and did not test for sex effects on habitat selection.

For each movement session and individual cougar, we estimated the speed in each vegetation type,

$$S_v = \sum_{i=1}^{n} (s_i \times a_v) / \sum_{i=1}^{n} a_v,$$

where n = number of movement segments during the session, s_i = the average speed (km/h) during each 15-min interval based on the straight-line distance between locations, and a_v = area of vegetation type v within each 100-m buffered segment, i. We used the unweighted average S_v across sessions for each cougar as an estimate of that animal's speed in a particular vegetation type. To determine whether the rankings of speeds in vegetation types were correlated with the ranking of selection for each vegetation type, we used Spearman's rank order correlation coefficient (r_s = test statistic, $\alpha < 0.05$). We also used a paired t-test to test for differences between male and female mean movement rates through each vegetation type (t = test statistic, $\alpha < 0.05$).

We calculated the angular deviation from a straight line for all consecutive movement segments for all cougars. To test whether the circular distribution of deviation angles during movements ≥100 m was nonuniform, we performed a Rao's (1976) spacing test of uniformity (U = test statistic, $\alpha < 0.05$). To determine whether mean movement distance was correlated with turning angle, we calculated an angular-linear correlation coefficient (Fisher 1993, Zar 1999; nr^2_{al} = test statistic, $\alpha < 0.05$).

We had an insufficient number of observations to investigate seasonal differences in patterns of selection during movements. Similarly, we had too few observations of daytime movement to compare nocturnal and daytime movements: we monitored all 17 individuals overnight, but only 5 cougars during diel sessions that included daylight hours.

Vegetation Types

Digital coverages of available vegetation types were acquired from Orange, Riverside, and San Diego counties. Vegetation polygons were identified by county personnel during 1990, 1992, 1993, and 1995 using LANDSAT Thematic Mapper and SPOT 2 satellite imagery, aerial photo interpretation, and field vegetation mapping surveys (ground-based and aerial). Although these data are nearly contemporaneous with our cougar locations, we checked all polygons classed as urban, disturbed, or agriculture in the vicinity of a session against field maps and notes, and made appropriate adjustments. We digitized and georeferenced all polygons using terrain-corrected satellite data and then digitally coded and projected these data as UTM coordinates (zone 11, North American Datum of 1927). These methods achieved a mean spatial accuracy of approximately 25 m and a minimum mapping unit between 0.2 and 2.0 ha. When possible, we more precisely delineated narrow riparian areas using the near infrared band of a SPOT image to detect greater leaf moisture content or by using hydrographic data layers. All vegetation types were categorized and classified by the 3 counties based on modifications to the Holland classification system (R. F. Holland. Preliminary Descriptions of the Terrestrial Natural Communities of California. California Department of Fish and Game, Nongame Heritage Program, Sacramento, California, USA, unpublished report). By consolidating infrequent vegetation types with similar types, our analyses used 9 general vegetation types: scrub, chaparral, grassland, riparian, forest, woodland, agriculture, urbanized (residential, industrial, or commercial developments), and disturbed (see Dickson 2001). We classified lakes, rivers, wetlands, vernal pools, beaches, and man-made watercourses (0.70% of the study area) within the riparian vegetation type. Cliff and rock habitats (0.04%) were most often adjacent to chaparral vegetation types, and so we reclassified these as such. Because coastal dunes (0.01%) were usually associated with scrub vegetation, we grouped these types together.

Topography

We merged 26 USGS 1:24,000 digital elevation models (DEMs) to describe elevation and slope of the study area. We derived the slope (in degrees) of a cell location from the DEM using the ArcView® Spatial Analyst extension (Environmental Systems Research Institute, Redlands, California, USA). On the scale of individual movements, we considered maximum slope to be the most appropriate measure of topographic roughness encountered by an individual cougar. To calculate the maximum slope encountered (used) by an individual during a movement segment, we generated 100 alternative segments (of length equal to the original and terminating at a randomly located point within 50 m of the start and end point of the original) within a movement segment buffer and intersected these alternative segments with the DEM to derive an average value of maximum slope. We assumed that the maximum slope available to an individual was the average maximum slope value for the 35 alternative segments intersected with the DEM. We used a paired t-test to assess topographic selection for slope during all movement sessions for all individuals ($\alpha < 0.05$). For each individual monitored for >1 session, we calculated the mean maximum slope encountered during each session and then averaged across sessions so that each animal contributed only 1 value to the statistical analysis.

Roads

We obtained 1995 U.S. Bureau of the Census Topologically Integrated Geographic Encoding and Referencing (TIGER) digital data coverages for all roads on the 3 counties. We modified these maps based on paper maps on which field crews had indicated accurate road location and condition (paved, dirt, absent) of mapped roads. To assess whether roads affected cougar movements, we calculated total paved and dirt road densities (m/km^2) for all buffered movement (used) and alternative (available) paths. For each session, we calculated road densities at each used and available segment. To determine available densities, we averaged across the 35 alternative segments. We used a paired *t*-test to determine whether mean road densities for each session differed ($\alpha <$ 0.05) between movements and alternative paths.

We analyzed road crossings by comparing the minimum number of crossings of 2-lane paved roads during a diel session to the number of crossings that would have occurred if the focal animal were indifferent to paved roads. We excluded freeway crossings from our analyses because 5 years of study documented only a single non-fatal freeway crossing (except via underpasses). To avoid having simulated paths cross paved driveways and residential roads, we restricted all simulations to a study area that was clipped to exclude residential areas within or abutting potential cougar habitat.

We inferred a single crossing for any movement segment that crossed a paved road. To estimate the expected number of crossings, we constructed a simple individual-based movement model, and we generated 50 simulated paths for each session, each with the same number of movement segments as the actual travel path. Each simulation started using the initial bearing of the actual movement path, giving each simulation a tendency to move in the direction that the focal animal moved. Each subsequent movement segment in the simulations used a circular deviation angle and displacement selected at random, with replacement, from the observed distributions (Fig. 2). If a simulated travel path encountered a study area boundary or residential area, we forced the contacting segment to reflect back into the study area at a random deviation angle. We used a paired *t*-test to determine whether the mean number of actual road crossings was less ($\alpha < 0.05$) than expected. For individuals monitored for >1 session, we calculated a mean for each session and then averaged across sessions so that each animal contributed only 1 value to the statistical analysis.

To examine whether cougars might exploit road crossing structures, such as underpasses or culverts, to trap prey, we examined the locations of all 5,562 daybed locations, 855 nocturnal static locations, and 145 cougar-killed prey carcasses in this study area during 1986–1992 (Beier and Barrett 1993, Beier 1995, Beier et al. 1995, Dickson and Beier 2002). We tallied the number of locations by type (daybed, static, carcass) that occurred within 300 m of a crossing structure under major roads (>2 lanes in each direction).

RESULTS

We analyzed 44 tracking sessions (29 nocturnal, 15 diel), including 22 sessions on 10 female cougars and 22 sessions on 7 male cougars (Table 1). Although most cougars were monitored for 3 or more sessions, 5 individuals were monitored for only 1 nocturnal or diel session. The behavior of these 5 animals was thus measured with relatively low precision. Imprecision in measurements decreases the power of statistical tests but does not increase risk of type I error (because these errors are subsumed in the residual sum of squares). Such risk is even lower for compositional analysis, which forced us to drop some of these animals from analyses when, for example, the individual did not use all vegetation types.

Movement Statistics

Total number of movement segments ≥50 m and static locations was 1,647 and 356, respectively. Following Beier et al. (1995) we assume that cougars were hunting during these sessions and that many static locations represented sites where cougars slowly stalked and attempted to ambush prey. Other static locations probably represented rest sites.

The mean number of movement segments per session was 36.4 (SD = 6.3) for females and 37.7 (SD = 7.7) for males. On average, tracking sessions lasted 19.9 hrs (SD = 5.1) for females and 17.3 hrs (SD = 1.9) for males. Total duration of movements during a session averaged 9.1 hrs (SD = 1.6) for females and 9.4 hrs (SD = 1.9) for males. During a session, female cougars traveled an average of 10.7 km (SD = 4.5) and males traveled 10.0

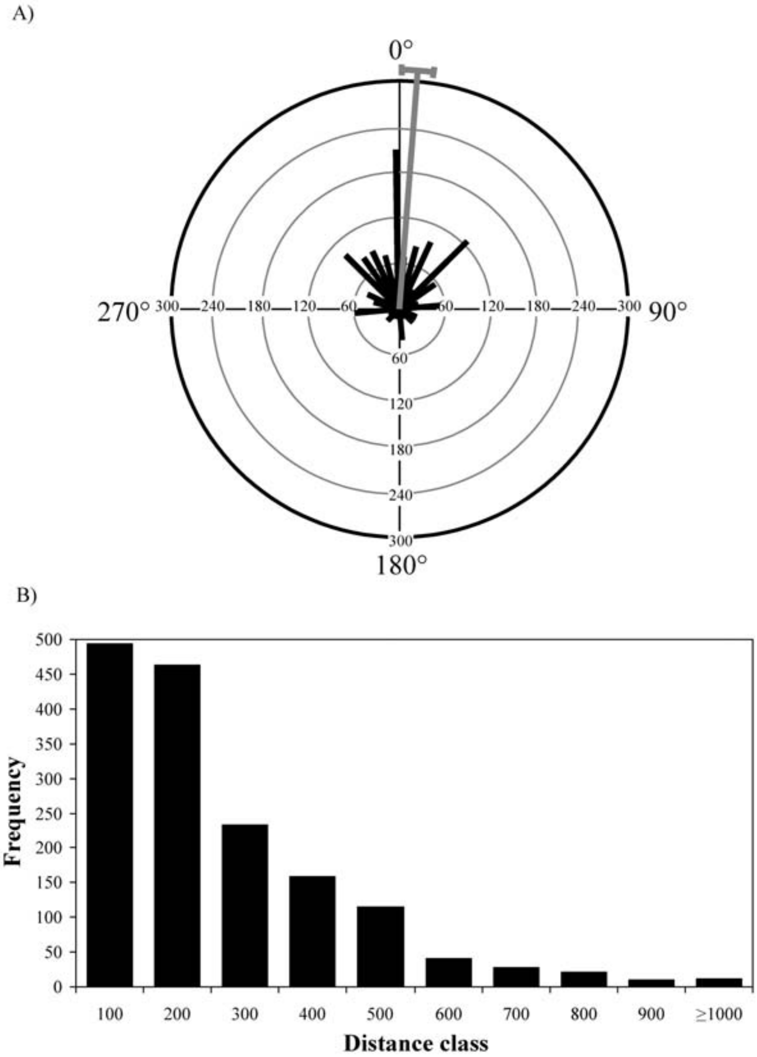

Fig. 2. (A) Frequency distribution of circular deviation angles for movements ≥100 m (*n* = 1,536) for 10 female and 7 male cougars during 44 radiotracking sessions in southern California, USA, 1988–1992. An angle of 0° indicates an animal did not deviate from a straight line. Mean deviation angle and +/– 95% confidence intervals are shown. (B) Frequency distribution of distance moved per 15 min; abscissa is lower bound of each 100-m distance class (*n* = 1,572).

km (SD = 3.0). Average time in static positions during a session was 10.8 hrs (SD = 5.1) for females and 7.9 hrs (SD = 3.5) for males, excluding the static intervals (of unknown duration) that occurred at the start and end of each session.

Movement segments between 50 and 100 m probably approached the resolution of triangulation. Because these short segments comprised only 0.4% of all movement segments, including these segments introduces little if any error to our analyses.

For 1,536 movement segments ≥100 m, cougars tended to move in a straight-line; the mean circular angle of deviation was 4.4° +/– 3.8 (95%CI; Fig. 2A), and the circular distribution of deviation angles was not uniform ($U = 351.8$, $P < 0.001$). During consecutive 15-min movement intervals, cougars often turned to the right or left; the average deviation angle during a session was 52.8° (SD = 47.8, n = 1,536). Distance traveled per 15 min (Fig. 2B) averaged 288 m (SD = 192, range = 100 – 2,059 m, n = 1,572), with 61% of movements <300 m. The distance moved was not correlated with turning angle ($nr^2_{al} = 4.13$, $r = 0.34$, $P > 0.10$, $n = 36$ angle classes of 10° each).

Influence of Vegetation Type

The habitat composition of travel paths used by cougars differed from the habitat composition of alternative segments ($-N\ln\Lambda = 15.00$, $P < 0.025$, df = 5, n = 9 females and 7 males; Fig. 3). Because forested, agricultural, and disturbed vegetation types were not available to some individuals, these types were dropped from all compositional analyses. Although riparian types ranked highest in the compositional analysis of habitat use during movements, use was statistically significant only in contrast with urbanized types. Chaparral and scrub types also were ranked above urbanized types. However, other contrasts were more ambiguous and difficult to interpret.

During intervals of stasis, cougar use of vegetation types was not statistically different from the habitat composition through which they traveled during movement intervals ($-N\ln\Lambda = 4.76$, $P > 0.25$, df = 4, $n = 8$ females and 7 males with ≥7 static locations). Urbanized vegetation types were available to only a few individuals and were excluded from this analysis. Although neither the omnibus test nor pairwise contrasts were significant ($P > 0.05$), chaparral (10%) and riparian vegetation types (27%) ranked higher than scrub, grassland, and woodland types during periods of stasis, and they were used as stopping points more often than they were encountered on travel paths.

Cougars moved slowest through riparian vegetation (grand mean = 1.07 km/hr), which was the type ranked highest in the compositional analysis of movements and fastest through urbanized types (1.49 km/hr), the lowest ranking type (Table 1; Fig. 4A). In all vegetation types, females moved faster than males ($t = 5.52$, $P < 0.001$, $n = 9$). There was a significant negative correlation between ranks for travel speed and selection for a vegetation type ($r_s = -0.89$, $P < 0.05$, $n = 6$; Fig. 4B).

Influence of Topography

During monitored intervals of movement, all cougars used maximum slopes that were more gentle than those available ($t = 7.38$, $P < 0.001$, $n = 17$). For indi-

Table 1. Mean travel speeds in 9 vegetation types for 10 female and 7 male cougars in the Santa Ana Mountain Range, California, USA, 1988–1992. "—" indicates vegetation type was not encountered on travel path.

Animal ID	Total no. of sessions monitored	Total no. of movement segments	Travel speed (km/hr) Scrub	Chaparral	Grassland	Riparian	Woodland	Forest	Agriculture	Urbanized	Disturbed	Mean travel speed (+/– 1SD)
F1	4	164	1.17	1.33	1.30	1.22	1.29	2.42	1.30	1.43	1.85	1.48 (0.41)
F2	4	142	1.22	1.06	1.42	1.11	1.30	—	1.19	1.23	1.29	1.23 (0.12)
F3	4	146	1.05	1.04	0.98	0.92	1.04	1.10	—	3.50	1.60	1.40 (0.87)
F4	2	68	0.84	0.87	0.79	0.77	0.48	0.90	—	0.60	0.74	0.75 (0.14)
F8	1	34	1.23	0.98	1.86	0.72	2.58	2.01	—	—	—	1.56 (0.70)
F10	1	28	0.78	0.99	—	0.98	1.03	—	0.63	1.16	—	0.93 (0.19)
F11	1	27	1.55	0.71	1.33	1.38	0.83	—	—	—	—	1.16 (0.37)
F17	2	87	1.05	0.98	1.02	1.10	1.09	1.16	1.74	1.05	1.09	1.14 (0.23)
F18	1	47	1.47	1.67	2.04	1.19	2.12	—	1.67	1.79	—	1.71 (0.32)
F19	2	74	1.54	1.64	1.28	1.50	1.48	1.03	—	1.40	—	1.41 (0.20)
Female mean (+/- 1SD)	2	82	1.19 (0.27)	1.13 (0.32)	1.34 (0.40)	1.09 (0.25)	1.32 (0.62)	1.44 (0.63)	1.31 (0.45)	1.52 (0.87)	1.32 (0.43)	1.29 (0.14)
M2	5	154	1.29	1.45	1.25	1.14	1.20	2.54	2.13	1.83	1.44	1.59 (0.48)
M5	1	26	0.81	0.73	1.12	1.13	0.83	—	—	—	0.97	0.93 (0.17)
M6	3	126	0.87	0.96	1.09	1.02	0.79	—	0.80	1.34	0.75	0.95 (0.20)
M9	2	97	1.33	1.22	1.25	1.17	1.54	1.02	—	1.56	2.22	1.41 (0.37)
M10	4	140	0.77	0.90	0.79	0.64	0.44	0.44	0.50	0.58	0.40	0.61 (0.18)
M12	3	116	1.05	1.01	1.42	1.21	1.09	0.85	0.56	0.85	0.99	1.00 (0.24)
M13	4	171	0.96	0.94	0.99	1.01	1.18	1.17	—	2.47	1.28	1.25 (0.51)
Male mean (+/- 1SD)	3	119	1.01 (0.22)	1.03 (0.24)	1.13 (0.20)	1.04 (0.19)	1.01 (0.36)	1.20 (0.79)	1.00 (0.77)	1.44 (0.68)	1.15 (0.58)	1.11 (0.14)
Grand mean (+/- 1SD)	3	97	1.11 (0.26)	1.09 (0.28)	1.25 (0.45)	1.07 (0.22)	1.19 (0.53)	1.33 (0.68)	1.17 (0.59)	1.49 (0.77)	1.22 (0.51)	1.21 (0.31)

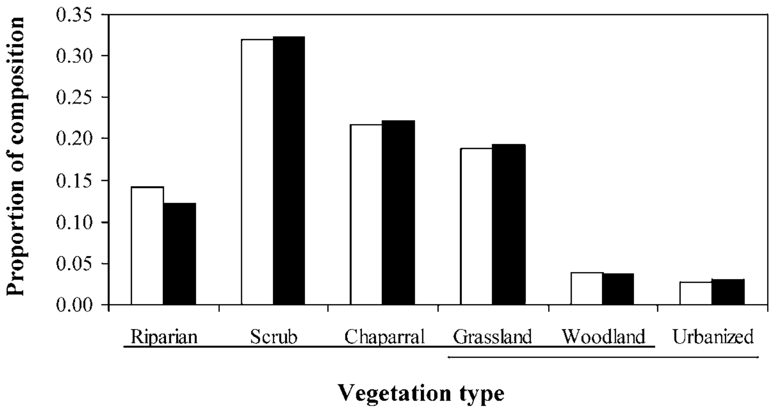

Fig. 3. Cougars (n = 9 females, 7 males) in the Santa Ana Mountain Range, California, USA, 1988–1992, tended to avoid human-dominated vegetation types and areas lacking understory woody plants during 15-min intervals when the animal moved ≥50 m. White bars indicate mean proportional utilization and black bars indicate mean proportional availability. Vegetation types are arranged from highest to lowest rank; underlining under names of vegetation types on the x-axis indicates vegetation types for which rankings are not significantly ($P > 0.05$) different.

vidual cougars, the mean available maximum slopes exceeded the used slopes by 0.71° to 3.54° (mean difference = 1.49°, SD = 0.81).

Influence of Roads

Total paved road density was about 21% lower on cougar travel paths (4.20 m/km^2, $\bar{x} = 0.10$ +/– 0.20 m/km^2 [SD]) compared to available paths (5.30 m/km^2, $\bar{x} = 0.12$ +/– 0.22 m/km^2; $t = -2.16$, $P = 0.04$, $n = 44$). Density of dirt roads was slightly higher on paths used by cougars (62.50 m/km^2, $\bar{x} = 1.42$ +/– 1.04 m/km^2) compared to available paths (59.17 m/km^2, $\bar{x} = 1.34$ +/– 0.78 m/km^2; $t = 1.48$, $P = 0.15$, $n = 44$). Buffered movement segments intersected dirt roads in all but 2 sessions, during which no dirt roads were available. All tracked individuals encountered or used dirt roads (368 occasions during 41 sessions).

Focal animals crossed 2-lane paved roads a total of 19 times; crossings involved 9 individual cougars and occurred during 11 of the 44 sessions, with a mean of 0.45 crossings per cougar per session (SD = 0.67, n = 17 individuals). In contrast, simulated paths had a mean of 1.29 crossings per cougar per session (SD = 1.37), a difference that was statistically significant ($t = -2.50$, $P = 0.012$). The simulated travel paths of all individuals crossed paved roads. Only 3 individuals (F2, F10, M10) crossed paved roads more often (1 crossing each) than expected (0.37, 0.12, 0.87, respectively), based on simulated paths.

Three of 5,562 daybed locations, 0 of 855 nocturnal static locations, 0 of 85 deer killed by cougars, and 2 of 60 small mammal kills (opossum, raccoon in these cases) were within 300 m of a crossing structure under a major highway. All 5 of these locations reflected the activities of a single female (F2) during the last days before her death, when she was apparently keying in on garbage-eating animals near a housing development, not on animals using the crossing structure. These numbers are lower than the 42 documented crossings via such structures (Beier and Barrett 1993, Beier 1995). Because we required cougar tracks or unambiguous radio signals to confirm a crossing, these 42 crossings underestimate the true frequency of these events.

DISCUSSION

Based on our observations, traveling cougars tended to continue moving in a consistent direction but often turned ~54° right or left, with few retrograde movements; movements averaged 288 m per 15-min interval and were not correlated with turning angle (Fig. 2). Our analysis of frequency of road crossings illustrates how these data can generate a null (random walk) model for hypothesis testing. These distributional data also can form the basis of more-sophisticated individually based movement models. Our results suggest that these advanced cougar movement models should reflect an aversion to paved roads and human-modified vegetation types, little differentiation among natural vegetation types, no aversion to dirt roads, and selection for gentle grades.

Our results support the assertion (Doak et al. 1992, Andren 1994, Dickson and Beier 2002) that habitat pattern has multi-scale impacts on the movement and distribution of animals. On the SAMR, Dickson and Beier (2002) identified strong patterns of selection by adult cougars for riparian areas at 2 spatial scales (based mostly on 1 static, diurnal location per animal per day). During the movement periods we analyzed here, riparian vegetation again ranked first, but several other natural vegetation types were statistically as

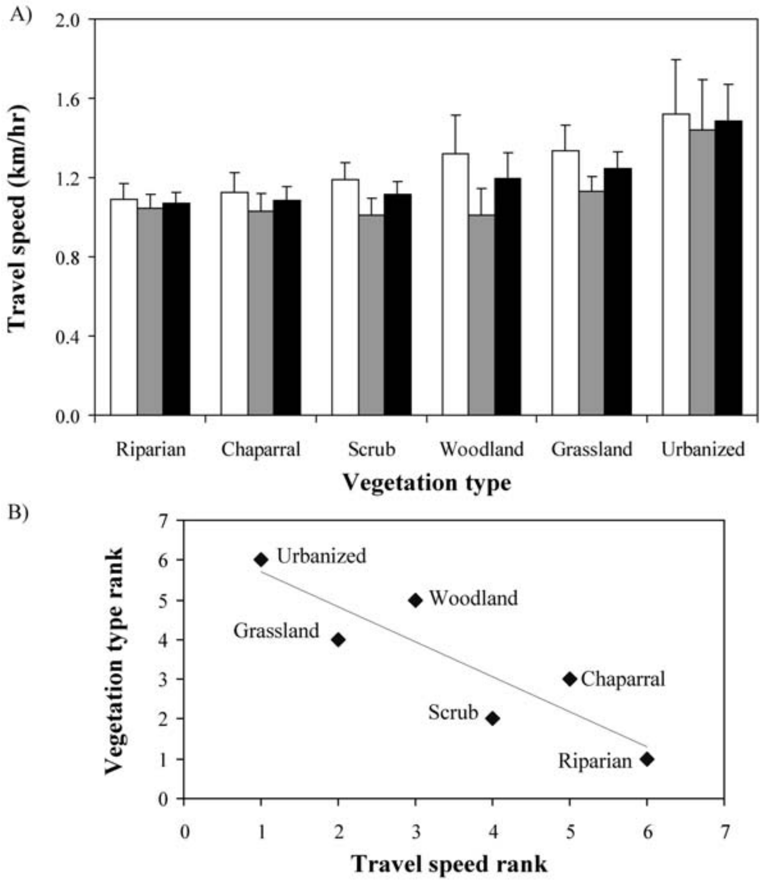

Fig. 4. Cougars in the Santa Ana Mountain Range tended to move more slowly through highly ranked vegetation types and more quickly through human-dominated types. (A) White bars indicate mean travel speed for females, gray bars indicate mean speed for males, and black bars indicate mean speed for the sexes combined. Error bars indicate +1 SE. Vegetation types are arranged from slowest to fastest based on the mean travel speed for the sexes combined. (B) The correlation between ranks for travel speed and vegetation type was statistically significant ($P < 0.05$).

preferred as riparian vegetation. Additionally, grasslands ranked below riparian, scrub, and chaparral vegetation types for cougar movements, but not with the statistical significance Dickson and Beier (2002) observed for diurnal locations. Thus, traveling cougars monitored over nocturnal or diel periods used a broader range of habitats than used for diurnal locations alone (typically daybed sites; Beier et al. 1995). Our findings support the argument of Comiskey et al. (2002) that analysis of diurnal locations provides limited information about cougar patterns of selection during the times they are most active. We conclude that habitat use of cougars (and other nocturnal carnivores) estimated solely by analysis of diurnal locations may not accurately reflect habitat preferences of hunting and traveling animals. Movement studies of nocturnal carnivores should include data collected during those periods when the animal is most active.

Although previous research using diurnal locations suggested that cougars avoided grasslands due to lack of cover (Logan and Irwin 1985, Laing 1988, Williams et al. 1995, Dickson and Beier 2002), grasslands may play a more important role during cougar movement. Grassland vegetation constituted 19% of the composition of used movement segments. Perhaps grasslands provide cougars with the means to more readily permeate areas already known to them or to stalk and pursue prey. Grassland vegetation types were also a common (19%) characteristic of habitat mosaics used during intervals of stasis, which in some cases probably represented stalking or attempts to ambush prey (Beier et al. 1995).

If animals tend to move more rapidly through environments that make them uncomfortable or that offer few resources, our results on travel speed through various vegetation types is consistent with the rankings based on compositional analysis. An analysis of habitat selection based on travel speed, unlike other analyses of habitat use, does not require an estimate of habitat availability. Estimating habitat availability invariably requires making arbitrary assumptions. For instance, we made the reasonable assumption that habitat availability could be estimated by the average habitat composition in 35 buffered vectors with length equal to the average distance moved during a session. It would have been equally reasonable to estimate availability by buffered vectors with length equal to the actual distance moved in a particular interval, or the average for all study animals. Our diligent search of the literature suggests that our study is the first attempt to make inferences about habitat use from travel speed for any terrestrial vertebrate, and we believe travel speed may offer an efficient tool for study of habitat selection patterns.

We found travel speed to be a useful complement to compositional analysis and other traditional methods of analyzing habitat selection. However, our single illustration of the method does not constitute a full exploration of its strengths and weaknesses. One important limitation of the travel speed method is that it cannot assess habitats the animal does not use at all. Similarly, travel speed cannot be used to assess animal response to fine-scale features such as paved roads.

Cougars consistently used travel paths that were less rugged than their general surroundings. This suggests that individuals consider the energetic cost of alternative paths and that they probably have a mental map of their surroundings. This is consistent with Beier's (1995) description of canyon bottoms and ridgelines as common travel routes for dispersing cougars. Hunting or traveling individuals minimize energetic expense by frequenting landscape features that cost the least.

The effectiveness of habitats to support cougars is reduced by human disturbance, particularly roads (Murphy et al. 1999). Our results indicate that 2-lane paved roads constrain cougar movement significantly but do not prevent movement. Indeed, vehicle collisions are the leading cause of mortality in this population, comprising 32% of all deaths of radiotagged cougars and their offspring (Beier and Barrett 1993). The problem is exacerbated by the placement of paved roads in preferred riparian habitats on the SAMR (Dickson and Beier 2002). Underpasses and other structures can facilitate cougar movements across paved roads (Beier 1993, Beier 1995, Foster and Humphrey 1995, Gloyne and Clevenger 2001), and we encourage efforts to construct or enhance crossing structures in preferred habitats.

Our data suggest that such structures are not exploited by predators in a way that creates a prey trap, supporting the conclusion of a recent review (Little et al. 2002). However, most crossings on our study area occurred where major roads crossed narrow, degraded habitat corridors, where cougars and their prey may not wish to linger. Cougars may behave differently where such crossing structures occur along roads passing through large blocks of intact habitat.

All individuals tracked during this study encountered or used dirt roads, and dirt road density was 8% higher on cougar travel paths than on available travel segments, suggesting that dirt roads do not inhibit, and may even promote, cougar movement. Back-tracking with hounds after our monitoring sessions confirmed that individuals frequently used dirt roads or trails to travel up to 2 km, especially in areas of dense scrub or chaparral (Beier 1995). In northern Florida, translocated cougars tended to cross light duty roads and trails in favor of all other road types (Belden and Hagedorn 1993). On study areas in northern Arizona and southern Utah, Van Dyke et al. (1986) reported that most cougars crossed most of the unimproved dirt roads within their home ranges. In addition to providing a path through dense scrub, dirt roads and trails may facilitate predator access to prey (James and Stuart-Smith 2000, Kinley and Apps 2001, Kerley et al. 2002). We believe that retaining or creating a dirt road or trail along the midline of a planned movement corridor would facilitate its use by cougars and minimize straying into adjacent human-dominated landscapes.

MANAGEMENT IMPLICATIONS

Our results suggest that riparian vegetation, and other vegetation types that provide horizontal cover, are desirable features in movement corridors, that dirt roads should not impede cougar use of corridors, that corridors should lie along routes with relatively gentle topography, and that cougars do not use road crossing structures to create prey traps. Managers and land-use planners are using these findings to design corridors to facilitate cougar movement in the South Coast ecoregion of California (Beier et al. 2005).

Because cougars will become extinct in even the largest core areas of this ecoregion if connectivity is severed (Beier 1996), cougars are an appropriate focal species for corridor design. However, because a corridor that serves cougars will not serve all species, we urge planners to consider a broad suite of focal species in designing landscape linkages (Beier et al. 2005).

Our frequency distributions of movement lengths and turning angles, in conjunction with the habitat preferences documented herein, are also being used to construct sophisticated individual-based movement models (in collaboration with J. Tracey and K. Crooks, Colorado State University). We hope these approaches can help quantify the influence of landscape features on other, large carnivores used as umbrella species for conservation planning.

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LITERATURE CITED

AEBISCHER, N. J., AND P. A. ROBERTSON. 1992. Practical aspects of compositional analysis as applied to pheasant habitat utilization. Pages 285–293 *in* I. G. Priede and S. M. Swift, editors. Wildlife telemetry: remote monitoring and tracking of animals. Ellis Horwood, Chichester, United Kingdom.

———, ———, AND R. E. KENWARD. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325.

AITCHISON, J. 1986. The statistical analysis of compositional data. Chapman & Hall, London, United Kingdom.

ANDERSON, A. E., D. C. BOWDEN, AND D. M. KATTNER. 1992. The puma on the Uncompahgre Plateau, Colorado. Colorado Division of Wildlife Technical Publication 40.

ANDREN, H. 1994. Effects of habitat fragmentation on birds and small mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355–366.

BARBOUR, M. G., AND J. MAJOR. 1995. Terrestrial vegetation of California. Fourth edition. Special Publication 9. California Native Plant Society, University of California, Davis, USA.

BEIER, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. Conservation Biology 7:94–108.

———. 1995. Dispersal of juvenile cougars in fragmented habitat. Journal of Wildlife Management 59:228–237.

———. 1996. Metapopulation modeling, tenacious tracking, and cougar conservation. Pages 293–323 *in* D. R. McCullough, editor, Metapopulations and wildlife management. Island Press, Washington, D.C., USA.

———, AND R. H. BARRETT. 1993. The cougar in the Santa Ana Mountain Range, California. Final report. Orange County Cooperative Mountain Lion Study, Department of Forestry and Resource Management, University of California, Berkeley, USA.

———, D. CHOATE, AND R. H. BARRETT. 1995. Movement patterns of mountain lions during different behaviors. Journal of Mammalogy 76:1056–1070.

———, K. PENROD, C. LUKE, W. SPENCER, AND C. CABAÑERO. 2005. South Coast missing linkages: restoring connectivity to wildlands in the largest metropolitan area in the United States. *In* K. R. Crooks and M. A. Sanjayan, editors. Connectivity and conservation. Cambridge University Press, London, United Kingdom.

BELDEN, R. C., AND B. W. HAGEDORN. 1993. Feasibility of translocating panthers into northern Florida. Journal of Wildlife Management 57:388–397.

BERGMAN, C. M., J. A. SCHAEFER, AND S. N. LUTTICH. 2000. Caribou movement as a correlated random walk. Oecologia 123:364–374.

BUNN A. G., D. L. URBAN, AND T. H. KEITT. 2000. Landscape connectivity: a conservation application of graph theory. Journal of Environmental Management 59:265–278 Sp. Iss.

COMISKEY, E. J., O. L. BASS, L. J. GROSS, R. T. MCBRIDE, AND R. SALINAS. 2002. Panthers and forests in south Florida: an ecological perspective. Conservation Ecology 6:18. Available online at http://www.consecol.org/vol6/iss1/art18.

CROOKS, K. R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology 16:488–502.

DEANGELIS, D. L., AND L. J. GROSS. 1992. Individual-based models and approaches in ecology: populations, communities, and ecosystems. Chapman and Hall, New York, USA.

DICKSON, B. G. 2001. Home-range and habitat selection by adult cougars in the Santa Ana Mountain Range of southern California. Thesis, Northern Arizona University, Flagstaff, USA.

———, AND P. BEIER. 2002. Home-range and habitat selection by adult cougars in southern California. Journal of Wildlife Management 66:1235–1245.

DOAK, D. F., P. C. MARINO, AND P. M. KAREIVA. 1992. Spatial scale mediates the influence of habitat fragmentation on dispersal success: implications for conservation. Theoretical Population Biology 41:315–336.

FISHER, N. I. 1993. Statistical analysis of circular data. Cambridge University Press, New York, USA.

FOSTER, M. L., AND S. R. HUMPHREY. 1995. Use of highway underpasses by Florida panthers and other wildlife. Wildlife Society Bulletin 23:95–100.

GLOYNE, C. C., AND A. P. CLEVENGER. 2001. Cougar (*Puma concolor*) use of wildlife crossing structures on the Trans-Canada highway in Banff National Park, Alberta. Wildlife Biology 7:117–124.

HEMKER, T. P., F. G. LINDZEY, AND B. B. ACKERMAN. 1984. Population characteristics and movement patterns of cougars in southern Utah. Journal of Wildlife Management 48:1275–1284.

JAMES, A. R. C., AND A. K. STUART-SMITH. 2000. Distribution of caribou and wolves in relation to linear corridors. Journal of Wildlife Management 64:154–159.

KERLEY, L. L., J. M. GOODRICH, D. G. MIQUELLE, E. N. SMIRNOV, H. B. QUIGLEY, AND M. G. HORNOCKER. 2002. Effects of roads and human disturbance on Amur tigers. Conservation Biology 16:97–108.

KINLEY, T. A., AND C. D. APPS. 2001. Mortality patterns in a subpopulation of endangered mountain caribou. Wildlife Society Bulletin 29:158–164.

LAING, S. P. 1988. Cougar habitat selection and spatial use patterns in southern Utah. Thesis, University of Wyoming, Laramie, USA.

LITTLE, S. J., R. G. HARCOURT, AND A. P. CLEVENGER. 2002. Do wildlife passages act as prey-traps? Biological Conservation 107:135–145.

LOGAN, K. A., AND L. L. IRWIN. 1985. Mountain lion habitats in the Big Horn Mountains, Wyoming. Wildlife Society Bulletin 13:257–262.

MECH, L. D. 1983. Handbook of animal radio-tracking. University of Minnesota Press, Minneapolis, USA.

MINTA, S. C., P. M. KAREIVA, AND A. P. CURLEE. 1999. Carnivore research and conservation: learning from history and theory. Pages 323–404 *in* T. W. Clark, A. P. Curlee, S. C. Minta, and P. M. Kareiva, editors. Carnivores in ecosystems: the Yellowstone experience. Yale University Press, New Haven, Connecticut, USA.

MURPHY, K. M., P. I. ROSS, AND M. G. HORNOCKER. 1999. The ecology of anthropogenic influences on cougars. Pages 77–101 *in* T. W. Clark, A. P. Curlee, S. C. Minta, and P. M. Kareiva, editors. Carnivores in ecosystems: the Yellowstone experience. Yale University Press, New Haven, Connecticut, USA.

NORMAN, T., A. FINEGAN, AND B. LEAN. 1998. The role of fauna underpasses in New South Wales. Pages 195–208 *in* G. L. Evink, P. Garrett, D. Zeigler, and J. Berry, editors. Proceedings of the international conference on wildlife ecology and transportation. Florida Department of Transportation, Tallahassee, USA.

PACE, R. M., III. 2001. Estimating and visualizing movement paths from radio-tracking data. Pages 189–206 *in* J. J. Millspaugh and J. M. Marzluff, editors. Radio tracking and animal populations. Academic Press, San Diego, California, USA.

PADLEY, W. D. 1990. Home ranges and social interactions of mountain lions in the Santa Ana Mountains, California. Thesis, California State Polytechnic University, Pomona, USA.

PAQUET, P. C., J. R. STRITTHOLT, N. L. STAUS, P. J. WILSON, S. GREWAL, AND B. N. WHITE. 2001. Feasibility of timber wolf reintroduction in Adirondack Park. Pages 47–64 *in* D. S. Maehr, R. F. Noss, and J. L. Larkin, editors. Large mammal restoration: ecological and social challenges in the 21st century. Island Press, Washington, D.C., USA.

RAO, J. S. 1976. Some tests based on arc-lengths for the circle. Sankhya, The Indian Journal of Statistics, Serial B(4) 38:329–338.

RETTIE, J. W., AND P. D. MCLOUGHLIN. 1999. Overcoming radiotelemetry bias in habitat-selection studies. Canadian Journal of Zoology 77:1175–1184.

RUTH, T. K., K. A. LOGAN, L. L. SWEANOR, M. G. HORNOCKER, AND L. J. TEMPLE. 1998. Evaluating cougar translocation in New Mexico. Journal of Wildlife Management 62:1264–1275.

SCHADT, S., F. KNAUER, P. KACZENSKY, E. REVILLA, T. WIEGAND, AND L. TREPL. 2002. Rule-based assessment of suitable habitat and patch connectivity for the Eurasian lynx. Ecological Applications 12:1469–1483.

SENFT, R. L., M. B. COUGHENOUR, D. W. BAILEY, L. R. RITTENHOUSE, O. E. SALA, AND D. M. SWIFT. 1987. Large herbivore foraging and ecological hierarchies. BioScience 37:789–799.

SWEANOR, L. L., K. A. LOGAN, AND M. G. HORNOCKER. 2000. Cougar dispersal patterns, metapopulation dynamics, and conservation. Conservation Biology 14:798–808.

TURCHIN, P. 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. Ecology 72:1253–1266.

———. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates, Sunderland, Massachusetts, USA.

VAN DYKE, F. G., R. H. BROCKE, AND H. G. SHAW. 1986. Use of road track counts as indices of mountain lion presence. Journal of Wildlife Management 50:102–109.

WHITE, G. C., AND R. A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, USA.

WIENS, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

———, N. C. STENSETH, B. VAN HORNE, AND R. A. IMS. 1993. Ecological mechanisms and landscape ecology. Oikos 66:369–380.

WILLIAMS, J. S., J. J. MCCARTHY, AND H. D. PICTON. 1995. Cougar habitat use and food habits on the Montana Rocky Mountain Front. Intermountain Journal of Sciences 1:16–28.

WITH, K. A. 1994. Ontogenetic shifts in how grasshoppers interact with landscape structure: an analysis of movement patterns. Functional Ecology 8:477–485.

ZAR, J. H. 1999. Biostatistical analysis. Fourth edition. Prentice-Hall, Upper Saddle River, New Jersey, USA.

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Conservation Thresholds for Land Use Planners

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INTRODUCTION

While there are many threats to biological diversity in the United States, the loss and fragmentation of habitats and ecosystems have become the most significant (Wilcove et al. 1998). The survival of plant and animal species and whether our natural systems will continue to provide essential services—recycling of nutrients, flood and pest control, and maintenance of clean air, water, and soil—significantly depends upon where and how land is used, converted, and managed. Land use change resulting from development and associated human activities (e.g., agriculture, grazing, forest harvesting, and hunting) often alters the abundances and varieties of native species; introduces novel and potentially detrimental species to an area; and disrupts natural water and nutrient cycles, and natural disturbance patterns (e.g., fire) (U.S. Geological Survey 1998).

> *"Spatial planning is most significant in nature conservation when 10-40% of the natural vegetation has been removed from a landscape."*
>
> Forman and Collinge (1997), Landscape and Urban Planning 37, p. 129

Everyday, land use planners are faced with decisions regarding whether and how land is developed, parcelized, and used, and in what pattern. For the most part, such land use decisionmaking occurs without taking into account individual and cumulative impacts to biological resources. Implementing biologically sensitive spatial planning early in the development process will help preserve our natural heritage for the future, since the most crucial time for planning is when the first 10 to 40 percent of the natural vegetation is altered or removed from the landscape (Forman and Collinge 1997). A growing interest exists among land use planners and developers to use the tools at their disposal to better protect biological diversity. However, these professionals often lack the necessary information to incorporate ecological principles into their decisionmaking and to transform their traditional planning approaches into progressive, ecologically-based conservation tools.

To encourage and facilitate better integration of ecological knowledge into land use and land management decisionmaking, the scientific community needs to provide planners with applicable ecological information and guidance. To this end, the Ecological Society of America (ESA) convened a committee of leading scientists to identify principles of ecological science relevant to land use and to develop guidelines for land use decisionmaking.[1] The result was the development of eight general guidelines to assist land use planners in evaluating the ecological consequences of their decisions (*see* Box 1).

Conservation guidelines, such as those established by the ESA Land Use Committee, are designed to be flexible and to apply to diverse land use situations. As a result, they tend to be general in nature. For ecological principles to be put into practice, however, land use planners will need more specific information on potential threshold responses of species and ecosystems to development activities, particularly in relation to habitat fragmentation. To facilitate the adequate preservation of contiguous or connected natural areas, land use planners will need to know what science tells them about the minimum sizes of habitat patches species need to survive, or the amount of habitat necessary for the long-term persistence of native populations and communities in a region. In addition, they need information about the adequate size and placement of habitat corridors that would facilitate species movement and colonization among disjunct habitat patches, and about recommended widths of riparian buffers to protect water quality and provide wildlife habitat. Similarly, knowing the extent to which edges influence natural habitats would help land use professionals evaluate the effective area of any given habitat patch or corridor. Other fragmentation thresholds—such as the maximum distance between isolated patches tolerable in a landscape before ecological processes and patterns become disrupted—would arm decisionmakers with specific parameters that could be incorporated into land use design and modeling.

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[1] "The Ecological Society of America (ESA) is a non-partisan, nonprofit organization of scientists founded in 1915 to: promote ecological science by improving communication among ecologists; raise the public's level of awareness of the importance of ecological science; increase the resources available for the conduct of ecological science; and ensure the appropriate use of ecological science in environmental decision making by enhancing communication between the ecological community and policy-makers."
As cited in Ecological Society of America. "About ESA." <www.esa.org> (31 July 2002).

Given the inherent complexity of ecological systems, scientists are understandably reticent about providing exact prescriptions for land use planning and design because answers vary depending on the species, ecosystem, or scale in question. Nevertheless, by not promoting the use of even partial knowledge about species or ecosystem responses to human disturbance and fragmentation, the result is that land use decisions—even the most well-intentioned—are being made completely uninformed by science.

BOX 1. GUIDELINES FOR LAND USE PLANNING AND MANAGEMENT

In the face of rapid land use change, the Ecological Society of America's Land Use Committee recommends that land use planners and developers take into consideration the following eight guidelines to evaluate the potential impact of their decisions on our natural systems (*see* Dale et al. 2000 for full discussion):

1. Examine the impacts of local decisions in a regional context.

The persistence of species and the sustainability of ecosystems are determined not only by immediate surroundings but also by larger landscape factors, such as how habitats are interspersed across the landscape. Thus, local land alterations may have broad-scale regional impacts. Land use planners should both identify the surrounding region that is likely to affect and be affected by a local project and examine how adjoining jurisdictions are using and managing their lands. Regional environmental data (e.g., land cover classes, hydrologic patterns, and habitats for species of concern) should be incorporated into the decision-making process to facilitate a regional assessment of impacts.

2. Plan for long-term change and unexpected events.

Ecological processes, such as nutrient cycling, energy flow patterns, and disturbance regimes, may function over lengthy and variable time scales. In addition, ecosystems change over time. As a result, impacts posed by land use decisions are often long-term and unpredictable. Impacts may be delayed and not fully realized until years or decades later, or they may be cumulative such that a "unique trajectory of events" results that could not have been predicted from any single event. The complexity and variability of ecosystem responses dictate that land use decisions consider potential occurrences and implications of unanticipated and long-term events (e.g., variations in weather and disturbance patterns).

3. Preserve rare landscape elements and associated species.

Rare landscape elements, such as wetlands, riparian and mountain zones, and old-growth forests, often provide critical habitats for rare and endangered species. To protect a region's biological diversity, the natural diversity within a landscape must be preserved. Land use planners should identify the location of rare and unique landscape elements, by methods such as inventory and analysis of vegetation types, geology, hydrology, and physical features, and by their associated species. Once such landscape elements are identified, development should be guided away from such areas and toward more common landscape features.

4. Avoid land uses that deplete natural resources over a broad area.

Depletion of natural resources over time will lead to the irreversible disruption of ecosystems and associated processes. Consequently, land use planning and development should strive to prevent the diminishment of natural resources (e.g., soil, water, and habitat types such as wetlands) in any given area by identifying vital or at-risk resources and by taking the necessary precautions to avoid actions that threaten resource sustainability. Certain land uses or land activities may be deemed altogether incompatible in particular settings.

5. Retain large contiguous or connected areas that contain critical habitats.

Large habitat patches typically support a greater diversity and abundance of plants and animals and can maintain more ecosystem processes than small patches. Large intact habitats provide more resources, allowing larger populations of a species to persist, thus, increasing the chance of survival over time. Parcelization of large habitats often decreases the connectivity of systems, negatively affecting the movement of species necessary for fulfilling nutritional or reproductive requirements. To counter such effects, large intact areas and small areas that are well connected to other critical habitats should be protected.

6. Minimize the introduction and spread of non-native species.

Non-native species often negatively affect the survival of native species and disrupt the functioning of ecosystems. The spread of non-natives is facilitated by the development of transportation infrastructure and by the creation of edge environments and artificial landscapes. Land use professionals should strive to minimize the potential introduction and spread of non-native species into natural environments.

7. Avoid or compensate for effects of development on ecological processes.

Development may not only cause site-specific impacts, but may also disturb regional ecological processes. Ecological processes, such as fire, grazing, dispersal patterns, and hydrologic cycles, help to sustain plant and animal populations across a landscape. Thus, land uses that could negatively affect other systems or lands through the disruption of these processes should be avoided while those that benefit or enhance ecological attributes should be encouraged.

8. Implement land use and land management practices that are compatible with the natural potential of the area.

The natural potential of a site, as determined in part by local physical and biologic conditions, should be factored into how land is used and managed. Land uses that do not take advantage of a site's natural potential or consider its limitations, will likely result in unnecessary resource loss and high economic costs.

For more information on ecological principles to guide land use planning decisionmaking, see Dale et al. (2000), Duerksen et al. (1997), and Dramstad et al. (1996).

FROM GUIDELINES TO THRESHOLDS

The Environmental Law Institute (ELI) surveyed existing scientific literature to determine whether a body of knowledge has emerged within the scientific community relevant and applicable to national land use decision-making, specifically pertaining to biological conservation thresholds. A literature search of the major ecological, conservation, and land use journals was conducted using the Science Citation Index (ISI Web of Science) using search terms under the following categories: habitat fragmentation,[2] buffers,[3] corridors,[4] ecological thresholds,[5] and indicator species.[6] To increase applicability to current land use decisionmaking in the states, the search was confined to studies pertaining to the continental United States, as well as articles published between 1990-2001, and pre-1990 articles commonly cited within the scientific community. Only those articles containing quantitative information directly relevant to determining conservation thresholds for land use planning and land management were considered.[7] In addition to the literature search, review papers found in the gray literature (e.g., those produced by land management and regulatory agencies) were also included when possible and applicable.

ELI found adequate information on potential ecological threshold measures for the following areas: habitat patch area, percent of suitable habitat, edge effects, and buffers. Corridor design is reviewed in brief; however, specific guidance on corridor size was not feasible given inadequate available information within the scientific literature. This survey reflects scientific information largely related to habitat fragmentation and landscape ecology issues, with a focus on the spatial relationships (e.g., size, shape, location) and interactions of land attributes over large geographic areas.[8] This review does not cover other important conservation elements such as how to account for the biological integrity or ecological significance of habitat patches, which land use planners should consider when determining which parcels of land to protect. In addition, the thresholds presented in this review does not adequately address the conservation of species or habitat types that are naturally rare or localized (e.g., those with patchy distributions or limited ranges).

This report summarizes the Institute's findings and provides a platform for identifying gaps in existing knowledge to help guide more in-depth ecological research directly applicable to land use planning. This report in no way attempts to misrepresent the complexity of species and ecosystem response to land conversion, degradation, and fragmentation by providing simplified prescriptions. Land use planners should cautiously interpret the presented threshold values and ranges and tailor them to their unique circumstances and geographic settings.

First and foremost, land use planners need to establish their priorities for conservation—whether they be water quality or quantity, wildlife habitat, or biodiversity. In addition, conservation targets need to be established—whether they be regionally rare or endangered species or unique landscape elements (e.g., wetlands, old growth forests, riparian zones), or other targets—because this will directly influence the value and scale of any threshold.[9] Thresholds should be chosen or developed to meet the needs of the resources a locality is most concerned with managing and conserving. Planners should place great emphasis on evaluating site-specific and regional physical and biological conditions that influence the resiliency of particular systems to human disturbance.

The threshold values presented in this report should not detract from the larger goals of conserving or restoring indigenous species, rare and representative habitats, ecosystem functions, and natural connectivity. Where possible, the ESA land use guidelines should be followed. Land use planners should strive to protect large, intact parcels of land, high quality and ecologically important habitat, and where appropriate, should connect protected natural areas. When development is deemed necessary, land use planners should promote more compatible land uses and avoid or minimize fragmenting habitat patches wherever possible.

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[2] To locate papers with potential habitat fragmentation threshold information, the following search terms were used: minimum habitat size, habitat size, habitat requirement, habitat fragmentation, patch size, minimum fragment size, island biogeography, landscape connectivity, habitat connectivity, and metapopulation theory.

[3] To locate papers with potential threshold information on buffer width, the following search terms were used: riparian buffer, wetland buffer, buffer zone, buffer distance, forest buffer, buffer width, and buffer size.

[4] To locate papers with potential threshold information on corridor width, the following search terms were used: fragment connectivity, boundary permeability, landbridge, highway overpass, highway underpass, stream cross, habitat corridor, corridor, migration corridor, riparian corridor, and underpass.

[5] To locate papers with potential ecological threshold information, the following search terms were used: ecological threshold, conservation threshold, environmental threshold, and landscape threshold.

[6] To locate papers with potential threshold information relevant to indicator species, the following search terms were used: indicator species, indicator species and habitat fragmentation, and indicator species and thresholds.

[7] The majority of the papers encountered and selected focus on terrestrial species and to a lesser extent freshwater aquatic communities.

[8] As defined by Risser et al. (1984), "Landscape ecology considers the development and dynamics of spatial heterogeneity, spatial and temporal interactions and exchanges across heterogeneous landscapes, influences of spatial heterogeneity on biotic and abiotic processes, and management of spatial heterogeneity."

[9] Thresholds presented in this report reflect a taxonomic bias in the scientific literature toward birds and mammals. Thus, for many of the recommended threshold values, these two animal groups are assumed to be the conservation targets.

BOX 2. DEFINITION OF TERMS

Biological diversity (or biodiversity) – the variety of life and its processes, which includes the abundances of living organisms, their genetic diversity, and the communities and ecosystems in which they occur (The Keystone Center 1991). Diversity at all levels from genes to ecosystems need to be maintained to preserve species diversity and essential ecosystem services like climate regulation, nutrient cycling, water production, and flood/storm protection (Dale et al. 2000).

Biological (or ecological) integrity – refers to a system's wholeness, including presence of all appropriate elements and occurrence of all processes at appropriate rates, that is able to maintain itself through time (Angermeier and Karr 1994).

Boundary – a zone comprised of the edges of adjacent ecosystems or land types (Forman 1995).

Corridor – a linear strip of a habitat that differs from the adjacent land on both sides, connecting otherwise isolated larger remnant habitat patches (Forman 1995, Fischer et al. 2000).

Buffers – linear bands of permanent vegetation, preferably consisting of native and locally adapted species, located between aquatic resources and adjacent areas subject to human alteration (Castelle et al. 1994, Fischer and Fischenich 2000).

Ecosystem – a geographic area including all the living organisms (e.g., people, plants, animals, and microorganisms), their physical surroundings (e.g., soil, water, and air), and the natural cycles (nutrient and hydrologic cycles) that sustain them. Ecosystems can be small (e.g., single forest stand) or large (e.g., an entire watershed including hundreds of forest stands across many different ownerships) (USFWS 1994).

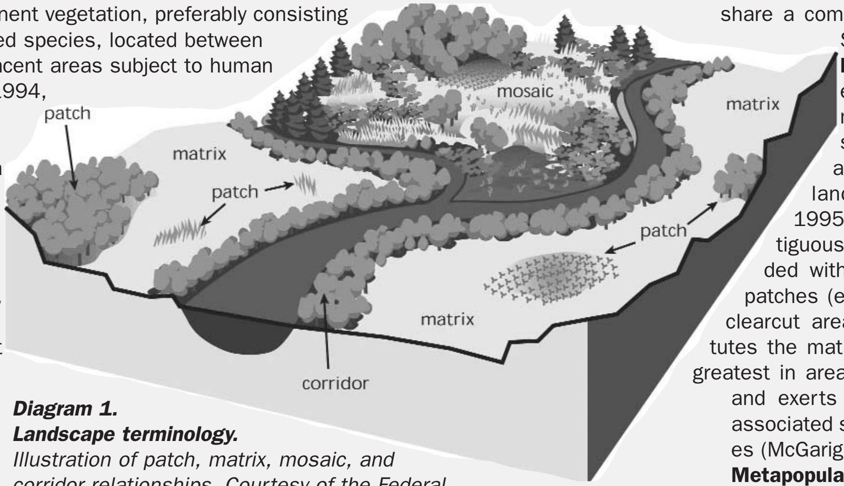

Diagram 1.
Landscape terminology.
Illustration of patch, matrix, mosaic, and corridor relationships. Courtesy of the Federal Interagency Stream Restoration Working Group (FISRWG), Stream Corridor Restoration: Principles, Processes, and Practices (10/98).

Ecosystem functions – the biophysical processes that take place within an ecosystem, apart from any human context (e.g. nutrient, energy, and hydrologic cycling; or soil formation).

Ecosystem services – refer to the ecosystem goods (e.g., food, and medicine) and services (e.g., climate regulation, water purification, and flood control) that humans derive benefit, directly or indirectly, from ecosystem functions (Costanza et al. 1997).

Ecosystem sustainability – the tendency of a system to be maintained or preserved over time without loss of decline to elements such as its structure, function, diversity, and production. Sustainability is widely regarded as economically and ecologically desirable and the only viable long-term pattern of human land use (Dale et al. 2000).

Edge – the portion of an ecosystem or habitat near its perimeter, where influences of the surroundings prevent development of interior/core-area environmental conditions (Forman 1995).

Edge effects – the negative influence (e.g., such as the profound modifications of biological and physical conditions) of habitat or ecosystem edges on interior conditions of habitat or on associated species (Meffe and Carroll 1997, Lindenmayer and Franklin 2002).

Habitat – consists of the physical features (e.g., topography, geology, stream flow) and biological characteristics (e.g., vegetation cover and other species) needed to provide food, shelter, and reproductive needs of animal or plant species (Duerksen et al. 1997).

Habitat fragmentation – the breaking up of previously continuous habitat (or ecosystem) into spatially separated and smaller parcels. Habitat fragmentation results from human land use associated with forestry, agriculture, and settlement, but can also be caused by natural disturbances like wildfire, wind, or flooding. Suburban and rural development commonly change patterns of habitat fragmentation of natural forests, grasslands, wetlands, and coastal areas as a result of adding fences, roads, houses, landscaping, and other development activities (Dale et al. 2000).

Landscape – a large heterogeneous land area (e.g., multiple square miles or several thousand hectares) consisting of a cluster of interacting ecosystems repeated in similar form (e.g., watershed) (Forman 1995, Duerksen et al. 1997).

Land use – the purpose to which land is used by humans (e.g., protected areas, forestry for timber production, plantations, row-crop agriculture, pastures, or human settlement) (Dale et al. 2000).

Local population – set of individuals of a species that live in the same habitat patch and interact with each other; most naturally applied to "populations" living in such small patches that all individuals practically share a common environment (Hanski and Simberloff 1997).

Matrix – the background ecosystem or land use type in a mosaic, characterized by extensive cover, high connectivity, and/or major control over the landscape functioning (Forman 1995). For example, in a large contiguous area of mature forest embedded with numerous small disturbance patches (e.g., timber harvest patches or clearcut areas), the mature forest constitutes the matrix element type because it is greatest in areal extent, is mostly connected, and exerts a dominant influence on the associated species and ecological processes (McGarigal 2003).

Metapopulation – a network of semi-isolated populations with some level of regular or intermittent migration and gene flow among them, in which individual populations may be extinct but then be recolonized from other subpopulations (Meffe and Carroll 1997).

Mosaic – a pattern of patches, linear corridors, and matrix in a landscape (Forman 1995).

Minimum viable population - The minimum viable population size is the smallest number of individuals required to maintain a population over the long-term (Forman 1995).

Non-native (or exotic) species – organisms (plants, animals, insects, and microorganisms) that occur in locations beyond their known historical, natural ranges or have been brought in from other continents, regions, ecosystems, or habitats (National Invasive Species Council 2001).

Patch – a relatively homogeneous type of habitat that is spatially separated from other similar habitat and differs from its surroundings (Forman 1995).

Remnant patch – habitat patches that escape disturbance (e.g., development) and are left remaining from an earlier more extensive span of habitat (e.g., woodlots in an agricultural area) (Dramstad et al. 1996).

Scale – the relative size or degree of spatial resolution of an area of interest. Small areas of interest (e.g., area around a house of single subdivision) are considered to be fine scale; in contrast to a larger area (e.g., a county or watershed), which is considered to be of coarse scale (Forman 1995, Duerksen et al. 1997).

Suitable habitat – habitat that meets the survival and reproductive needs of a species, allowing for a stable or growing population over time (Lamberson et al. 1994).

THRESHOLDS FOR LAND USE PLANNING: ADDRESSING HABITAT FRAGMENTATION

Varying shapes and configuation of habitat patches resulting from habitat fragmentation, Buchanan, Alabama. Courtesy of John R. Tolliver, USDA Forest Service, www.forestryimages.org.

Habitat fragmentation severely threatens biodiversity and ecosystem functioning wherever humans dominate the landscape. Land use planners play a significant role in determining whether and how landscapes and ecosystems are fragmented or maintain natural connectivity.

Habitat fragmentation is the process whereby contiguous natural areas are reduced in size and separated into discrete parcels. Fragmentation results from a reduction in the area of the original habitat due to land conversion for other uses, such as residential and commercial development. It also occurs when habitat is divided by roads, railroads, drainage ditches, dams, power lines, fences or other barriers that may prohibit the free movement and migration of plant and animal species (Primack 1993, Forman 1995). When habitat is destroyed, a patchwork of habitat fragments is left behind, often resulting in patches that are isolated from one another in a modified and inhospitable landscape matrix.[10] Fragmentation causes the microclimate to be altered due to changes in solar radiation, wind, and humidity; habitat patches become more isolated with a growing distance between remnant patches; and the resulting landscape is modified by changes in size and shape of the resulting patches (Saunders et al. 1991). These changes have varying impacts on species persistence and ecosystem sustainability.

Groups of organisms respond differently to habitat fragmentation. Some species, such as game species like white-tailed deer and bobwhite quail (referred to as edge species), may actually thrive under altered conditions (Bolger et al. 1997). However, many other species—often rare species and habitat specialists—are negatively affected. Species that depend upon the interior of forests, prairies, wetlands or other natural habitats will be absent from landscapes that lack sufficient natural areas containing true core habitat (Meffe and Carroll 1997). Although a fragmented landscape may enhance the abundance of certain generalist species, overall, fragmentation threatens the maintenance of biodiversity and the functioning of natural systems (Soulé 1991, Forman 1995).

To the detriment of many species, particularly those that are area-sensitive, habitat patches may lack the range of resources necessary to support permanent populations (Primack 1993, Forman 1995). Habitat fragmentation will reduce the foraging and nesting ability of animals and can lead to the rapid loss of species due to the creation of barriers to dispersal and colonization. In a fragmented landscape, normal dispersal will be disrupted when the land surrounding the remaining patches is inhospitable to species formerly thriving in the contiguous habitat (e.g., because it is degraded or is home to predators). For example, many bird species that dwell in the forest interior will not cross even short distances of open areas (Askins 1995). When species migration and dispersal is limited, new immigrants are less likely to supplement diminishing populations, thereby, increasing extinction vulnerability (Askins 1995).

The negative effects of habitat fragmentation are compounded by an altered physical environment (*see* "Edge Effects"). Land conversion and land transformation can cause major alterations in hydrologic regimes, mineral and nutrient cycles, radiation balance, wind and dispersal patterns, and soil stability (Harris 1984 as cited in Collinge 1996; Hobbs 1993 *as cited in* Forman 1995). Changes in such ecosystem properties and processes in turn affect native species composition, abundance, and long-term persistence, further degrading the biodiversity and the integrity of the affected natural areas.

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[10] Matrix is the background ecosystem or land use type in a mosaic, characterized by extensive cover, high connectivity, and/or major control over the landscape functioning (Forman 1995) (see Box 2).

UNDERSTANDING THE EFFECTS OF FRAGMENTATION

Over the past 25 years, the scientific community has devoted much energy to understanding the various components of fragmentation—the influence of fragment size, shape, configuration, heterogeneity, connectivity, among other factors—and how they effect the sustainability and persistence of species and natural processes in a landscape. Ideally, scientists would understand the influence and interaction of these characteristics on the continued survival of species and the integrity of ecosystems. Due to gaps in scientific knowledge, available information was only found within the literature to present potential threshold responses related to patch area, proportion of suitable habitat, edge effects, and buffers.

This paper provides land use decisionmakers with concrete information culled from the scientific literature in order to translate the land use guideline #5 offered by the Ecological Society of America (*see* Box 1) for on-the-ground practice. Recommendations on "how to retain large contiguous or connected areas that contain critical habitat" are presented, with specific information on how to best protect habitat patches and sufficient natural area, to minimize edge effects, and to design riparian buffers and habitat corridors.

HABITAT PATCHES

A common consequence of land development is the fragmentation of an originally connected natural landscape into a mosaic of disconnected habitat patches.[11] The size of the remaining habitat fragments significantly influences the type, abundance, and diversity of species that can persist in the affected region. In general, large patches better sustain wildlife populations and ecosystem functions over time than small patches. Holding other factors constant—such as patch shape, condition, and configuration—larger areas of habitat tend to support larger population sizes and a greater number of interior, specialist, and native species due to increased habitat diversity and more core area (Harris 1984, Dramstad et al. 1996, Forman 1995). The probability of a species population being extirpated generally increases with decreasing patch size.[12] This is due to the tendency of larger patches to retain a greater array of the natural resources and ecological functions provided by healthy ecosystems than smaller patches with more edge, increased susceptibility to invasion by exotics or predators, and more disturbed conditions (Soulé 1991, Metro 2001) (*see* "Edge Effects"). Area-sensitive forest bird species in the mid-Atlantic United States, for example, have been found to exhibit lower species diversity and higher extinction and turnover rates in landscapes with smaller mean forest patch size (Boulinier et al. 2001).

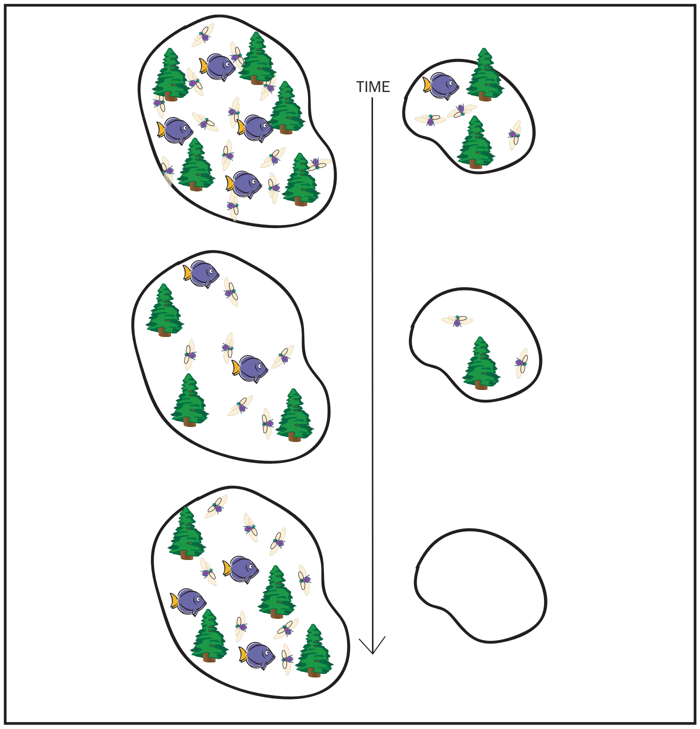

Diagram 2. Patch size and local extinction. *Probability of a local species population going extinct increases with decreasing habitat patch size. A larger patch generally supports a larger population size for a given species than a smaller patch, making it less likely that the species will go locally extinct in the larger patch. Modified from Dramsted et al (1996), Landscape Ecology Principles in Landscape Architecture and Land-Use Planning, p. 20.*

In general, to ensure the survival of individual species, population levels must remain large enough to protect against extinction from random natural events (e.g., floods, fires, droughts) and to maintain sufficient genetic variation to adapt to changing environmental conditions (e.g., changes in rates of predation, competition, disease, and food supply) (Gilpin and Soulé 1986, Meffe and Carroll 1997). A common tool used to determine the size of a population(s) needed to ensure long-term survival is a Population Viability Analysis (PVA). A PVA uses quantitative methods to predict the likely future status of a population or set of populations of conservation concern—often those that are at risk of extinction (Morris et al. 2002). This technique can take into account the many environmental, demographic, and genetic variables that determine extinction probabilities for individual species (Meffe and Carroll 1997).

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[11] A patch is a relatively homogeneous type of habitat that is spatially separated from other similar habitat and differs from its surroundings (Forman 1995).

[12] What is being discussed in this report is to the local extinction of a species population from a particular habitat or region (termed extirpation or population extinction), rather than the overall elimination of the species worldwide (termed global extinction).

Because plant and animal population size is the best predictor of extinction probability, habitat patches should be large enough to maintain viable populations of important species—including rare, endangered, and economically important species—and to maintain the ecological processes that support these communities. Based on Population Viability Analyses, general guidelines have been proposed for minimum viable population sizes:[13] 1) populations less than 50 individuals being too small and vulnerable to extinction due to their rapid loss of genetic variability and inability to withstand natural catastrophes; and 2) populations of 1,000 to 10,000 individuals being adequate to ensure long-term persistence (Meffe and Carroll 1997). Such numbers, however, should be viewed with scrutiny because much debate still exists about what size constitutes a minimum viable population for the many different species that make up natural systems (Saunders et al. 1991).

MANAGING FOR ADEQUATE HABITAT PATCH SIZE

For purposes of this review, minimum patch area is the smallest habitat patch that should be protected in order to sustain a species, a diversity of species or communities, or functioning of ecosystems. The literature suggests that, depending on the species or habitat in question, minimum critical patches range from as little as 0.0004 hectares (0.001 acres) (based on the needs of certain invertebrates) up to 220,000 hectares (550,000 acres) (based on the needs of certain mammals) to sustain target species or communities (*see* Appendix B). This wide range reveals that a generic "minimum" critical patch size or habitat requirement does not exist; thresholds are entirely dependent on the target species in question.

Ultimately, the amount of habitat necessary to maintain healthy wildlife populations varies according to many factors, such as taxonomic group, body size, foraging and resource requirements, and dispersal patterns of the species (Bender et al. 1998). Taxonomic groups, such invertebrates and plants, which have smaller dispersal ranges and tend to respond to their environment at smaller spatial scales, are reported to need less habitat area (e.g., less than 10 hectares or 25 acres) (McGarigal and Cushman 2002).

Larger patch areas are recommended to support bird, mammal, and fish species. Minimum habitat requirements for birds ranged from one hectare up to 2,500 hectares (6,250 acres), with the majority (75 percent) of the values found within the literature to be under 50 hectares (125 acres).[14] Minimum patch size required by mammals ranges from one hectare to 10 hectares for small mammals and up to 220,000 hectares for large-bodied or wide-ranging mammals (e.g., bears, cougars). Larger bodied vertebrates and wide-ranging predators tend to require larger territories to meet resource and reproductive needs (Soulé 1991). Minimum habitat area is greater for predators, such as bears, with recommended patch sizes greater than 900 and 2,800 hectares and cougars with 220,000 hectares (Mattson 1990, Mace et al. 1996, Beier 1993, respectively).[15] In contrast, estimates for habitat requirements for small mammals, such as rodents and rabbits, varied from one hectare to 10 hectares (Soulé et al. 1992, Barbour and Litvaitis 1993, Bolger et al. 1997). Only one study was found to provide evidence on possible watershed area needed to sustain fish species, finding that suitable patch sizes larger than 2,500 hectares might increase the chance of bull trout occurrence in Idaho (Rieman and McIntyre 1995).

Overall, the majority of the findings in this survey pertain to birds and mammals (*see* "A Closer Look at Habitat Patch Size" in Appendix A for specific information on numbers and trends). Few studies were found to recommend patch sizes to sustain plant, invertebrate, or fish populations. Keeping in mind this sample represents a narrow array of species and habitats, the protection of habitat patches of 55 hectares (137.5 acres) or more appears to capture 75 percent of species requirements reviewed in this select survey (*see* Figure 1). Such minimum land parcels, however, are not likely to capture particularly area-sensitive species, like wide-ranging predators or particularly sensitive interior bird species, found to need habitat patches greater than 2,500 hectares (or about 6,175 acres) (Trine 1998, Mattson 1990, and Beier 1993).

Given the great scientific uncertainty and gaps in the knowledge base on minimum habitat requirements of species and ecosystems, land use planners should adopt a conservative approach. The goal should be to maintain sufficiently large intact and well-connected habitat patches that would support the most area-sensitive species, species of greatest environmental concern (e.g., rare, threatened, or endangered species), or focal species, such as keystone species,[16] link species,[17] or umbrella species.[18] Declines in these groups of organisms may have wide ranging implications, negatively affecting the persistence of other associated species and ecosystems (Dale et al. 2000).

Land use planners should carefully consider the conservation needs of species with large-area or specialized life history requirements or that depend upon a combination of different habitats (e.g., large-ranging predators; interior species, or rare species); these species are likely to survive only in rel-

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[13] The minimum viable population size is the smallest number of individuals required to maintain a population over the long-term (Forman 1995); for example, the size of a population that would have a 95 percent probability of persisting for 100 years (Boyce 1992).

[14] Recommended conservation threshold values are based on the goal of capturing 75 percent of the requirements found for species, communities, and habitats surveyed in this literature review; thus, the third quartile was used by calculating the value for which 75 percent of the threshold values lie below this value (after numerical ranking).

[15] One hectare is equal to approximately 2.5 acres.

[16] Keystone species are species that have greater effects on ecological processes than would be predicted by their abundance or biomass alone (Dale et al. 2000).

[17] Link species are species that exert critical roles in the transfer of matter and energy across trophic levels of a food web or that provide critical links for energy transfer within complex food webs (Dale et al. 2000).

[18] Umbrella species are species that either have large area requirements or use multiple habitats and thus overlap the habitat requirements of other species (Dale et al. 2000).

atively large areas or in very specific habitat types (potentially very small, localized areas), which should be actively targeted for protection (Saunders et al. 1991, Ruggierro et al. 1994, Collinge 1996). To help guide conservation planning, umbrella species (e.g., vertebrate mammals such as cougars and grizzly bears) have been proposed as targets for conservation, because their protection may ensure the protection of other secondary species (Franklin 1993). By protecting areas large enough to maintain viable populations of wide-ranging species, sufficient habitat may be maintained to ensure survival of other species dependent on the same habitat. Land use planning that allows for the persistence of focal species—like rare and endangered species, keystone or umbrella species—may help direct land conservation. Land use planners will need the help of local biologists to identify appropriate focal and area-sensitive species in their region to better implement habitat conservation strategies.

> *Land use planners should strive to protection and maintain habitat patches larger than 55 hectares (137.5 acres).*

Even though protecting large expanses of connected habitat is the ultimate goal, this may not be practicable in the often highly developing landscapes in which land use planners often find themselves working. In these settings, land use professionals should try and conserve what habitat remains and, where possible, work with land management agencies and land trusts to identify potential areas for habitat restoration. Working to conserve even the smallest remaining natural areas is important, particularly in human-dominated landscapes. A series of small- or medium-sized reserves may capture a greater diversity of habitat types, environmental heterogeneity, and biological diversity than the preservation of one large fragment (Tscharntke et al. 2002) (*see* "Role of small patches"). Protecting natural habitats with the greatest conservation significance locally and regionally—regardless of size—is vital to preserving biological diversity and ecosystem services. No matter how small habitat patches may be, they still have ecological and/or aesthetic values, whether providing habitat for small organisms like amphibians or insects; providing green space for recreational activities; helping moderate temperature and provide shade in urban areas; or decreasing run-off from streets, pavements, and other impermeable surfaces.

Other Patch Area Design Considerations

The size of any given habitat patch is only one factor determining whether or not the patch will support species persistence, biological diversity, and ecosystem functions. Other factors to consider are the shape, location/configuration, condition, and boundaries of patches, as well as the role of small habitat patches. The following is general guidance on ways to counteract the negative impacts of habitat fragmentation and habitat loss at a landscape scale.

- **Patch shape:** Patch size and shape determine the distance of the patch's edge to the habitat interior and the amount of core area remaining in any remnant habitat patch (*see* "Edge Effects") (Collinge 1996). Shape determines the edge to interior ratio of a habitat patch, which should be as low as possible to minimize edge effects (Wilcove et al. 1986, Saunders et al. 1991, Collinge 1996). Circular habitat reserves are recommended to minimize contact between the protected core habitat and adjacent environmental or human pressures (Wilcove et al. 1986). In contrast, long, thin remnants have proportionally more edge, and thus, more negative edge effects (Forman and Godron 1981, Saunders et al. 1991).

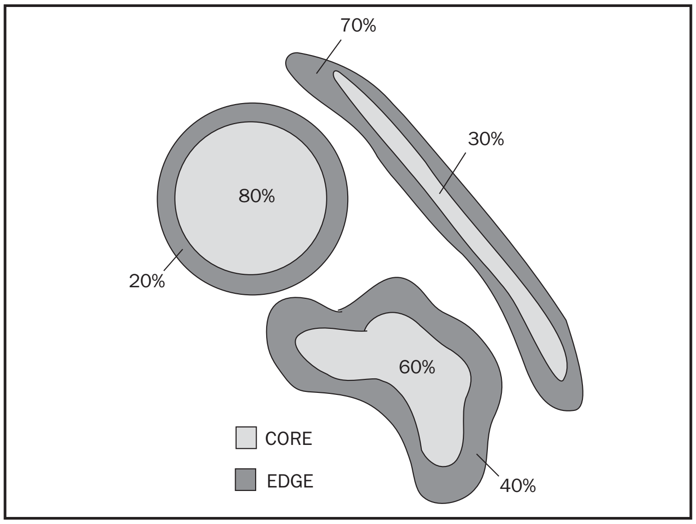

Diagram 3. Patch shape and edge. *The edge to interior ratio of a habitat patch is affected by patch shape. A more convoluted, irregular, or linear patch will have a higher proportion of edge, thus, increasing the number of edge species and decreasing the number of interior species.*

- **Patch location/configuration:** The landscape context in which patches reside may have an even greater effect on the function and sustainability of a habitat fragment than the characteristics of the patch itself (Forman 1995). The distances between suitable habitat patches and the nature of the matrix between these patches will influence species survival (Ruggiero et al. 1994, Andren 1997). In general, more connected habitats are better than isolated habitats because patches in close proximity are likely to enhance species dispersal, recolonization, and persistence (Fahrig and Merriam 1994). Even where wildlife populations may decline or disappear in isolated patches due to random events or patch conditions, recolonization may occur if species are able to successfully disperse from nearby habitat (Pulliam et al. 1992). To maintain demographic linkages, suitable patches should be positioned to provide stop-over points or "stepping stones" for species dispersal (Forman and Godron 1981). The allowable distance between patches will depend upon individual species' dispersal capabilities, which vary within and among species groups (Ruggiero et al. 1994, Bender et al. 1998). When making land use planning decisions, practitioners should consider the contribution of patches to the overall landscape structure and how well the location of any given patch relates or links to other patches (Dramstad et al. 1996).

- **Boundary zone:** The contrast between a patch edge and the surrounding landscape matrix (also referred to as the boundary zone) affects the severity of edge effects and the dispersal abilities of wildlife populations. The higher the contrast between patch types or patches and their surrounding matrix, the greater the edge effects (Franklin 1993). Boundaries in a landscape could be either "hard" or "soft." Hard boundaries usually result from human activities, such as clearcutting and development, and have linear borders with high vegetation contrast, such as between a forest and cultivated field. Soft edges, which dominate natural landscapes, tend to have varying degrees of structural contrast with curved habitat boundaries (Forman 1995). To minimize edge effects at the local scale and facilitate the movement of species between a patch and the surrounding matrix, land use planners should mimic naturally occurring edges and provide gradual thinning of vegetation (e.g., smaller shrubs grading into larger shrubs and taller trees at the edge of a wooded patch) rather than an abrupt transition from vegetated to denuded areas (Forman and Godron 1981, Forman 1995, Duerksen et al. 1997).

- **Patch condition:** The quality of the habitat patch itself will also influence the ability of remnant species and systems to persist or function over the long-term (Fahrig and Merriam 1994, Forman 1995). Large patches with degraded habitat—such as those dominated by non-native species, or with diminished biological diversity, severe erosion, or modified hydrologic patterns—may have less conservation value than small patches of high biological integrity.[19] The biological integrity of land parcels and whether or not they contain unusual or distinctive landscape features (e.g., cliffs, caves, meadows, thermal features, and vernal pools), old-growth forests or mature habitats, or rare, threatened, or endemic species, are also factors that land use planners should consider when selecting which lands to conserve (Dramstad et al. 1996, Duerksen 1997, Lindenmayer and Franklin 2002).

- **Role of small patches:** While large patches generally are recommended to provide sufficient habitat to sustain populations of species—particularly area-sensitive species—small patches also play a vital role in regional conservation. Although larger patches may contain greater habitat diversity than smaller ones, a collection of multiple small patches may capture a greater array of habitats, and perhaps more rare species, than a single large habitat patch (Forman and Godron 1981, Saunders et al. 1991, Forman 1995, Tschartnke et. al. 2002). Small wetlands of less than two hectares, for example, can support surprisingly high species richness of amphibians (Richter and Azous 1995 as cited in Metro 2001). Proximity to core habitat and local habitat heterogeneity, rather than riparian habitat area, may better predict reptile and amphibian richness (Burbink et. al. 1998). In addition, small isolated riparian habitat patches have been found to be vital stop-over sites for en-route migratory birds in the southeastern United States (Skagen et al. 1998). If strategically positioned between larger habitat patches, smaller patches can serve as "stepping stones" to allow for greater species dispersal and recolonization (Murphy and Weiss 1988; Burel 1989 and Potter 1990 as cited in Fahrig and Merriam 1994; Forman 1995).

Many of the above described factors influence not only the effective habitat patch size, but also other fragmentation thresholds, such as the proportion of suitable habitat or the amount of edge in a landscape. Thus, land use planners should keep these design considerations in mind when interpreting the thresholds presented below.

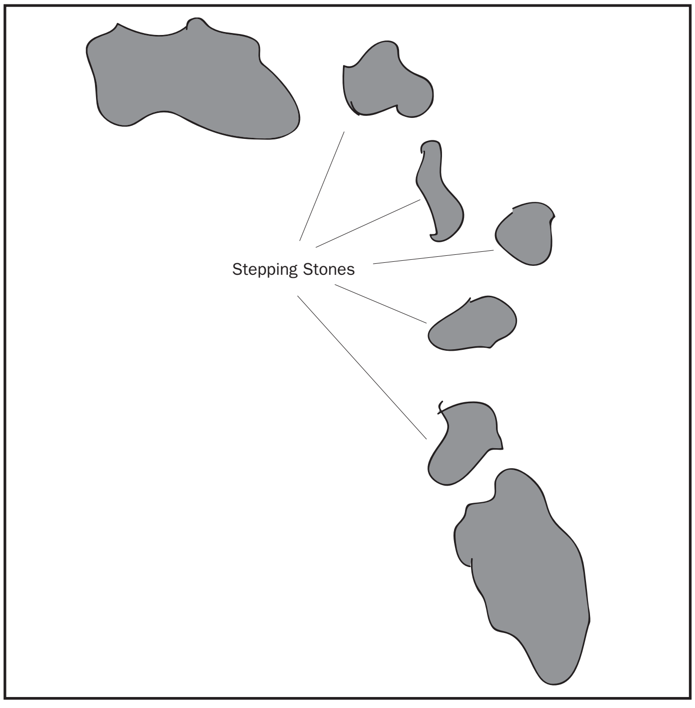

Diagram 4. Stepping stone patches. *Protecting habitat patches strategically positioned between larger habitat patches can be a way to enhance species dispersal and colonization in a landscape, and to increase local species population persistence. Modified from Duerksen et al. (1997), Habitat Protection Planning: Where the Wild Things Are, p 14.*

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[19] Biological integrity refers to "a system's wholeness, including presence of all appropriate elements and occurrence of all processes at appropriate rates" (as cited in Angermeier and Karr 1994).

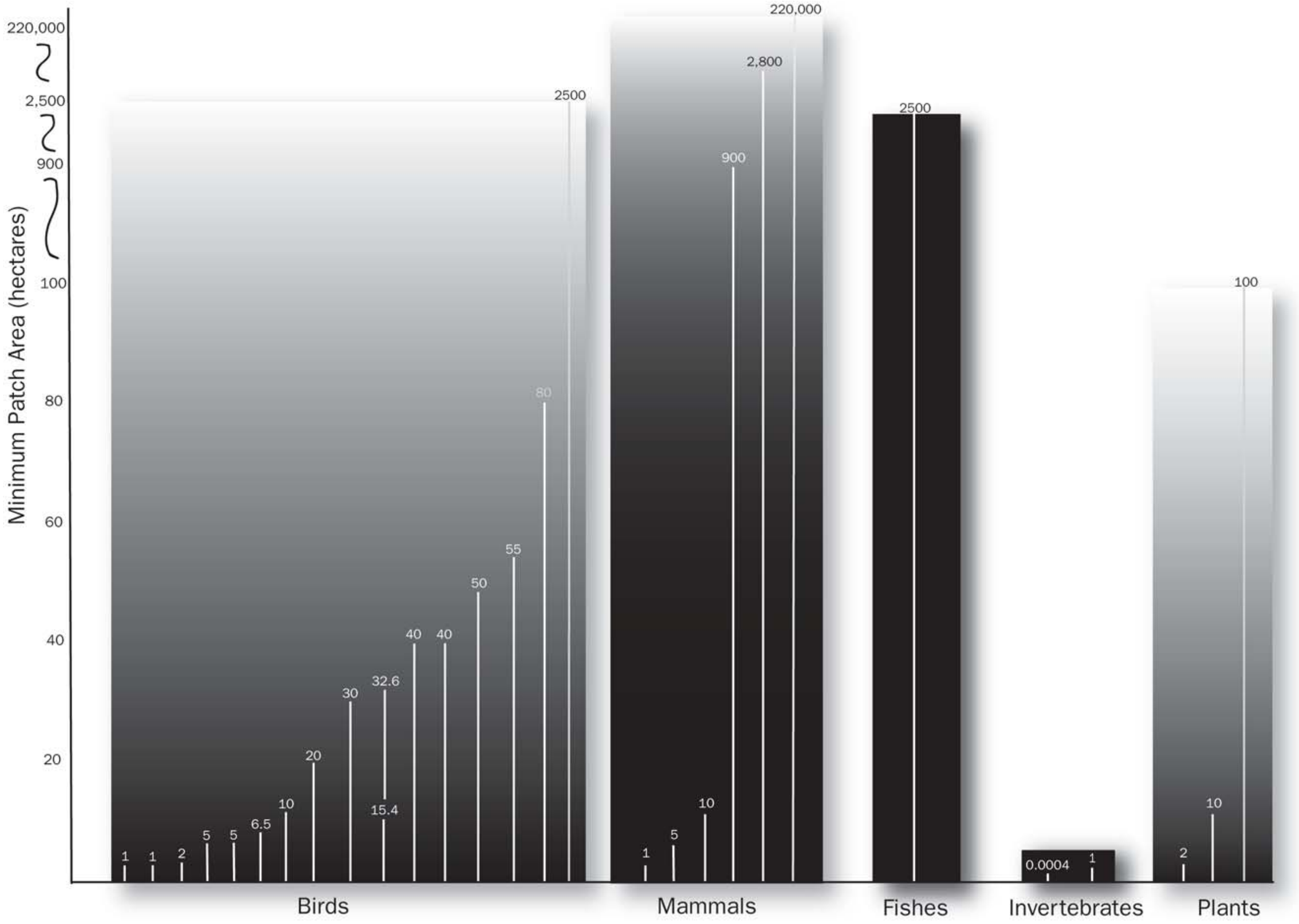

Figure 1. Minimum patch area requirements (in hectares) needed to maintain populations or communities of birds, mammals, fishes, invertebrates, or plants species in the United States, as cited in the scientific literature. Numbers represent the recommended minimum patch area sizes; two numbers along one line indicate a recommended range (*see* Appendix A for specific findings). Lines extend from zero to the recommended minimum patch area sizes to indicate the span of habitat needed for protection.

SUITABLE HABITAT IN LANDSCAPE

Landscapes are complex assemblages of many habitat fragments that together help sustain large-scale biological systems. As a result, meeting minimum patch sizes for species in a given landscape may be inadequate to ensure their persistence (Fahrig 2001). The configuration and nature of the landscape surrounding a patch also greatly determine whether a region will support species persistence and diversity (Lindenmayer and Franklin 2002).

In addition to considering the size of patches, land use planners must consider the total amount of suitable habitat in a given landscape. Local populations of plants and animals are often linked together by dispersal, essentially forming a larger "metapopulation" (Hanski and Simberloff 1997).[20] Individual species from such subpopulations migrate between habitat patches, interacting and breeding with other individuals, which influences the overall survivorship of the species in a region. In addition, the quality and availability of habitat patches can greatly determine the viability of a metapopulation. Some habitat patches may be of higher quality allowing for the local species population to benefit from higher reproductive rates than death rates. These "source" populations produce excess individuals that could emigrate into neighboring patches to settle and breed, thus, expanding the overall population and helping to buffer it from local extirpation. On the other hand, some habitat patches may be of poor quality, where local productivity is less than mortality. Referred to as "sink" populations, these areas lack immigration of individuals from source populations, leading to the extirpation of the local population (Pulliam 1988). For species populations that exhibit a metapopulation structure, land use planners should strive to protect existing source habitat patches, as well as restore habitat that may serve to support future source populations. However, land use planners should be cautious not to designate critical habitat solely by the proportion of the local population present; a source habitat could support as little as 10 percent of the metapopulation, which is responsible for maintaining the other 90 percent of the total population (Pulliam 1988). Rather, land use planners should work with ecologists to identify source habitat by demographic characteristics (e.g., death and birth rates of species).

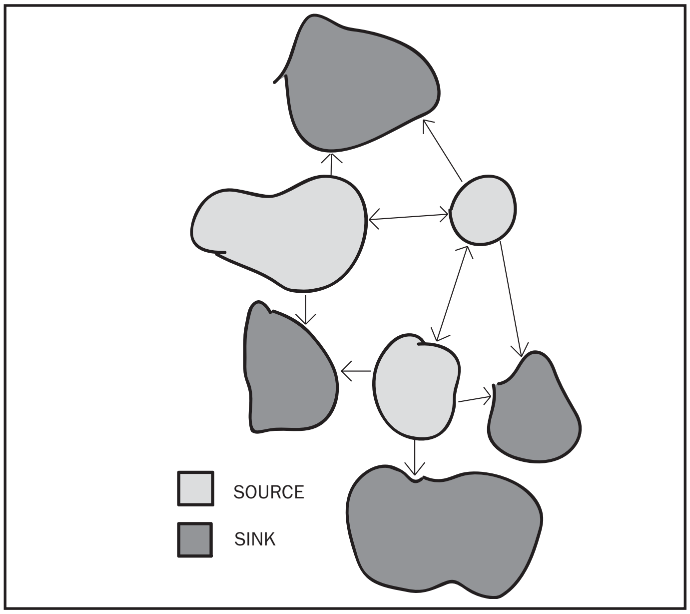

Diagram 5. Metapopulation and Source/Sink Dynamics. *Local populations of organisms in different habitat patches may be linked demographically, forming an interdependent metapopulation. "Source" habitat patches, which supplement local populations in "sink" habitat patches, should be targeted for protection. Ideally, land use planners should protect entire metapopulations. Modified from Mette and Carroll (1994), Principles of Conservation Biology, p 188.*

Metapopulation theory reveals that the local extinction of a subpopulation can be prevented by occasional immigration from neighboring patches, termed the "rescue effect," which is considered important in maintaining small populations and high levels of species diversity (Brown and Kodric-Brown 1977, Stevens 1989). Local extinctions may commonly occur within small habitat patches; about 10-20 percent of certain local populations of plants, arthropods, amphibians, birds, and small mammals within various habitat types have been found to go extinct per year (Fahrig and Merriam 1994). Thus, a set of interconnected habitat patches should be conserved to sustain sufficiently large metapopulations that would allow for regional species persistence.[21] Habitat patches must also be configured to facilitate dispersal and recolonization between patches, particularly those used for breeding and foraging (Saunders et al. 1991, Fahrig and Merriam 1994, Boulinier et al. 2001, Fahrig 2001). Land use planners should strive to identify particular subpopulations, habitat patches, or links between isolated patches that are critical for the maintenance of the overall metapopulation of priority species (Meffe and Carroll 1997).

Not only is the quality of the habitat patches themselves important, but also the condition of the matrix between isolated habitat patches. If the matrix is able to support populations of species present in the original contiguous habitat or allows for adequate species dispersal or migration between fragments, then communities in remnant patches may retain diverse and viable populations of native plants and animals (Askins 1995). Estimating the proportion of suitable habitat in a landscape is a larger scale method of determining how much suitable habitat should be conserved to ensure the persistence of species in a region.

Managing for the Amount of Necessary Habitat in a Landscape

Scientists generally offer recommendations on the proportion of suitable habitat that should be conserved in a

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[20] A metapopulation is a set of local populations that interact by individuals moving between the local populations (or subpopulations) (Hanski and Gilpin 1991).

[21] A local extinction refers to the extinction of a single, local population in a given geographic area; a local extinction does not entail that the entire species has gone extinct within its known range.

landscape based on two scientific trends. First, species disappear in a landscape with the loss of a certain amount of habitat, and different species go extinct at different thresholds of habitat loss (Fahrig 2002). Thus, scientists have estimated extinction thresholds to determine the proportion of suitable habitat needed to sustain specific species.[22] The "extinction threshold" is the minimum amount of habitat required for a population to persist in a region below which the population will go extinct (Fahrig 2001, Fahrig 2002).[23] Extinction thresholds are essentially the converse of population viability estimates derived from PVAs (described above).

Second, threshold values may be based on the amount of habitat below, which the negative effects of habitat fragmentation may compromise species persistence. This is termed "habitat fragmentation thresholds" (Andrén 1994, Fahrig 1998). As the proportion of suitable habitat decreases in a landscape, the reduction in patch sizes and the increasing isolation of these fragments begins to significantly affect the abundance, distribution, or diversity of species in the landscape due to alterations in species movement or the spread of disturbance (e.g., wildfire, flooding, invasion by exotic species), among other factors (Gustafson and Parker 1992, Andrén 1994). The recommendations presented in this review are largely based on existing literature reviews of both extinction thresholds and habitat fragmentation thresholds (*see* Andrén 1994, Fahrig 2001).

Studies of suitable habitat range between 5 percent to 80 percent of the landscape depending on the species, geographic region, and parameters in question (*see* Appendix C). Seventy-five percent of the surveyed studies reported that suitable habitat should be up to 50 percent of the total landscape, whereas 50 percent of the studies reported at least 20 percent of habitat (*see* Figure 2). Given the constraints presented by the available literature (*see* "A Closer Look at Proportion of Suitable Habitat" in Appendix A for explanation on limitations), the conservation of greater proportions of habitat—such as a minimum of 60 percent—is recom-

BOX 3. PLANNING AT THE RIGHT SCALE

Natural communities vary greatly in the area in which they occur. In order to determine which land parcels and how much habitat to protect, land use planners should plan at the appropriate scale for the target system or species. Ideally, planning would occur across multiple scales to capture the greatest habitat and species diversity (*see* Box 2 for a definition of scale).

1. Coarse scale

Certain habitats and species, termed "matrix" habitats and "coarse-scale" species, will require planning to occur at a very large scale to capture their wide-ranging needs. Natural communities—such as spruce-fir forests (Northeast), longleaf pine forests (Southeast), tallgrass prairie (Midwest), and sagebrush (West)—can span as much as one million contiguous acres. Matrix communities are historically dominant habitat and exist across widespread physical gradients, such as broad ranges of elevation, precipitation, and temperature. Coarse-scale species (also termed wide-ranging species) require large areas to access the quantity of habitat or the different habitat types needed for survival (e.g., prairie chicken, fox, badger, marten, and pike minnow). Migratory species (e.g., migratory birds or salmon) and top-level predators (e.g., caribou, wolves, and bears) may depend upon not only matrix communities, but also associated habitat patches (described below), connecting corridors, and aquatic systems. To address the needs of such expansive communities and wide-ranging species, land use planners will need to take a landscape scale and regional approach; an area of several thousand acres up to one million acres may need to be conserved. This scale of planning will likely demand an inter-jurisdictional perspective and inter-municipal cooperation.

2. Intermediate scale

Planning may need to occur at a smaller scale—on the order of several hundred to a thousand acres—to conserve "large patch" community types and "intermediate-scale" species. Occurring in large patches, but not as vast an area as matrix types, are communities like red maple-black ash swamps or northern hardwood forests. Large patch communities may span a thousand acres but are bound by certain physical factors (e.g., coastal salt marshes being defined by low topographic position and predictable tides) or by a single dominant ecological process (e.g., fire, flooding, or drainage). Intermediate-scale species are those that depend on a single large patch or several different kinds of habitats (e.g., amphibians that depend on both wetland and upland complexes).

3. Fine scale

Land use planners will need to plan at a more "fine" or site-specific scale to ensure that "small patch" communities and local-scale species are protected. Small patch communities are communities that naturally occur in narrow, localized, or discrete areas (e.g., fens, bogs, glades, caves, or cliffs) or occur only where specific or narrow physical factors and local environmental conditions are present (e.g., seepages, outcrops, certain types of soil). Local-scale species are species with limited movement and dispersal abilities or specific habitat needs that restrict their populations to a single community or habitat type. Belonging to this category are many rare and threatened species, insects, and plants. Occurrences of small patch communities and local-scale species may be found in only a couple of acres up to several hundred acres.

Given the natural variability in occurrence of communities and species and their wide-ranging geographic needs land use planners will need to plan at multiple scales to capture the biological diversity of a region, as well as to plan at the right scale for designated conservation targets.

The conservation thresholds found within this literature survey are predominately based on matrix and large patch communities, as well as coarse- and intermediate-scale terrestrial species. Thus, the findings and recommendations in this report do not fully address the conservation needs for small patch communities, local-scale species, and aquatic environments. To ensure the protection of restricted communities and rare species, land use planners will need to collaborate with local ecologists to identify priority conservation areas for their region.

The above information is based on research by The Nature Conservancy (TNC) (see Poiani and Richter 2000, and TNC 1998).

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[22] From a species perspective, suitable habitat has been interpreted as habitat utilized for nesting, with associated expected birth and death rates that allow for a stable or growing population (Lamberson et al. 1994).

[23] The extinction threshold may be estimated by: 1) the minimum amount of habitat below which the equilibrium population is zero; or 2) the minimum amount of habitat below which the probability of longterm population survival is less than one (Fahrig 2002).

mended to sustain long-term populations of area-sensitive species and rare species.

Scientists have proposed that more robust species (e.g., large dispersal range, high fecundity, high survivorship)—usually the more common widespread species—may persist in even the most extensively fragmented systems with only 25 to 50 percent of suitable habitat. In contrast, rare species and habitat specialists like the Northern spotted owl may require up to 80 percent of suitable habitat to persist in a region (Lande 1987, Lande 1988, Lamberson et al. 1992). Land use planners should take into account the more sensitive and rare species within their region to develop critical thresholds for proportions of suitable habitat relevant to their geographic setting (Mönkkönen and Reunanen 1999). Such an approach may also provide for the protection of more common and robust species that depend on similar habitat types.

Land use planners should strive to conserve at least 20% to 60% of natural habitat in a landscape.

In addition to the proportion of suitable habitat, other considerations should be factored into land use decisionmaking, such as the spatial arrangements of remaining habitat patches and the matrix between patches. In landscapes that are highly fragmented—including most urban, suburban, and even rural areas with less than 30 percent of remaining suitable habitat—the spatial arrangement of habitat patches greatly affects species survival (Andrén 1994). For example, wetland bird communities are found to depend not only on their local habitat, but also on the amount of wetlands within a surrounding three kilometer buffer (Fairbairn and Dinsmore 2001).

The condition of the surrounding matrix in which habitat patches are embedded also influences the effective size of the remaining fragments and the degree to which the patches are isolated (Andrén 1994, Lindenmayer and Franklin 2002). In turn, these factors affect whether or not species will be able to successfully disperse among habitat patches and whether important ecosystem processes, such as fire and hydrologic cycling, will occur on the landscape (Fahrig and Merriam 1994) (*see* "Patch location/configuration").

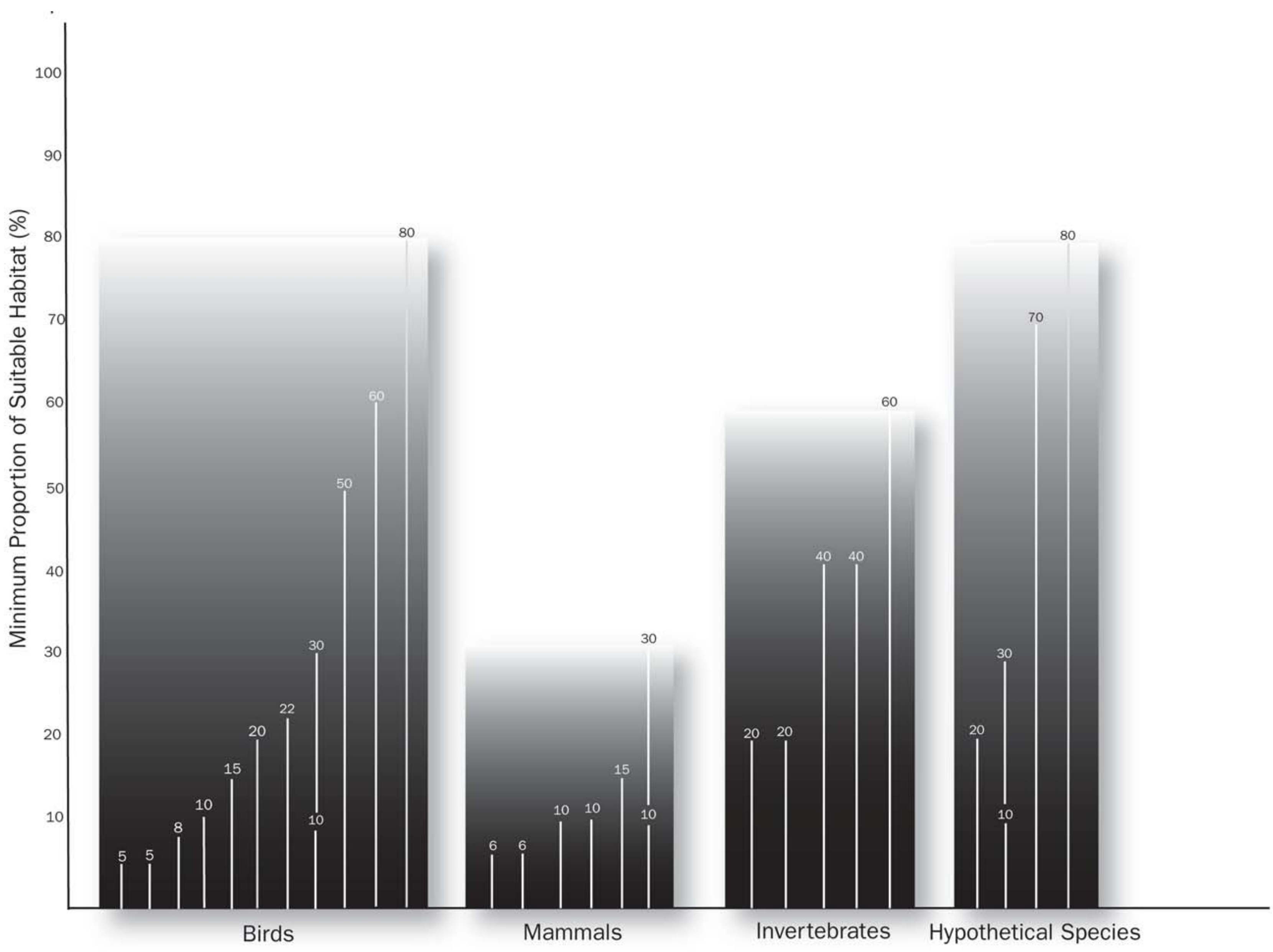

Figure 2. Recommended minimum proportions of suitable habitat (in percentages) needed to maintain populations or communities of birds, mammals, invertebrates, or hypothetical species (as determined by models) in the United States, as cited in the scientific literature. Numbers represent the recommended minimum proportions of habitat; two numbers along one line indicate a recommended range (*see* Appendix B for specific findings). Lines extend from zero to the recommended proportion to indicate the span of habitat needed for protection.

EDGE EFFECTS

Habitat fragmentation inevitably results in the creation of edge environments. Edges occur where a habitat—such as a forest, prairie, or wetland—meets a road, clearcut, housing development, or some other natural or artificial transition or boundary (Soulé 1991). Habitat fragments differ from the original contiguous natural habitat in that they have a greater amount of edge per area and the habitat core is closer to an edge environment. Patch edges may have significantly different conditions than the contiguous system or habitat interior, with altered fluxes of wind, sun exposure, water, and nutrients that greatly affect animal and plant communities (Saunders et al. 1991, Murcia 1995). This change in energy, nutrient, or species flow results from increased amounts of edge and reduced interior habitat, and has been termed the "edge effect."

Increased amounts of edge along habitats create a disturbed environment that allows for the establishment of pest and predator species, which penetrate the fragment interior and adversely affect the diversity and abundance of interior species (Primack 1993). Mammalian predators (e.g., raccoons, foxes, coyotes, feral cats), egg-eating birds (e.g., crows and blue jays), and brood parasitizers (e.g., brown-headed cowbirds) concentrate their hunting along forest edges, thus, increasing the intensities of predation on native species (Soulé 1991).[24] Habitat fragmentation also increases the vulnerability of remnant patches to invasion by exotic and pest species (Soulé 1991, Askins 1995). Higher frequency and intensity of disturbances, like fire and wind damage, may also result due to increased edge (Soulé 1991). Edges like roads and trails introduce such disturbances as pedestrian, pet, and vehicular traffic, causing animals to avoid such areas (Duerksen et al. 1997). Each of these edge effects has significant impact on the vitality and composition of the species in the remaining habitat patch.

Information on environmental and species response to edges helps determine how large patch sizes should be designed to provide sufficient interior habitat, as well as how far development, such as roads, trails, and housing, should be from remnant core areas.

MANAGING FOR EDGE INFLUENCE

The intensity of edge effects has been measured by a number of different methods. The influence of an edge (termed "edge influence") may be defined as the distance between the border to the point where microclimate and vegetation do not significantly differ from the interior conditions of the habitat. From a species perspective, edge influence may be defined as the distance from an edge to the area where species densities, survival rates, or reproductive rates do not differ from those in the interior habitat (Forman 1995, Murcia 1995). Edge influence has also been measured by the behavioral response of animal movement, such as flushing distance, from a disturbance associated with edge environments.[25]

Creation of edge by deforestation, Willamette National Forest, Oregon. Photo courtesy of Steve Holmer, American Lands Alliance.

The intensity of edge effects is influenced by many physical factors, such as the shape and size of the patch, the direction the edge faces (i.e., aspect), and the structural contrast of its boundaries (Soulé 1991). As discussed earlier, larger, circular patches will have more interior habitat and less edge than a rectangular or oblong patch of the same size (Forman and Godron 1981) (*see* "Patch shape"). The orientation of edges affect the amount of exposure to solar radiation, with edges facing the equator tending to have wider edge influence (Forman and Godron 1981, Murcia 1995). The more structurally different the boundaries between different habitat types, the greater the edge effects.

To decrease the influence of edge, buffers are recommended to "soften" the transition between natural and artificial environments (*see* "Boundary zone"). A remnant forest patch directly abutting cropland or urban development will have significant edge effects in contrast to a forest adjacent to a buffer of small shrubs or secondary vegetation. In addition, some habitat types may be more susceptible to negative edge effects; for example, grasslands have been found to exhibit wider edges than forest edges (Forman 1995).

Scientists offer a wide range of findings on the distance edge effects penetrate into ecosystems in the United States, with results ranging from only eight meters up to five kilometers. Based on the response of birds to edge environments, edge effects may penetrate into a habitat patch from about 16 meters up to almost 700 meters; mammals may avoid edge environments from 45 meters up to 900 meters; and microclimate changes may extend from eight meters up to 240 meters into habitat (*see* Appendix E). The majority of the surveyed studies (75 percent) estimates edge influence to be approximately 230 meters or less (*see* Figure 3).

Based on this select review, land use planners should take a conservative approach to mitigating edge effects. To pro-

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[24] Cowbird females lay their eggs in the nests of other bird species, relying on these hosts to incubate and raise their chicks. Brown-headed cowbirds have been found to parasitize over 220 host species. (*see* http://www.audubon.org/bird/research/cowbird-info.html).

[25] Flushing distance is the distance that an animal may flee in response to a disturbance, such as in response to pedestrian or pets on a trail or vehicular traffic on roads (Duerksen et al. 1997)

To avoid the negative effects of edges, land use planners should consider buffering up to 230 to 300 meters around edge peripheries.

vide for sufficient suitable habitat, land use planners should buffer remnant patches by at least 300 meters from all edge peripheries, particularly for matrix and large patch community remnants; naturally small patch communities may not require such a wide buffer (*see* Box 3). The area within the buffer should not be counted as suitable habitat provided for species conservation. In addition, roads, trails, and other development should be placed at least 300 meters away from interior habitat to minimize impact. Ideally, land use planners and ecologists should work collaboratively to determine the intensity of edge effects by the response of species or groups of species that are most sensitive to patch size in the ecosystems or regions of concern (Forman 1995). Measuring edge distance by the most sensitive species—often vertebrates of conservation concern—would mean that the influence of edges may actually be hundreds or thousands of meters, thus, requiring much larger patch sizes to meet habitat requirements.

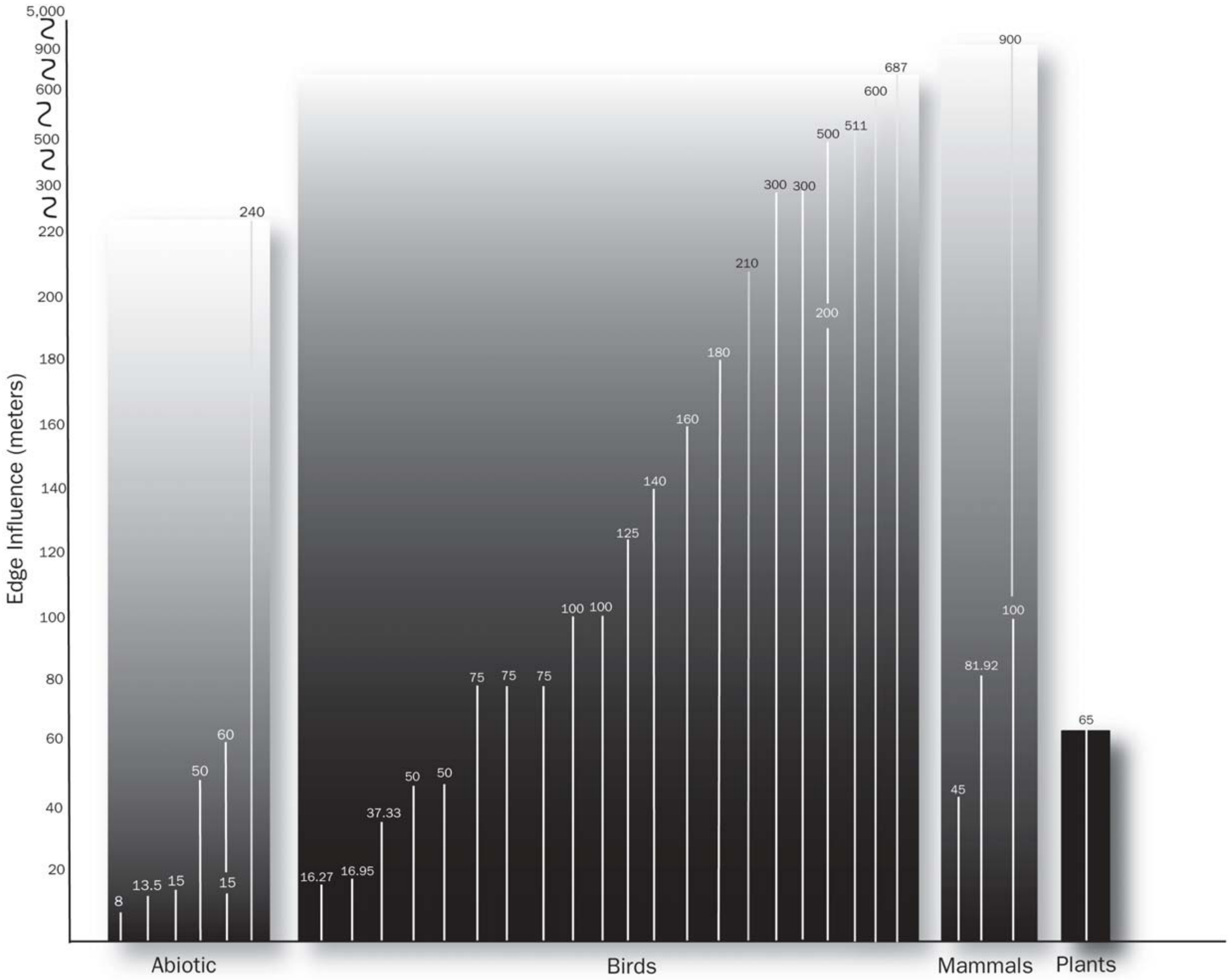

Figure 3. Distances (in meters) that edge effects penetrate into habitats in the United States, as cited in the scientific literature. Edge width is measured by abiotic, bird, mammal, or plant responses; abiotic responses include microclimate changes, such as changes in temperature, humidity and light. Numbers represent edge width distance findings; two numbers along one line indicate a range of edge width distance (*see* Appendix C for specific findings). Lines extend from zero to the determined edge widths to indicate the span of habitat that is affected by edge effects.

RIPARIAN BUFFERS

Although generally comprising a small proportion of the landscape—often less than 1 percent—riparian areas are regional hot spots that support a disproportionately high number of wildlife species and provide a wide array of ecological functions and values (Naiman et al. 1993, Fischer and Fischenich 2000, National Research Council 2002). The support of high levels of species diversity and ecological processes in these areas is due in part to regular disturbance events, like floods, as well as to climatic and topographic variation and the availability of water and nutrients (Naiman et al. 1993).

Riparian areas are ecosystems adjacent to or near flowing water, such as rivers, lakes, shorelines, and some wetlands. They are transitional areas between aquatic and upland terrestrial systems and exhibit gradients in environmental conditions, ecological processes, and living organisms (National Research Council 2002). Unfortunately, riparian systems are continuously threatened by adjacent or upstream human activities. For example, agricultural, industrial, or urban development can increase levels of light, temperature, stormwater runoff, sedimentation, pollutant loading, and erosion, which degrade water quality and diminish suitable aquatic habitat (Castelle et al. 1994). In the last 200 years, over 80 percent of riparian land in North America and Europe has disappeared (Naiman et al. 1993).

To ameliorate the negative impacts of adjacent land uses, a common regulatory and management practice is to establish protected areas, or buffers, around aquatic resources like rivers, streams, lakes, and wetlands. At least 15 states and seven local jurisdictions in the United States have adopted riparian buffer regulations, protecting widths ranging from six meters to over 300 meters in size (Johnson and Ryba 1992).

Buffers are vegetated zones, usually linear bands of permanent vegetation, preferably native species, located between aquatic resources and adjacent areas subject to human alteration (Castelle et al. 1994, Fischer and Fischenich 2000). Buffers can help regulate riparian microclimate and provide necessary shading for the in-stream growth and reproduction of aquatic life; stabilize stream banks and prevent channel erosion; provide organic litter (e.g., leaf litter) and woody debris, which are important sources of food and energy for fish and aquatic invertebrate communities; remove or regulate sediment, nutrients, or other contaminants (e.g., pesticides, herbicides) from runoff; provide flood attenuation and storage to decrease damage to property; and provide wildlife habitat (Castelle et al. 1994, O'Laughlin and Belt 1995, Wenger 1999, Fischer and Fischenich 2000, National Research Council 2002).

Riparian buffer establishment, North Hather Creek, Innoko, Alaska. Courtesy of U.S. Fish and Wildlife Service.

Managing for Adequate Buffer Width

Recommended buffer widths are commonly determined by one of two methods: uniform versus variable widths. Uniform-width buffers are commonly adopted because they are easier to enforce, require less specialized knowledge, time, and resources to administer, and allow for greater regulatory predictability (Castelle et al. 1994). Uniform widths are often based on a single resource protection goal, usually related to water quality. In contrast, with variable-width buffers, the size or width of the strip is adjusted along its length to account for multiple functions, adjacent land use, and site and stream conditions. The width of the strip may be adjusted depending on the value of the aquatic resources, the intensity of surrounding land use, and the type and condition of vegetation, topography, soils, or hydrology, among other variables. For example, a larger width may be required for buffers surrounding more pristine or highly valued wetlands or streams; in close proximity to high impact land use activities; or with steep bank slopes, highly erodible soils, or sparse vegetation (Castelle et al. 1994, Fischer and Fischenich 2000).

> *Land use planners should strive to establish 100-meter wide riparian buffers to enhance water quality and wildlife protection.*

Although the method of varying buffer width is generally believed to provide more adequate protection for aquatic resources, it may be less efficient because variable strips can retain less material than a uniform-width buffer of equivalent average width (Weller et al. 1998). Thus, providing policymakers with scientific guidance on uniform buffer widths allows for the implementation of practicable land management practices that protect aquatic resources.

For this report, riparian buffer widths are measured from the top of the bank or level of bankfull discharge of one side of a water body;[26] therefore, a 50 meter buffer on a 10 meter stream would create a zone at least 110 meters wide (Wenger 1999, Fischer and Fischenich 2000).

As with other conservation thresholds, the scientific literature does not support an ideal buffer width applicable in all circumstances. This survey found recommended buffer widths ranging from one meter up to 1600 meters, with 75 percent of the values extending up to 100 meters (*see* "A Closer Look at Buffer Width" in Appendix E for further discussion). At minimum, a riparian buffer should encompass "the stream channel and the portion of the terrestrial landscape from the high water mark towards the uplands where vegetation may be influenced by elevated water tables or flooding, and by the ability of soils to hold water" (Naiman et al. 1993).

The necessary buffer size varies considerably based on the specific management goal. In general, recommended buffer sizes are significantly greater if the intent is to protect ecological functions, such as providing wildlife habitat and supporting species diversity, as opposed to water quality functions.

Based on the majority of scientific findings, land use practitioners should plan for buffer strips that are a minimum of 25 meters in width to provide nutrient and pollutant removal; a minimum of 30 meters to provide temperature and microclimate regulation and sediment removal; a minimum of 50 meters to provide detrital input and bank stabilization; and over 100 meters to provide for wildlife habitat functions.[27] To provide water quality and wildlife protection, buffers of at least 100 meters are recommended (*see* Figure 4).

Other Buffer Design Considerations

The width of any given buffer is just one aspect, albeit important, which determines its ability to provide a variety of functions. Other factors to consider are the linear extent, vegetation composition, and level of protection of buffers. The following is general guidance on the design and development of buffers.

- **Vegetation:** Buffers should have diverse vegetation that is both native and well-adapted to the region. Maintaining a diverse array of species and vegetation structure (e.g., herbaceous ground cover, understory saplings, shrubs, and overstory trees) is recommended to allow for greater tolerance to possible fluctuations in environmental conditions (e.g., water levels, temperature, herbivory), and to provide for greater ecological functions (e.g., wildlife habitat) (see Fischer and Fischenich 2000 for further guidance on vegetation type, diversity, and propagation techniques).
- **Extent:** In part, the effectiveness of a buffer in meeting management objectives is a function of the linear extent of the aquatic system that is protected (Wenger 1999). Protection efforts should prioritize the establishment of continuous buffer strips along the maximum reach of stream, rather than focusing on widening existing buffer fragments (Weller et al. 1998). Protection of the headwater streams as well as the broad floodplains downstream is also recommended. Headwater streams and downstream floodplains generally encompass less than 10 percent of total landmass; thus, this level of protection is practicable (Naiman et al. 1993). Ideally, buffers

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[26] The bankfull discharge is the maximum level of discharge that a stream channel can convey without flowing onto its floodplain. This stage plays a vital role in forming the physical dimensions of the channel because the flows near the bankfull stage move the most sediment over the long-term and the processes of sediment transport and deposition are the most active in forming the channel (Dunne and Leopold 1978).

[27] While a 100-meter buffer is recommended to provide for adequate wildlife values, some natural riparian habitat is too narrow to support such an area. In these cases, land use planners should consider the utility of narrower buffers, especially where they might function as wildlife corridors (see "Habitat Connectivity").

should extend along all perennial, intermittent, and ephemeral streams, lakes, shorelines, and adjacent wetlands (Weller et al. 1998, Wenger 1999), so long as such buffering would not create detrimental upland habitat fragmentation as might be the case in areas of high stream densities (Lindenmayer and Franklin 2002).

- **Buffer protection:** To ensure that buffers function adequately, all major sources of disturbance and contamination should be excluded from the buffer zone, including dams, stream channelization, water diversions and extraction, heavy construction, impervious surfaces, logging roads, forest clear cutting, mining, septic tank drain fields, agriculture and livestock, waste disposal sites, and application of pesticides and fertilizers (Wenger 1999, Pringle 2001). Another consideration is the level of legal protection afforded to the area. Whether the buffer is in preservation status or protected under a conservation easement that allows for some level of activity, for example, will also determine its ability to provide desired functions.

BOX 4. UNDERSTANDING THE EFFECTS OF LAND USE

The many different uses of land—whether for agriculture, silviculture, recreation/open space, or commercial or residential development—will have varying impacts on the ecosystems, habitats, and species in a region. The types, extent, and combinations of land uses within a matrix will affect the viability of habitat patch sizes, the amount of suitable habitat, the severity of edge effects, and the utility of buffers and corridors in a given landscape.

Certain land use types are likely to be more compatible with biodiversity conservation in certain landscapes, depending on the natural arrangement of physical features, habitats, and species, and the effect of previous land uses (Forman 1995). A study on breeding bird communities in central Pennsylvania, for example, found that forests within agricultural landscapes had fewer forest-associated species, long-distance migrants, forest-canopy and forest-understory nesting species, and a greater number of edge species than forest landscapes primarily disturbed by silviculture, irrespective of the effect of disturbance (Rodewald and Yahner 2001). In Colorado, ranchlands and protected reserves were found to be more compatible with species of conservation concern (including songbirds, carnivores, and plant communities) than exurban developments, which tended to support only human-adapted species (Maestas et al. *in press*).

To plan for long-term sustainability, land use planners will need more guidance on the level of compatibility of different land uses in various regions and ecosystems. As a general rule, a landscape mosaic should be planned first according to its ecological constraints (e.g., water availability, forest and soil productivity, natural flooding/fire cycles) and natural site potential (e.g., natural potential for productivity and for nutrient and water cycling) (Dale et. al. 2000). In terms of hierarchical planning, a general recommendation is for land use planners to first plan "for water and biodiversity; then for cultivation, grazing, and wood products; then for sewage and other wastes; and finally for homes and industry" (Forman 1995 *as cited in* Dale et al. 2000, p.658).

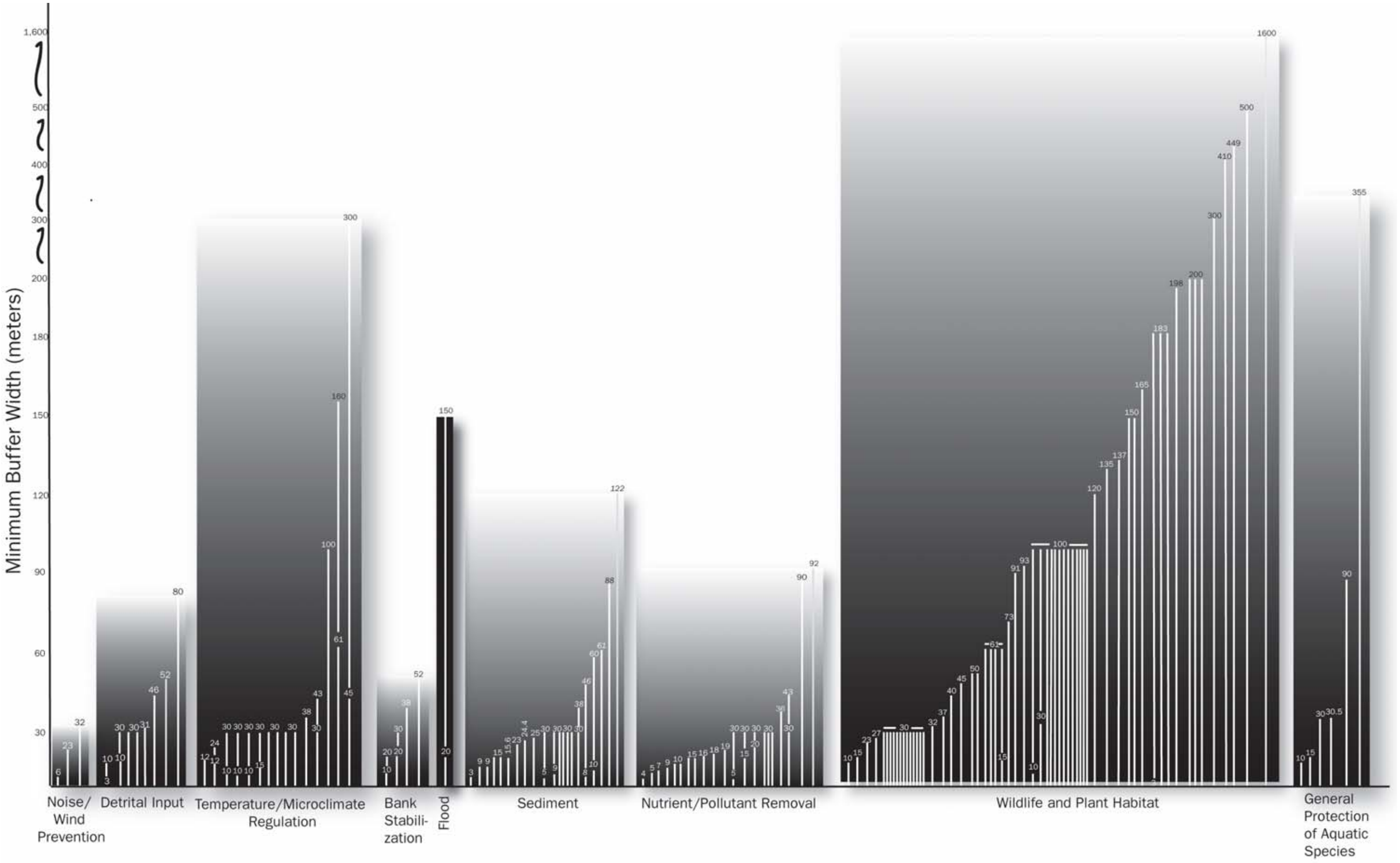

Figure 4. Recommended minimum riparian buffers (in meters) from each side of a water body (e.g. stream bank) needed to prevent noise/wind damage; provide detrital input; moderate temperature/microclimate; stabilize banks; provide flood attenuation; control sediment; reduce nutrients/pollutants; and provide wildlife habitat functions and general protection of aquatic systems in the United States, as cited in the scientific literature. Numbers represent the recommended minimum buffer widths; two numbers along one line indicate a recommended range (*see* Appendix D for specific findings). Lines extend from zero to the recommended buffer widths to indicate the span of habitat needed for protection.

HABITAT CONNECTIVITY

Conservation biologists generally agree that species viability and diversity are enhanced by well-connected habitats (Fahrig and Merriam 1985, Gilpin and Soulé 1986, Primack 1993, Noss and Cooperrider 1994, Meffe and Carroll 1997, Beier and Noss 1998, Lehtinen et al. 1999). Because small, isolated reserves are unlikely to maintain viable populations over the long-term, and because climate change and disturbances require that organisms be able to move over large distances, corridors are recommended as one conservation measure to counter the negative effects of habitat fragmentation and patch isolation (Noss 1991).

Not only can riparian buffers help ensure water quality protection and habitat for plants and animals adjacent to waterbodies, but they can also act as dispersal routes for species and connect remnant patches.[28] Although riparian corridors are useful for some terrestrial wildlife, linkages outside riparian areas may be required to maintain connectivity for non-associated upland species (McGarigal and McComb 1992).

Corridors (also referred to as conservation corridors, wildlife corridors, or dispersal corridors) are intended to permit the direct spread of many or most taxa from one region to another (Brown and Gibson 1983 *as cited in* Noss 1991). They should facilitate foraging movements, seasonal migrations, dispersal and recolonization, and escape from disturbance (Saunders et al. 1991, Soulé 1991). Whether or not corridors actually provide connectivity will depend largely on the species in question and its dispersal capabilities and movement patterns across the landscape (Saunders et al. 1991). Given the species-specific nature of this issue, generalizations about the biological value of corridors are under debate among the scientific community (Noss 1987, Simberloff and Cox 1987, Simberloff et al. 1992, Franklin 1993, Beier and Noss 1998) (for further discussion *see* Appendix A "Further Analysis").

MANAGING FOR OPTIMAL CORRIDOR WIDTH

An important design consideration when maintaining or establishing habitat corridors is width. Corridor width can influence the dispersal behavior of species, resulting in changes in home range size, shape, and use. In addition, corridor width is positively correlated with the abundance and species richness for birds, mammals, or invertebrates (Lindenmayer and Franklin 2002). As is true for other conservation thresholds, in general, the wider the better. Wider corridor bands are recommended to provide interior habitat conditions, which allows for the movement and/or habitation of interior species. In addition, greater habitat area is more likely to provide sufficient cover for species from predators, domestic animals, or human disturbance (Forman and Godron 1981). Corridors that are too narrow may consist entirely of edge, thus, deterring the use by interior or area-sensitive species or causing an increase in mortality from predation (Wilcove et al. 1986).

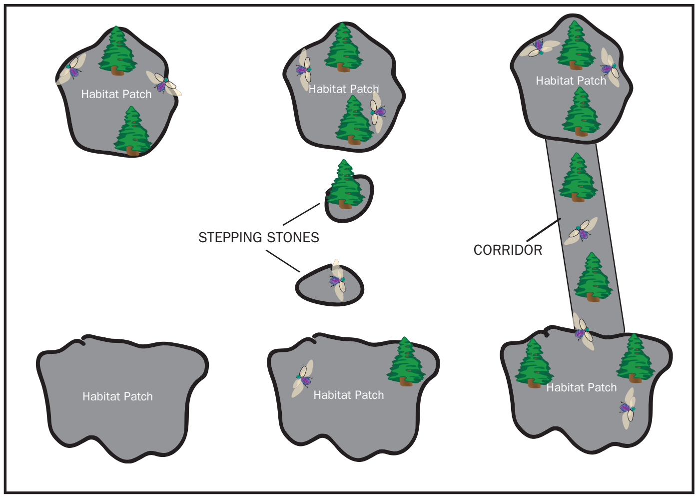

Diagram 6. Habitat Connectivity. *Habitat connectivity can be increased by the protection of stepping stone patches or by the establishment of a corridor. Modified from Dramsted et al. (1996), Landscape Ecology Principles in Landscape Architecture and Land-Use Planning, p. 37.*

Although corridor width has been identified as an important design element, few studies explicitly examined minimum corridor width requirements. This survey found a limited number of studies that provide indirect evidence on effective corridor sizes, however, none of the reviewed studies explicitly tested different corridor widths with the goal of determining an optimal size. Although they did not directly examine recommended corridor width, three studies did find corridor widths of 32 meters and 100 meters to encourage the movement of butterflies and reduce species turnover rates for breeding birds, respectively (Haddad and Baum 1999, Haddad 1999 for butterflies; Schmiegelow et al. 1997 for birds).

Data limitations on the relationship between corridor width and species response prevent the development of recommendations on optimal corridor size. For any given set width, corridor effectiveness will vary with other attributes, such as length, habitat continuity, habitat quality, and topographic position in the landscape, among other factors (Lindenmayer and Franklin 2002) (*see* "Other Corridor Design Considerations").

First and foremost, land use planners should strive to limit the degree of isolation between existing habitat patches and optimize the natural connectivity to allow for the dispersal of sensitive native species through the most appropriate means. This may be done by establishing habitat corridors, maintaining specific structural conditions within the landscape, or setting aside stepping stone patches (Lindenmayer and Franklin 2002) (*see* "Inter-patch distance").

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[28] A riparian corridor is a strip of vegetation adjacent to an aquatic system that connects two or more larger patches of habitat through which an organism is likely to move (Fischer et al. 2000). Corridors are not only riparian but also can be positioned in upland environments as well.

Simultaneously, land use planners should minimize the connectivity of artificial habitats like clearcuts, agricultural fields, and roadsides that tend to spread exotic and pest species (Noss 1991).

OTHER CORRIDOR DESIGN CONSIDERATIONS

Corridor width is one important factor that determines whether a corridor will enhance landscape connectivity. Other factors to consider are the condition of the landscape matrix, the distances between remnant patches, and the extent and configuration of the corridors themselves.

- **Condition of landscape matrix:** The landscape matrix in which corridors are embedded greatly influences corridor use. If conditions in the matrix are suitable (e.g., sufficient original vegetation cover exists), then species reliance on corridors may be minimized. On the other hand, if matrix conditions are inhospitable or degraded (e.g., are highly developed or fragmented; have disrupted ecological processes or disturbed conditions; or are highly invaded by exotic species), then corridor systems linking remnant patches may be required to retain landscape connectivity (Rosenburg et al. 1997 *as cited in* Lindenmayer and Franklin 2002). Given that land use planners often work in extensively developed or developing areas, the latter case is the most likely. Understanding the relationship between the landscape matrix and the movements of target organisms will be fundamental in determining the best placement of corridors to enhance connectivity (Lindenmayer and Franklin 2002).

- **Inter-patch distance:** The distance between remnant patches will affect the conservation value of corridors. When distances between remnant patches are short as compared to the movement ability of target species, a stepping stone approach may be the most effective mechanism for promoting dispersal (*see* “Patch location/configuration”). On the other hand, if the distance separating habitat fragments is relatively far, corridors may be the right mechanism to provide landscape connectivity (Haddad 2000).

- **Corridor configuration and extent:** Networks of intersecting corridors may provide for more effective migratory pathways, allowing greater opportunities for animal foraging and predator avoidance (Forman and Godron 1981). Ideally, a corridor would “encompass the entire topographic gradient and habitat spectrum from river to ridgetop” (Noss 1991). Such an expansive corridor network may allow for the representation of different native habitat and land cover types in a region. In addition, having such a broad system of corridors would help enhance overall resiliency in case of the destruction of individual corridors by unexpected disturbances (Noss 1991).

BOX 5. CONSERVATION THRESHOLDS: A STARTING POINT

The following summarizes findings from a select sample of scientific papers pertinent to species and ecosystems in the United States on critical thresholds related to minimum habitat patch area, proportion of suitable habitat, edge influence, and riparian buffer width. Recommendations are based on the goal of capturing 75 percent of the requirements found for species, communities, and habitats surveyed; thus, the third quartile was used by calculating the value for which 75 percent of the threshold values lie below this value (after numerical ranking). These guidelines should be interpreted very cautiously because they are based on a small sample, and may not be applicable for specific species, habitats, and geographic settings of concern. Land use planners and land managers should consider these results as a baseline from which to launch more tailored and in-depth assessments.

Habitat Patch Area

In general, land use planners should strive to maintain and protect habitat patches greater than 55 hectares (137.5 acres). The goal should be to maintain larger parcels greater than 2,500 hectares (or about 6,175 acres) to protect more area-sensitive species.

Proportion of Suitable Habitat

In general, land use planners should strive to conserve at least 20 percent up to 50 percent of the total landscape for wildlife habitat, where possible.[‡] The conservation of greater proportions of habitat—such as a minimum of 60 percent—may be needed to sustain long-term populations of area-sensitive species and rare species.

Edge Influence

In general, to avoid the negative effects of edges on habitats, land use planners should consider establishing buffer zones up to at least 230 to 300 meters from the periphery of edges.

Riparian Buffer Width

In general, land use planners should plan for riparian buffer strips that are a minimum of 25 meters in width to provide for nutrient and pollutant removal; a minimum of 30 meters to provide temperature and microclimate regulation and sediment removal; a minimum of 50 meters to provide detrital input and bank stabilization; and over 100 meters to provide for wildlife habitat functions. To provide water quality and wildlife protection, buffers of at least 100 meters are recommended.

Landscape Connectivity

Land use planners should strive to reduce the distances between habitat patches and to optimize the natural connectivity of the landscape. This may be done by establishing habitat corridors that connect previously isolated patches; by maintaining the natural, structural conditions within the landscape; or by setting aside stepping stone patches. Simultaneously, land use planners should minimize the connectivity of artificial habitats like clearcuts, agricultural fields, and roadsides.

[‡] The 50 percent recommendation is based on capturing 75 percent of the threshold values surveyed; 20 percent is based on capturing 50 percent of threshold values surveyed. The latter recommendation is provided because land use planners are often working in highly developed regions where protecting 50 percent or more of the landscape is impractical.

RECOMMENDATIONS FOR FUTURE RESEARCH AND ACTION

THE ROLE OF THE SCIENTIFIC COMMUNITY

More scientific research is needed to help inform specific land use decisions being made everyday in the United States—decisions that significantly determine the future of domestic biodiversity. This survey of the scientific literature found that out of all land management strategies geared toward reducing the effects of urbanization and sprawl, the most substantial guidance available is on how to best develop riparian buffers. Conversely, science offers very little consensus opinion to land use planners on how to determine which habitat patches to conserve and where; the amount of habitat to protect in a region or conversely the maximum amount of impervious surface to allow; the ways in which to mitigate against the negative consequences of habitat edges; or how best to design and plan for corridors. In addition, because development will continue to occur and because private lands are increasing becoming more important in species conservation, more information is needed on the level of compatibility of the various types and combinations of land uses with biodiversity. To better inform decisionmaking, the scientific community needs to provide more specific information to land use practitioners on how to implement ecologically conscious growth.

> *"Fragmentation effects are difficult to translate into management rules-of-thumb for several reasons: (1) they tend to be highly specific to the taxa, spatial scales, and ecological processes considered; (2) they vary according to the landscape type and its structure; and (3) their influence on species distribution and abundance may be obscured by local effects such as changes to certain microhabitat features (e.g., habitat degradation)."*
>
> Villard (2002), Ecological Society of America, Ecological Applications 12(2), p.319

In addition, scientists should address the taxonomic bias in the literature. A recent review of 134 papers on habitat fragmentation found that over half of the research focuses on birds, the vast majority being songbirds. Mammals and plants come second, making up about 18 percent; invertebrates and reptiles/amphibians are the most understudied, with only 9 percent and 4 percent, respectively (McGarigal and Cushman 2002). Our survey found similar results. Most of the fragmentation research used for this study looks at the effects of fragmentation on bird species and, to a lesser extent, mammals. Sixty-six percent of the surveyed research on edge effects; 57 percent on patch area; 44 percent on proportion of suitable habitat; and 32 percent of the wildlife papers on buffers measured effects on bird species. Mammals made up 24 percent of the research on proportion of suitable habitat; 21 percent on patch area; 11 percent of research on buffers; and 9 percent on edge effects. Fish, invertebrate, and plant response made up anywhere from zero to 13 percent of the research. This focus has left particularly large gaps in research on reptiles and amphibians, invertebrates, and plants.

If the scientific community wishes to help curtail the loss and endangerment of species, then it will need to start addressing other taxonomic groups. The most at-risk species in the United States are flowering plants and freshwater species. In terms of species numbers, flowering plants have by far the greatest number of at-risk species (over 5,000 species are at-risk). In terms of the proportion, species that rely on freshwater habitats—mussels, crayfishes, stoneflies, amphibians, and fishes—exhibit the highest level of risk. With only 14 percent of bird species being at risk and 16 percent of mammal species, these groups are the least threatened (Master et al. 2000).

Above all else, this literature search reveals the inadequacy of the information currently available for land use planners to use in their day-to-day decisions, which have profound effects on biological diversity. The scientific community should be commended for developing theories, such as metapopulation concepts, which have important implications for applied management like endangered species recovery. However, due to the simplified assumptions implied within metapopulation models, their application to real landscapes is severely limited (Fahrig and Merriam 1994). In addition, whether metapopulations are actually common in real landscapes is largely unknown (Lindenmayer and Franklin 2002). Similarly, the SLOSS debate on whether a single large reserve is better than a group of small ones, which consumed the academic community for many years, failed to produce concrete management recommendations (Forman 1995).[29] In order for ecological principles to be put into practice, land use professionals will need general rules of thumb and specific guidelines to implement on-the-ground.

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[29] SLOSS stands for Single Large Or Several Small, which refers to whether conservation reserves are best designed as one large tract of protected land versus several smaller tracts of the equivalent area (Meffe and Carroll 1997).

Only about 10 percent of the papers reviewed in this survey provided quantitative information useful for developing conservation thresholds relevant to land use planning. Similarly, most of the papers published in the Journal of Applied Ecology during a large proportion of the last 30 years have been devoid of practical applications or management recommendations (Pienkowski and Watkinson 1996). Given the complexity surrounding habitat fragmentation, it is understandable that the scientific community is apprehensive about presenting or extrapolating research findings such that they can be easily applied to land use planning and management. Scientists even warn that providing general thresholds "may be more dangerous than useful because many species can be lost if the threshold is determined by averaging over the requirements of many species" (Mönkkönen and Reunanen 1999).

Without adequate information on land use thresholds, land use decisionmaking will continue to be uninformed by the best available science. Although reaching consensus in the scientific community on these thresholds may be an impractical goal, if enough resources are directed to answer specific land use threshold questions, research results may begin coalescing on some general range of values, which would provide useful guidance. Hopefully, this literature review will prompt scientific research that is relevant to and usable by everyday land use practitioners.

THE ROLE OF THE POLICY COMMUNITY

Although more scientific study is needed to provide ecologically-based and scientifically defensible advice on land use planning and land management thresholds, substantial research has already been conducted. The policy community could play a more active role as a conduit between the scientific community and land use planners—to help interpret the available research, help with dissemination, and communicate back to scientists on research gaps and needs. Periodical reviews of the literature, such as this survey, should be conducted to provide land use planners and land management practitioners with the most up-to-date and best available scientific information. In addition, where possible, scientific research will need to be translated into easily applied management recommendations. To ensure that land use decisions are well-informed, mechanisms should be in place to communicate current scientific understanding to the general public. Scientific institutes, such as the National Academy of Sciences, among others, should conduct or commission studies on areas where particular research gaps are found. Clear arguments, particularly those that are economically based, need to be conveyed to the land use community so that they understand why they should make land use decisions with biodiversity in mind.

THE ROLE OF THE LAND USE PLANNING COMMUNITY

The failure of land use planners to communicate their needs to the scientific community may be another reason that science inadequately addresses land use planning concerns. Land use practitioners should be encouraged to better communicate with scientists about the type of information that they need and in what format it would be most useful. An exchange about what is working on-the-ground and what is not, and about public concerns regarding land use alteration and biodiversity, would be of great benefit.

However, given the diverse habitat requirements of species and the great uncertainty and unpredictability of species and ecosystem response to habitat alteration, land use planners should not wait for the development of *the magical threshold value* before applying known general ecological guidelines, such as those presented by the Ecological Society of America's Land Use Committee. To ensure that our natural resources will be conserved for future generations, spatial planning needs to proceed immediately using the best available information.

Land use planners should err on the side of caution and adopt the most conservative threshold ranges, particularly since factors, such as global climate change, are likely to intensify land use impacts. The future change of our climate —predicted to rise globally by an average about 4° Fahrenheit (2° Celsius) by the year 2100—is likely to alter the level and timing of temperature and precipitation and to increase the frequency of environmental disturbances (like floods, droughts, hurricanes, and fires), causing shifts in suitable ecosystem and species ranges, as well as the composition of species and flows of energy and nutrients (Field et. al. 1999). For species and ecosystems to be able to withstand such drastic environmental perturbations, sufficient intact and well-connected habitat will be essential. Thus, larger patch sizes, greater habitat area, wider buffers, and more corridors are likely required under future global warming than presented in this review.

Land use planners should realize that, ultimately, there is no replacement for site-specific assessments. It is both difficult and often misleading to develop thresholds that generalize across landscapes and across ecoregions (Mönkkönen and Reunanen 1999). Since thresholds will fail to be meaningful when generalized across landscapes, ecosystems, and states, thus unable to capture the unique variation in nature, land use planners and managers need to work in close collaboration with ecologists (Mönkkönen and Reunanen 1999). Land use professionals should use the articles and research highlighted in this review only to the extent that they are appropriate for their region and to launch more in-depth analyses. This review predominately covers thresholds and guidelines for planning at a large (coarse) scale. This report, however, does not focus on the conservation of rare or localized species or habitat types, and species other than birds and mammals. It does not provide guidance on how to protect lands of greatest biological value. Rather than simply adopting the types of measures discussed in this review, land use planners should collaborate with scientists to better protect small patch communities and local-scale species and to better identify site-specific and regional conservation needs.

Although land use planners are asked to make local, site-specific decisions on a daily basis, it is still vital to maintain a landscape perspective. Numerous, small development projects that independently may not contribute to significant habitat loss, degradation, or fragmentation, may cumulatively have devastating consequences. Site-specific land use decisions would be more ecologically mindful if better informed by scientific information. Yet, to really make a difference for biodiversity, land use planners will need to begin considering their cumulative and landscape-scale impacts.

Biodiversity needs to be a central component directly considered in all land use and community planning projects. An overarching land use vision with a statewide or county-wide blueprint for protecting ecosystems, representative and rare species, and broader patterns of biodiversity would serve as an important framework to guide the implementation of the specific thresholds outlined in this report. For example, Florida developed a model that identifies areas with priority conservation significance and landscape linkages (i.e., corridors) captures most of the major ecological communities and known occurrences of rare species for the entire state (Hoctor et al. 2000). Conserving regional biodiversity and accounting for land use impacts over a large scale—both spatially and temporally—will likely require inter-municipal cooperation and state-level leadership, as in the case of Florida.

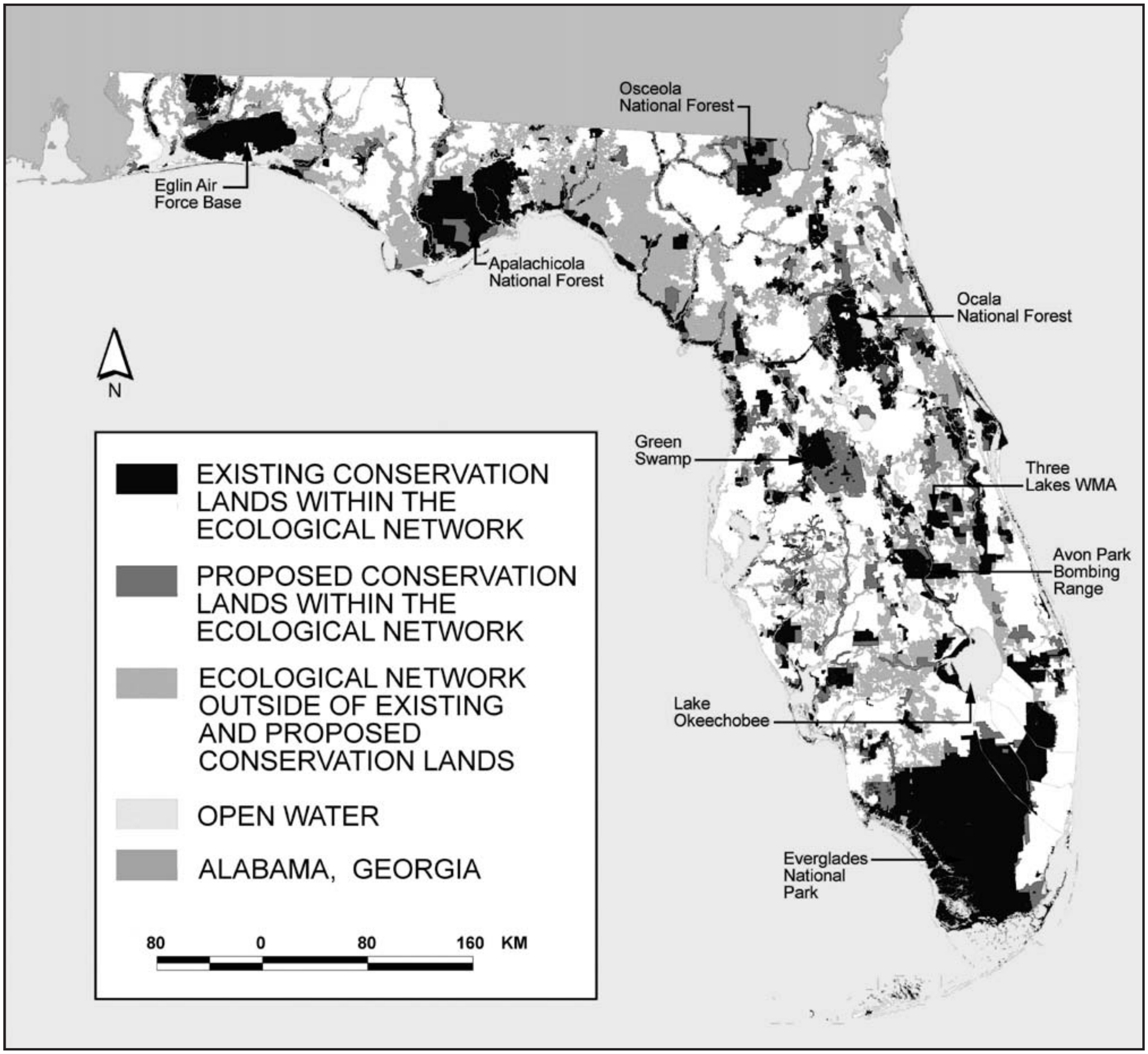

Diagram 7. Florida Ecological Network. *Results from the Florida Statewide Greenways GIS decision support model. Courtesy of the University of Florida.*

CONCLUSION

Land use decisions have profound effects on biological diversity. Land use planners, however, have many opportunities to tailor their traditional land use tools to better address biodiversity conservation. To the extent possible, planning decisions should be based on the best available science. Although the current scientific literature provides much guidance to land use planners on how to incorporate ecological knowledge into their actions, significant gaps exist in the information provided by the scientific community. The more that is known about how human mediated fragmentation impacts ecosystems, the more it is revealed that species and communities interact in complex, dynamic, and often unpredictable ways on multiple temporal and spatial scales. For science to meet the needs of local land use planners, on-going and dedicated collaboration needs to exist between the scientific, policy, and land use planning communities. Although a consensus may never develop in the scientific community on broad conservation thresholds, more effective and targeted guidance can be developed to help land use planners make more ecologically informed decisions. Without this information, little incentive exists for land use planners and land managers to factor biodiversity considerations into their decisions at all.

LITERATURE CITED

Ambuel, B., and S. A. Temple. 1983. Area-dependent changes in bird communities and vegetation of southern Wisconsin forests. Ecology 64:1057-1068.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: A review. Oikos 71:355-366.

Andren, H. 1997. Population response to landscape change depends on specialization to different habitat elements. Oikos 80:193-196.

Askins, R. 1995. Hostile landscapes and the decline of migratory songbirds. Science 267:1956-1957.

Askins, R., M. Philbrick, and D. Sugeno. 1987. Relationship between the regional abundance of forest and the composition of forest bird communities. Biological Conservation 39:129-152.

Aune, K., and W. Kasworm. 1989. Final Report on East Front Grizzly Bear Study. Montana Department of Fish, Wildlife, and Parks, Helena.

Barbour, M., and J. Litvaitis. 1993. Niche dimensions of New England cottontails in relation to habitat patch size. Oecologia 95:321-327.

Beier, P. 1993. Determining minimum habitat areas and habitat corridors for cougars. Conservation Biology 7:98-108.

Beier, P. 1995. Dispersal of juvenile cougars in fragmented habitat. Journal of Wildlife Management 59:228-237.

Beier, P., and R. F Noss. 1998. Do habitat corridors provide connectivity? Conservation Biology 12:1241-1252.

Bender, D.J., T.A. Contreras, and L. Fahrig. 1998. Habitat loss and population decline: A meta-analysis of the patch size effect. Ecology 79:517-533.

Bennett, A. 1998. Linkages in the Landscape: The Role of Corridors and Connectivity in Wildlife Conservation. IUCN, Gland, Switzerland.

Bodie, J., and R. Semlitsch. 2000. Spatial and temporal use of floodplain habitats by lentic and lotic species of aquatic turtles. Oecologia 122:138-146.

Bohning-Gaese, K., M. Taper, and J. Brown. 1993. Are declines in North American insectivorous songbirds due to causes on the breeding range? Conservation Biology 7:76-86.

Bolger, D. , A. Alberts, and M. Soulé. 1991. Occurrence patterns of bird species in habitat fragments: Sampling, extinction, and nested subsets. Am. Nat. 137:155-166.

Bolger, D. , A. Alberts, R. Sauvajot, P. Potenza, C. McCalvin, D. Tran, S. Mazzoni, and M. Soulé. 1997. Response of rodents to habitat fragmentation in coastal southern California. Ecological Applications 7(2):552-563.

Bosakowski, T., D. Smith, and R. Speiser. 1992. Nest sites and habitat selected by Cooper's hawks, *Accipiter cooperii*, in northern New Jersey and southeastern New York. Canadian Field-Naturalist 106(4):474-479.

Bottom, D. , P. Howell, and J. Rogers. 1983. Final Report: Fish Research Project Oregon Salmonid Habitat Restoration. Oregon Department of Fish and Wildlife, Portland.

Boulinier, R., J. Nichols, J. Hines, J. Sauer, C. Flather, and K. Pollock. 2001. Forest fragmentation and bird community dynamics: Inference at regional scales. Ecology 82(4):1159-1169.

Bowne, D., J. Pales, and G. Barrett. 1999. Effects of landscape spatial structures on movement patterns of the hispid cotton rat (*Sigmodon hispidus*). Landscape Ecology 14:53-65.

Boyce, M. 1992. Population viability analysis. Annual Review of Ecology and Systematics 23:481-506.

Brazier, J., and G. Brown. 1973. Buffer strips for stream temperatures control. Forest Research Lab, Oregon State University, Corvallis.

Brittingham, M., and S. Temple. 1983. Have cowbirds caused forest songbirds to decline? BioScience 33:31-35.

Broderson, J. 1973. Sizing Buffer Strips to Maintain Water Quality, Master of Science Thesis. University of Washington, Seattle.

Brosofske, K., J. Chen, R. Naiman, and J. Franklin. 1997. Harvesting effects on microclimatic gradients from small streams to uplands in western Washington. Ecological Applications 7:1188-1200.

Brothers, T. 1993. Fragmentation and edge effects in central Indiana old-growth forests. Natural Areas Journal 13:268-275.

Brothers, T., and A. Spingarn. 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. Conservation Biology 6(1):91-100.

Brown, J., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: Effect of immigration on extinction. Ecology 58:445-449.

Brown, J., and A. Gibson. 1983. Biogeography. The C.V. Mosby Co., St. Louis, Missouri.

Brown, M., and J. Dinsmore. 1986. Implications of marsh size and isolation for marsh bird management. J. Wildl. Manage. 50(3):392-397.

Budd, W. , P. Cohen, P. Saunders, and S. Frederick. 1987. Stream corridor in the Pacific Northwest: Determination of stream-corridor widths. Environmental Management 11(5):587-597.

Buhlmann, K. 1998. Ecology, Terrestrial Habitat Use, and Conservation of a Freshwater Turtle Assemblage Inhabiting a Seasonally Fluctuating Wetland with Emphasis on Life History of *Deirochelys reticularia*, Doctor of Philosophy Dissertation. University of Georgia, Athens.

Burbrink, F., C. Phillips, and E. Heske. 1998. A riparian zone in southern Illinois as a potential dispersal corridor for reptiles and amphibians. Biological Conservation 86:107-115.

Burel, F. 1989. Landscape structure effects on carabid beetles spatial patterns in western France. Landscaping Ecology 2:215-226.

Burke, V., and J. Gibbons. 1995. Terrestrial buffer zones and wetland conservation: A case study of freshwater turtles in a Carolina bay. Conservation Biology 9:1365-1369.

Castelle, A., C. Conolly, M. Emers, E. Metz, S. Meyer, M. Witter, S. Mauermann, T. Erickson, and S. Cooke. 1992. Wetland Buffers: Use and Effectiveness. Publication No. 92-10. Washington Department of Ecology, Shorelands and Coastal Zone Management Program, Olympia.

Castelle, A. , A. Johnson, and C. Conolly. 1994. Wetland and stream buffer size requirements - A review. Journal of Environmental Quality 23:878-882.

Cederholm, C. 1994. A suggested landscape approach for salmon and wildlife habitat protection in western Washington riparian ecosystems. Pages 78-90 *in* A.Carey and C. Elliott, eds. Washington Forest Landscape Management Project Progress Report. Washington Department of Natural Resources, Olympia.

Chen, J., J. Franklin, and T. Spies. 1995. Growing season microclimatic gradients from clearcut edges into old-growth Douglas-Fir forests. Ecological Applications 5:74-86.

Collinge, S. 1996. Ecological consequences of habitat fragmentation: Implications for landscape architecture and planning. Landscape and Urban Planning 36:59-77.

Corbett, E. and J. Lynch. 1985. Management of streamside zones on municipal watersheds. Pages 187-190 *in* R. Johnson, C. Ziebell et al., eds. Riparian Ecosystems and their Management: Reconciling Conflicting Uses. First North American Riparian Conference (1985), Tucson, Arizona.

Corley, C., G. Frasier, M. Trlica, F. Smith, and E. Taylor. 1999. Technical note: Nitrogen and Phosphorus in runoff from two montane ripari an communities. Journal of Range Management 52:600-605.

Crist, T., and R. Ahern. 1999. Effects of habitat patch size and temperature on the distribution and abundance of ground beetles (Coleoptera: Carabidae) in an old field. Environmental Entomology 28(4):681-689.

Dale, V., S. Brown, R. Haeuber, N. Hobbs, N. Huntly, R. Naiman, W. Riesbsame, M. Turner, and T. Valone. 2000. Ecological Society of America report: Ecological principles and guidelines for managing the use of land. Ecological Applications 10:639-670.

Desbonnet, A., P. Pogue, V. Lee, and N. Wolf. 1994. Vegetated Buffers in the Coastal Zone. A Summary Review and Bibliography. Coastal Resources Center Technical Report No. 2064. University of Rhode Island, Narragansett, RI.

Dickson, J. 1989. Streamside zones and wildlife in southern U.S. forests. Pages 131-133 *in* G. Gresswell, B. Barton, and J. Kershner, eds. Practical Approaches to Riparian Resource Management: An Educational Workshop. U.S. Bureau of Land Management, Billings, Montana.

Dillaha, T., R. Reneau, S. Mostaghimi, and D. Lee.1989. Vegetative filter strips for agricultural nonpoint source pollution control. Trans. ASAE 32:513-519.

Dooley, J., and M. Bowers. 1998. Demographic responses to habitat fragmentation: Experimental tests at the landscape and patch scale. Ecology 79(3):969-980.

Doyle, R., G. Stanton, and D. Wolf. 1977. Effectiveness of forest and grass buffer strips in improving the water quality of manure polluted runoff. ASAE, Paper 77-2501. ASAE, St. Joseph, Michigan.

Dramstad, W., J. Olsen, and R. Forman. 1996. Landscape Ecology Principles in Landscape Architecture and Land-Use Planning. Island Press, Washington, DC.

Duerksen, C., D. Elliott, N. Hobbs, E. Johnson, and J. Miller. 1997. Habitat Protection Planning: Where the Wild Things Are. American Planning Association, Chicago, IL.

Dunne, T., and L. Leopold. 1978. Water in Environmental Planning. Freeman and Co., San Francisco, CA.

Ecological Society of America. “About ESA.” <www.esa.org> (31 July 2002).

Elfstrom, B. 1974. Tree Species Diversity and Forest Island Size on the Piedmont of New Jersey, Masters Thesis. Rutgers University, New Brunswick, NJ.

Erman, D., J. Newbold, and K. Ruby. 1977. Evaluation of Streamside Bufferstrips for Protecting Aquatic Organisms. Water Resource Center, Contr. 165, Univ. of Calif., Davis, CA.

Fahrig, L., 1998. When does fragmentation of breeding habitat affect population survival? Ecological Modeling 105:273-292.

Fahrig, L. 2001. How much habitat is enough? Biol. Conservation 100:65-74.

Fahrig , L. 2002. Effect of habitat fragmentation on the extinction threshold: A synthesis. Ecological Applications 12:346-353.

Fahrig, L. and, G. Merriam. 1985. Habitat patch connectivity and population survival. Ecology 66:1762-1768.

Fahrig, L. and, G. Merriam. 1994. Conservation of fragmented populations. Con. Bio. 8:50-59.

Fairbairn, S., and J. Dinsmore. 2001. Local and landscape-level influences on wetland bird communities of the prairie pothole region of Iowa, USA. Wetlands 21:41-47.

FEMAT (Forest Ecosystem Mangement Assessment Team). 1993. Aquatic ecosystem assessment: Riparian ecosystem components. Forest Ecosystem Management: An Ecological, Economic, and Social Assessment. Report of the Forest Ecosystem Management Assessment Team. 1993-793-071. USDA Forest Service, Washington, DC.

Fennessey, M., and J. Cronk. 1997. The effectiveness and restoration potential of riparian ecotones for the management of nonpoint source pollution, particularly nitrate. Critical Reviews in Environmental Science and Technology 27(4):285-317.

Field, C., G. Daily, F. Davis, S. Gaines, P. Matson, J. Melack, N. Miller. 1999 (November). Confronting Climate Change in California: Ecological Impacts on the Golden State. The Union of Concerned Scientists and the Ecological Society of America, Washington, D.C. <http://www.ucsusa.org/publication.cfm?publicationID=7>

Fischer, R. 2000. Width of riparian zones for birds. Ecosystem Management and Restoration Research Program Technical Notes Collection. U.S. Army Engineer Research and Development Center, Vicksburg, Mississippi. <www.wes.army.mil/el/emrrp>

Fischer, R. and J. Fischenich. 2000 (April). Design recommendations for corridors and vegetated buffer strips. U.S. Army Corps Engineer Research and Development Center, Vicksburg, MS, ERCD TN-EMRRP-SR-24.

Fischer, R., C. Martin, and J. Fischenich. 2000 (August). Improving riparian buffer strips and corridors for water quality and wildlife. Pages 457-462 *in* P. Wigington and R. Beschta, eds. Riparian ecology and mangement in multi-land use watersheds. American Water Resources Association, Middleburg, Virginia, TPS-00-2.

Forman, R. 1995. Land Mosaics: The Ecology of Landscape and Regions. Cambridge University Press, Cambridge.

Forman, R., A. Galli and C. Leck. 1976. Forest size and avian diversity in New Jersey woodlots with some land use implications. Oecologia 26:1-8.

Forman, R., and M. Godron. 1981. Patches and structural components for a landscape ecology. Bioscience 31:733-740.

Forman, R., and S. Collinge. 1997. Nature conserved in changing landscapes with and without spatial planning. Landscape and Urban Planning 37:129-135.

Franklin, J. 1993. Preserving biodiversity: Species, ecosystems, or landscapes? Ecological Applications 3:202-205.

Franklin, J., and R. Forman. 1987. Creating landscape patterns by forest cutting: Ecological consequences and principles. Landscape Ecology 1:5-18.

Furfey, R., J. Budhabhatti, and L. Putnam. 1997 (July). Policy Analysis and Scientific Review for Title 3 of the Urban Growth Management Functional Plan: Water Quality and Floodplain Management Conservation. Metro, Portland, OR.

Gaines, D. 1974. Review of the status of the yellow-billed cuckoo in California: Sacramento Valley populations. Condor 76:204-209.

Galli, A.E., C. Leck and, R. Forman. 1976. Avian distribution patterns in forest islands of different sizes in central New Jersey. Auk 93:356-64.

Gardner, R., B. Milne, M. Turner, and R. O’Neill. 1987. Neutral models for analysis of broad-scale landscape pattern. Landscape Ecology 1:19-28.

Ghaffarzadeh, M., A. Robinson, and R. Cruse. 1992. Vegetative filter strip effects on sediment deposition from overland flow. Agronomy Abstracts. ASA, Madison, WI.

Gilpin, M., and M. Soulé. 1986. Minimum viable population: Processes of species extinction. Pages 19-34 *in* M. Soulé, ed. Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates, Sutherland, MA.

Gregory, S., G. Lamberti, D. Erman, K. Koski, M. Murphy, and J. Sedell. 1987. Influence of forest practices on aquatic production. Pages 233-255 *in* E. Salo and T. Cundy, eds. Streamside management: Forestry and Fishery Interactions. Coll. Forest Resources Contribution 57. Univ. of Washington, Institute of Forest Resource, Seattle, WA.

Gresswell, R., B. Barton, and J. Kershner, eds. Practical Approaches to Riparian Resource Management: An Educational Workshop. U.S. Bureau of Land Management, Billings, Montana.

Grismer, M. 1981. Evaluating dairy waste management systems influence on fecal coliform concentration in runoff, Masters Thesis. Oregon State University, Corvallis, OR.

Groffman, P., A. Gold, T. Husband, R. Simmons, and W. Eddleman. 1990. An Investigation into Multiple Uses of Vegetated Buffer Strips. Publication No. NBP-90-44. Dept. of Nat. Res. Sci., University of Rhode Island, Kingston, RI.

Gustafson, E., and G. Parker. 1992. Relationships between landcover proportion and indices of landscape spatial pattern. Landscape Ecology 7:101-110.

Haddad, N. 1999. Corridor use predicted from behaviors at habitat boundaries. The American Naturalist 153:215-227.

Haddad, N. 1999. Corridor and distance effects on interpatch movements: A landscape experiment with butterflies. Ecological Applications 9:612-622.

Haddad, N. 2000. Corridor length and patch colonization by a butterfly, Junonia coenia. Conservation Biology 14:738-745.

Haddad, N., and K. Baum. 1999. An experimental test of corridor effects on butterfly densities. Ecological Applications 9:623-633.

Hagar, J. 1999. Influence of riparian buffer width on bird assemblages in western Oregon. Journal of Wildlife Management 63:484-496.

Hannon, S., and F. Schmiegelow. 2002. Corridors may not improve the conservation value of small reserves for most boreal birds. Ecological Applications 12(5):1457-1468.

Hansen, A., D. Urban, and B. Marks. 1992. Avian community dynamics: The interplay of landscape trajectories and species life histories. Pages 170-195 *in* A. Hansen, and F. di Castri, eds. Consequences for Biotic Diversity and Ecological Flows. Springer-Verlag, New York.

Hanski, I. 1994. A practical model of metapopulation dynamics. Journal of Animal Ecology 63:151-162.

Hanski, I., and M. Gilpin. 1991. Metapopulation dynamics: Brief history and conceptual domain. Biological Journal of the Linnean Society 42:3-16.

Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain and application to conservation. Pages 5-26 *in* I. Hanski, and M. Gilpin, eds. Metapopulation Biology: Ecology, Genetics and Evolution. Academic Press, London.

Harris, L. 1984. The Fragmented Forest: Island Biogeography Theory and the Preservation of Biotic Diversity. University of Chicago Press, Chicago, IL.

Harris, R. 1985. Vegetative barriers: An alternative highway noise abatement measure. Noise Control Engineering Journal 27:4-8.

Hartley, M., and M. Hunter, Jr. 1998. A meta-analysis of forest cover, edge effects, and artificial nest predation rates. Conservation Biology 12(2):465-469.

Henderson, M., G. Merriam, and J. Wegner. 1985. Patchy environments and species survival: Chipmunks in an agricultural mosaic. Biol. Cons. 31:95-105.

Hennings, L. 2001. Riparian bird communities in Portland, Oregon: Habitat, urbanization, and spatial scale patterns, Masters Thesis. Oregon State University Department of Fisheries and Wildlife, Corvallis, OR.

Herkert, J. 1994. The effects of habitat fragmentation on midwestern grassland bird communities. Ecological Applications 4(3):461-471.

Herson-Jones, L., M. Heraty, and B. Jordan. 1995. Riparian Buffer Strategies for Urban Watersheds. Metropolitan Washington Council of the Governments, Washington, D.C.

Hewlett, J., and J. Fortson. 1982. Stream temperatures under an inadequate buffer strip in the southeast Piedmont. Water Resources Bulletin 18:983-988.

Hickman, T., and R. Raleigh. 1982. Habitat suitability index models: Cutthroat trout. U.S. Department of Interior, Fish Wildlife Service. FWS/OBS-82/10.5.

Hobbs, R. 1992 (November). The role of corridors in conservation: Solution or bandwagon? Tree 7(11):389-392.

Hobbs, R. 1993. Effects of landscape fragmentation on ecosystem processes in the western Australian wheatbelt. Biological Conservation 64:193-201.

Hoctor, T., M. Carr, and P. Zwick. 2000. Identifying a linked reserve system using a regional landscape approach: The Florida ecological network. Conservation Biology 14(4):984-1000.

Hodges, M., Jr., and D. Krementz. 1996. Neotropical migratory breeding bird communities in riparian forests of different widths along the Altamaha River, Georgia. The Wilson Bulletin 108:496-506.

Holmes, T., R. Knight, L. Stegall, and G. Craig. 1993. Responses of wintering grassland raptors to human disturbance. Wildl. Soc. Bull. 21:461-478.

Hoover, J., M. Brittingham, and L. Goodrich. 1995. Effects of forest patch size on nesting success of wood thrushes. The Auk 112(1):146-155.

Hopkins, P., and N. Webb. 1984. The composition of the beetle and spider faunas on fragmented Calluna-heathland. Journal of Applied Ecology 21:935-946.

Horner, R., and B. Mar. 1982. Guide for Water Quality Impact Assessment of Highway Operations and Maintenance. Report No. WA-RD-39.14. Washington Department of Transportation, Olympia.

Howe, R. 1984. Local dynamics of bird assemblages in small forest habitat islands in Australia and North America. Ecology 65:1585-1601.

Jacobs, T. and J.W. Gilliam. 1985. Riparian losses of nitrate from agricultural drainage waters. Journal of Environmental Quality 14:472-478.

Janzen, D. 1986. The eternal external threat. Pages 286 - 303 *in* M. Soulé, ed. Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates, Sunderland, MA.

Jenkins, S. 1980. A size-distance relation in food selection by beavers. Ecology 61:740-746.

Johnson A., and D. Ryba. 1992. A Literature Review of Recommended Buffer Widths to Maintain Various Functions of Stream Riparian Areas. King County Surface Water Management Division, King County, Washington.

Jones, J., J. Lortie, and U. Pierce, Jr. 1988. The identification and mangement of signiciant fish and wildlife resources in southern coastal Maine. Maine Department of Inland Fish and Wildlife, Augusta.

Joyal, L., M. McCollough, and M. Hunter. 2001. Landscape ecology approaches to wetland species conservation: A case study of two turtle species in southern Maine. Conservation Biology 15(6):1755-1762.

Jules, E. 1998. Habitat fragmentation and demographic change for a common plant: Trillium in old-growth forest. Ecology 79(5):1645-1656.

Karr, J., and I. Schlosser. 1977. Impact of Near Stream Vegetation and Stream Morphoology on Water Quality and Stream Biota. Document No. EPA-600/3-77-097. U.S. Environmental Protection Agency, Athens, GA.

Kasworm, W., and T. Manley. 1990. Road and rail influences on grizzly bears and black bears in northwest Montana. International Conference on Bear Research and Management 8:79-85.

Keller, C., C. Robbins, and J. Hatfield. 1993. Avian communities in riparian forests of different widths in Maryland and Delaware. Wetlands 13:137-144.

Kilgo, J., R. Sargent, B. Chapman, and K. Miller. 1998. Effect of stand width and adjacent habitat on breeding bird communities in bottom-and hardwoods. Journal of Wildlife Management 62:72-83.

Knutson K., and V. Naef. 1997. Management recommendations for Washington's priority habitats: Riparian. Washington Department of Fish and Wildlife, Olympia, WA.

Lamberson, R., R. McKelvey, B. Noon, and C. Voss. 1992. A dynamic analysis of spotted owl viability in a fragmented forest landscape. Conservation Biology 6:505-512.

Lamberson, R., B. Noon, C. Voss, and K. McKelvey. 1994. Reserve design for territorial species: The effects of patch size and spacing on the viability of the northern spotted owl. Conservation Biology 8:185-195.

Lande, R. 1987. Extinction thresholds in demographic models of terrestrial populations. American Naturalist 130:624-635.

Lande, R. 1988. Demographic models of the northern spotted owl (*Strix occidentalis caurina*). Oecologia 75:601-607.

Laurance, W., and E. Yensen. 1991. Predicting the impacts of edge effects in fragmented habitats. Biological Conservation 55:77-92.

Laurence, W., R. Bierregaard, C. Gascon, R. Didham, A. Smith, A. Lynam, V. Viana, T. Lovejoy, K. Sieving, J. Sites, M. Anderson, M. Tocher, E. Kramer, C. Restrepo, and C. Moritz. 1997. Tropical forest fragmentation: Synthesis of diverse and dynamic discipline. Pages 502- 525 *in* W. Laurence and R. Bierregaard, eds. Tropical Forest Remnants: Ecology, Management, and Conservation of Fragmented Communities. University of Chicago Press, Chicago, IL.

Lehtinen, R., S. Galatowitsch, and J. Tester. 1999. Consequences of habitat loss and fragmentation for wetland amphibian assemblages. Wetlands 19(1):1-12.

Lidicker, W.Z. 1999. Responses of mammals to habitat edges: An overview. Landscape Ecology 14:333-343.

Lindenmayer, B., and J. Franklin. 2002. Conserving Forest Biodiversity: A Comprehensive Multiscaled Approach. Island Press, Washington DC.

Lomolino, M., J. Brown, and R. Davis. 1989. Island biogeography of montane forest mammals in the American southwest. Ecology 70:180-194.

Lovejoy, T., and D. Oren 1981. The minimum critical size of ecosystems. Pages 7- 12 *in* R. Burgess and D. Sharpe, eds. Forest Island Dynamics in Man-Dominated Landscapes. Springer-Verlad New York, Inc., New York.

Lovejoy, T., and J. Rankin, R. Bierregaard, K. Brown, L. Emmons, and M. van der Voort. 1984. Extinctions. Pages 295-325 *in* M. Niteki, ed. Ecosystem Decay of Amazon Remnants. University of Chicago Press, Chicago, IL.

Lowrance, R. 1992. Groundwater nitrate and denitrification in a coastal plain riparian forest. Journal of Environmental Quality 21:266-271.

Lowrance, R., R. Todd, J. Fail, O. Hendrickson, R. Leonard, and L. Asmussen. 1984. Riparian forests as nutrient filters in agricultural watersheds. BioScience 34:374-77.

Lynch, J., and D. Whigham. 1984. Effects of forest fragmentation on breeding bird communities in Marlyand, USA. Biol. Cons. 28:287-324.

Lynch, J., E. Corbett, and K. Mussallem. 1985. Best management practices for controlling nonpoint-source pollution on forested watersheds. Journal of Soil and Water Conservation 40:164-167.

Mace, R., J. Waller, T. Manley, L. Lyon, and H. Zuuring. 1996. Relationships among grizzly bears, roads, and habitat in the Swan Mountains, Montana. Journal of Applied Ecology 33:1395-1404.

Madison, C., R. Blevins, W. Frye, and B. Barfield. 1992. Tillage and grass filter strip effects upon sediment and chemical losses. Agronomy Abstracts. ASA, Madison, Wisconsin.

Maestas, J., R. Knight, and W. Gilbert. 2003 (in press). Biodiversity across a rural land-use gradient. Conservation Biology, *in press.*

Master, L., B. Stein, L. Kutner, and G. Hammerson. 2000. Vanishing assets: Conservation status of U.S. species. Pages 92-118 *in* B. Stein, L. Kutner, and J. Adams, eds. Precious Heritage: The Status of Biodiversity in the United States. Oxford University Press, New York.

Matlack, G. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. Biological Conservation 66:185-194.

Mattson, D. 1990. Human impacts on bear habitat use. International Conference on Bear Research and Management 6:105-110.

Mattson, D., R. Knight, and B. Blanchard. 1987. The effects of developments and primary roads on grizzly bear habitat use in Yellowstone National Park, Wyoming. International Conference on Bear Research and Management 7:259-273.

May, C. 2000. Protection of stream-riparian ecosystems: A review of the best available science. Pages B2-B51 *in* Kitsap County. Kitsap Peninsula Salmonid Refugia Study. Port Orchard, Washington.

McDade, J., F. Swanson, W. McKee, J. Franklin, and J. Van Sickle. 1990. Source distances for coarse woody debris entering small streams in western Oregon and Washington. Canadian Journal of Forest Research 20:326-330.

McGarigal, K. 2003. "Landscape Structure and Spatial Pattern Analysis for ARC/INFO." <www.innovativegis.com/products/fragstatsarc/aboutlc.htm> (24 February 2003).

McGarigal, K. and W. McComb. 1992. Streamside versus upslope breeding bird communities in the central Oregon Coast Range. Journal of Wildlife Management 56:10-23.

McGarigal, K., and S. Cushman. 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. Ecological Applications 12:335-345.

McIntyre, N. 1995. Effects of forest patch size on avian diversity. Landscape Ecology 10(2):85-99.

McLellan, B., and D. Shackleton. 1988. Grizzly bears and resource extraction industries: Effects of roads on behavior, habitat use and demography. Journal of Applied Ecology 25:451-460.

Meffe, G., and C. Caroll. 1997. Principles of Conservation Biology, 2nd Edition. Sinauer Associates, Sunderland, MA.

Meier, A., S. Bratton, and D. Duffy. 1995. Possible ecological mechanisms for loss of vernal-herb diversity in logged eastern deciduous forests. Ecological Applications 5:935-946.

Metro Regional Services. 2001 (August). Metro's Scientific Literature Review for Goal 5. Metro, Portland, Oregon.

Meyer, C., and S. Miller. 2002 (June). Use of fragmented landscapes by marbled murrelets for nesting in southern Oregon. Conservation Biology 16(3):755-766.

Miller, S., R. Knight, and C. Miller. 1998. Influence of recreational trails on breeding bird communities. Ecological Applications 8(1):162-169.

Miller, S., R. Knight, and C. Miller. 2001. Wildlife responses to pedestrians and dogs. Wildlife Society Bulletin 29(1):124-132.

Milligan, D. 1985. The Ecology of Avian Use of Urban Freshwater Wetlands in King County, Washington, Masters Thesis, University of Washington, Seattle.

Mills, L. S. 1996. Fragmentation of a natural area: Dynamics of isolation for small mammals on forest remnants. Pages 199-218 *in* R. Wright, ed. National Parks and Protected Areas: Their role in Environmental Protection. Blackwell Sci. Pub. Cambridge, MA.

Mitchell, F. 1996. Vegetated buffers for wetlands and surface waters: Guidance for New Hampshire municipalities. Wetlands Journal 8:4-8.

Mitchell, C., M. Turner, and S. Pearson. 2002. Effects of historical land use and forest patch size on mymechores and ant communities. Ecological Applications 12(5):1364-1377.

Mitsch, W., and J. Gosselink. 1993. Wetlands, 2nd Edition. Van Nostrand Reinhold, New York.

Mönkkönen, M., and P. Reunanen. 1999. On critical thresholds in landscape connectivity: A management perspective. Oikos 84(2):302-305.

Moring, J. 1982. Decrease in stream gravel permeability after clear-cut logging: An indication of intragravel conditions for developing salmonid eggs and alevins. Hydrobiologia 88:295-298.

Morris, W., P. Bloch, B. Hudgens, L. Moye, and J. Stinchcombe. 2002. Population viability analysis in endangered species recovery plans: Past use and future improvements. Ecological Applications 12(3):708-712.

Mudd, D. 1975. Touchet River Wildlife Study, Bulletin No. 4. Applied Research Section, Environmental Management Division, Washington Game Department.

Murcia, C. 1995. Edge effects in fragmented forests: Implications for conservation. Trends Ecological Evolutions 10:58-62.

Murphy, D., and S. Weiss. 1988. Ecological studies and the conservation of the Bay checkerspott butterfly, *Euphydryas editha bayensis*. Biological Conservation 46:183-200.

Murphy, D., and B. Noon. 1992. Integrating scientific methods with habitat conservation planning: Reserve design for northern spotted owls. Ecological Applications 2:3-17.

Naiman, R., H. Décamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecological Applications 3(2):209-212.

National Invasive Species Council (NISC). 2001 (January). Management Plan: Meeting the Invasive Species Challenge. National Invasive Species Council, Washington, D.C.

National Research Council (NRC). 2002. Riparian Areas: Functions and Strategies for Management. National Academy Press, Washington, DC.

National Resources Conservation Service (NRCS). 1995. Riparian Forest Buffers. U.S. Department of Agriculture, Washington, DC.

Naugle, D., K. Higgins, S. Nusser, and W. Johnson. 1999. Scale-dependent habitat use in three species of prairie wetland birds. Landscape Ecology 14:267-276.

Naugle, D., R. Johnson, M. Estey, and K. Higgins. 2001. A landscape approach to conserving wetland bird habitat in the prairie pothole region of eastern South Dakota. Wetlands 21:1-17.

Nelson, S., and T. Hamer 1995. Nest success and the effects of predation on marbled murrelets. Pages 89-97 *in* C. Ralph, G. Hunt, M. Raphael, and J. Piatt, eds. Ecology and Conservation of the Marbled Murrelet, General Technical Report PSW-GTR-152. U.S. Forest Service, Albany, CA.

Newbold, J., D. Erman, and K. Roy. 1980. Effect of logging on macroinvertebrates in streams with and without buffer strips. Can. J. Fish. Aquat. Sci. 37:1076-1085.

Nichols, D., T. Daniel, D. Edwards, P. Moore, and D. Pote. 1998. Use of grass filter strips to reduce 17-estradiol in runoff from fescue-applied poultry litter. Journal of Soil and Water Conservation 53:74-77.

Nieswand, G., R. Hordon, T. Shelton, B. Chavooshian, and S. Blarr. 1990. Buffer strips to protect water supply reservoirs: A model and recommendations. Water Resources Bulletin 26(6):959-966.

Nilsson, S. 1978. Fragmented habitat, species richness and conservation practice. Ambio 7:26-27.

Nilsson, S. 1986. Are bird communities in small biotope patches random samples from communities in large patches? Biol. Cons. 38:179-204.

Norris, D., and B. Stutchbury. 2001. Extraterritorial movements of a forest songbird in a fragmented landscape. Conservation Biology 15(3):729-736.

Noss, R. 1987. Corridors in real landscapes: A reply to Simberloff and Cox. Conservation Biology 1:159-164.

Noss, R. 1991. Landscape connectivity: Different functions at different scales. Pages 27-40 *in* W. Hudson, ed. Landscape Linkages and Biodiversity. Defenders of Wildlife, Washington, DC.

Noss, R., and L. Harris. 1986. Nodes, networks, and MUMs: Preserving diversity at all scales. Environ. Management 10:299-309.

Noss, R., and A.Cooperrider. 1994. Saving Nature's Legacy: Protecting and Restoring Biodiversity. Island Press, Washington, DC.

Odell, E., and R. Knight. 2001. Songbird and medium-sized mammal communities associated with exurban development in Pitkin County, Colorado. Conservation Biology 15(4):1143-1150.

O'Laughlin, J., and G. Belt. 1995. Functional approaches to riparian buffer strip design. Journal of Forestry 93(2):29-32.

Osborne, L., and D. Kovacic. 1993. Riparian vegetated buffer strips in water-quality restoration and stream management. Freshwater Biology 29:243-258.

Paton, P. 1994. The effect of edge on avian nest success: How strong is the evidence? Conservation Biology 8:17-26.

Pearson, S., and D. Manuwal. 2001. Breeding bird response to riparian buffer width in managed pacific northwest Douglas-Fir forests. Ecological Applications 11:840-853.

Petersen, R., L. Deusen, S. M. Keller, and P. A. Knudsen. 1989. A new approach to riparian management in Washington state. Pages 11-15 *in* R. Gresswell, B. Barton, and J. Kershner, eds. Practical Approaches to Riparian Resource Management: An Educational Workshop. U.S. Bureau of Land Management, Billings, Montana.

Pienkowski, M., and A. Watkinson. 1996. The Application of Ecology. Journal of Applied Ecology 33:1-4.

Poiani, K., and B. Richter. 2000. Functional landscapes and the conservation of biodiversity. Working Papers in Conservation Science. The Nature Conservancy, Conservation Science Division. <http://www.conserveonline.org/2000/11/b/en/WP1.pdf>

Pollock, M., and P. Kennard. 1998. A Low-Risk Strategy for Preserving Riparian Buffers Needed to Protect and Restore Salmonid Habitat in Forested Watersheds of Washington State, Version 1.1. 10,000 Years Institute, Bainbridge Island, Washington.

Potter, M. 1990. Movement of North Island brown kiwi (*Apteryx austalis mantelli*) between forest fragments. New Zealand Journal of Ecology 14:17-24.

Primack, R. 1993. Essentials of Conservation Biology. Sinauer Associates, Sutherland, MA.

Pringle, C. 2001. Hydrologic connectivity and the management of biological reserves: A global perspective. Ecological Applications 11(4):981-998.

Pulliam, H. 1988. Sources, sinks and population regulation. American Naturalist 132:652-661.

Pulliam, H., J. Dunning, and J. Liu. 1992. Population dynamics in complex landscapes: A case study. Ecological Applications. 2:165-177.

Raleigh, R. 1982. Habitat Suitability Index Models: Brook Trout. FWS/OBS-82/10.24. U. S. Department of Interior, U.S. Fish and Wildlife Service.

Raleigh, R., Hickman, R. Solomon, and P. Nelson. 1984. Habitat Suitability Information: Rainbow Trout. FWS/OBS082/10.60. U.S. Department of Interior, Fish and Wildlife Service.

Raleigh, R., W. Miller, and P. Nelson. 1986. Habitat Suitability Index Models: Chinook Salmon. FWS/OBS-82/10.122. U.S. Department of Interior, Fish and Wildlife Service.

Ranney, J., M. Bruner, and J. Levenson, 1981. The importance of edge in the structure and dynamics of forest islands. Pages 68-95 *in* R. Burgess and D. Sharpe, eds. Forest Island Dynamics In Man Dominated Landscapes. Springer, New York.

Richardson, C., and C. Miller. 1997. Recommendations for protecting raptors from human disturbance: A review. Wildlife Society Bulletin 25:634-638.

Richter, K., and A. Azous. 1995. Amphibian occurrence and wetland characteristics in the Puget Sound Basin. Wetlands 15:305-312.

Rieman, B., and J. McIntyre. 1995. Occurrence of bull trout in naturally fragmented habitat patches of varied size. Transactions of the American Fisheries Society 124:285-296.

Robbins, C., D. Dawson, and B. Dowell. 1989. Habitat area requirements of breeding forest birds of the middle Atlantic states. Wildlife Monographs 103:1-34.

Roby, K., D. Erman, and J. Newbold. 1977. Biological Assessment of Timber Management Activity Impacts and Buffer Strip Effectiveness on National Forest Streams of Northern California. USDA Forest Service, California Region.

Rodewald, A., and R. Yahner. 2001. Influence of landscape composition on avian community structure and associated mechanisms. Ecology 82(12):3493-3504.

Rodgers, J., and H. Smith. 1997. Buffer zone distances to protect foraging and loafing waterbirds from human disturbance in Florida. Wildlife Bulletin Society 25:139-145.

Rosenburg, D., B. Noon, and E. Meslow. 1997. Biological corridors: Form, function, and efficacy. Bioscience 47:677-687.

Rudolph, D., and J. Dickson. 1990. Streamside zone width and amphibian and reptile abundance. The Southwest Journal 35(4):472-476.

Ruggiero, L., G. Hayward, and J. Squires. 1994. Viability analysis in biological evaluations: Concepts of population viability analysis, biological population, and ecological scale. Conservation Biology 8(20):364-372.

Saunders, D., R. Hobbes, and C. Margules. 1991. Biological consequences of ecosystem fragmentation: A review. Conservation Biology 5:18-31.

Schaefer, J., M. Brown, R. Hamann, and J. Tucker. 1991. A natural resources management and protection plan for the Econlockhatchee River Basin. Pages 145-150 *in* L. Adams and D. Leedy, eds. Wildlife Conservation in Metropolitan Environments, National Institute for Urban Wildlife, Columbia, MD.

Schellinger, G., and J. Clauses. 1992. Vegetative filter treatment of dairy barnyard runoff in cold region. Journal of Environmental Quality 21:40-45.

Schmiegelow, K.., C. Machtans, and S. Hannon. 1997. Are boreal birds resilient to forest fragmentation? An experiment study of short-term community responses. Ecology 78:1914-1932.

Semlitsch, R. 1998. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. Conservation Biology 12:1113-1119.

Shisler, J., R. Jordan, and R. Wargo. 1987. Coastal wetland buffer delineation. New Jersey Department of Environmental Protection, Trenton, NJ.

Simberloff, D., and J. Cox. 1987. Consequence and costs of conservation corridors. Conservation Biology 1:63-71.

Simberloff, D., J. Farr, J. Cox, and D. Mehlman. 1992. Movement corridors: Conservation bargains or poor investments. Conservation Biology 6:493-504.

Skagen, S., C. Melcher, W. Howe, and F. Knopf. 1998. Comparative use of riparian corridors and oases by migrating birds in southeast Arizona. Conservation Biology 12:896-909.

Small, M. 1982. Wildlife management in riparian habitats. Publication of the Maine Agricultural Experimental Station, Orono, ME.

Smith, A. 1974. The distribution and dispersal of pikas: Consequences of insular population structure. Ecology 55:1112-1119.

Smith, A. 1980. Temporal changes in insular populations of the pika (*Ochotona prineps*). Ecology 61:8-13.

Soulé, M. 1991. Land use planning and wildlife maintenance: Guidelines for conserving wildlife in an urban landscape. Journal of the American Planning Assoc. 57(3):313-323.

Soulé, M., D. Bolger, A. Alberts, R. Sauvajot, J. Wright, M. Sorice, and S. Hill. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. Conservation Biology 2:75-92.

Soulé, M., A. Alberts, and D. Bolger. 1992. The effects of habitat fragmentation on chaparral plants and vertebrates. Oikos 63:39-47.

Spackman, S., and J. Hughes. 1995. Asessment of minimum stream corri dor width for biological conservation: Species richness and distribution along mid-order streams in Vermont. Biol. Conserv. 71:325-332.

Spence, B., G. Lomnicky, R. Hughes, and R. Novitzki. 1996. An ecosystem approach to salmonid conservation. TR-4501-96-6057. ManTech Environmental Research Services Corp, Corvallis, OR.

Stauffer, D. and L. Best. 1980. Habitat selection by birds of riparian communities: evaluating effects of habitat alterations. Journal of Wildlife Management 44(1):1-15.

Steinblums, I., H. Froehlich, and J. Lyons. 1984. Designing stable buffer strips for stream protection. Journal of Forestry 82:49-52.

Stevens, G. 1989. The latitudinal gradient in geographic range: How so many species coexist in the tropics. Am. Nat. 133:240-256.

Stewart, J., D. Downes, L. Wang, J. Wierl, and R. Bannerman. 2000 (August). Influences of riparian corridors on aquatic biota in agricultural watersheds. Pages 209-214 *in* P.J. Wigington and R. L. Beschta, eds. International Conference on Riparian Ecology and Management in Multi-Land Use Watersheds, American Water Resources Association, Portland, OR.

Summerville, K., and T. Crist. 2001. Effects of experimental habitat fragmentation on patch use by butterflies and skippers (lepidoptera). Ecology 82:1360-1370.

Tassone, J. 1981. Utility of hardwood leave strips for breeding birds in Virginia's central piedmont, Masters Thesis. Virginia Polytechnic Institute and State University, Blacksburg, VA.

The Keystone Center. 1991. Final Consensus Report of the Keystone Policy Dialogue on Biological Diversity on Federal Lands. The Keystone Center, Keystone, Colorado.

The Nature Conservancy (TNC). 1998. Northern Appalachian/Boreal Ecoregion Plan. *Unpublished.*

Todd, A. 2000 (August). Making decisions about riparian buffer width. Pages 445-450 *in* P.J. Wigington and R. L. Beschta, eds. International Conference on Riparian Ecology and Management in Multi-Land Use Watersheds, American Water Resources Association, Portland, OR.

Trine, C. 1998. Wood thrush population sinks and implications for the scale of regional conservation strategies. Conservation Biology 12(3):576-585.

Triquet, A., G. McPeek, and W. McComb. 1990. Songbird diversity in clearcuts with and without riparian buffer strip. Journal of Soil and Water Conservation 45:500-503.

Tscharntke, T., I. Steffan-Dewenter, A. Kruess, and C. Thies. 2002. Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. Ecological Applications 12(2):354-363.

USDA Soil Conservation Service (SCS). 1982. Filter strip (acre). Filter Strip 393.

U.S. Fish and Wildlife Service (USFWS). 1994. “Ecosystems.” <http://daphne.fws.gov/ecosystem/ecosystem.htm> (24 February 2003).

U.S. Geological Survey. 1998. Status and Trends of the Nation’s Biological Resources, Volume 1. U.S. Department of the Interior, U.S. Government Printing Office, Washington, D.C.

Vander Haegen, W., and R. Degraaf. 1996. Predation on artificial nests in forested riparian buffer strips. Journal of Wildlife Management 60:542-550.

Villard, M. 2002. Habitat fragmentation: Major conservation issue or intellectual attractor? Ecological Applications 12(2):319-320.

Washington Department of Ecology (WDOE). 1981. Western Washington urban stream assessment. Washington Department of Ecology, Office of Water Programs, Water Quality Planning, Olympia, WA.

Weaver, J., P. Paquet, and L. Ruggiero. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. Conservation Biology 10(4):964-976.

Weddell, B. 1991. Distribution and movements of Columbian ground squirrels (*Spermophilus columbianus (Ord)*): Are habitat patches like islands? Journal of Biogeography 18:385-394.

Weins, J. 1989. Spatial scaling in ecology. Functional Ecology 3:385-397.

Weller, D., T. Jordan, and D. Correll. 1998. Heuristic models for material discharge from landscapes with riparian buffers. Ecological Applications 8:1156-1169.

Wenger, S. 1999 (March 5). A Review of the Scientific Literature on Riparian Buffer Width, Extent and Vegetation. Institute of Ecology, University of Georgia, Athens, GA.

Whitcomb, R., C. Robbins, J. Lynch, B. Whitcomb, M. Klimkiewicz, and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of the eastern deciduous forest. Pages 125-205 *in* R. Burgess, and M. Sharpe, eds. Forest Island Dynamics in Man-Dominated Landscapes. Springer, New York.

Wiens, J., R. Schooley, and R. Weeks, Jr. 1997. Patchy landscapes and animal movements: Do beetles percolate? Oikos 78:257-264.

Wilcove, D., C. McLellan, and A. Dobson. 1986. Habitat fragmentation in the temperate zone. Pages 237-256 *in* M. Soulé, ed. Conservation Biology: The Science of Scarcity and Diversity. Sinauer Associates, Sunderland, MA.

Wilcove, D., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. BioScience 48:607-615.

Wilson, L. 1967. Sediment removal from flood water by grass filtration. Transactions of the American Society of Agricultural Engineers 10(1):35-37.

With, K. 1997. The application of neutral landscape models in conservation biology. Conservation Biology 11:1069-1080.

With, K., and T. Crist. 1995. Critical thresholds in species responses to landscape structure. Ecology 76:2446-2459.

With, K., D. Pavuk, J. Worchuck, R. Oates, and J. Fisher. 2002. Threshold effects of landscape structure on biological control in agroecosystems. Ecological Applications 12(1):52-65.

Woodard, S., and C. Rock. 1995. Control of residential stormwater by natural buffer strips. Lake and Reservoir Management 11:37-45.

Young, R., T. Huntrods, and W. Anderson. 1980. Effectiveness of vegetated buffer strips in controlling pollution from feedlot runoff. Journal of Environmental Quality 9:483-497.

Zeigler, B. 1988. Interdepartmental Report–Wetland Buffers: Essential for Fish and Wildlife. Habitat Management Division, Washington State Department of Wildlife, Olympia, WA.

APPENDIX A. FURTHER ANALYSIS

Titles and abstracts of 1,458 papers within scientific and land use planning journals were reviewed to determine whether they provide specific information on conservation thresholds that could help guide land use planning in the United States. A total of 160 papers (11 percent) were selected for inclusion in this study: 20 papers with quantitative information on minimum patch area; 27 papers on minimum proportion of suitable habitat; 25 papers on edge width distance; and 88 papers on minimum buffer width.[30]

A CLOSER LOOK AT HABITAT PATCH SIZE

Only 20 papers were found in the scientific literature to provide specific information on minimum patch area requirements pertaining to ecoregions within the United States; these papers provided 28 citations on threshold patch size.[31] The majority of papers that address habitat patch size focus primarily on estimating the area of habitat needed to sustain specific target species—as measured by species occurrence, population densities, or breeding success—and to a lesser extent species diversity or community assemblages. As reported in previous literature reviews, little is known about the amount of patch area needed to maintain essential ecosystem functions, such as primary productivity, nutrient and hydrologic cycling, or disturbance regimes (Forman 1995).

This survey reveals a taxonomic bias in scientific literature. Out of the total 28 citations, 16 citations (57 percent) pertain to birds and six citations (21 percent) to mammals. Minimum patch area requirements reported in the literature ranged from one hectare to over 2,500 hectares for birds, and from one hectare to over 220,000 hectares for mammals. Only two studies provide three relevant citations on patch size requirements for plant species: an estimated two hectares needed to sustain a representative tree community type (Elfstrom 1974), and at least 10 hectares needed to conserve an old growth forest if surrounded by secondary forest, or 100 hectares if surrounded by clearcuts (Harris 1984). Two additional studies provide patch area information for invertebrates, which indicate that habitat requirements for invertebrates may range from a minimum of 0.0004 hectares (four meters squared) up to one hectare. One study provides information for fishes, predicting a 50 percent chance of bull trout occurrence in watershed patches larger than 2,500 hectares (Rieman and McIntyre 1995).

Reported habitat patch size thresholds vary widely, even within the same taxonomic group and for the same species. This lack of convergence on minimum critical patch size reflects the large range of habitat needs exhibited by different species across different ecosystems and that species response to habitat fragmentation is very complex. This natural and inherent complexity is compounded by the lack of consistency in methodology researchers used to measure minimum habitat requirements—with differing study designs as well as parameters measured. Minimum patch area is commonly determined for target species by measuring species occurrence on a site, species densities, or nesting/breeding success. To a lesser extent studies evaluate the persistence of species diversity or community assemblages. Since different parameters are measured, different results are produced. For example, according to this survey, neotropical wood thrushes require anywhere from one hectare up to greater than 2,500 hectares of habitat depending on the variable measured (evidence of breeding versus nesting success and occurrence of nesting predation) (Robbins et al. 1989 and Trine 1998).

By in large, this review reiterates a viewpoint expressed by the scientific community several years ago: simply not enough is known about minimum critical size that should be protected in order to maintain species diversity and species composition in any given ecosystem (Lovejoy and Oren 1981 *as cited in* Saunders et al. 1991; Noss and Harris 1986). Given the lack of information on the habitat patch size requirements of species, communities, or ecosystems in the United States, land use planners should work with land and natural resource agencies and local scientists to identify the habitat patches most in need of protection.

A CLOSER LOOK AT PROPORTION OF SUITABLE HABITAT

Twenty-seven papers were encountered within the scientific literature reporting extinction or habitat fragmentation thresholds on the proportion of suitable habitat needed for an array of species. The papers surveyed provide 26 different estimates of the amount of habitat needed, depending on the species and taxa in question, and the parameter measured. The majority of findings—42 percent (11 citations)—relate to the amount of habitat recommended to maintain bird

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[30] These numbers only include papers that provided specific threshold information, which was factored into the assessment (see Appendices). Review papers and background papers are not included in these figures if they failed to provide relevant quantitative information.

[31] Because papers provide multiple findings/recommendations related to minimum patch area size requirements, the number of papers does not necessarily equal the number of citations.

species or populations. Based on this review, bird species in the United States may require anywhere from 5 percent to 80 percent of suitable remaining habitat.

The second most commonly researched group is mammals. About 23 percent of the findings (six citations) pertained to mammalian response to habitat loss and habitat isolation, which suggests that this taxonomic group may require anywhere from 6 percent to 30 percent of suitable habitat. This range, however, should not be considered representative for all mammalian groups, because it only includes small mammals (e.g., chipmunks, rabbits, squirrels) (*see* Appendix C). An important focal group—wide-ranging predators and large-bodied mammals—failed to be represented in this select review, thus, the proportions are skewed to the smaller range relevant to smaller bodied mammals.

Four studies (five citations) provide thresholds for invertebrates, ranging from 20 percent up to 60 percent of required protected habitat. Additionally, four studies base their findings on models predicting response by hypothetical species, which reveal that threshold responses may occur anywhere from as large a range as 20 percent to 90 percent of habitat loss.

As revealed by the diverse range of values offered by scientists, it is clear that no common threshold exists for the amount of habitat needed to support different populations of species or needed to minimize the negative effects of habitat fragmentation in a landscape. The lower range of proportions (e.g., 5 to 30 percent) tend to be habitat fragmentation thresholds, as determined by evidence that species are in some way negatively affected by habitat loss or habitat isolation. A significant proportion of these studies is based on predicted species response to habitat loss and fragmentation by models (at least seven of the citations). The larger proportions (e.g., 60 to 80 percent) tend to be based on models that predict the amount of habitat needed to sustain long-term species persistence or to prevent the consequences of extensive habitat fragmentation in a landscape.

Given the sparse and diverse findings, land use planners should apply these thresholds with great caution. As reported in earlier reviews, most of the habitat fragmentation studies are performed during short time periods (e.g., one or two seasons), and only provide a snap shot of how species may respond to habitat loss and isolation (Andrén 1994). In these studies, the damage to populations resulting from habitat alteration could have occurred previously (Mönkkönen and Reunanen 1999)—particularly for historically modified landscapes like eastern deciduous forests (Meier et al. 1995, Mitchell et al. 2002). Thus, the long-term consequences of fragmentation are likely not revealed in this select review because a time lag often exists between the fragmentation of a landscape and the associated response by species, populations, or systems (Andrén 1994).

CLOSER LOOK AT EDGE INFLUENCE

Twenty-five studies surveyed provide 32 findings on the distance that edges might affect habitats in the United States. Like the other conservation thresholds, the focal species of choice is birds. Sixty-six percent of the findings (21 citations within 12 articles) measure the influence of edges related to bird response, revealing that edge influence for birds extends anywhere from about 16 meters to up to almost 700 meters. Studies measuring bird or bird nest abundance report that edge effects extend between 180 and 687 meters where as those measuring predation and nesting success range from 50 to beyond 600 meters. Bird response (e.g., flushing distance) to disturbances such as roads and human traffic extends from 16.27 meters to 300 meters.

Secondarily, the influence of edges is measured by abiotic responses. Edge effects based on microclimate conditions —such as changes in light, temperature, humidity, nutrients, and moisture—are found to extend from eight meters up to 240 meters based on five studies (six citations) (Ranney et al. 1981, Laurance and Yensen 1991, Brothers and Spingarn 1992, Matlack 1993, and Chen et al. 1995).

To a lesser extent, the scientific literature provides information on the effects of edges on mammals and plants. Three studies have found that mammals avoid edge environments from at least 45 meters to 900 meters. For example, studies reveal that wide-ranging grizzly bears are displaced from 100 to 900 meters due to traffic along roadways (Mills 1996, Miller et al. 2001, and Weaver et al. 1996). One study provides evidence on the influence of edges on plant communities, finding that almost no recruitment of seedlings occurs within 65 meters of forest clear-cut edges in Oregon (Jules 1998).

Within this review, no single study is found to report edge influence in relation to invertebrate communities in the United States. As is true for the other thresholds, research has been conducted more extensively in tropical forests outside of the United States, and may serve to address knowledge gaps. For example, a study in Brazil reveals that edge effects may be more intense for invertebrate groups. Edge effects may penetrate up to 50 meters as measured by bird density; 80 meters as measured by soil moisture; 100 meters as measured by canopy height, foliage density, and leaf-litter invertebrate abundance and richness; 200 meters as measured by leaf-litter invertebrate species composition and invasion of disturbance adapted beetles; and 250 meters for invasion of disturbance-adapted butterflies (Laurance et al. 1997).

To get a better handle on the intensity of edge influence in the United States and, consequently, the amount of habitat needed to reduce the effects of edges and related disturbances, land use planners will need more site-specific guidance from ecologists. Land use planners and land managers will also need more information on effective measures that can be taken to better "soften" the many different types of edges affecting the large array of habitat types in the United States.

A CLOSER LOOK AT BUFFER WIDTH

Eighty-eight papers (156 citations) are found to provide recommendations on riparian buffer widths.[32] Of all the conservation thresholds surveyed, buffer prescriptions are the most studied and best documented. Substantial research has been conducted on the effective size of buffers, particularly related to water quality considerations, to assist regulatory and land management agencies in developing scientifically sound minimum buffer width (Castelle et al. 1994). Several literature reviews have been conducted to help inform state and local governments in developing riparian protection plans and ordinances (*see* Johnson and Ryba 1992, Furfey et al. 1997, Wenger 1999, Fischer 2000, Fischer et al. 2000, and Metro 2001). In April 2000, the U.S. Army Corp of Engineers released national recommendations for riparian buffer strip and riparian corridor design (Fischer and Fischenich 2000). This baseline research significantly informed the buffer width recommendations in this report.

One review offers the following buffer prescriptions: a three to 10 meter buffer to provide detrital input; 10 to 20 meters for stream stabilization; five to 30 meters for water quality protection; 20 to 150 meters for flood attenuation; and 30 to 500 meters or more for riparian habitat (Fischer and Fischenich 2000). The Institute's review reveals wider buffer ranges to provide a variety of functions, with a range of six to 32 meters to reduce noise and wind damage; 10 to 52 meters to stabilize stream banks; three to 80 meters to provide detrital input; four to 92 meters to remove nutrients and pollutants; three to 122 meters to remove sediments; 20 to 150 meters to provide flood attenuation; 10 to 300 meters to regulate temperature and microclimate; and three to 1600 meters to provide wildlife habitat (*see* Appendix E).

Findings in this review primarily relate to river and stream systems, however, a small number of papers explicitly address wetlands (*see* Buhlmann 1998 and Joyal et al. 2001). Although not all wetlands lie within riparian zones (e.g., isolated wetlands), they serve as vital resources and provide essential functions, such as flood storage, water purification, sediment trapping, and wildlife habitat (Mitsch and Gosselink 1993). Thus, placing buffers around these areas to protect them from nearby development activities is also advised.

Predicting the adequacy of a buffer strip to provide sufficient wildlife habitat and to protect natural species diversity is quite challenging. The width recommendations primarily focus on birds and are based on various methods—ranging from determining species presence or nesting within the area to determining species abundance, diversity, or community assemblages. Few studies attempt to measure species survival over time; thus, it is questionable whether the recommended buffers will ensure persistence of the target species and communities over the long-term.

As mentioned above, the actual effective size and adequacy of any given buffer is determined by the management target, as well as other site-specific factors, such as site and watershed conditions; intensity of adjacent land use; slope steepness; stream order; soil characteristics (depth, texture, erodibility, moisture, pH); floodplain size and frequency of inundation; hydrology; buffer characteristics (e.g., type, density, and structure of vegetation, and buffer length); and landowner/manager objectives (Naiman et al. 1993, Castelle et al. 1994, Wenger 1999, Todd 2000). For example, larger buffers may be necessary when the buffer strip is in poor condition (e.g., comprised of sparse exotic vegetation, disturbed/erodible soils); is located on steep bank slopes (e.g., greater than 10 percent to 15 percent);[33] is surrounded by intense land uses; or is located within watersheds with increased impervious surfaces that results in high nutrient, chemical, and sediment inputs, and runoff (e.g., adjacent to urban/suburban areas or intensive agricultural farmland). Such factors should be considered when evaluating the applicability of the general recommended buffer sizes (*see* Wenger 1999, Fischer and Fischenich 2000, Metro 2001). In addition, management decisions should not only be based on site-specific characteristics but also on basin or watershed level needs to maintain the hydrologic connectivity and natural variability of these systems (Naiman et al. 1993, Pringle 2001). [34]

A CLOSER LOOK AT CORRIDORS

To determine whether or not corridors are effectively enhancing species conservation, scientists evaluate whether (and how) patch occupancy, species abundance and diversity, colonization, and immigration rates change with and without the presence of corridors (Beier and Noss 1998).

Many studies lend support to the premise that corridors retain important species or provide faunal habitat (Bennett 1998). Few studies, however, provide clear evidence that corridors are required for species movement in landscapes (Hobbs 1992). Many species simply do not respond or require corridors (Rosenburg et al. 1997, Bowne et al. 1999, Hannon and Schmiegelow 2002). For example, male-hooded warblers preferentially travel across open areas, even in

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[32] Some papers recommend multiple buffer widths, for example, they may suggest different widths for different species or functions of concern. Thus, the number of papers does not equal the number of citations.

[33] Herson-Jones et al. 1995 (found that greater than 10 percent slopes are steep slopes) and Nieswand et al. 1990 (found that greater than 15 percent slopes are steep) (as cited in Wenger 1999).

[34] Hydrologic connectivity refers to water-mediated transfer of matter, energy, or organisms within or between elements of the hydrologic cycle (Pringle 2001).

landscapes with corridors connecting habitat patches (Norris and Stutchbury 2001). For species like the Northern spotted owl, which has been found to disperse randomly, the presence of corridors will likely not enhance its survival (Murphy and Noon 1992 *as cited in* Lindenmayer and Franklin 2002). Because of the complexity of animal behavior, land use planners should not assume that establishing corridors between habitat patches in a region will automatically guarantee enhanced and effective dispersal and recolonization among the separated wildlife populations.

The benefits of corridors should be weighed against their potential repercussions. Scientists warn that corridors may potentially transmit diseases, fires, or other catastrophes among habitats and populations, as well as increase invasions by non-native invasions or exposure to predation (Simberloff and Cox 1987, Noss 1991, Noss and Cooperrider 1994). To add to the complexity of this issue, many corridor studies—both those that claim corridor benefits and those that claim costs—suffer from design flaws that limit their ability to discern the real conservation value of corridors (Beier and Noss 1998).

A recent scientific review is able to shed some light on the corridor controversy; a review by Beier and Noss (1998) presents evidence from well-designed studies that suggest that corridors seem to be providing sufficient connectivity to enhance the viability of wildlife populations. Conversely, a lack of evidence backs the assertion that the presence of corridors actually has a greater adverse impact than their absence (Beier and Noss 1998, Hobbs 1992). Although wildlife corridors should not be automatically assumed to be an essential component of all land conservation strategies (Lindenmayer and Franklin 2002), planners should consider corridors as one potentially valuable conservation tool (Beier and Noss 1998, Hobbs 1992).

APPENDIX B. MINIMUM PATCH AREA

Minimum patch area requirements (in hectares) found within the scientific literature (as of December 2001) to maintain populations or communities of animal or plant species in the United States. One hectare is about 2.5 acres.

TAXA	PATCH AREA	FINDING	STATE	CITATION
Birds				
	≥ 1 ha	Minimum area requirement for breeding wood thrushes is 1 ha, although nesting success on fragments of that size would be extremely low.	MD, PA, VA, WV	Robbins et al. 1989
	> 1	Five species of chaparral-requiring birds were supported by census plots larger than 1 ha.	CA	Soulé et al. 1992
	≥ 2 ha (seed-eating birds) ≥ 40 ha (insect-eating birds)	The minimum area point[1] for insect-eating birds was estimated to be at least 40 ha, in contrast to 2 ha for seed-eating birds. This is interpreted as the habitat size needed to support a representative bird community.	NJ	Forman et al. 1976[2] Galli et al. 1976[2]
	≥ 5 ha (marsh)	Ten of the 25 species did not occur in marshes less than 5 ha.	IA	Brown and Dinsmore 1986
	≥ 5, ≥ 30, ≥ 40, ≥ 50, ≥ 55 ha	Estimates of minimal area requirements for five area-sensitive species ranged from 5 to 55 ha.	IL	Herkert 1994
	≥ 6.5 ha, 15.4 -32.6 ha	Black tern required 6.5 ha in heterogeneous landscapes, but required 15.4 - 32.6 ha in homogeneous landscapes.	SD	Naugle et al. 1999
	≥ 10 ha (forest)	Forest patches ≥ 10 ha had much greater bird diversity than patches < 3.25 ha	GA	McIntyre 1995
	> 80 ha	In fragments < 80 ha, nesting success was low (43%), and nest predation was high (56%).	PA	Hoover et al. 1995
	< 20 ha, >2500 ha	Based on a study of cowbird parasitism and nest predation on 3 large forest tracts (1100 - 2200 ha) in southern Illinois, maintaining wood thrush populations in the midwest might require > 2500 ha reserves. In the east even a small woodlot (< 20ha) may sustain a population.	IL	Trine 1998
Mammals				
	> 1 ha	Control plots larger than 1 ha supported most species of rodents.	CA	Soulé et al. 1992
	≥ 5 ha	Cottontails may become vulnerable to extinction if large patches ≥ 5.0 ha are not maintained.	NH	Barbour and Litvaitis 1993
	≥ 10 ha	Fragments < 10 ha did not support populations of native rodents.	CA	Bolger et al. 1997

TAXA	PATCH AREA	FINDING	STATE	CITATION
	≥ 900 ha (9 km2)	More than 80% of bear sitings occurred in blocks of undisturbed habitat ≥ 9 km^2.	MT	Mace et al. 1996[3]
	≥ 2800 ha (28 km2)	Grizzly bears in the Yellowstone ecosystem should have security blocks 28 km^2 in size.	MT, ID, WY	Mattson 1990[3]
	≥ 220,000 ha (2200 km2)	Model predicts low extinction risk for cougars in areas as small as 2200 km^2, but w/ increasing risk with little immigration.	CA	Beier 1993
Fishes				
	> 2500	Found support that suitable patch size (as defined by watersheds above 1600 m elevation) influences the occurrence of bull trout. Predicted probability of occurrence is 0.5 for patches larger than 2500 ha.	ID	Rieman and McIntyre 1995
Invertebrates				
	≥ .0004 ha (4m2)	Vegetation patches ≥ 4m^2, as well as open areas, were important to the distribution and abundance of carabid beetles.	OH	Crist and Ahern 1999
	≥ 1 ha	Observed minimum patch size for occupancy by populations of 3 butterfly species is 1 ha.	model	Hanski 1994
Plants				
	≥ 2 ha (5 acres)	Minimum area point[1] for tree communities was estimated to be about 2 ha.	NJ	Elfstrom 1974[2]
	≥ 10, ≥ 100 ha	Conserving an old-growth forest might require 10 ha if surrounded by comparable forest, but 100 ha if surrounded by a clearcut.	—	Harris 1984[4]

— Indicates that the geographic location was not determined because the recommendation was cited secondarily from another review article.

model indicates that the research was conducted through modeling and therefore is not specific to any geographic area.

[1] Minimum area point is the point on a species-area curve, which shows the relationship between species number and habitat area, where there is an abrupt change in the slope. The minimum area point has been considered an index of how large a community must be to representative of the community type (Forman 1995).

[2] *As cited in* Forman 1995

[3] *As cited in* Weaver et al. 1996

[4] *As cited in* Franklin 1993

APPENDIX C. PROPORTION OF SUITABLE HABITAT

Recommended minimum proportions of suitable habitat found within the scientific literature (as of December 2001) to maintain long-term persistence of viable populations or communities of species or to minimize the negative consequences of habitat fragmentation in the United States.

TAXA	PROPORTION OF SUITABLE HABITAT	FINDING	STATE	CITATION
Birds				
	≥ 5%	When < 5% of area was covered by habitat, there was an effect on bird density.	WI	Ambuel and Temple 1983[1]
	≥ 5%	When < 5% of area was covered by habitat, there was an effect on bird community.	—	Howe 1984[1]
	> 8%	When 8% of area was covered by habitat, there was an effect on land bird community.	—	Nilsson 1978[1] Nilsson 1986[1]
	≥ 10%	When < 10% of area was covered by habitat, there was an effect on species richness.	—	Soulé et al. 1988[1] Bolger et al. 1991[1]
	>10-30%	The negative effects of patch size and isolation on native species may not occur until the landscape consists of only 10-30% of the original habitat.	review	Andrén 1994
	> 15%	When 15% of area was covered by habitat, there was an effect on bird density.	—	Askins et al. 1987[1]
	> 20%	When 20% of area was covered by habitat, there was an effect on bird community.	MD	Lynch and Whigham 1984[1]
	> 22%	When 22% of area was covered by habitat, there was an effect on land bird community	—	Whitcomb et al. 1981[1]
	> 50%	Numerous species were more likely to inhabit wetlands in landscapes where less than 50% of the upland matrix was tilled.	SD	Naugle et al. 2001
	≥ 60%	A model assuming 60% suitable habitat suggests a high likelihood for the longterm persistence of Northern spotted owls.	model	Lamberson et al. 1994
	> 80%	Metapopulation model predicted that the Northern spotted owl population would go extinct if the proportion of old-growth forest was reduced to less than 20% of landscape.	model	Lande 1988[4] Lamberson et al. 1992[4]
Mammals				
	> 6%	When 6% of area was covered by habitat, there was an effect on chipmunk density.	—	Henderson et al. 1985[1]
	> 6%	When 6% of area was covered by habitat, there was an effect on pika abundance.	—	Smith 1974[1] Smith 1980[1]
	≥ 10%	When < 10% of area was covered by habitat, there was an effect on mammal species richness.	—	Soulé et al. 1992[1]
	> 10%	When 10% of area was covered by habitat, there was an effect on Columbian ground squirrel presence/absence.	—	Weddell 1991[1]
	> 10-30%	The negative effects of patch size and isolation on the native species may not occur until the landscape consists of only 10 –30% of the original habitat.	review	Andrén 1994
	> 15%	When 15% of area was covered by habitat, there was an effect on small mammal presence.	—	Lomolino et al. 1989[1]

TAXA	PROPORTION OF SUITABLE HABITAT	FINDING	STATE	CITATION
Invertebrates				
	≥ 20%	The threshold for changes in movement patterns of beetles occurred at 20% coverage of cells.	CO	Wiens et al. 1997
	≥ 20%	Clover patches became significantly more isolated below 20% habitat, which disrupted the predator foraging behavior of ladybird beetles, decreasing their ability to serve as biocontrol agents of aphids.	model	With et al. 2002
	≥ 40%	Habitat specialists of grasshoppers exhibited limited movement and disjunct populations—which can affect population persistence—when preferred habitat occupied less than 40% of the landscape.	model	With and Crist 1995
	≥ 40, ≥ 60%	Rare species were disproportionately affected by fragmentation and did not occur in patches with less than 40% habitat. Over half of the species were never observed in plots with less than 60% habitat remaining.	OH	Summerville and Crist 2001
Hypothetical Species				
	> 10-30%	As habitat loss continues beyond the threshold (occurring somewhere in the range of 70-90% habitat loss) decline in population performance should become much more severe. But model predicts that habitat fragmentation begins to occur when about 60% of original vegetation remains.	model	Gardner et al. 1987[2]
	≥ 20%	The threshold value of habitat amount is 20% habitat, below which the effects of habitat fragmentation on population persistence may become evident.	—	Andrén 1994[3] Fahrig 1998[3]
	> 70%	Models of forest landscapes forecast that patches of old-growth forest can become fragmented even when about 70% of the landscape cover remains.	model	Franklin and Forman 1987
	> 80%	Terrestrial species with low demographic potential could not persist in landscape even with 80% of suitable habitat in landscape.	model	Lande 1987[4]

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model indicates that the research was conducted through modeling and therefore is not specific to any geographic area.

review indicates papers that base recommendation on a survey of the literature.

[1] *As cited in* Andrén 1994

[2] *As cited in* Dooley and Bowers 1998

[3] *As cited in* Fahrig 2001

[4] *As cited in* With and Crist 1995

APPENDIX D. EDGE INFLUENCE

Distances (in meters) that edge effects penetrate into habitats in the United States as found within the scientific literature (as of December 2001), according to abiotic, bird, mammal, and plant response.

TAXA/SUBJECT	EDGE INFLUENCE	FINDING	STATE	CITATION
Abiotic				
	8 m	Microclimatic differences ceased to exist beyond 8 m into forest fragments.	IN	Brothers and Spingarn 1992
	13.3 m	Model indicated that elevated soil temperatures may extend up to 13.3 m from edge.	model	Laurance and Yensen 1991
	≥ 15 m	In deciduous forest patches, microclimate changes were estimated to extend at least 15 m from the forest edge to the interior.	WI	Ranney et al. 1981[2]
	50 m	Significant edge effects were detected in light, temperature, litter moisture, vapor pressure deficit, humidity, and shrub cover, affecting the forest microenvironment up to 50 m from the edge.	PA, DE	Matlack 1993
	15-60 m (solar radiation) > 240 m (humidity and wind speed)	Solar radiation gradients extend 15–60 m into upland old-growth forest and humidity and wind speed gradients at > 240 m.	—	Chen et al. 1995[9]
Birds				
	16.27 m, 16.95 m, 37.73 m	Maximum flushing* distance in response to pedestrians and dogs was 16.27 m (American robin), 16.95 m (vesper sparrow), and 37.73 m (western meadowlark).	CO	Miller et al. 2001
	50 m	Predation and parasitism rates are often significantly greater within 50 m of an edge.	—	Paton 1994[3]
	50 m	Murrelet nest success was higher when nests were more than 50 m from the forest edge.	—	Nelson and Hamer 1995[4]
	75 m	Estimated that edge-related nest predation extended 75 m into forested buffer strip.	ME	Vander Haegen and Degraaf 1996
	75 m, 100 m	For the majority of species found to have reduced numbers near trails due to nest predation and brood parasitism by brown-headed cowbirds, the zone of influence of trails appears to be around 75 m; however, Townsend's Solitaires exhibited reduced numbers as far as 100 m away from trail.	CO	Miller et al. 1998
	75 m, 125 m, 140 m, 160 m, 210 m, 300 m	Buffer zones that would prevent flushing by approximately 90% of the wintering individuals of a species are: American kestrel, 75 m; merlin, 125 m; prairie falcon, 160 m; rough-legged hawk, 210 m; ferruginous hawk, 140 m; and golden eagle, 300 m.	CO	Holmes et al. 1993
	100 m	Flushing distances of waterbirds in response to pedestrians, all-terrain vehicles, automobiles, and boats, indicate that human disturbance extends up to 100 m.	FL	Rodgers and Smith 1997

TAXA/SUBJECT	EDGE INFLUENCE	FINDING	STATE	CITATION
	180 m	Avian densities were altered up to 180 m away from homes on the perimeter of ex-urban developments.	CO	Odell and Knight 2001
	200–500 m	The abundance of interior habitat bird species was reduced within 200 to 500 m of an edge.	CA	Bolger et al. 1997b[1]
	≥ 300 m	Nest parasitism by brown-headed cowbirds decreased with distance away from forest edge but extended ≥ 300 m into the forest.	—	Brittingham and Temple 1983[5]
	511 m, 687 m	Most Cooper hawk nests occurred 511 m from paved roads and 687 m from human habitation.	Northeast	Bosakowski et al. 1992
	600 m	Effect of increased predation extends 600 m into habitat.	—	Wilcove et al. 1986[1]
Mammals				
	≥ 45 m	The influence of a clearcut on small mammals (California red-backed vole and deer mouse) extends at least 45 m into the forest from its edge.	—	Mills 1996[6]
	81.92 m	Maximum flushing distance of mule deer in response to pedestrians and dogs was 81.92 meters.	CO	Miller et al. 2001
	100–900 m	Human traffic along open roads displaces most grizzly bears from 100–900 meters.	—	Mattson et al. 1987[7] McLellan and Shackleton 1988[7] Aune and Kasworm 1989[7] Kasworm and Manley 1990[7] Mace et al. 1996[7]
Plants				
	65 m	Populations in forest remnants within 65 m of forest clear-cut edges have almost no recruitment of young plants.	OR	Jules 1998
General				
	5000 m	In different habitats and for different taxa, edge effects may penetrate up to 5 km.	—	Janzen, 1986[8]

* Flushing distance is the distance that an animal may flee in response to a disturbance, such as in response to pedestrian or pets on a trail or vehicular traffic on roads.

— Indicates that the geographic location was not determined because the recommendation was cited secondarily from another review article.

model indicates that the research was conducted through modeling and therefore is not specific to any geographic area.

[1] *As cited in* Metro 2001.

[2] *As cited in* Collinge 1996

[3] *As cited in* Hartley and Hunter 1998

[4] *As cited in* Meyer and Miller 2002

[5] *As cited in* Robbins et al. 1989

[6] *As cited in* Lidicker 1999

[7] *As cited in* Weaver et al. 1996

[8] *As cited in* Laurance and Yensen 1991

[9] *As cited in* Brosofske et al. 1997

APPENDIX E. RIPARIAN BUFFER WIDTH

Recommended minimum riparian and wetland buffer widths (in meters) to maintain water quality and wildlife functions within ecoregions of the United States, as found within the scientific literature (as of December 2001).

FUNCTION	TAXA/SUBJECT	BUFFER WIDTH	CITATION
Miscellaneous			
	Noise	≥ 6 m (mature evergreen)	Harris 1985[3]
	Wind damage prevention	≥ 23 m	Pollock and Kennard 1998[3]
	Noise	≥ 32 m (heavily forested)	Groffman et al. 1990[5]
Detrital Input			
	Organic litterfall	1/2 SPTH	FEMAT 1993[3]
	Large Woody Debris	1 SPTH	FEMAT 1993[3]
	Large Woody Debris	1 SPTH	Spence et al. 1996[3]
	Woody Debris	3–10 m	Fischer and Fischenich 2000
	Woody Debris	10–30 m	Wenger 1999
	Organic litterfall	≥ 30 m	Erman et al. 1977[3]
	Woody Debris	≥ 30 m (forested watersheds)	Pollock and Kennard 1998[3]
	Woody Debris	≥ 31 m	Bottom et al. 1983[4]
	Woody Debris	≥ 46 m	McDade et al. 1990[3]
	Organic litterfall	≥ 52 m	Spence et al. 1996[3]
	Woody Debris	≥ 80 m	May 2000[3]
Temperature and microclimate regulation			
	Microclimate	3 SPTH	FEMAT 1993[3]
	Shade	10–30 m	Osborne and Kovacic 1993[3]
	Temperature control	10–30 m	Wenger 1999
	Water temperature	10–30 m	Castelle et al. 1994
	Shade	11–24 m	Brazier and Brown 1973[5]
	Water temperature	≥ 12 m	Corbett and Lynch 1985[4]
	Water temperature	15–30 m	Hewlett and Fortson 1982[4]
	Shade	23–38 m	Steinblums et al. 1984[5]
	Shade	≥ 30 m	Spence et al. 1996[3]
	Shade	≥ 30 m	FEMAT 1993[3]
	Shade	≥ 30 m	May 2000[3]
	Maintenance of water temperature within 1°C of former mean	≥ 30 m	Lynch, Corbett, and Mussalem 1985[1]
	Water temperature	30–43 m	Jones et al. 1988[4]
	Air temperature, solar radiation, wind, humidity	≥ 45–300 m	Brosofske et al. 1997
	Microclimate regulation	≥ 100 m	May 2000[3]
	Microclimate regulation	61–160 m	Knutson and Naef 1997[3]
Bank Stabilization			
	Bank Stabilization	1/2 SPTH	FEMAT 1993[3]
	Bank Stabilization	10–20 m	Fischer and Fischenich 2000

FUNCTION	TAXA/SUBJECT	BUFFER WIDTH	CITATION
	Stream/channel stabilization	20–30 m	Corbett and Lynch 1985[4]
	Stream stabilization/sediment control	≥ 38 m	Cederholm 1994[3]
	Bank Stabilization	≥ 52 m	Spence et al. 1996[3]
Flood Attenuation			
	Floodplain storage	20–150 m	Fischer and Fischenich 2000
Sediment Removal			
	Sediment removal	≥ 3m (sand), ≥ 15 m (silt), ≥ 122m (clay)	Wilson 1967[5]
	Sediment removal	5–30 m	Fischer and Fischenich 2000
	Sediment removal	8–46 m (depending on slope)	SCS 1982[4]
	Sediment (85% removal)	≥ 9 m (grass filter strips, 7%, 12% slopes)	Ghaffarzadeh et al. 1992[4]
	Suspended solids (84% removal)	≥ 9 m (vegetated filter strip)	Dillaha et al. 1989[1]
	Sediment removal	9–30 m	Wenger 1999
	Sediment removal	10–60 m	Castelle et al. 1994
	Sediment removal	≥ 15 m	Budd et al. 1987[4]
	Sediment removal	≥ 15.6 m	Broderson 1973[4]
	Sediment removal	≥ 23 m	Schellinger and Clausen 1992[4]
	Suspended sediment (92% removal)	≥ 24.4 m (vegetated buffer)	Young et al. 1980[4]
	Sediment removal	≥ 25 m	Desbonnet et al. 1994[4]
	Sediment removal	≥ 30 m	Erman et al. 1977[3]
	Sediment removal	≥ 30m	Moring 1982[3]
	Sediment removal	≥ 30 m	May 2000[3]
	Sediment (75% removal)	30–38 m	Karr and Scholosser 1977[4]
	Sediment (75–80% removal)	≥ 30 m	Lynch, Corbett, and Mussalem 1985[1]
	Sediment (80% removal)	≥ 61 m (grass filter strip and vegeated buffers)	Horner and Mar 1982[1]
	Sediment (50% removal)	≥ 88 m	Gilliam 1988[4]
Nutrient/Pollutant Removal			
	Nitrogen, Phosphorus, Potassium, and Fecal Bacteria	≥ 4 m (grass filter strip and forested buffers)	Doyle et al. 1997[1]
	Nitrates and Phosphates (90% removal)	≥ 5 (grass filter strip)	Madison et al. 1992[1]
	Nutrient removal	5–30 m	Fischer and Fischenich 2000
	Nitrates (almost complete removal)	≥ 7 m	Lowrance 1992[1]
	Removal of Phosphorus (79%) and Nitrogen (73%)	≥ 9 m (vegetated filter strip)	Dillaha et al. 1989[1]
	Nitrogen and Phosphorus	≥ 10 m	Corley et al 1999[1]
	Nutrient and Metal	≥ 10 m	Petersen et al. 1992[4]
	Nutrient removal	10—90 m	Castelle et al. 1994
	Nitrate Concentrations	15–30 m	Wenger 1999

FUNCTION	TAXA/SUBJECT	BUFFER WIDTH	CITATION
	Nutrient and metal	≥ 15 m	Castelle et al. 1992[4]
	Phosphorus	≥ 15 m (hardwood buffer)	Woodard and Rock 1995[1]
	Nutrient and metal	≥ 16 m	Jacobs and Gilliam 1985[4]
	Estradiol (98% decrease)	≥ 18 m (grass filter strip)	Nichols et al. 1998[1]
	Nitrogen and Phosphorus (80 and 89% removal, respectively)	≥ 19 m (riparian forest buffer)	Shisler, Jordan, and Wargo 1987[1]
	Nitrates (up to 100%)	20–30 m	Fennessy and Cronk 1997[3]
	Fecal coliform reduction	23–92 m	SCS 1982[5]
	Pollutant removal	≥ 30 m	May 2000[3]
	Fecal coliform reduction	≥ 30 m	Grismer 1981[5]
	Nutrient reduction to acceptable levals	≥ 30 m	Lynch, Corbett, and Mussalem 1985[1]
	Nutrient and metal removal	30–43 m	Jones et al. 1988[5]
	Nutrient and metal removal	≥ 36 m	Young et al. 1980[4]
Wildlife and Plant Species			
	General wildlife	3–183 m	FEMAT 1993[3]
	General wildlife habitat	≥ 10 m	Petersen et al. 1992[5]
	General species diversity	10–100 m	Castelle et al. 1994
	General bird habitat	≥ 15 m	Milligan 1985[5]
	Fish (Cutthroat trout, rainbow trout, and steelhead)	15–61 m	Knutson and Naef 1997[3]
	Birds	≥ 15–200 m	Stauffer and Best 1980
	Aquatic wildlife habitat	20–150 m	Fischer and Fischenich 2000
	General wildlife habitat	≥ 23 m	Mudd 1975[5]
	General wildlife habitat	≥ 27 m	WDOE 1981[5]
	Invertebrates (aquatic insects)	≥ 30 m	Erman et al. 1977[3]
	Invertebrates (macroinvertebrate diversity)	≥ 30 m	Gregory et al. 1987[3]
	Fish (cutthroat trout)	≥ 30 m	Hickman and Raleigh 1982[3]
	Invertebrates (benthic communities)	≥ 30 m	Newbold et al. 1980[5]
	Amphibians (frogs and salamanders)	≥ 30 m (riparian forest buffer)	NRCS 1995[3]
	Fish (brook trout)	≥ 30 m	Raleigh 1982[5]
	Fish (rainbow trout)	≥ 30 m	Raleigh et al. 1984[3]
	Fish (chinook salmon)	≥ 30 m	Raleigh et al. 1986[5]
	Invertebrates (benthic communities)	≥ 30 m	Roby et al. 1977[5]
	Amphibians, Reptiles, Vertebrates	≥ 30 m (riparian forest buffer)	Rudolph and Dickson 1990[1]
	Fish (salmonid egg development)	≥ 30 m	Spackman and Hughes 1995[1]
	Plants (vascular plant diversity)	≥ 30 m	Spackman and Hughes 1995[1]
	Fish (fish diversity and densities)	≥ 30 m	Stewart et al. 2000
	Mammals (beavers)	30–100 m	Jenkins 1980[9]
	General wildlife habitat	≥ 32 m	Groffman et al. 1990[5]
	Birds (Willow flycatcher nesting)	≥ 37.5 m	Knutson and Naef 1997[3]

FUNCTION	**TAXA/SUBJECT**	**BUFFER WIDTH**	**CITATION**
	Birds (diversity and assemblages)	≥ 40 m	Hagar 1999
	Birds (assemblages and persistence)	≥ 45 m	Pearson and Manuwal 2001
	Mammal (gray squirrel)	≥ 50 m	Dickson 1989[1]
	Birds (neotropical migrants, interior species)	≥ 50 m	Tassone 1981[3]
	Birds (raptors)	50–1600 m	Richardson and Miller 1997[7]
	Fish (trout, salmon)	≥ 61 m	Castelle et al. 1992[3]
	Mammals (deer)	≥ 61 m	NRCS 1995[3]
	General wildlife	≥ 61 m	Zeigler 1988[5]
	Mammals (small)	67–93 m	Jones et al. 1988[5]
	Reptiles (gravid mud turtles, Florida cooters, slider turtles)	≥ 73 m (90% protection)	Burke and Gibbons 1995
	Birds	75–200 m	Jones et al. 1988[3]
	Mammal (beaver)	≥ 91 m	NRCS 1995[3]
	Mammals (large)	≥ 100 m	Jones et al. 1988[5]
	Birds (neotropical migrants)	≥ 100 m	Fischer 2000
	Wildlife habitat	≥ 100 m	Fischer, Martin, and Fischenich 2000; and Fischer and Fischenich 2000
	Birds (yellow-billed cuckoo breeding habitat)	≥ 100 m	Gaines 1974[2]
	Birds (neotropical migrant diversity and functional assemblages)	≥ 100 m	Hodges and Krementz 1996
	Birds (forest bird nesting habitat)	≥ 100 m	Keller et al. 1993
	Reptiles (Western pond turtle nesting habitat)	≥ 100 m (stream buffer)	Knutson and Naef 1997[3]
	Aquatic wildlife	≥ 100 m	May 2000[3]
	Birds (red-shouldered hawk and forest bird breeding habitat)	≥ 100 m	Mitchell 1996[2]
	Birds (pileated woodpecker nesting habitat)	≥ 100 m	Small 1982[3]
	Birds (neotropical migrant abundance)	≥ 100 m	Triquet, McPeek, and McComb 1990[2]
	Terrestrial riparian wildlife communities	100–300 m (300 m for forest interior species)	Wenger 1999
	Reptiles (spotted turtles nesting habitat)	120 m (wetland buffer)	Joyal et al. 2001
	Reptiles (turtles)	≥ 135 m (wetland buffer)	Buhlmann 1998[1]
	Birds (Pileated woodpecker)	≥ 137 m	Castelle et al. 1992[3]
	Birds (species diversity)	≥ 150 m	Spackman and Hughes 1995[2]
	Birds (reduce edge-related nest predation)	≥ 150 m	Vander Haegen and DeGraaf 1996
	Amphibians (salamanders)	≥ 165 m	Semlitsch 1998
	Birds (Bald eagle, nesting ducks, herons, sandhill cranes)	≥ 183 m	Knutson and Naef 1997[3]
	Mammals (fawning of mule deer)	≥ 183 m	Knutson and Naef 1997[3]

FUNCTION	TAXA/SUBJECT	BUFFER WIDTH	CITATION
	Plants (minimize non-native vegetation)	≥ 198 m	Hennings 2001[3]
	Birds (Rufous-sided towhee)	≥ 200 m	Knutson and Naef 1997[3]
	Reptiles (Blanding's turtles nesting habitat	≥ 410 m (wetland buffer)	Joyal et al. 2001
	Reptiles (False map turtles, slider turtles, lotic turtles dispersal)	≥ 449 m	Bodie and Semlitsch 2000
	Birds (complete assemblages)	≥ 500 m	Kilgo et al. 1998[1]
General Protection of Aquatic Systems			
	Multiple functions	1–90 m	Todd 2000
	Multiple functions	≥ 10 m	Fischer and Fischenich 2000
	Multiple functions	≥ 15 m	Fischer, Martin, and Fischenich 2000
	Multiple functions	30 m	Furfey et al. 1997
	Sediment/contaminant control, general water quality maintenance	30.5 m (+0.61 m per 1% slope)	Wenger 1999
	Wetland and river integrity	≥ 335 m	Schaefer et al. 1991[6]

SPTH, or site potential tree height, is used as a standard measurement to allow for multiple riparian functions. SPTH is measured in various ways. FEMAT (1993) defines SPTH the height of a site potential tree as the average maximum height of the tallest dominant trees of 200 years or more of age for a given site class (*For further discussion, refer to Metro 2001*).

[1] *As cited in* Fischer and Fischenich 2000.

[2] *As cited in* Fischer 2000.

[3] *As cited in* Metro 2001.

[4] *As cited in* Furfey et al. 1997

[5] *As cited in* Johnson and Ryba 1992

[6] *As cited in* Burke and Gibbons 1995

[7] *As cited in* Fischer, Martin, and Fischenich 2000

[8] *As cited in* Hagar 1999

[9] *As cited in* Allen 1983

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Fractured Genetic Connectivity Threatens a Southern California Puma (*Puma concolor*) Population

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Abstract

Pumas (*Puma concolor;* also known as mountain lions and cougars) in southern California live among a burgeoning human population of roughly 20 million people. Yet little is known of the consequences of attendant habitat loss and fragmentation, and human-caused puma mortality to puma population viability and genetic diversity. We examined genetic status of pumas in coastal mountains within the Peninsular Ranges south of Los Angeles, in San Diego, Riverside, and Orange counties. The Santa Ana Mountains are bounded by urbanization to the west, north, and east, and are separated from the eastern Peninsular Ranges to the southeast by a ten lane interstate highway (I-15). We analyzed DNA samples from 97 pumas sampled between 2001 and 2012. Genotypic data for forty-six microsatellite loci revealed that pumas sampled in the Santa Ana Mountains (n = 42) displayed lower genetic diversity than pumas from nearly every other region in California tested (n = 257), including those living in the Peninsular Ranges immediately to the east across I-15 (n = 55). Santa Ana Mountains pumas had high average pairwise relatedness, high individual internal relatedness, a low estimated effective population size, and strong evidence of a bottleneck and isolation from other populations in California. These and ecological findings provide clear evidence that Santa Ana Mountains pumas have been experiencing genetic impacts related to barriers to gene flow, and are a warning signal to wildlife managers and land use planners that mitigation efforts will be needed to stem further genetic and demographic decay in the Santa Ana Mountains puma population.

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Introduction

Genetic diversity, demography, and abundance – biological characteristics that influence population viability – can vary across a species' distribution. Species that are generally perceived as wide-ranging and abundant are sometimes relegated to status as "least conservation concern", in spite of indicators signaling concern and frequently, lack of data. Pumas (*Puma concolor*; also known as mountain lion, cougar, and in Florida, panther) epitomize this dilemma. Although pumas in California have not been subjected to hunting since 1972, and were designated as a Specially Protected Mammal in 1990 [1], there is minimal active management and little scientifically validated data on statewide or regional population numbers. Pumas in southern California have one of the lowest annual survival rates among any population in North America, on par with rates seen in hunted populations (unpublished data). They are under increasing threats from habitat loss and fragmentation, and mortality from vehicle strikes, depredation permits, poaching, public safety kills, wildfire, and poisoning [2,3]. Timely evaluation of potential threats to population viability is imperative in order to prioritize conservation activities to prevent collapse of some populations.

The human population of southern California is over 20 million [4] and expected to exceed 30 million by 2060 [5]. This increasing population will likely result in further loss, fragmentation, and degradation of natural habitats in the region. Habitat fragmentation south of greater Los Angeles has effectively turned the Santa Ana Mountain range in mostly Orange and Riverside counties into a 'mega-fragment' of habitat, surrounded to the west, north, and east by dense urban land uses. The only remaining montane and foothill habitat linkage connecting the Santa Ana Mountain range to other mountains of the Peninsular Range is a southeasterly swath of habitat bisected by a very heavily traveled 10-lane highway, Interstate 15 (I-15) (Figure 1).

Population viability of pumas in the Santa Ana Mountains (a geography henceforth referred to as distinct from the broader Peninsular Ranges to the east) has been of conservation concern

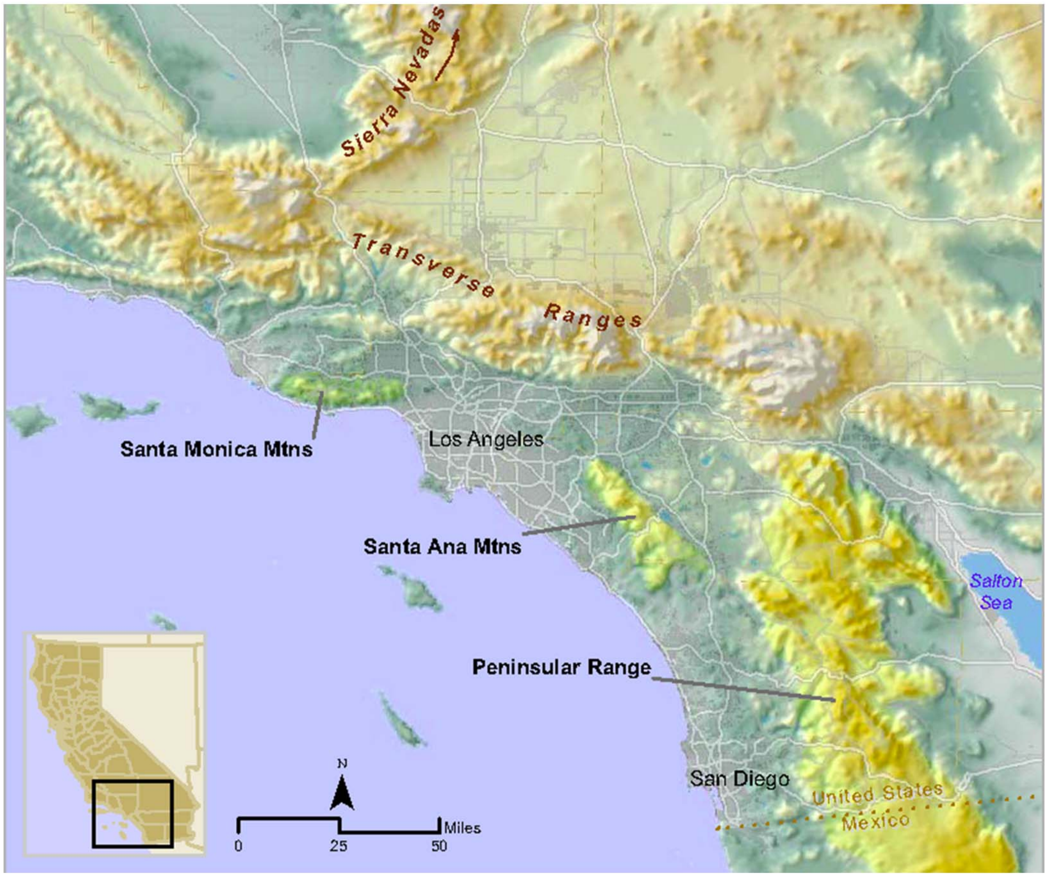

Figure 1. Topographic map depicting location of Santa Ana Mountains, eastern Peninsular Ranges in southern California, and adjacent regions. Inset shows location in the state of California.
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for decades. Population monitoring and modeling in the 1980s highlighted that urbanization and highways were fragmenting puma habitat (e.g., [6]), and that in turn motivated efforts to protect habitat connectivity in the region (e.g., [7,8]). As part of a statewide assessment of puma genetic diversity and population structure, Ernest et al. [9] employed an 11-locus microsatellite panel and found that, for a limited sample size (n = 14) Santa Ana pumas had lower genetic diversity than other populations in California. Since 2001, pumas in the region have been the subject of an ongoing study by the Karen C. Drayer Wildlife Health Center of the University of California, Davis (UCD) School of Veterinary Medicine. Telemetry data from 74 pumas in the UCD study has confirmed that minimal connectivity (only one GPS-collared puma over ten years was documented to transit successfully; unpublished data) exists between the Santa Ana Mountains and the eastern Peninsular Ranges across I-15, confirming that previous connectivity concerns were warranted.

We conducted a detailed appraisal of the genetic diversity, relatedness, and population structure of southern California puma populations. Using 97 samples collected over 12 years as part of the UCD study, and a 46-locus microsatellite panel, we evaluated levels of genetic diversity, estimated effective population sizes and tested whether genetic data supported a hypothesis of recent bottleneck in the populations. We assessed whether genetics reflected our telemetry observations of infrequent puma crossings of I-15 between the Santa Ana Mountains and the Peninsular Ranges to the east. Additionally we explored inter-population gene flow at multiple time scales by employing methods that reflect recent (a few generations) and more historical (tens or more generations). Finally, we tested our hypothesis that the Santa Ana population had lower genetic diversity than those sampled from other regions in California.

Materials and Methods

Samples

We obtained blood or tissue samples for analysis of nuclear DNA from pumas captured for telemetry studies, and from those found dead or killed by state authorities for livestock depredation or public safety in San Diego, Orange, Riverside, and San Bernardino counties of southern California (n = 97) during 2001–2012 (Figure 2). Pumas captured for telemetry were captured and sampled as detailed in [10]. Forty-two samples were collected to the west of I-15 in the Santa Ana Mountains, and 55 samples were collected in the Peninsular Ranges to the east of I-15. A small number of additional samples were collected from deceased animals in San Bernardino County just to the north of the Peninsular Range across Interstate Highway 10. For population genetic comparisons with pumas sampled elsewhere throughout California, a 257 sample subset of our statewide puma DNA data archive was employed (regions and sample sizes detailed in Table 1 and depicted in Figure 1 in [9])

Ethics Statement

Animal handling was carried out in strict accordance with the recommendations and approved Protocol 10950/PHS, Animal

Table 1. Genetic diversity summary statistics for southern California pumas (n = 97) relative to other populations in California (n = 257).

Sampling Region	Abbrev.		N	Na	AR	Ho	He	I	%P
North Coast	**NC**	**Mean**	29	3.6	2.0	0.41	0.44	0.80	98%
		SE		0.2	0.1	0.03	0.03	0.05	
Modoc Plateau & Eastern Sierra Nevada	**MP-ESN**	**Mean**	51	4.2	2.4	0.52	0.54	0.98	100%
		SE		0.3	0.1	0.03	0.03	0.05	
Western Sierra Nevada	**WSN**	**Mean**	47	4.2	2.4	0.47	0.51	0.95	98%
		SE		0.2	0.2	0.03	0.03	0.06	
Central Coast: north	**CC-N**	**Mean**	83	3.2	1.9	0.41	0.41	0.70	98%
		SE		0.2	0.1	0.03	0.03	0.06	
Central Coast: central	**CC-C**	**Mean**	21	3.4	2.1	0.43	0.46	0.81	96%
		SE		0.2	0.1	0.03	0.03	0.05	
Santa Monica Mountains	**CC-S**	**Mean**		2.2	1.7	0.38	0.33	0.53	76%
Central Coast: South		**SE**	26	0.1	0.1	0.04	0.03	0.05	
Peninsular Range-East	**PR-E**	**Mean**	55	3.1	2.0	0.43	0.41	0.74	87%
		SE		0.2	0.2	0.04	0.04	0.07	
Santa Ana Mountains	**SAM**	**Mean**	42	2.3	1.6	0.33	0.32	0.54	80%
		SE		0.2	0.1	0.03	0.03	0.05	

Abbrev. = region abbreviations used in Tables and Figures. Mean with standard error (SE). N = sample size. Na = average number of different alleles per locus. AR = allelic richness, standardized to sample size. Ho = observed heterozygosity. He = expected heterozygosity. I = Shannon's information index (Sherwin et al 2006). %P = percent of polymorphic loci. Regions are detailed further in text and generally follow California Bioregions designations. (http://biodiversity.ca.gov/bioregions.html).

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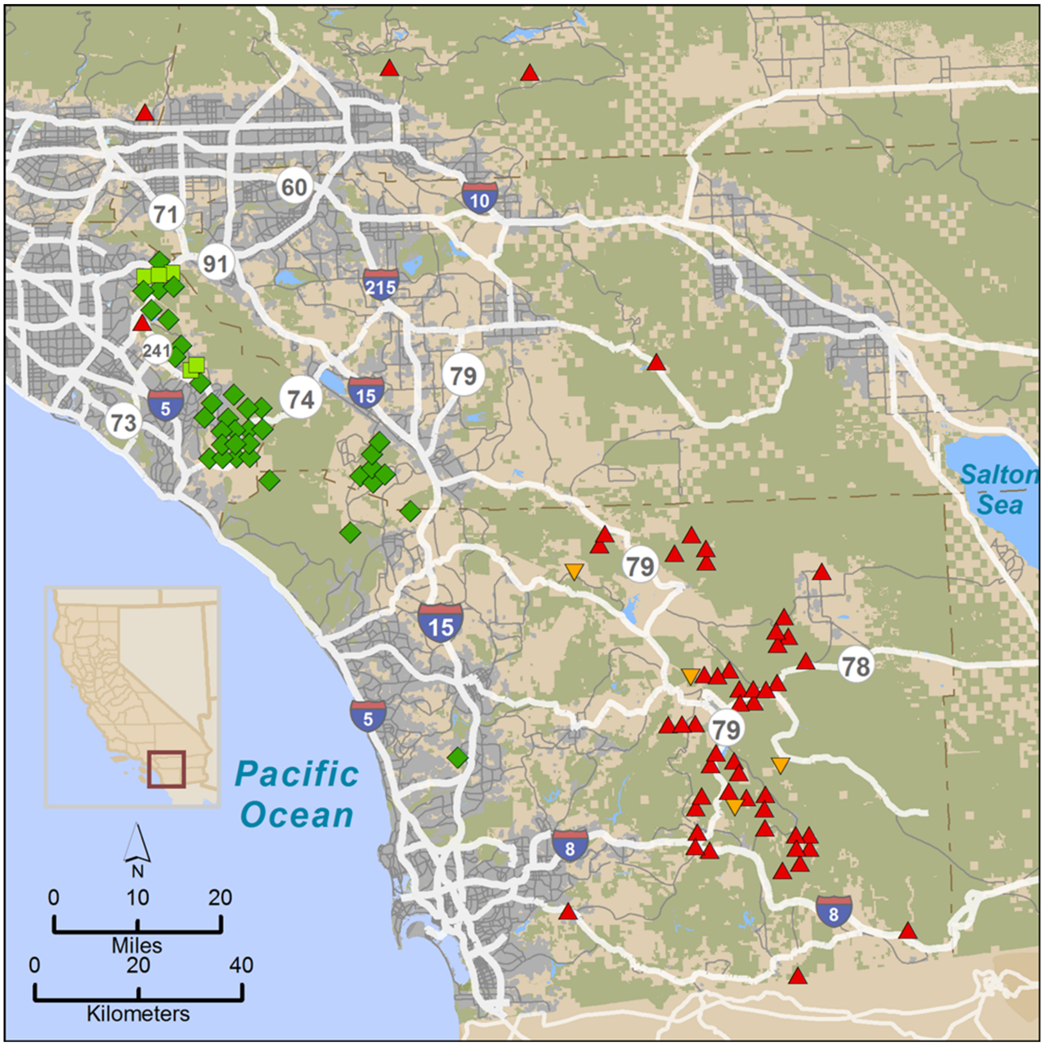

Figure 2. Map of puma capture locations in the Santa Ana Mountains and eastern Peninsular Ranges of southern California. Colors of symbols represent genetic group assignment inferred from Bayesian clustering analysis (STRUCTURE analysis, see Figure 4). Genetic group A-1 = green diamonds; A-2 = red triangles (apex at top). One male puma (M86) captured in the Santa Ana Mountains had predominant genetic assignment to the A-2 (red) genetic group. Five individuals (light green squares) captured in the Santa Ana Mountains had partial assignment to the A-2 group (M91, F92, M93, M97 and F102). Molecular kinship analysis showed that M86 and a female (F89) captured in the Santa Ana Mountains were parents of pumas M91, F92, and M93 (captured in the Santa Ana Mountains). Puma M97 assigned in parentage to M86 and F61, while F102 had unknown parentage (no parentage assignments; due possibly to her death early in project prior to collection of most of the samples). Three individuals (orange triangles, apex at bottom), had partial assignment (however, less than 20%) to A-1.
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Welfare Assurance number A3433-01, with capture and sampling procedures approved by the Animal Care and Use Committee at the University of California, Davis (Protocol #17233), and Memoranda of Understanding and Scientific Collecting Permits from the California Department of Fish and Wildlife (CDFW). Permits and permissions for access to conserved lands at puma capture and sampling sites were obtained from CDFW, California Department of Parks and Recreation, The Nature Conservancy, United States (US) Fish and Wildlife Service, US Forest Service, US Bureau of Land Management, US Navy/Marine Corps, Orange County Parks Department, San Diego County Parks Department, San Diego State University, Vista Irrigation District, Rancho Mission Viejo/San Juan Company, Sweetwater Authority, California Department of Transportation (CalTrans), and the City of San Diego Water Department.

DNA Extraction and Microsatellite DNA data collection

Whole genomic DNA was extracted using the DNeasy Blood & Tissue Kit (QIAGEN, Valencia, CA, USA). Fifty microsatellite DNA primers were initially screened for this project. Forty-six loci that performed well in multiplex PCR (using the QIAGEN Multiplex PCR kit; QIAGEN) and conformed to expectations for Hardy-Weinberg and linkage equilibria were selected for ultimate analysis [11,12,13]. One sex-identification locus (Amelogenin) was used to confirm sex in samples from degraded puma carcasses [14].

PCR products were separated with an ABI PRISM 3730 DNA Analyzer (Applied Biosystems Inc., Foster City, CA, USA) with each capillary containing 1 µL of a 1:10 dilution of PCR product and deionized water, 0.05 µL GeneScan-500 LIZ Size Standard and 9.95 µL of HiDi formamide (both products Applied Biosystems Inc.) that was denatured at 95°C for 3 min. Products

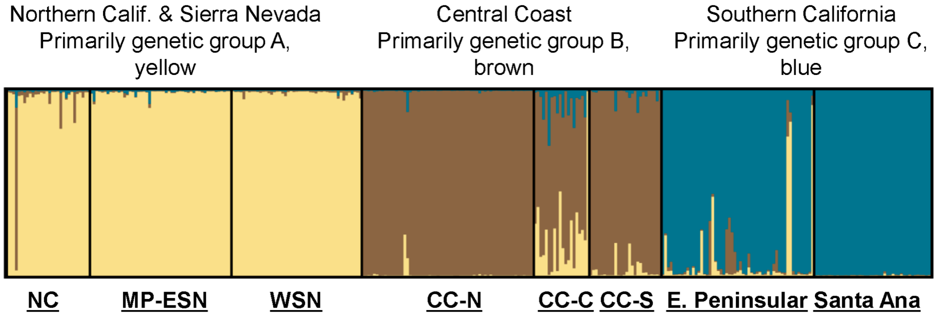

Figure 3. California puma population genetic structure. STRUCTURE bar plot displaying the genetic clustering relationship of southern California pumas relative to others in California. Three major genetic groups, A (blue, on right), B (brown, in center), and C (yellow, on left), are evident for analysis of 354 individuals sampled throughout California. Abbreviations: NC = North Coast, MP-ESN = Modoc Plateau & Eastern Sierra Nevada, WSN = Western Sierra Nevada, CC-N = Central Coast: north, CC-C = Central Coast: central, CC-S = Central Coast: South (Santa Monica Mountains), PR-E = Peninsular Range-East, SAM = Santa Ana Mountains. The plot is organized by grouping individuals in order of their geographic region sampling source. Proportional genetic assignment for each puma is represented by a vertical bar, most easily visualized for pumas that genetically assigned to a group different from most others sampled in its region (for example one individual with over 80% brown and 8% blue near far left of group A). Pumas primarily from the Sierra Nevada Range and northern California are represented by group A (yellow), group B (brown) includes primarily Central Coast pumas and group C (blue) represents primarily southern California pumas (Santa Ana Mountains and eastern Peninsular Ranges).
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were visualized with STRand version 2.3.69 [15]. Negative controls (all reagents except DNA) and positive controls (well-characterized puma DNA) were included with each PCR run. Samples were run in PCR at each locus at least twice to assure accuracy of genotype reads and minimize risk of non-amplifying alleles. For >90% samples, loci that were heterozygous were run at least twice and homozygous loci were run at least three times.

Genetic diversity

The number of alleles (Na), allelic richness (AR; incorporates correction for sample size), observed heterozygosity (Ho), expected heterozygosity (He), Shannon's information index [16], and tests for deviations from Hardy-Weinberg equilibrium were calculated using software GenAlEx version 6.5 [17,18]. Shannon's information index provides an alternative method of quantifying genetic diversity and incorporates allele numbers and frequencies. Testing for deviations from expectations of linkage equilibrium was conducted using Genepop 4.2.1 [19], and we tested for the presence of null alleles using the program ML RELATE [20]. We assessed significance for calculations at alpha = 0.05 and used sequential Bonferroni corrections for multiple tests [21] in tests for Hardy-Weinberg and linkage equilibria.

The average probability of identity (PID) was calculated two ways using GenAlEx: 1) assuming random mating (PID_{RM}) without close relatives in a population [22], and 2) assuming that siblings with similar genotypes occur in a population (PID_{SIBS}) [23]. Probability of identity is the likelihood that two individuals will have the same genetic profile (genotype) for the DNA markers used. PID_{SIBS} is considered conservative since it probably conveys a higher likelihood; however, we recognized that siblings occurred in these populations.

Assessing population structure and genetic isolation

We used a Bayesian genetic clustering algorithm (STRUCTURE version 2.3.4 [24,25]) to determine the likely number of population groups (K; genetic clusters) and to probabilistically group individuals without using the known geographic location of sample collection. We used the population admixture model with a flat prior and assumed that allele frequencies were correlated among populations, and ran 50,000 Markov chain Monte Carlo repetitions following a burnin period of 10,000 repetitions. First,

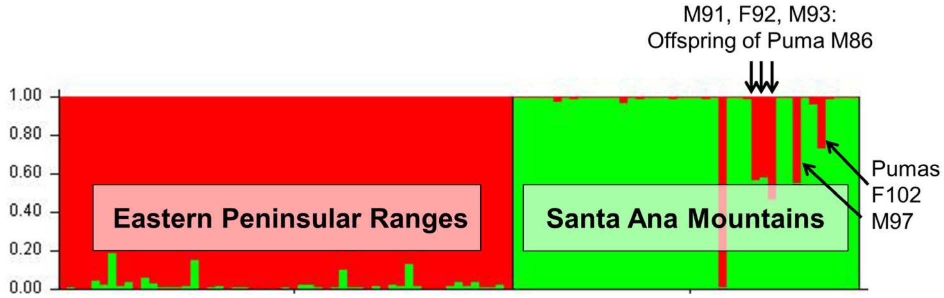

Figure 4. Southern California puma population genetic structure. Bar Plot displaying results of STRUCTURE analysis focused on genotypic data from 97 southern California pumas (the blue block from Figure 3). With removal of the strong genetic signal from northern California and Central Coast samples (see Figure 3), two distinct southern California groupings were inferred, C-1 (green, on right) and C-2 (red, on left). These reflect the two regions: Santa Ana Mountains to the west of I-15 (predominantly genetic group C-1) and eastern Peninsular Ranges to the east of I-15 (predominantly genetic group C-2). Genetic clustering is dependent on genetic variance among samples included in the analysis. One male puma (M86) captured in the Santa Ana Mountains has predominant genetic assignment to the C-2 (red) genetic group (the predominant genetic cluster for PR-E), and five others had partial assignment to the C-2 group (M91, F92, M93, M97 and F102). Molecular kinship analysis showed that M86 and a female (F89) assigning to the C-1 genetic group were parents of pumas M91, F92, and M93 (all were captured in the Santa Ana Mountains).
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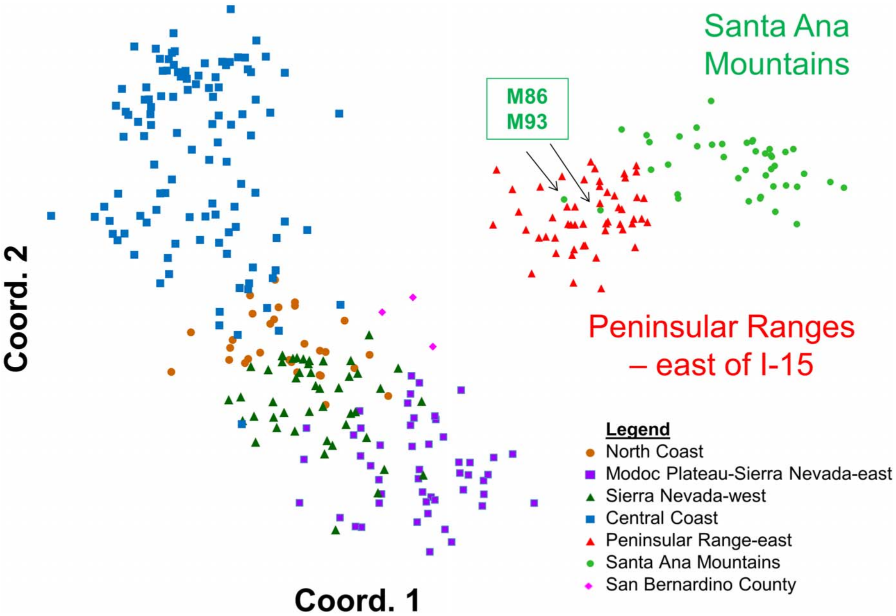

Figure 5. Principal Coordinates analyses (PCoA) constructed using genetic covariance matrices (GenAlEx) for 354 California puma genetic profiles including 97 from southern California. Patterns displayed for first two axes of variation within the genetic data set. Each point, color-coded to its sampling region, represents an individual puma. Note that colors in PCoA diagrams reflect geographic source of samples and not STRUCTURE genetic cluster assignment. Abbreviations and sample sizes per Table 1. Arrows denote pumas described in Figure 4.
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an analysis including 354 statewide puma genotypes (97 from southern California and 257 from other regions) was run to estimate the probability of one through 10 genetic clusters (K), with each run iterated three times. Second, given the output of the statewide run, we ran an analysis using only the 97 southern California puma genotypes to estimate the probability of one through five K, with each run iterated three times. Employing STRUCTURE HARVESTER [26] we averaged log probability

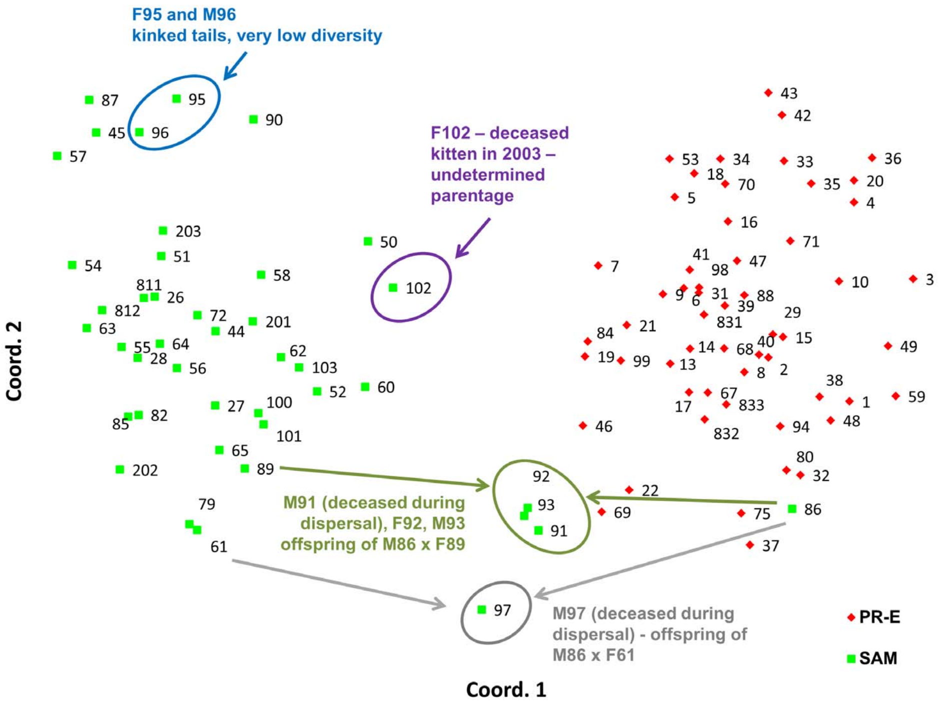

Figure 6. Principal Coordinates analyses (PCoA) via covariance matrices for 97 southern California puma genetic profiles as conducted in GenAlEx. Patterns displayed for first two axes of variation within the genetic data set. Each point represents an individual puma, and has sample identification number and color-coding to sampling region. Note that colors in PCoA diagrams reflect geographic source of samples and not STRUCTURE genetic cluster assignment. Abbreviations and sample sizes per Table 1.
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Table 2. Wright's F_{ST} values indicate that southern California mountain lion populations are genetically distinct from other populations in California.

	NC	MP-ESN	WSN	CC-N	CC-C	CC-S	PR-E	SAM
North Coast (NC)	0							
Modoc Plateau & Eastern Sierra Nevada (MP-ESN)	0.09	0						
Western Sierra Nevada (WSN)	0.05	0.03	0					
Central Coast: north (CC-N)	0.13	0.14	0.12	0				
Central Coast: central (CC-C)	0.08	0.09	0.06	0.07	0			
Santa Monica Mountains (CC-S)	0.17	0.15	0.12	0.14	0.10	0		
Peninsular Range-East (PR-E)	0.13	0.08	0.09	0.12	0.09	0.16	0	
Santa Ana Mountains (SAM)	0.18	0.16	0.17	0.19	0.17	0.27	0.07	0

Note that one of the geographically closest puma populations, Santa Monica Mountains, has highest F_{ST} with the Santa Ana population, evidence of high genetic isolation for both regions. Probability, P(random> = data) based on 9999 permutations for all values are <0.001. Abbreviation definitions and sample sizes are included in Table 1.

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of the data given K, log Pr(X|K), statistics across the multiple runs for each of the K estimates. In each case (statewide and southern California), we selected the K value of highest probability by identifying the set of values where the log Pr(X|K) value was maximized and subsequently selected the minimum value for K that did not sacrifice explanatory ability [27,28,29]. We defined membership to a cluster based upon the highest proportion of ancestry to each inferred cluster.

To further assess and visualize genetic relationships among regions and individuals, we performed principal coordinates analyses (PCoA) via covariance matrices with data standardization [30] using GenAlEx. This is a technique that allowed us to explore and plot the major patterns within the data sets. The PCoA process located major axes of variation within our multidimensional genotype data set. Because each successive axis explains proportionately less of the total genetic variation, the first two axes were used to reveal the major separation among individuals. Employing Genalex software, a pairwise, individual-by-individual genetic distance matrix was generated and then used to create the PCoA.

Wright's F-statistic, $F_{ST,}$ was calculated to appraise how genetic diversity was partitioned between populations. As implemented in GenAlEx, we used Nei's [31] formula, with statistical testing options offered through 9999 random permutations and bootstraps.

Detecting migrants

We used GENECLASS2 version 2.0.h [32] to identify first-generation migrants, i.e. individuals born in a population other than the one in which they were sampled. Genetic clusters identified during STRUCTURE analysis were treated as putative populations. GENECLASS2 provides different likelihood-based test statistics to identify migrant individuals, the efficacy of which depends on whether all potential source populations have been sampled. We first calculated the likelihood of finding a given individual in the population in which it was sampled, L_h, assuming all populations had not been sampled. We then calculated L_h/L_{max}, the ratio of L_h to the greatest likelihood among the populations [33], which has greater power when all potential source populations have been sampled. The critical value of the test statistic (L_h or L_h/L_{max}) was determined using the Bayesian approach of Rannala and Mountain [34] in combination with the resampling method of Paetkau et al. [33]; i.e., Monte Carlo simulations carried out on 10,000 individuals with the significance level set to 0.01.

Testing for bottlenecks and inferring effective population size

We tested for evidence of recent population size reductions in Santa Ana Mountains and eastern Peninsular Range regions with one-tailed Wilcoxon sign-rank tests for heterozygote excess in the program BOTTLENECK version 1.2.02 [35]. The program evaluates whether the reduction of allele numbers occurred at a rate faster than reduction of heterozygosity, a characteristic of populations which have experienced a recent reduction of their effective population size (Ne) [35,36]. This bottleneck genetic signature is detectable by this test for a finite time, estimated to be less than 4 times Ne generations [37]. These tests were performed using the two-phase (TPM, 70% step-wise mutation model and 30% IAM) model of microsatellite evolution and 10,000 iterations.

We then estimated contemporary Ne for each of the two regions based on gametic disequilibrium with sampling bias correction [38] using LDNE version 1.31 [39]. Ne is formally defined as the size of the ideal population that would experience the same

Table 3. Effective population size estimations and indications of recent genetic bottlenecks in southern California pumas.

	Mode	TPM	Ne (P-CI; JK-CI)
Santa Ana Mtns	Shifted mode	0.009	5.1 (3.3–6.7; 3.3–6.6)
Peninsular Range, East	Normal L	0.19	24.3 (21.7–27.3; 20.6–28.8)

Listed by column are p-values for population bottleneck tests (Wilcoxon sign-rank test; BOTTLENECK) assuming the two-phase (TPM) model of microsatellite evolution. Effective size (Ne) estimations (95% CI) based on data from 42 microsatellite loci. The Santa Ana Mountains population exhibited clear evidence of a population bottleneck. Effective population size estimate using the point estimate linkage disequilibrium method of (LDNE, Waples 2006) with 95% confidence intervals (CI) for both parametric (P) and jackknifed (JK) estimates.

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amount of genetic drift as the observed population [40]. These analyses excluded alleles occurring at frequencies ≤ 0.05, and we used the jackknife method to determine 95% confidence intervals [38].

Relatedness analyses: pairwise coefficient and internal

Molecular kinship analysis was conducted using a number of software packages. Pairwise relatedness among individuals was evaluated using the algorithm of Lynch and Ritland [41], with reference allele frequencies calculated and relatedness values averaged within each southern California population, as implemented in GenAlEx. Partial molecular kinship reconstruction was conducted using a consensus of outputs from the GenAlEx pairwise relatedness calculator, ML Relate [20], CERVUS version 3.0.3 [42], and Colony version 2.0.3.1 [43,44]. Individual genetic diversity (also called internal relatedness) was assessed using Rhh [45] as implemented in R statistical software [46]. This is a measure of genetic diversity within each individual (an estimate of parental relatedness [47], and we averaged over individuals for each of the two regions of southern California. Significance of differences between means was evaluated using t tests.

Results

Forty-two of the 46 loci that we employed were polymorphic in southern California and selected for the subsequent analyses. The average probabilities of identity with assumptions of either random mating (PID_{RM}) or mating among sibs (PID_{SIBS}) across the 42 loci for the eastern Peninsular Ranges were (PID_{RM}) 6.3×10^{-22} and (PID_{SIBS}) 3.1×10^{-10}, and for the Santa Ana Mountains were (PID_{RM}) 2.8×10^{-15} and (PID_{SIBS}) 1.1×10^{-7} respectively. These very small values indicate that the panel of genetic markers provided very high resolution to distinguish individuals. For example, given this data the probability of seeing the same multi-locus genotype in more than one puma was less than one in nine million for Santa Ana Mountains pumas.

Genetic diversity

Measures of genetic variation including allelic diversity, heterozygosity, Shannon's information index, and polymorphism, were lower for Santa Ana pumas than most of those tested from other regions of California (Table 1). Such low genetic diversity indicators were approached only by pumas in the Santa Monica Mountains (Ventura and Los Angeles Counties), a neighboring remnant puma population in the north Los Angeles basin (Figure 1).

Population Structure

Bayesian clustering analysis (STRUCTURE; Figure 3 of statewide puma genetic profiles (n = 354), including 97 from southern California, also support genetic distinctiveness of Santa Ana Mountains and eastern Peninsular Range pumas from other populations in the state. Three main genetic groups (A, B, and C) were evident in the analysis (Figure 3) The 97 pumas sampled in southern California (right-hand set of bars in Figure 3, with samples from Santa Ana and eastern Peninsular Range pumas labeled) predominantly cluster within genetic group C. The Santa Ana pumas assign very tightly to group C (0.996 average probability assignment), while pumas of the eastern Peninsular Ranges showed more variable assignment (0.93 average probability assignment), with 9 individuals (16%) having less than 0.90 assignment. Pumas sampled in the Central Coast of California (which included Santa Monica Mountains pumas) make up the central set of bands, and those individuals predominantly assign to the genetic group B. Pumas sampled in the other regions of California (North Coast Ranges, Modoc Plateau, western Sierra

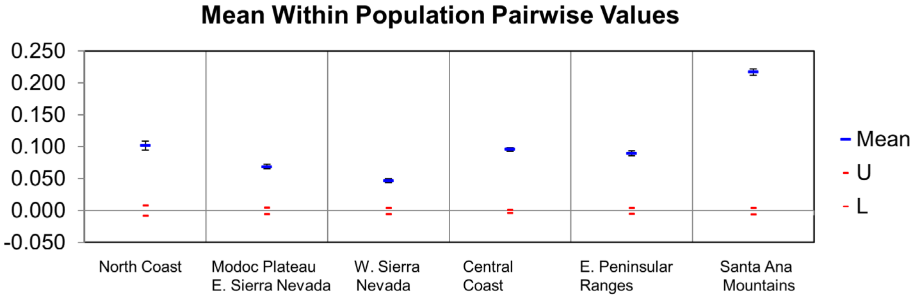

Figure 7. Average pairwise relatedness (r; blue bars with confidence intervals) for pumas sampled in southern California relative to other regions in California. Algorithm of Lynch and Ritland (1999) as implemented in GenAlEx. Expected range for "unrelated" is shown as red bars with confidence intervals. The average relatedness of Santa Ana Mountain pumas is higher than those sampled in Peninsular Ranges east of I-15 and for any other region tested in California. Relatedness in the Santa Ana Mountains pumas approaches second order family relationship (half sibs, niece-aunt, grandparent-grandchild, etc.). Abbreviations listed in Table 1.

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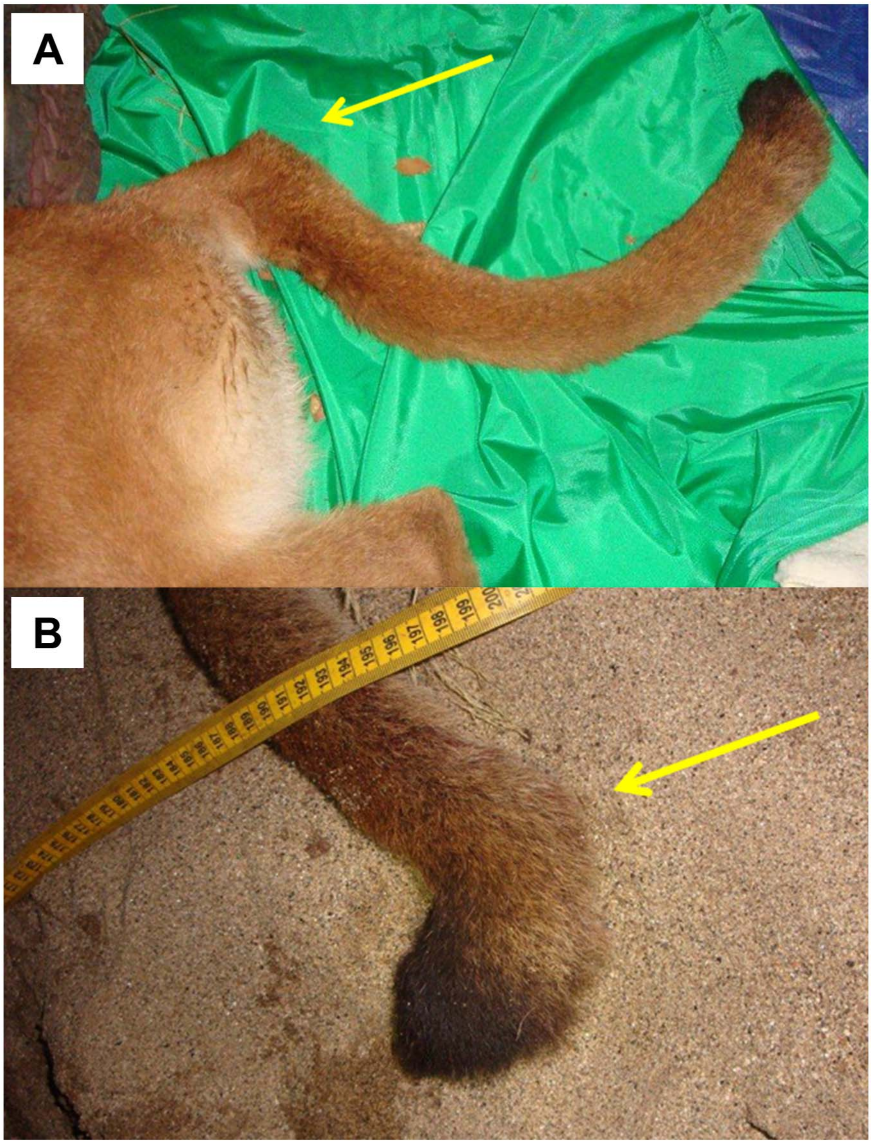

Figure 8. Photographs of kinked tails of pumas F95 (a) and M96 (b). Arrows indicate kink sites. Puma F95 had tail kink at base of tail and Puma M96 had tail kink near distal tip of tail. These two pumas had among the lowest genetic diversity measured in this study.
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Nevada, and eastern Sierra Nevada) predominantly cluster with the genetic group A. Notably, there are individuals sampled in each geographic area which cluster with a genetic group that is not the dominant one in that area, suggesting dispersal events and/or genetic exchange that have occurred to varying degrees in each region.

A STRUCTURE analysis focused only on genetic data from the 97 southern California pumas indicated two distinct genetic groups (C-1 and C-2 shown in Figure 4). Pumas sampled in the eastern Peninsular Range region east of I-15 group primarily with C-2 and those of the Santa Ana Mountain region on the west side of I-15 group with C-1. An exception to the consistent genetic clustering was an adult male (M) puma (M86), that was captured in the Santa Ana Mountains but clustered with pumas from the eastern Peninsular Ranges (primarily genetic group C-2). Five other pumas captured in the Santa Ana Mountains had a 30–50% assignment to the C-2 group (M91, F92, M93, M97 and F102). Molecular kinship analysis showed that M86 and a female (F89) captured in the Santa Ana Mountains and assigned to the C-1 genetic group were the likely parents of three of these pumas (M91, F92, and M93) (results of relatedness and kinship analyses). M86 also was the likely parent of another puma in the group (M97), an offspring of another female (F61) that was sampled in Santa Ana Mountains and clustered with the C-1 genetic group. F102 was a <1 year old female killed by a vehicle in 2003 prior to collection of the majority of samples from adults in the Santa Ana Mountains.

Principal coordinates analysis of statewide puma genetic profiles ($n = 354$) (PCoA; Figure 5) allowed graphical examination of the first two major axes of multivariate genetic variation, and confirmed and added detail to the genetic distinctiveness of southern California pumas relative to others in California. The PCoA also reinforced the distinctiveness of pumas sampled in the Santa Ana Mountains from those sampled in the eastern Peninsular Ranges. Most pumas sampled in the Santa Ana Mountains align in a cloud of data points distinct from the eastern

Peninsular Range pumas, and were the most genetically distant from all other pumas tested in California (Figure 5). The analysis also confirms the STRUCTURE findings that M86 who was sampled in the Santa Ana Mountains genetically aligns with the pumas sampled in the Peninsular Ranges, as does one of his offspring, M93 (see Figure 6 for additional detail). The PCoA position of data points for three pumas sampled in the San Bernardino Mountains north of Peninsular Ranges (pink diamonds in Figure 5) illustrates an intermediate genetic relationship between pumas from the rest of California and pumas sampled in the eastern Peninsular Ranges and Santa Ana Mountains, and suggests that they may represent transitional gene flow signature between southern California and regions to the north and east.

PCoA analysis of only the samples collected in the Santa Ana and Peninsular Ranges (Figure 6) confirms the findings from the STRUCTURE analysis indicating genetic distinctiveness of these two populations despite geographic proximity. Siblings M91, F92, and M93 (offspring of F89 and M86 according to our kinship reconstructions) as well as M97 (likely offspring of a female puma captured in the Santa Ana Mountains, F61, and M86, according to kinship reconstructions) are located graphically midway between their parents' PCoA locations.

Genetic isolation

Wright's F_{ST} calculations (Table 2) indicate that Santa Ana Mountains pumas are the most isolated of those tested throughout California ($p = 0.0001$). Despite the short distance (as short as the distance across the I-15 Freeway) between the Santa Ana Mountains and the eastern Peninsular Range region, F_{ST} was surprisingly high (0.07) given the very close proximity of the two regions (separated only by an interstate highway). The Santa Monica Mountains pumas and Santa Ana Mountains pumas had the highest F_{ST} (0.27; lowest gene flow) of all pairwise comparisons in the state, demonstrating a high level of genetic isolation between these regions.The Santa Monica Mountains and Santa Ana Mountains are less than 100 km direct distance apart, through the center of Los Angeles. However the more likely distance for puma travel between these two mountain ranges, avoiding urban areas and maximizing upland habitat, would likely exceed 300 km (estimated using coarse measurements on Google Earth, Google, Inc.).

Detection of migrants

GENECLASS2 identified four individuals as first-generation migrants ($P<0.01$), four with the L_h method (pumas F75, M80, M86, and M99), and one with the L_h/L_{max} ratio (M86, which was detected using both likelihood methods). Pumas F75, M80, and M99 were all captured from the San Bernardino Mountains (Figure 2) at the northern extent of the study region, yet clustered with individuals from the Eastern Peninsular Range during STRUCTURE analysis. Their migrant designation may suggest immigration from populations north of Los Angeles and/or a distinct genetic population within the San Bernardino region. Puma M86 was captured in the Santa Ana Mountains, but assigned strongly to the eastern Peninsular Range genetic cluster, indicating a seemingly clear population of origin. This individual assignment is in accord with the clustering results from STRUCTURE (Figure 4).

Evidence of genetic bottlenecks

The Santa Ana Mountains population exhibited clear evidence of a population bottleneck (Table 3; Wilcoxon sign-rank test for heterozygote excess, and detection of a shift in the allele frequency distribution mode [36]; BOTTLENECK software). The eastern Peninsular Range mountain lions did not show a strong signature of a bottleneck.

Effective population size

Effective population size (Ne) estimations using the linkage disequilibrium method (LDNe program) were 5.1 for the Santa Ana Mountains population and 24.3 for mountain lions in the eastern Peninsular Ranges. Statistical confidence intervals for both regions, given the genetic data, were tight (Table 3).

Relatedness: pairwise coefficient and internal

The average pairwise coefficient of relatedness (r, Figure 7) was highest in Santa Ana Mountains pumas relative to all others tested in California (0.22; 95% confidence interval of 0.22–0.23), a level that approaches second order kinship relatedness (half-sibs, grantparent/grandchild, aunt-niece, etc). The value for the eastern Peninsular Ranges was 0.10 (confidence interval of 0.09–0.10), less than that of third order relatives (first cousins, great-grandparent/great grandchild). Other regions of California averaged similar or lower values to those of eastern Peninsular Ranges (Figure 7).

Among pumas sampled in the Santa Ana Mountains, the population average (0.14) for internal relatedness as implemented in rHH software was significantly higher (t test; $p = 5.8 \times 10^{-6}$) than for those sampled in the eastern Peninsular Ranges (0.001). Of a group of six pumas which clustered near one another in PCoA (Figure 6), five have among the lowest individual genetic diversity measured in southern California (Puma ID [Internal Relatedness value: F45 [0.37], F51 [0.37], M87 [0.28], F90 [0.21], F95 [0.38], and M96 [0.33]). Notably, pumas F95 and M96 (highest internal relatedness) were observed with kinked tails at capture in the Santa Ana Mountains (Figure 8).

Discussion

Pumas of the Santa Ana Mountains are genetically depauperate, isolated, and display signs of a recent and significant bottleneck. In general, coastal California puma populations have less genetic diversity and less gene flow from other populations than those farther inland [9] (Table 1). This study showed that two coastal populations (Santa Ana Mountains and Santa Monica Mountains) had particularly low genetic variation and gene flow from other regions. Lack of gene flow is likely due in part to natural barriers to puma movement: geography and habitat (Pacific Ocean to the west; less hospitable desert habitat bounding certain regions, etc.). However, our data suggest that anthropogenic developments on the landscape are playing a large role in genetic decay in the Santa Ana Mountains puma population. As large solitary carnivores with sizable habitat requirements, pumas are extremely sensitive to habitat loss and fragmentation [48,49].

The genetic bottleneck in the Santa Ana Mountains pumas is estimated at less than about 80 years, depending on definitions of effective population size (Ne) and puma generation time. Luikhart and Cornuet [37] state that the bottleneck signatures decay after "4 times Ne [here estimated to be 5.1] generations". Logan and Sweanor [50] estimated generation time for their New Mexico population of pumas to be 29 months (2.4 years) for females. If an allowance of 2.4–4.0 years is made for generation times (unknown) in the Santa Ana Mountains population, the maximum estimated time since a bottleneck would be about 40–80 years. This was a period of tremendous urban development and multi-lane highway construction in southern California, particularly I-15 [51]. It is likely that the potential for connectivity between the Santa Ana Mountains and the Peninsular Range-East region will continue to be eroded by ongoing increases in traffic volumes on I-15, and conversion of unconserved lands along the I-15 corridor by development and agriculture [8,48,52].

An isolated population of pumas in the Santa Monica Mountains to the north of the Santa Ana Mountains also exhibit low values relative to other western North American populations (see Table 2 in [53]. Santa Monica pumas are isolated by urbanization of a megacity and busy wide freeways (Ventura county, including greater Los Angeles region [53]. Multiple instances of intraspecific predation, multiple consanguineous matings (father to daughter, etc.), and lack of successful dispersal highlight a suite of anthropogenic processes also occurring in the Santa Ana Mountains. Our collective findings of kinked tails *and* very low genetic diversity in Santa Ana pumas F95 and M96 may portend manifestations of genetic inbreeding depression similar to those seen in Florida panthers [54,55]; however recognizing that kinked tails can have non-genetic etiologies.

Our analyses suggest that the Santa Ana Mountains puma population is highly challenged in terms of genetic connectivity and genetic diversity, a result hinted at in Ernest et al. [9] and now confirmed to be an ongoing negative process for this population. This compounds the demographic challenges of low survival rates and scant evidence of physical connectivity to the Peninsular Ranges east of I-15 (unpublished data). Beier [6] documented these same challenges during the 1990's, and data from the ongoing UCD study suggest the trends have accelerated. Substantial habitat loss and fragmentation has occurred and is continuing to occur; Burdett et al. [10] estimated that by 2030, approximately 17% of puma habitat that was still available in 1970 in southern California will have been lost to development, and fragmentation will have rendered the remainder more hazardous for pumas to utilize. Riley et al [53] document a natural "genetic rescue" event: the 2009 immigration and subsequent breeding success of a single male to the Santa Monica Mountains. This introduction of new genetic material into the population was paramount to raising the critically low level of genetic diversity, as also exemplified by the human-mediated genetic augmentation of Florida Panthers with Texas puma stock [56].

These findings raise concerns about the current status of the Santa Ana Mountains puma population, and the longer-term outlook for pumas across southern California. In particular, they highlight the urgency to maintain – and enhance – what connectivity remains for pumas (and presumably numerous other species) across I-15. Despite warnings [6,9] about potential serious impacts to the Santa Ana Mountains puma population if concerted conservation action was not taken, habitat connectivity to the Peninsular Ranges has continued to erode. We are hopeful that these new genetic results will motivate greater focus on connectivity conservation in this region. Indeed, the Santa Ana Mountains pumas may well serve as harbingers of potential consequences throughout California and the western United States if more attention is not paid to maintaining connectivity for wildlife as development progresses.

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Author Contributions

Conceived and designed the experiments: HBE TWV WMB. Performed the experiments: HBE TWV MRB WMB. Analyzed the data: HBE TWV MRB. Contributed reagents/materials/analysis tools: HBE TWV SAM WMB. Contributed to the writing of the manuscript: HBE TWV SAM MRB WMB.

References

1. Mansfield TM, Torres SG (1994) Trends in mountain lion depredation and public safety threats in California. Paper 33. Proceedings of the Sixteenth Vertebrate Pest Conference, Santa Clara, CA. Editors: WS Halverson and AC Crabb. University of California, Davis.
2. Riley SPD, Pollinger JP, Sauvajot RM, York EC, Bromley C, et al. (2006) FAST-TRACK: A southern California freeway is a physical and social barrier to gene flow in carnivores. Mol Ecol 15: 1733–1741.
3. Riley SPD, Bromley C, Poppenga RH, Uzal FA, White L, et al. (2007) Anticoagulant exposure and notoedric mange in Bobcats and Mountain Lions in urban Southern California. J Wildl Manage 71: 1874–1884.
4. U.S. Census Bureau (2012) 2010 Census of Population and Housing, Summary Population and Housing Characteristics, CPH-1-6, California, U.S. Government Printing Office, Washington, DC.
5. California Department of Finance (2013) New Population Projections: California to surpass 50 million in 2049. Press release. Available: http://www.dof.ca.gov/research/demographic/reports/projections/p-1/documents/Projections_Press_Release_2010-2060.pdf Accessed 2 December 2013.
6. Beier P (1995) Dispersal of juvenile cougars in fragmented habitat. J Wildl Manage 59: 228–237.
7. Luke C, Penrod K, Cabanero CR, Beier P, Spencer W, et al. (2004) A Linkage Design for the Santa Ana-Palomar Mountains Connection. Unpublished report. San Diego State University, Field Station Programs and South Coast Wildlands. Available at: http://www.scwildlands.org/reports/SCML_SantaAna_Palomar.pdf.
8. Morrison SA, Boyce WM (2009) Conserving connectivity: Some lessons from mountain lions in southern California. Conserv Biol 23: 275–285.
9. Ernest HB, Boyce WM, Bleich VC, May B, Stiver SJ, et al. (2003) Genetic structure of mountain lion (Puma concolor) populations in California. Conserv Genet 4: 353–366.
10. Burdett CL, Crooks KR, Theobald DM, Wilson KR, Boydston EE, et al. (2010) Interfacing models of wildlife habitat and human development to predict the future distribution of puma habitat. Ecosphere 1: 1.
11. Ernest HB, Penedo MCT, May BP, Syvanen M, Boyce WM (2000) Molecular tracking of mountain lions in the Yosemite Valley region in California: genetic analysis using microsatellites and faecal DNA. Mol Ecol 9: 433–441.
12. Kurushima JD, Collins JA, Well JA, Ernest HB (2006) Development of 21 microsatellite loci for puma (Puma concolor) ecology and forensics. Mol Ecol Notes 6: 1260–1262.
13. Menotti-Raymond M, David VA, Lyons LA, Schaffer AA, Tomlin JF, et al. (1999) A genetic linkage map of Microsatellites of the domestic cat (Felis catus). Genomics 57: 9–23.
14. Pilgrim KL, Mckelvey KS, Riddle AE, Schwartz MK (2005) Felid sex identification based on noninvasive genetic samples. Mol Ecol Notes 5: 60–61.
15. Toonen RJ, Hughes S (2001) Increased throughput for fragment analysis on an ABI Prism 377 automated sequencer using a membrane comb and STRAND software. BioTechniques 31: 1320–1324.
16. Sherwin WB, Jabot F, Rush R, Rossetto M (2006) Measurement of biological information with applications from genes to landscapes. Mol Ecol 15: 2857–2869.
17. Peakall R, Smouse PE (2006) GenAlEx 6: genetic analysis in Excel. Population genetic software for teaching and research. Mol Ecol Notes 6, 288–295.
18. Peakall R, Smouse PE (2012) GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research – an update. Bioinformatics 28: 2537–2539.
19. Rousset F (2008) genepop'007: a complete re-implementation of the genepop software for Windows and Linux. Mol Ecol Resour 8: 1755–0998.
20. Kalinowski ST, Wagner AP, Taper ML (2006) ML-RELATE: a computer program for maximum likelihood estimation of relatedness and relationship. Mol Ecol 6: 576–579.
21. Rice WR 1989. Analysing tables of statistical tests. Evolution 43: 223–5.

22. Taberlet P and Luikart G (1999), Non-invasive genetic sampling and individual identification. Biol J Linn Soc 68: 41–55.
23. Waits LP, Luikart G, Taberlet P (2001) Estimating the probability of identity among genotypes in natural populations: cautions and guidelines. Mol Ecol 10: 249–56.
24. Pritchard JK, Stephens M, Donnelly P (2000). Inference of population structure using multilocus genotype data. G3 155: 945–959.
25. Hubisz MJ, Falush D, Stephens M, Pritchard J (2009) Inferring weak population structure with the assistance of sample group information. Mol Ecol Resour 9: 1322–1332.
26. Earl DA, vonHoldt BM (2012) STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. Conserv Genet Resour 4: 359–361.
27. Pritchard JK, Wen W (2002) Documentation for structure version 2.3.4. As viewed June 1 2013: http://pritch.bsd.uchicago.edu.
28. Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Mol Ecol 14: 2611–2620.
29. Waples RS, Gaggiotti O (2006) What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. Mol Ecol 15, 1419–1439.
30. Orloci L (1978) Multivariate analysis in vegetation research. 2nd ed. Dr W. Junk. The Hague. 451 p.
31. Nei M (1977) F-statistics and analysis of gene diversity in subdivided populations. Ann Hum Genet 41: 225–233.
32. Piry S, Alapetite A, Cornuet JM, Paetkau D, Baudouin L (2004) GENECLASS2: A software for genetic assignment and first-generation migrant detection. J Hered 95: 536–539.
33. Paetkau D, Slade R, Burdens M, Estoup A (2004) Genetic assignment methods for the direct, real-time estimation of migration rate: a simulation-based exploration of accuracy and power. Mol Ecol 13: 55–65.
34. Rannala B, Mountain JL (1997) Detecting immigration by using multilocus genotypes. Proc Natl Acad Sci USA 94: 9197–9201.
35. Cornuet JM, Luikart G (1997) Description and power analysis of two tests for detecting recent population bottlenecks from allele frequency data. G3 144: 2001–2014.
36. Luikart G, Allendorf FW, Cornuet JM, Sherwin WB (1998) Distortion of allele frequency distributions provides a test for recent population bottlenecks. J Hered 89: 238–247.
37. Luikart G, Cornuet JM (1998) Empirical evaluation of a test for identifying recently bottlenecked populations from allele frequency data. Conserv Biol 12: 228–237.
38. Waples RS (2006) A bias correction for estimates of effective population size based on linkage disequilibrium at unlinked gene loci. Conserv Genet 7: 167–184.
39. Waples RS, Do C (2008) LDNE: a program for estimating effective population size from data on linkage disequilibrium. Mol Ecol Resour 8: 753–756.
40. Wright S (1969) Evolution and the Genetics of Population. Vol 2. The Theory of Gene Frequencies. University of Chicago Press.
41. Lynch M, Ritland K (1999) Estimation of pairwise relatedness with molecular markers. G3 152: 1753–1766.
42. Kalinowski ST, Taper ML, Marshall TC (2007) Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Mol Ecol 16: 1099–1006.
43. Jones OR, Wang J (2010) COLONY: a program for parentage and sibship inference from multilocus genotype data. Mol Ecol Resour 10: 551–555.
44. Wang J (2012) Computationally efficient sibship and parentage assignment from multilocus marker data. G3 191: 183–194.
45. Alho JS, Välimäki K, Merilä J (2010) Rhh: an R extension for estimating Multilocus heterozygosity and heterozygosity–heterozygosity correlation. Mol Ecol Resour 10: 720–72.
46. R Development Core Team (2011) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
47. Amos W, Worthington Wilmer J, Fullard K, Burg TM, Croxall JP (2001) The influence of parental relatedness on reproductive success. Proc R Soc Lond B - Biol Sci 268: 2021–2027.
48. Beier P (1993) Determining Minimum Habitat Areas and Habitat Corridors for Cougars. Conserv Biol 7: 94–108.
49. Crooks KR (2002) Relative Sensitivities of Mammalian Carnivores to Habitat Fragmentation. Conserv Biol 16: 488–502.
50. Logan K and Sweanor L (2001) Desert Puma: Evolutionary Ecology And Conservation Of An Enduring Carnivore. Island Press. 464.
51. Barbour E (2002) Metropolitan growth planning in California, 1900–2000. Public Policy Institute of California. San Francisco, California. 246.
52. Beier P (1996) Metapopulation modeling, tenacious tracking, and cougar conservation. In McCullough DR, editor, Metapopulations and wildlife management. Washington DC: Island Press. 293–323.
53. Riley SPD, Serieys LEK, Pollinger J, Sikich J, Dalbeck L, et al. Individual behaviors dominate the dynamics of an urban mountain lion population isolated by roads. Curr Biol 24: 1989–1994.
54. Roelke ME, Martenson JS, O'Brien SJ. (1993). The consequences of demographic reduction in the endangered Florida panther. Curr Biol 3: 340–350.
55. Culver M, Hedrick PW, Murphy K, O'Brien S Hornocker MG. (2008) Estimation of the bottleneck size in Florida panthers. Anim Conserv 11: 104–110.
56. Johnson WE, Onorato DP, Roelke ME, Land ED, Cunningham M, et al. (2010). Genetic restoration of the Florida panther. Science 329, 1641–1645.

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California Red-Legged Frog (*Rana draytonii*) Movement and Habitat Use: Implications for Conservation

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ABSTRACT.—**Nonbreeding habitats are critically important for *Rana draytonii*, especially for individuals that breed in temporary bodies of water. We radiotracked 123 frogs to evaluate seasonal habitat use. Individual frogs were continuously tracked for up to 16 months. Some individuals remained at breeding ponds all year, but 66% of female and 25% of male frogs moved to nonbreeding areas, even when the breeding site retained water. Frogs at our main study site moved 150 m (median), roughly the distance to the nearest suitable nonbreeding area. The greatest straight-line distance traveled was 1.4 km, although the presumed distance traveled was 2.8 km. Females were more likely than males to move from permanent ponds (38% of females, 16% of males), but among dispersing frogs, males and females did not differ in distance moved. Some frogs left breeding sites shortly after oviposition (median = 12 days for females, 42.5 days for males), but many individuals remained until the site was nearly dry. Fog provided moisture for dispersal or migration throughout the summer. Our data demonstrate that maintaining populations of pond-breeding amphibians requires that all essential habitat components be protected; these include (1) breeding habitat, (2) nonbreeding habitat, and (3) migration corridors. In addition, a buffer is needed around all three areas to ensure that outside activities do not degrade any of the three habitat components.**

Rana draytonii (California Red-Legged Frog) was once an abundant frog throughout much of central and southern California and is believed to have inspired Mark Twain's fabled story "The Celebrated Jumping Frog of Calaveras County." Now this frog is rare in both the Sierra Nevada foothills and the southern portion of its range (Jennings and Hayes, 1994). In parts of the central Coast Range, there are still large, vigorous populations, some of which probably rival those present 200 years ago (Fellers, 2005). *Rana draytonii* was federally listed as a Threatened species on 24 June 1996, and the recovery plan states that it ". . . has been extirpated from 70 percent of its former range . . . Potential threats to the species include elimination or degradation of habitat from land development and land use activities and habitat invasion by non-native aquatic species" (U.S. Fish and Wildlife Service, 2002:iv).

Rana draytonii use ponds or pools for breeding during the wet season (December through March) and ponds, riparian areas, or other aquatic habitats during the rest of the year. In Marin County, stock ponds are the most commonly used breeding sites. There is only one published report on migration or nonbreeding habitat requirements for this frog. Bulger et al. (2003) described movements of 56 *R. draytonii* in a coastal area about 100 km south of San Francisco. They found that 80–90% of the frogs remained at one breeding site all year. Frogs radiotagged at nonbreeding sites often moved in a straight-line between breeding and upland habitats without apparent regard to intervening vegetation or topography. Frogs traveled overland up to 2,800 m, and Bulger et al. (2003) recommended a 100 m buffer zone around breeding sites.

The California Red-Legged Frog recovery plan outlines the necessary actions for recovery. One task is to "conduct research to better understand the ecology of the California Red-Legged Frog including the use of uplands, dispersal habits, and overland movements" (U.S. Fish and Wildlife Service, 2002:84). This is a concern not only for *R. draytonii*, but also for many endangered and nonendangered vertebrates that migrate between breeding and nonbreeding areas. This includes salamanders (*Ambystoma*; Madison, 1997; *Triturus*; Joly et al., 2001), frogs (*Rana*; Richtor et al., 2001; Pope et al., 2000), snakes (*Farancia*; Gibbons et al., 1977), turtles (Burke and Gibbons, 1995; Bodie, 2001), and many species of passerine birds (Keast and Morton, 1980). Lamoureux and Madison (1999) made the point that studies need to examine amphibian habitat requirements at all times of the year not just during the breeding season. We designed our study to address this concern for *R. draytonii.*

MATERIALS AND METHODS

Study area.—Our study was conducted in Marin County, California, 45 km northwest of

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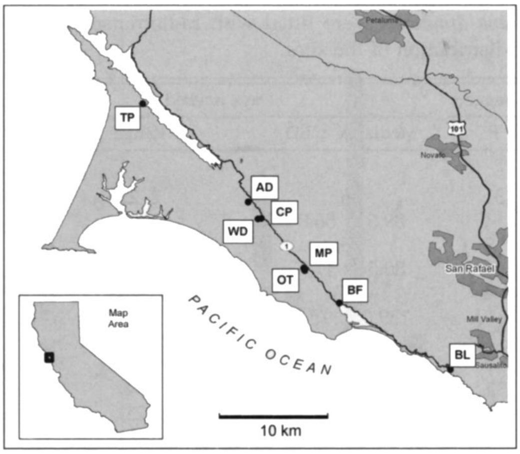

FIG. 1. Sites where California Red-Legged Frogs (*Rana draytonii*) were radiotagged at Point Reyes National Seashore and Golden Gate National Recreation Area, Marin County, California. Site descriptions are listed in Table 1.

San Francisco. All sites were within 6 km of the ocean and located at either Point Reyes National Seashore or Golden Gate National Recreation Area (Fig. 1). The local climate is Mediterranean, with an average annual rainfall of 100 cm that largely occurs between November and March. Mean monthly temperatures range from 8.6°C (December) to 16.6°C (August/September) at the headquarters of Point Reyes National Seashore in Olema Valley (National Park Service weather records). Most frogs ($N = 112$) were tagged in the Greater Olema Valley (Olema Valley and Pine Gulch Valley; 38°01′41″N, 122°46′50″E). To evaluate movement and habitat use in areas with contrasting habitats, nine frogs were tagged at Big Lagoon (37°51′36″N, 122°34′29″E), and two were tagged at Tomales Point (38°09′19″N, 122°54′43″E; Fig. 1).

Most of the Greater Olema Valley was characterized by a mixture of grazed and ungrazed grasslands interspersed with seasonal drainages with California bay (*Umbellularia californica*) and coast live oak (*Quercus agrifolia*). The west side of the valley was predominantly a Douglas fir forest (*Pseudotsuga menziesii*). Olema and Pine Gulch Creeks had well-defined riparian zones composed of California bay, red alder (*Alnus rubra*), willow (*Salix* spp.), big-leaf maple (*Acer macrophyllum*), and Douglas fir, with an understory dominated by blackberry (*Rubus discolor*), poison oak (*Toxicodendron diversilobum*), stinging nettles (*Urtica dioica*), and western sword fern (*Polystichum munitum*). Within the valley, there were 24 *R. draytonii* breeding sites. Fourteen of these were artificial stock ponds, and the others were naturally occurring ponds or marshes. Aquatic vegetation was predominantly cattails (*Typha* spp.), pennywort (*Hydrocotyle verticillata*), and rushes (*Juncus* spp.). About half of the ponds were seasonal, whereas the others usually held water all year. Study sites within the Olema Valley were selected to represent a range of habitats and because there was a sufficiently large *R. draytonii* population at each of the study sites.

The Big Lagoon study site consisted of a cattail marsh with a seasonal creek (Green Gulch Creek) that flowed into it. The marsh had several small areas where water depth was 1.0–1.5 m during the winter, but most of the marsh was covered by < 0.25 m of water, even during the wet season. A levee on the north side separated the marsh from a permanent creek (Redwood Creek), but a set of culverts allowed water to enter the marsh during higher winter flows. Water retention in the marsh varied with rainfall but was also influenced by how much water the National Park Service allowed to pass through flood gates on the culverts. The Tomales Point study site was a nonbreeding site at a seasonal seep. The dominant vegetation was coyote brush (*Baccharis pilularis*), with a few wax myrtle (*Myrica californica*). The nearest breeding pond was 650 m away.

Field methods.—Frogs were caught at night either with a dip net or by hand. We marked each frog with a passive integrated transponder (PIT) tag (TX1400L, Biomark, Meridian, ID; www.biomark.com) for individual identification and recorded sex, snout–vent length (SVL), and mass. Each frog was radiotagged by attaching a transmitter (model BD-2G, Holohil Systems Ltd., Carp, Ontario, Canada; www.holohil.com) to a belt of aluminum beaded chain that was slipped over the frog's extended rear legs and up onto the waist (Rathbun and Murphey, 1996). The transmitters were either a dull green or light brown color. The aluminum belt was painted flat black to eliminate reflections. The smallest frog we radiotagged was 32 g, and the mass of the transmitter and belt was approximately 2.1 g (6% of the frog's mass). When possible, we recaptured frogs before the battery died (20-week life) and fitted a new transmitter. We tagged frogs during all months of the year except August, with most being tagged just prior to, or during, the December to March breeding season.

A total of 123 individual frogs was radiotagged (47 females, 76 males) between 5 November 1997 and 1 May 2003 at eight sites (Table 1). Twenty-three frogs were consecutively fitted with two transmitters, six frogs with three transmitters, and one frog wore six

TABLE 1. Sites where California Red-Legged Frogs (*Rana draytonii*) were fitted with radiotransmitters in Marin County, California. Figure 1 shows the geographic distribution of the sites.

		Number of frogs tagged		Days tracked	
Site name	Habitat	M	F	Median x̄ ± SD	Range
Greater Olema Valley					
CP	Permanent pond	44	31	86 89.6 ± 56.0	2–229
MP	Seasonal pond	19	9	76 80.5 ± 47.3	12–191
AD	Seasonal pond	2	4	127 139.0 ± 75.0	63–253
BF	Seasonal pond	2	2	112 109 ± 74.9	28–184
WD	Permanent pond	0	1	134	134
OT	Permanent pond	1	0	121	121
All sites	–	68	47	83 91.3 ± 56.1	5–253
Big Lagoon					
BL	Permanent marsh	9	0	68 66.8 ± 36.8	16–130
Tomales Point					
TP	Seasonal seep and ditch	0	2	283	68–498

consecutive transmitters. Seventy-eight percent of all transmitters (N = 166) were recovered. Three frogs (two females, one male) lost their transmitters but were subsequently recaptured and outfitted with new transmitters 54, 244, and 493 days later. This yielded 126 telemetry histories. We generally located radiotagged frogs twice weekly; more often when the frogs were making regular movements. We recaptured frogs every 3–4 weeks to check for injuries and ensure proper fit of the transmitter belt. Frogs were radiotagged for 91 days (median) at the Olema Valley study sites and for 67 and 283 days at the Big Lagoon and Tomales Point sites, respectively.

Frogs were located using a TR-2 receiver (Telonics, Mesa, AZ; www.telonics.com) or an R-1000 receiver (Communication Specialists, Inc., Orange, CA; www.com-spec.com) with a directional "H" or three-element yagi antenna. Fine scale location of transmitters was accomplished with a partially stripped coaxial cable inserted into a length of PVC pipe that was used as a probe (Fellers and Kleeman, 2003). Radio locations were only determined during the day.

Frog locations were plotted on a 7.5′ USGS topographic map by noting proximity to a mapped feature or permanent local landmark (e.g., dead snag, fence corner). On a few occasions, locations were initially determined using a Garmin 12XL GPS unit (Garmin International Inc., Olathe, Kansas, www.garmin.com), but these locations were later visited and mapped on a topographic map using local landmarks. Telemetry data were analyzed by plotting coordinates on digitized USGS topographic maps (1:24,000 scale) using Topo! software (National Geographic TOPO! Maps, San Francisco, California; maps.nationalgeographic.com/topo). Unless otherwise noted, movements represent straight-line distances between successive locations. For some frogs, we also calculated a longer distance moved based on locations between breeding and nonbreeding sites. For example, frogs found at several successively further distances along a riparian corridor were presumed to have followed the creek between sites. This typically resulted in a longer distance moved than would be obtained using a straight-line distance and is referred to as presumed distance. Statistical analysis was conducted using Statistix (Version 7, Analytical Software, Tallahassee, Florida; www.statistix.com/home.html). We used α = 0.05 to evaluate statistical significance.

Olema Creek passed within 110 m of our main study site (CP) in Olema Valley (Fig. 1). To evaluate use of nonbreeding habitat, we conducted nocturnal surveys along all or part of a 4.8-km segment of Olema Creek where it flowed past our study area. One or two observers walked the creek while carefully searching both pools and stream banks for frogs. Observers used a combination of spotlights and binoculars to locate animals (Corben and Fellers, 2001). Radiotelemetry was not used as part of these nocturnal surveys. We believe that most of the frogs we located used the adjacent pond (CP) for breeding because (1) it

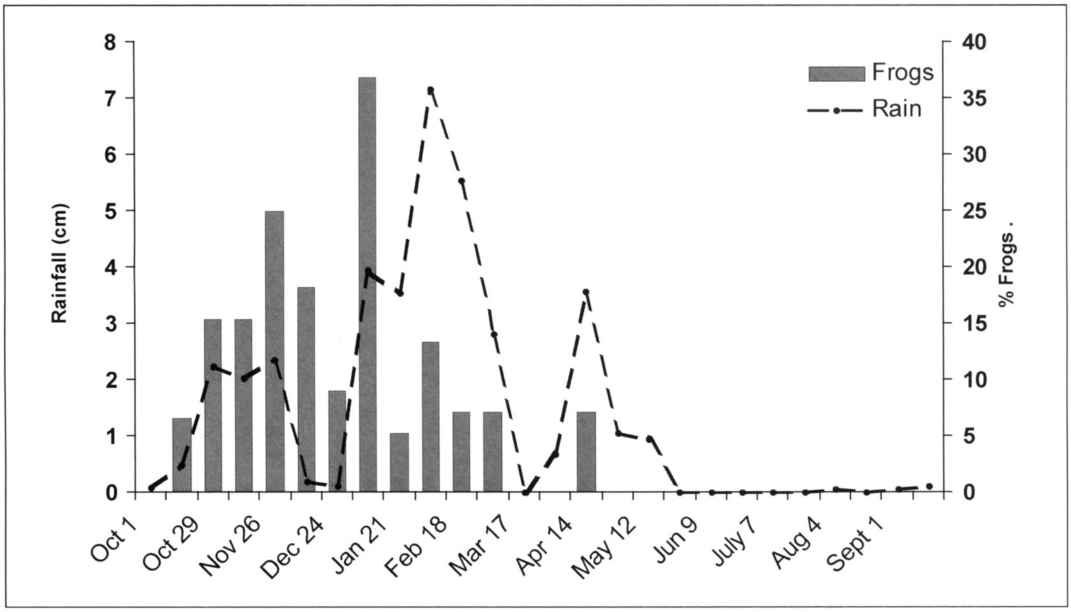

FIG. 2. Biweekly rainfall and the percent of radiotagged *Rana draytonii* that moved ≥30 m between October 1999 and September 2000.

was the closest breeding site and (2) some of the frogs found along the creek had been fitted with radiotransmitters at the pond.

RESULTS

Frogs made small-scale movements (<30 m) throughout the year. Movements of <30 m could be made without leaving the breeding sites; hence, they were considered local, nondispersal. Movements ≥30 m generally coincided with winter rains, although some frogs did not move until their seasonal habitat was on the verge of completely drying. In general, frogs moved toward breeding ponds with the onset of heavy winter rains. Frogs departed from breeding ponds at varying times throughout the rainy season, with some frogs remaining at permanent ponds all year. Some frogs made large-scale movements during the dry season (May through October), as seasonal breeding sites dried. A regression of the percent of frogs that moved ≥30 m versus rain showed that more frogs moved with higher amounts of rain ($P = 0.006$). We show rainfall and movements for the 1999–2000 season (Fig. 2), the year we had the most frogs simultaneously radiotagged.

Frog movements in the greater Olema Valley.— One hundred fifteen frogs were tracked for a mean of 91 days each (range = 5–253, Table 1). Median distance moved from the breeding site was 0 m, but for the 36 frogs that moved ≥30 m, the median was 150 m (range = 30–1400 m, Table 2, Fig. 3). In many cases, frogs almost certainly moved more than the straight-line distance between sites. This was confirmed with individuals that were located in transit. Presumed distance moved for those frogs that moved ≥30 m was 185 m (median, range = 30–1400 m).

A higher proportion of radiotagged females moved ≥30 m than males (13 of 68 males, 23 of 47 females, $\chi^2 = 11.49$, df = 1, $P < 0.01$). For frogs that moved ≥30 m, distance traveled was not significantly different for males ($N = 13$) and females ($N = 23$; median = 210 vs. 140 m, respectively; Wilcoxon rank sum $T = 1.22$, $P = 0.22$). Because some frogs lost their transmitters or were killed by predators (see below), the median distance moved might be greater than what we measured. Of the 36 frogs that moved ≥30 m, 22 (11 males, 11 females) reached a destination where they remained for at least two weeks. For these frogs, median distance traveled was 175 m. The median for these males and females was not significantly different (210 vs. 120 m; Wilcoxon rank sum $T = 0.56$, $P = 0.58$), in part because of the large variability in distance traveled.

A higher proportion of females left breeding sites than males. At our main study site (CP), nine of 21 (43%) females left the breeding site, whereas only four of 25 (16%) males departed. Females left the breeding site sooner than males (1, 5, 5, 5, 12, 55, 60, 76, 92 days for females [median = 12]; 31, 38, 47, 69 days for males

TABLE 2. Distance moved for 110 California Red-Legged Frogs (*Rana draytonii*) with radiotransmitters at three study sites in Marin County, California. Sixteen frogs radiotagged at nonbreeding sites are not included in this tabulation.

		Distance moved for frogs that moved ≥30 m						Frogs that moved <30 m
	Sex	Minimum	Median	Maximum	Mean	SD	*N*	*N*
Olema Valley								
CP	Males	200	240	490	293	135	4	31
CP	Females	100	320	1400	421	416	10	14
MP	Males	270	270	270	270	–	1	18
MP	Females	150	150	150	150	0	2	7
AD	Males	–	–	–	–	–	0	2
AD	Females	30	80	90	70	28	4	0
BF	Males	80	80	80	80	–	1	1
BF	Females	40	95	150	95	78	2	0
WD	Males	–	–	–	–	–	0	0
WD	Females	–	–	–	–	–	0	1
OT	Males	560	560	560	560	–	1	0
OT	Females	–	–	–	–	–	0	0
Big Lagoon								
BL	Males	30	105	390	158	136	6	3
	Females	–	–	–	–	–	0	0
Tomales Point								
TP	Males	–	–	–	–	–	0	0
TP	Females	30	40	50	40	14	2	0

[median = 42.5]), but the sample size was small, and the difference was not significant ($T = 0.61$, df = 11, $P = 0.55$).

Some of the dispersing frogs moved well away from the breeding site. One female (10.7 cm SVL) left the pond at our main study area (CP), crossed Olema Creek (the primary nonbreeding area) and stopped at a pond 320 m from the breeding pond. Two females (10.9 and 10.1 cm SVL) moved from CP, across Olema Creek and eventually resided in marshes, 0.88 and 1.02 km from the breeding site. Another female (10.6 cm SVL) moved down Olema Creek and up a small tributary for a total distance of 2.8 km (see individual case histories below).

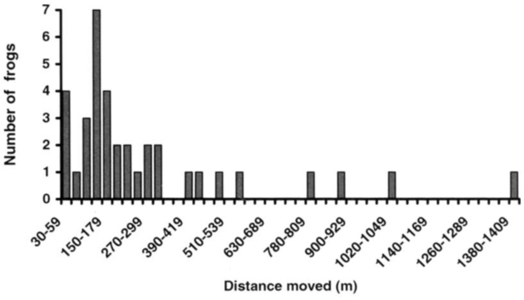

FIG. 3. Straight-line distance moved for all radiotagged Greater Olema Valley frogs that traveled ≥30 m. Median = 185 m, $N = 36$.

Fourteen of the breeding sites in the Greater Olema Valley were stock ponds surrounded by pastures. At these sites, all frogs that left the breeding site had to cross heavily grazed grassland to reach another pond or the riparian area. Frogs moved directly across these fields, typically traveling the most direct route to their destination. Movements of 100–200 m across open grasslands were common. With one exception, movements taking more than one night were along riparian corridors. One frog, however, spent five days sitting in a small clump of rushes in an open grassland (45 m from the breeding pond) before moving another 100 m to a small riparian area where it spent the next 50 days.

In two instances, we radiotagged females that appeared to have recently laid eggs (i.e., gaunt sides, conspicuously loose skin). Both frogs left the breeding pond within two days and moved to a seasonal marsh 800 m away. One frog took 32 days (5 December 1997 to 5 January 1998), whereas the other took five days (14–19 January 2000). A gravid female was fitted with a transmitter at a seasonal pond on 29 January 2001. By 8 February 2001, she had moved to an adjoining swale dominated by rushes. When captured on 28 February 2001, she had laid her eggs, as indicated by a sudden drop in mass. By 3 April 2001, she had moved 150 m to a riparian area where she remained until the transmitter was removed on 1 August 2001.

Frog movements at Big Lagoon.—The nine male frogs at this site moved a median distance of 70 m (0–390 m, Table 2). Frogs made small-scale movements (<30 m) throughout the time they were radiotagged (26 December 2002 through 3 June 2003). Most movements were between three of the deeper parts of the marsh, but one frog moved 390 m up Green Gulch Creek (when part of the marsh dried), to a seasonal creek that flowed into the marsh system. The other frogs moved to the only remaining pool at the west edge of the marsh, 50–75 m away. Most frogs did not use the riparian zone along the adjacent Redwood Creek. One individual spent four weeks there, and another frog moved to the riparian zone just before it lost its transmitter. We found frogs in the riparian area during only one nocturnal survey, although we regularly found them in the marsh or adjacent cattails.

Frog movements at Tomales Point.—The two female frogs radiotagged at this site (6.7 and 10.6 cm SVL) were relatively sedentary and apparently did not move to a breeding site. They had transmitters for an average of 283 days (68 and 498 days). Both frogs moved >30 m, with a mean of 65 m (Table 2). Although it might have been possible for the female that we tracked for 498 days to have moved to a breeding pond, laid eggs, and returned to her nonbreeding site without our noticing her absence, the gradual increase in mass throughout the time we tracked her indicated that this did not happen, and she apparently did not breed during the time we radiotracked her.

Use of riparian habitat.—On six of the 21 nocturnal stream surveys, there were ≥4 frogs per 100 m of stream, and one survey located seven frogs per 100 m (2 September 1999). Because radiotagged frogs known to be present (i.e., located during the same day by telemetry and also found along the creek on subsequent days) were frequently not seen during nocturnal surveys, the number of frogs along the creek was greater than what we observed, but it is not possible to determine by how much. For example, during a nocturnal survey on 5 July 2000, we observed one of the radiotagged frogs known to be along the creek, but we did not find two other radiotagged frogs whose presence had been confirmed earlier that day. Similarly, a nocturnal survey on 3 August 2000 did not detect either of two radiotagged frogs known to be present earlier that day; however, two untagged adults and nine subadults (<5.5 cm SVL) were observed. Nocturnal surveys also suggested that frogs tended to concentrate along portions of the creek nearest the breeding sites (Fig. 4).

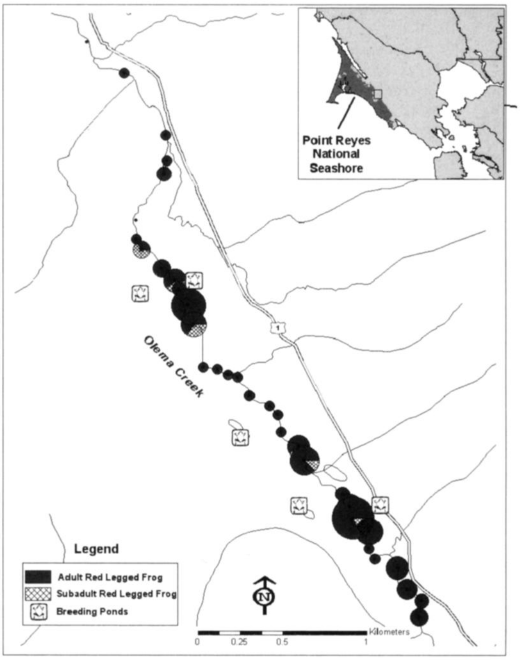

FIG. 4. Distribution of *Rana draytonii* along Olema Creek as detected during nocturnal surveys 4–6 October 1999. The distribution of frogs was similar during other surveys. Circles represent frogs, and size of each circle indicates relative number of frogs.

Diurnal behavior.—We conducted our radiotracking during the day and were frequently able to confirm visually the exact location of frogs with transmitters. This allowed us to evaluate diurnal microhabitat use. It was not unusual to find California Red-Legged Frogs basking in full sun, immediately adjacent to the water. Although we observed this behavior primarily at breeding ponds, occasionally frogs were found in similar situations in nonbreeding riparian areas.

Frogs that were not basking used a variety of cover. In permanent ponds, they sat entirely underwater in the deeper portions of the pond (>0.75 m), usually in association with the emergent vegetation. At sites with deeper water, *R. draytonii* sat on the bank in close proximity to the water. In shallow, seasonal ponds (<0.4 m deep), frogs were usually under vegetation (e.g., rushes, blackberries, hedge nettles [*Stachys ajugoides*]) at the edge of the pond. In seeps or seasonal streams, frogs were found under blackberry thickets interspersed with poison oak, coyote brush, hedge nettles, stinging nettles, and mats of rushes. Along permanent streams, frogs were found in or near pools with a depth of >0.5 m and associated with structurally complex cover (e.g., root mass, logjam, or overhanging bank). When on stream banks, frogs sat under dense vegetation as far as 2 m from the water's edge. Vegetation was predominantly western swordfern, blackberry, hedge nettle, and giant horsetail (*Equisetum telmateia*).

Predation.—We documented two predation events and had circumstantial evidence for three others. A Great Blue Heron (*Ardea herodia*) ate two radiotagged frogs sometime between 4 and 18 January 2000 (Fellers and Wood, 2004). Three other frogs appeared to have been killed by predators. The skin, bones, and transmitter of one frog were found at the base of a guano-stained fence post, along with a number of raptor pellets. Two frogs appeared to have been killed by mammalian predators, although we have no definitive proof. We found the skin, internal organs, PIT tag, and transmitter of a frog in a riparian corridor, and we found pieces of skin, internal organs, and the transmitter of another frog. One frog appeared to have been stepped on by a large, hoofed animal, probably one of the cows that grazed in the pasture. We found the anterior two-thirds of the frog in a pasture; the posterior portion of the frog had been crushed into the ground. Although we did not observe any predation during our nocturnal surveys along Olema Creek, we regularly observed raccoons (*Procyon lotor*), Black-Crowned Night Herons (*Nycticorax nycticorax*), river otters (*Lutra canadensis*), and nonnative rats (*Rattus* spp.). At breeding sites, we observed Great Blue Herons, but other potential predators probably visited the ponds and marshes at times.

Injuries from transmitters.—Twenty frogs had injuries from transmitter belts (17% of radiotagged frogs). The most common injury consisted of small abrasions on the dorsum or, less frequently, a midventral abrasion. The wounds generally healed within two weeks if frogs were fitted with transmitter belts with one additional bead. Eleven of the injured frogs were reweighed at the time the wound was noticed, and all frogs had gained mass since their initial capture. We reweighed 23 uninjured frogs with transmitters; 18 (78%) gained mass after initial capture, two (9%) had no change, and three (13%) lost mass. The mean mass gain for these frogs was 21%, and mean mass loss was 8.5%. Overall, we do not believe that the minor injuries caused by the transmitter belt interfered with frog behavior.

Individual case histories.—The frog that was radiotagged for the longest time had a transmitter for 16 months. When first caught on 12 May 1999, the female frog weighed 42.5 g and was 7.3 cm SVL. It grew steadily and was 77.7 g and 8.9 cm when last captured on 14 June 2000.

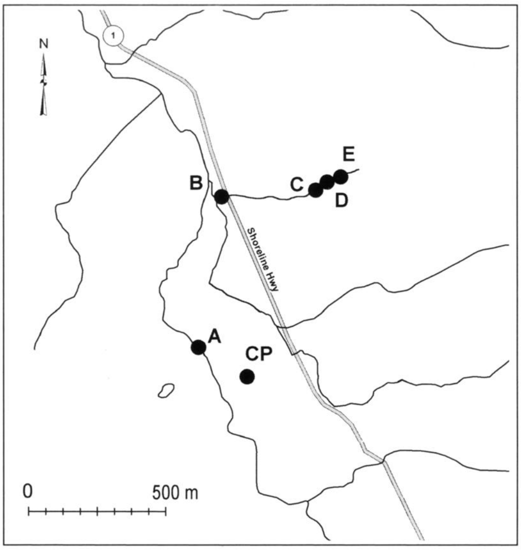

FIG. 5. Movements of a female radiotagged *Rana draytonii* that was captured at a breeding pond (CP) and subsequently moved to sites A–E. The frog was 10.5 cm (SVL) and was tagged during the breeding season (19 January 1999). The straight-line distance from CP to E was 1.4 km, but the presumed distance moved was 2.8 km.

The frog was caught in a puddle (1.0 × 0.3 m, 15 cm deep) that had formed in a rut created by a roadside seep along an abandoned dirt road on Tomales Point (site TP, Fig. 1). For 16 months, this frog made frequent, small (2–10 m) movements, within a 200-m^2 area surrounding the seep. The furthest the frog moved was 110 m. It used a variety of microhabitats: underwater in the puddle, underground in small mammal burrows, partially buried in duff beneath wax myrtle and coyote brush, and sitting in small clumps of grass. Although this frog was an adult female, it did not move to the nearest known breeding pond (650 m away) during the winter of 1999–2000. On 1 September 2000, the transmitter was found in the grass beneath a coyote brush, 6 m from where the frog had last been found. We could not determine whether the transmitter had fallen off or whether the frog had met a predator.

One frog moved at least 1.4 km. This was a female (10.5 cm SVL) tagged at a breeding pond (CP) during the breeding season (19 January 1999). On 23 January 1999, she was located under a fallen tree, 240 m away in Olema Creek. On 30 January 1999, she had moved a minimum of 650 m to a pool in a small tributary of Olema Creek (Fig. 5). It is quite likely that the frog followed Olema Creek to the tributary, which would have required a movement of 1.0 km to reach that point. By 14 February 1999, the frog had moved either across a two-lane, paved country road or under the road through a culvert. She then moved up a small, seasonal drainage, 430 m from her previous location. The presumed distance traveled by this frog was 2.8 km. The frog stayed in this drainage and was often found under blackberry brambles and thickets of poison oak along the stream. The transmitter and remains of the frog were found on 14 June 1999, apparently the victim of avian predation (see Predation above).

Discussion

The California Red-Legged Frog recovery plan emphasizes protection and recovery of breeding habitat (U.S. Fish and Wildlife Service, 2002), and most protection efforts have focused on breeding sites. One challenge in managing *R. draytonii* has been the paucity of data on habitat use beyond the breeding site, thus making it difficult to evaluate requirements for nonbreeding habitat and connecting migration corridors. Our study provides insights into *R. draytonii* movement and habitat use in a coastal environment and establishes a basis for making decisions about habitat protection.

Migration of *R. draytonii* from the breeding sites we studied was highly variable. Some frogs remained at breeding ponds all year, whereas others spent only a few days. Two-thirds of female frogs and 25% of male frogs moved from breeding areas. Bulger et al. (2003) found that 80–90% of *R. draytonii* remained at one breeding site all year. In our study, frogs at sites that held water only seasonally often lingered until the site was on the verge of drying completely. Because all our study sites were in an area where summer fog is the norm (E. J. Null, NOAA Technical Memorandum, NWS WR-126, 1995; Lundquist and Bourcy, 2000), frogs could move throughout much of the summer with little risk of desiccation. Once along the riparian corridor, frogs used a range of microhabitats that provided both cover and moisture, especially blackberry thickets, logjams, and root tangles at the base of standing or fallen trees. Regular summer dispersal across open grassland is in contrast to what Rothermel and Semlitsch (2002) reported for juvenile *Ambystoma* and *Bufo* in Missouri where desiccation appeared to be a significant factor affecting amphibian dispersal across fields adjacent to their artificial pools.

There was a wide range of migration distances (30–1400 m, straight-line). Our main study pond was 110 m from a riparian zone that provided suitable nonbreeding habitat (CP, Fig. 1). For frogs that moved at least 30 m from the pond, the median movement was 150 m. Relatively short movements from breeding sites was also suggested by the nocturnal surveys of riparian vegetation along Olema Creek (Fig. 4) where we found more frogs in areas adjacent to breeding sites. At Big Lagoon, where nonbreeding habitat was immediately adjacent to breeding sites in the marsh, the median distance moved was 68 m, and none of the frogs went more than 390 m. These short movements were similar to Columbia Spotted Frogs (*Rana luteiventris*); Pilliod et al. (2002) found no significant difference between males ($\bar{x}$ = 367 m moved) and females ($\bar{x}$ = 354 m). Bartelt et al. (2004) reported that male Western Toads (*Bufo boreas*) traveled shorter distances from breeding ponds than females (581 m ± 98 and 1105 m ± 272, respectively). Because there is relatively little data on these species, it is not possible to determine whether the differences are species-specific or dependent on the local landscape.

When frogs moved beyond the minimum distance to reach a suitable nonbreeding area, some followed riparian corridors, whereas others moved directly toward sites where they stayed through the nonbreeding season. Because most frogs moved from a breeding pond, across a grazed pasture, to a riparian area, they did not have the option of following a waterway during their initial movement. This is similar to Bulger et al. (2003), where frogs mostly moved in a straight line without apparent regard to intervening vegetation or topography. However, there were a few individuals in each study that moved primarily along a creek.

During our nocturnal surveys of Olema Creek, some frogs were well hidden by cover, whereas others sat fully exposed on top of logs or even on the sandy edge of the creek, places where California Red-Legged Frogs were rarely seen during the day. It is unclear why some individuals spent hours exposed to predation when good cover was only 1–2 m away. A frog in the open would have a wider field of view to detect and capture prey, perhaps partially mitigating the risk of predation. We documented predation by a Great Blue Heron, had evidence of predation by a raptor, and suspect that two other frogs succumbed to mammal predators. Additionally, we occasionally observed predators along Olema Creek including raccoons, Black-Crowned Night Herons, river otters, and nonnative rats (*Rattus* spp.). At a marsh that was not part of this study, we regularly observed night herons, and *R. draytonii* were so skittish that we have never been able to capture a single individual.

Based on their findings that 60% of the radiotagged frogs stayed within 30 m of their breeding sites, Bulger et al. (2003) recommend a 100-m buffer with an array of suitable habitat elements around breeding sites. Although that might work well at their study area, we do not believe that a simple, symmetrical buffer is typically adequate. At our main study site, a 100-m buffer would not include any suitable nonbreeding habitat. Because the pond completely dries every 4–5 years, such a buffer would result in the elimination of the local population. By contrast, the Big Lagoon site has suitable nonbreeding habitat immediately adjacent to the marsh. At that site, maintaining the marsh habitat and the natural water levels would likely be adequate for long-term survival.

Three important conclusions from our study are that (1) most frogs move away from breeding sites, but only a few move farther than the nearest suitable nonbreeding habitat; (2) the distance moved is highly site-dependent, as influenced by the local landscape; and (3) land managers should not use average dispersal or migration distances (from our study, or any other) to make decisions about habitat requirements. A herpetologist familiar with *R. draytonii* ecology needs to assess the local habitat requirements.

Recommendations.—Maintaining populations of pond-breeding amphibians, such as *R. draytonii*, requires that all essential habitat components be protected. These include (1) breeding habitat, (2) nonbreeding habitat, and (3) migration corridors. In addition, a buffer is needed around all three areas to ensure that outside activities do not degrade any of the three habitat components.

For *R. draytonii*, nonbreeding habitats must have several characteristics: (1) sufficient moisture to allow amphibians to survive throughout the nonbreeding season (up to 11 months), (2) sufficient cover to moderate temperatures during the warmest and coldest times of the year, and (3) protection (e.g., deep pools in a stream or complex cover such as root masses or thick vegetation) from predators such as raptors (hawks and owls), herons, and small carnivores.

Breeding habitat has been well described (U.S. Fish and Wildlife Service, 2002; Stebbins 2003) and receives most of the management attention (US Fish and Wildlife Service, 2002). However, nonbreeding areas are equally important because some *R. draytonii* spend only a week or two at breeding sites, yet nonbreeding habitat is frequently ignored and is generally not well understood. Aside from our study, Bulger et al. (2003) are the only ones to publish details on the use of nonbreeding habitat by *R. draytonii*. Additional research on nonbreeding habitat is needed, especially in other parts of range where *R. draytonii* occupy a diversity of ecotypes.

Migration corridors are frequently not considered in management planning for California Red-Legged Frogs. Our work and that of Bulger et al. (2003) indicate that *R. draytonii* migration corridors can be less "pristine" (e.g., closely grazed fields, plowed agricultural land) than the other two habitat components. Bulger et al. (2003) observed that *R. draytonii* did not avoid or prefer any landscape feature or vegetation type. They tracked frogs that crossed agricultural land, including recently tilled fields and areas with maturing crops. Our study site did not encompass such a diversity of habitats, but frogs readily traversed pastureland that surrounded the breeding sites. While conducting other research, we observed five frogs crossing a recently burned field as they moved toward a breeding pond during the first rain of the season (25 October 2004). Both our study and that of Bulger et al. were conducted at study sites near the Pacific Ocean where summer fog and high relatively humidity reduce the risk of desiccation for dispersing amphibians (E. J. Null, NOAA Technical Memorandum, NSW, WR-126, 1995; Lundquist and Bourcy, 2000). Though desiccation was probably not a problem for frogs in our study, amphibians are often faced with a variety of hazards including roads (Gibbs, 1998; Vos and Chardon, 1998), degradation of habitat (Vos and Stumpel, 1995; Findlay and Houlahan, 1997; Gibbs, 1998), and predation (Gibbs, 1998), as well as desiccation (Rothermel and Semlitsch, 2002; Mazerolle and Desrochers, 2005).

Buffers are often described as the area that frogs use near breeding sites. Such usage combines migration corridors and nonbreeding habitat, as well as the adjacent area necessary to protect these areas. We believe that it is important to identify each habitat component separately and then include a buffer that is sufficiently large to maintain the integrity of each habitat type. Such a buffer cannot be defined as a standard distance but rather as an area sufficient to maintain the essential features of the amphibian habitat. Hence, a riparian area adjacent to a forest undergoing clear-cut logging would need a relatively large buffer to protect it from increased sedimentation and the increased temperature fluctuations that occur after logging. Less severe habitat modifications adjacent to amphibian habitat could be accommodated with a narrower buffer (deMaynadier and Hunter, 1995, 1999; Gibbs, 1998).

Buffers are typically described as a fixed-width boundary around breeding sites (Semlitsch and Bodie, 2003). However, the distribution of habitat components is rarely symmetrical

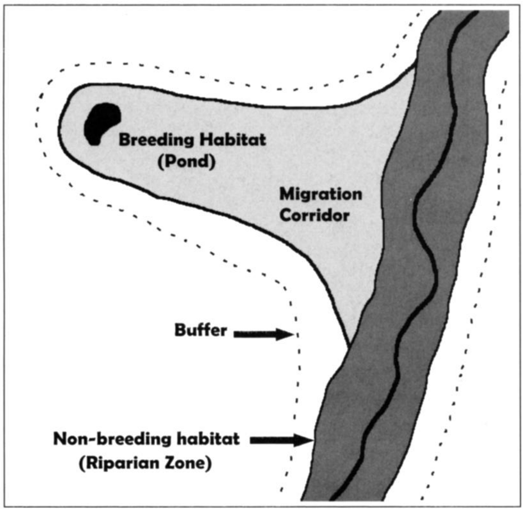

FIG. 6. Stylized diagram of typical *Rana draytonii* habitat showing the critical habitat components and the required asymmetrical buffer.

(e.g., a pond with frogs dispersing in all directions to surrounding nonbreeding area). At all of our study sites, frogs moved primarily in one direction, often toward the nearest riparian area, similar to what Rothermel and Semlitsch (2002) reported. As suggested by Regosin et al. (2005), protecting frog habitat in these situations requires an asymmetrical conservation area (Fig. 6). Because it is often not obvious from casual inspection what areas frogs are relying upon, delineating each habitat component and determining the size of a suitable buffer requires either an expert opinion from a field biologist with extensive experience with the species of interest or a field study to monitor radiotagged frogs.

The design of protected areas is often developed with the unstated assumption that only the most sedentary frogs can or need to be protected. The resulting systematic loss of individuals that move the farthest can have unexpected and unwanted effects (Gill, 1978; Berven and Grundzien, 1990). Long-distance dispersers are the individuals most likely to reach distant breeding sites and, hence, provide the genetic diversity that is important for survival of small populations. Additionally, those same dispersers are the individuals that would colonize sites where frogs have been lost because of random events that periodically extirpate local populations. By consistently selecting against frogs that disperse the greatest distances, the effective size of a metapopulation is reduced and the size of the effective breeding population is smaller; smaller breeding populations have a greater likelihood of extirpation (Gill, 1978; Sjogren, 1991).

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LITERATURE CITED

BARTELT, P. E., C. R. PETERSON, AND R. W. KLAVER. 2004. Sexual differences in the post-breeding movements and habitats selected by Western Toads (*Bufo boreas*) in southeastern Idaho. Herpetologica 60:455–467.

BERVEN, K. A., AND T. A. GRUDZIEN. 1990. Dispersal in the Wood Frog (*Rana sylvatica*): implications for genetic population structure. Evolution 44:2047–2056.

BODIE, J. R. 2001. Stream and riparian management for freshwater turtles. Journal of Environmental Management 62:443–455.

BULGER, J. B., N. J. SCOTT JR., AND R. B. SEYMOUR. 2003. Terrestrial activity and conservation of adult California Red-legged Frogs *Rana aurora draytonii* in coastal forests and grasslands. Biological Conservation 110:85–95.

BURKE, V. J., AND J. W. GIBBONS. 1995. Terrestrial buffer zones and wetland conservation: a case study of freshwater turtles in Carolina Bay. Conservation Biology 9:1365–1369.

CORBEN, C., AND G. M. FELLERS. 2001. A technique for detecting eyeshine of amphibians and reptiles. Herpetological Review 32:89–91.

DEMAYNADIER, P. G., AND M. L. HUNTER JR. 1995. The relationship between forest management and amphibian ecology: a review of the North American literature. Environmental Reviews 3:230–261.

———. 1999. Forest canopy closure and juvenile emigration by pool-breeding amphibians in Maine. Journal of Wildlife Management 63:441–450.

FELLERS, G. M. 2005. *Rana draytonii* Baird and Girard 1852, California Red-Legged Frog. *In* M. Lannoo (ed.), Amphibian Declines: The Conservation Status of United States Species. Volume 2, pp. 552–554. University of California Press, Berkeley.

FELLERS, G. M., AND P. M. KLEEMAN. 2003. A technique for locating and recovering radiotransmitters at close range. Herpetological Review 34:123.

FELLERS, G. M., AND L. WOOD. 2004. *Rana aurora draytonii* (California Red-Legged Frog) predation. Herpetological Review 35:163.

FINDLAY, C. S., AND J. HOULAHAN. 1997. Anthropogenic correlates of species richness in Southeastern Ontario wetlands. Conservation Biology 11:1000–1009.

GIBBONS, J. W., J. W. COKER, AND T. M. MURPHY. 1977. Selected aspects of the life history of the Rainbow Snake (*Farancia erytrogamma*). Herpetologica 33:276–281.

GIBBS, J. P. 1998. Amphibian movements in response to forest edges, roads, and streambeds in southern New England. Journal of Wildlife Management 62:584–589.

GILL, D. E. 1978. The metapopulation ecology of the Red-Spotted Newt, *Notophthalmus viridescens*. Ecological Monographs. 48:145–166.

JENNINGS, M. R., AND M. P. HAYES. 1994. Amphibian and Reptile Species of Special Concern in California., California Department of Fish and Game, Inland Fisheries Division, Rancho Cordova.

JOLY, P., C. MIAUD, A. LEHMANN, AND O. GROLET. 2001. Habitat matrix effects on pond occupancy in newts. Conservation Biology 15:239–248.

KEAST, A., AND E. S. MORTON (eds.). 1980, Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation. Smithsonian Institution Press, Washington, DC.

LAMOUREUX, V. S., AND D. M. MADISON. 1999. Overwintering habitats of radio-implanted Green Frogs, *Rana clamitans*. Journal of Herpetology 33:430–435.

LUNDQUIST, J. D., AND T. B. BOURCY. 2000. California and Oregon Humidity and Coastal Fog. Proceedings, 14th Conference on Boundary Layers and Turbulence. Aspen, CO.

MADISON, D. M. 1997. The emigration of radio-implanted Spotted Salamanders, *Ambystoma maculatum*. Journal of Herpetology 31:542–552.

MAZEROLLE, M. J., AND A. DESROCHERS. 2005. Landscape resistance to frog movements. Canadian Journal of Zoology 83:455–464.

PILLIOD, D. S., C. R. PETERSON, AND P. I. RITSON. 2002. Seasonal migration of Columbia Spotted Frogs (*Rana luteiventris*) among complementary resources in a high mountain basin. Canadian Journal of Zoology 80:1849–1862.

POPE, S. E., L. FAHRIG, AND H. G. MERRIAM. 2000. Landscape complementation and metapopulation effects on Leopard Frog populations. Ecology 81:2498–2508.

RATHBUN, G. B., AND T. G. MURPHEY. 1996. Evaluation of a radio-belt for ranid frogs. Herpetological Review 27:187–189.

REGOSIN, J. V., B. S. WINDMILLER, R. N. HOMAN, AND J. M. REED. 2005. Variation in terrestrial habitat use by four pool-breeding amphibian species. Journal of Wildlife Management 69:1481–1493.

RICHTER, S., J. E. YOUNG, R. A. SEIGEL, AND G. N. JOHNSON. 2001. Post-breeding movements of the Dark Gopher Frog, *Rana sevosa* Goin and Netting: implications for conservation and management. Journal of Herpetology 35:316–321.

ROTHERMEL, R. B., AND R. D. SEMLITSCH. 2002. An experimental investigation of landscape resistance of forest versus old-field habitats to emigrating juvenile amphibians. Conservation Biology 16: 1324–1332.

SEMLITSCH, R. D., AND J. R. BODIE. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation Biology 17:1219–1228.

SJOGREN, P. 1991. Extinction and isolation gradients in metapopulations: the case of the Pool Frog (*Rana lessonae*). Biological Journal of the Linnean Society 42:135–147.

STEBBINS, R. C. 2003. A Field Guide to Western Reptiles and Amphibians., Houghton Mifflin, New York.

U.S. FISH AND WILDLIFE SERVICE. 2002. Recovery plan for the California Red-Legged Frog (*Rana aurora draytonii*). U.S. Fish and Wildlife Service, Portland, OR.

VOS, C. C., AND J. P. CHARDON. 1998. Effects of habitat fragmentation and road density on the distribution pattern of the Moor Frog, *Rana arvalis*. Journal of Applied Ecology 35:44–56.

VOS, C. C., AND A. H. P. STUMPEL. 1995. Comparison of habitat-isolation parameters in relation to fragmented distribution patterns in the Tree Frog (*Hyla arborea*). Landscape Ecology 11:203–214.

Accepted: 20 January 2007.

CALIFORNIA

Gov. Newsom slams PG&E over ‘unacceptable’ power outages and failure to fix systems

Residents pick up meals Wednesday from one of the few food trucks operating in the Sonoma, Calif., area after Pacific Gas & Electric Co. initiated widespread power outages. (Brittany Hosea-Small / AFP/Getty Images)

OCT. 10, 2019
8:26 PM

Gov. Gavin Newsom tore into Pacific Gas & Electric Co. on Thursday, calling the mass power outages “unacceptable” and the result of the bankrupt utility’s own long legacy of mistakes.

“What’s happened is unacceptable. And it’s happened because of neglect. It’s happened because of decisions that were deferred, delayed or not made by the largest investor-owned utility in the state of California and one of the largest in the nation,” he said at a news conference. “This current operation is unacceptable. The current conditions and circumstances are unacceptable.”

For parts of Thursday, more than 1 million Californians remained without power after the state’s largest utility shut off electricity in an attempt to prevent windblown power lines from sparking devastating wildfires. PG&E said late Thursday that 738,000 customers remained without power and that it was restoring service in many areas.

Newsom said PG&E’s failure to maintain its system created the need for the outages.

“It’s decisions that were not made that have led to this moment in PG&E’s history and the state of California as it relates to our major investor-owned utility,” Newsom said. “This is not, from my perspective, a climate change story as much as a story about greed and mismanagement over the course of decades. Neglect. A desire to advance not public safety but profits.”

Responding to widespread criticism over the blackouts, the utility’s chief executive, Bill Johnson, said he was focused on PG&E’s future, not it’s past. He joined the company in April.

"I didn't come here to deal with the past. I came here to help improve the future," he said. "I haven't delved into all those matters."

He added: "There are many things we need to do better than we did this time. Communicate better, with as much notice as possible, as much clarity as frequently as possible. We did not deliver on that commitment at this time. Our website crashed. Maps were inconsistent or incorrect."

Residents had already rushed to empty store shelves looking for batteries and water and had lined up for gas to prepare for the looming outage. They did laundry, ran dishwashers and vacuumed, fearful they would not have power for several days. Some stuffed refrigerators and freezers with ice so they would stay colder longer. Others emptied food into coolers.

But their lights stayed on, while their frustrations mounted.

The steady alerts that power would be shut off at specific times — only to have it remain on — proved more unnerving than the actual loss of electricity for some.

Mary Carey, a lawyer who lives in a wooded East Bay community, compared the situation to knowing a "meteorite is on the way, but it won't hit for 12 hours."

Kevin Marker, 66, a retired businessman, had another take: "I think PG&E is just getting back at people."

By Thursday morning, the utility had turned off power to customers in Alameda, Alpine, Contra Costa, Mariposa, San Joaquin, San Mateo, Santa Clara, Santa Cruz, Stanislaus and Tuolumne counties.

It also had restored power to about 125,000 customers across the state, including 74,000 in Humboldt County. Still, officials warned, more areas could see blackouts, depending on weather conditions. The utility is still considering cutting off about 4,000 customers in the southern portion of its coverage area in Kern County.

Fierce winds blew through several counties in Northern California on Thursday, the kind of gusts that bend treetops and cause cars to swerve.

In response, the National Weather Service issued a red-flag warning for much of the region, cautioning residents to expect northerly winds between 15 and 30 mph, with gusts up to 50 mph, and very low daytime humidity. The warning is in effect through Friday.

Where PG&E may shut off power

The high winds and dry weather create ideal fire conditions, authorities warn, with the potential to transform a spark into a raging inferno. PG&E fears windblown electrical lines could spark fires if power is not cut.

About two hours northwest of Sacramento in Clearlake, residents entered their second full day without power. At the local Safeway, which had a generator to provide electricity, customers searched for ice and charcoal hoping to save or cook the groceries in their refrigerators.

At a nearby senior center, PG&E set up a charging station in a back room for cellphones and medical equipment. At least 150 people had visited Wednesday, said representative Conrad Asper. By lunchtime Thursday, there had been more than 250.

Paul Spillane, 79, expressed what was a common sentiment at the center: frustration with PG&E.

“I think it’s an outrage,“ he said of the blackouts. “I say it’s the three most miserable days I’ve had since I’ve been up here. I haven’t been eating properly or anything.“

Amee Peterson, 66, said she feels so dirty from a lack of hot showers that she's considering boiling water on the barbecue to wash her hair. On Wednesday night, she ate cake for dinner because she couldn't cook. Peterson, who has post-traumatic stress disorder, fibromialgia and other conditions, said she received automated calls warning her of the blackout, but they were not specific. When the power cut out at 1 a.m. while she was reading a book, she was surprised. Even more frustrating, she said, has been the lack of clarity on when power might return.

"There is no idea when it's coming back on," she said.

The utility has warned that some customers may be in the dark for up to five days, even after the winds subside, as crews check equipment and repair fallen lines before restoring electricity.

CALIFORNIA

Full coverage: California power outages

Oct. 9, 2019

The PG&E blackout marks the largest power shut-off to date as California utilities attempt to reduce the risk of wildfires that have charred thousands of acres, caused billions of dollars in damage and spurred cries for widespread change in how electricity is delivered over the state's aging grid.

Equipment malfunctions have been tied to some of the state's most destructive and deadliest fires, including the 2017 wine country blazes and last year's Camp fire, which devastated the town of Paradise and killed 85 people.

In January, PG&E filed for Chapter 11 bankruptcy protection, anticipating multibillion-dollar legal claims stemming from the Camp fire, which also destroyed nearly 14,000 homes. A month later, officials at the utility acknowledged that its equipment probably sparked that blaze.

At a news conference Wednesday evening, PG&E officials signaled that these types of massive shut-offs during fire season might be the new normal.

Sumeet Singh, vice president of PG&E's community wildfire safety program, said customers should anticipate similar shutdowns in the future until the utility has finished its wildfire safety plan, "unless the weather changes significantly and the vegetation condition and the fuel-loading condition, and land and the forest management, changes significantly within the state."

"We understand that this power shut-off is difficult for our customers and communities. Please check on your neighbors, friends and family and know that we will work safely, and quickly as possible, to restore power across the region," Singh said.

The power shut-offs have prompted backlash, with some residents saying they create a whole new set of dangers as they try to keep up with news about fires. Critics worry that communications and evacuations will be hampered when the power is out, especially if traffic signals don't work and cellphone service is affected.

There also was concern about how those with health issues who rely on electrically powered medical equipment to stay alive would cope without power.

State Sen. Jerry Hill (D-San Mateo) said Thursday that he sent a letter to the California Public Utilities Commission asking the panel to conduct a review of how PG&E decided which areas should lose power and how the blackouts were rolled out.

"Many questions remain unanswered as the state reels from the consequences of this decision by PG&E, chief among them why is PG&E alone in making this decision?" Hill wrote to the commission.

The outage prompted UC Berkeley to cancel classes for a second consecutive day. University officials say some buildings are running on generator power for "life safety, animal care and support of critical research infrastructure." However, the generators cannot power the entire campus.

The Oakland Zoo also remained closed after the region lost power overnight. The zoo had closed ahead of the planned blackout, and staff rushed out to purchase additional generators to power exhibits for animal safety. The gas they have will power the generators for about four days, Darren Minier, assistant director of animal care, told the San Francisco Chronicle.

In Southern California, residents have anxiously watched how the power shutdowns have affected other parts of the state, wondering if it was a glimpse of what was to come for them.

Southern California Edison on Thursday began preventive power outages across its service area. Given the strong Santa Ana winds forecast for the area, the utility said, power could be cut off to more than 173,000 customers in parts of nine counties in Southern and Central California: Los Angeles, San Bernardino, Riverside, Orange, Ventura, Kern, Tulare, Inyo and Mono.

Times staff writers Jaclyn Cosgrove, Anita Chabria and Patrick McGreevy contributed to this report.

CALIFORNIA

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Small brush fire ignites in El Sereno as firefighters battle the Saddleridge blaze

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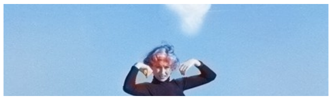

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CALIFORNIA

Saddleridge fire explodes to 4,700 acres, burns 25 homes in San Fernando Valley

By HANNAH FRY, LEILA MILLER, MATTHEW ORMSETH, JOSEPH SERNA

OCT. 11, 2019

9:41 AM

A fast-moving brush fire continued its destructive march into the northern foothills of the San Fernando Valley on Friday, burning at least 25 homes, closing freeways and forcing thousands to flee.

The Saddleridge fire, which broke out late Thursday in Sylmar amid strong Santa Ana winds, spread rapidly overnight west into Porter Ranch and other communities, burning more than 4,700 acres at a rate of roughly 800 acres per hour, Los Angeles Fire Department Chief Ralph Terrazas said early Friday.

“These weather conditions are significant,” Terrazas said. “You can imagine the embers from the wind have been traveling at significant distances, which cause other fires to start.”

Mandatory evacuations have been issued to roughly 23,000 homes making up a huge swath of neighborhoods north of the 118 Freeway from Tampa Avenue all the way to the Ventura County line — an area covering 100,000 residents.

L.A. County Fire Department
@LACoFDPIO

#SaddleridgeFire Los Angeles County Firefighters working all out! A physical and mental delivery from Camp 12 personnel creating a fuel break in an extreme fire behavior environment.

This highlights the challenges of night firefighting @LACOFD @Angeles_NF @LAFD @LASDHQ @LAPDHQ

1,397 9:27 AM - Oct 11, 2019

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One firefighter suffered a minor injury to his eye, and a man in his late 50s died after suffering a heart attack while talking with firefighters early Friday, Terrazas said. Authorities could not confirm reports that the man was trying to fight the fire from his home before he was stricken.

Saddleridge fire resources

Evacuation zones, evacuation centers, school and road closures

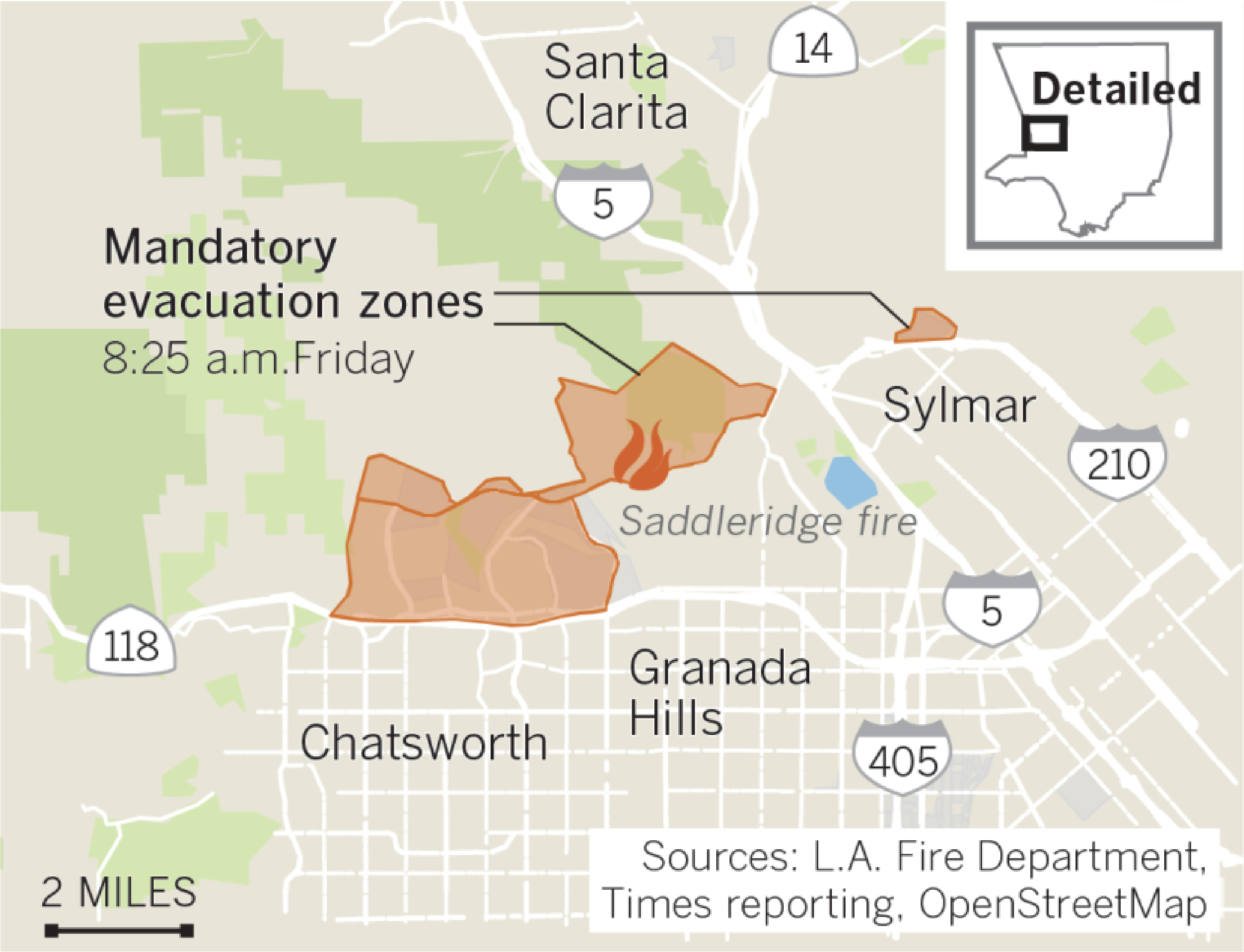
Map: Wildfires currently burning in California

More than 1,000 firefighters from multiple agencies were attacking the blaze Friday from the air and ground. Officials deployed helicopters and amphibious firefighting aircraft known as Super

Scoopers, while ground crews manned bulldozers to cut containment lines into nearby hillsides in an effort to slow the fire's spread. At least one air tanker blanketed fire retardant across the ridges.

However, unrelenting winds gusting up to 50 mph, low humidity and rising temperatures — which can dry out brush that fuels the fire — put crews at a disadvantage. Officials said they expect it will take days to get the blaze under control.

"Nobody is going home right away," Terrazas said.



The L.A. Fire Department has established these evacuation zones for the Saddleridge fire near Sylmar. They are current as of 5 a.m. Friday Oct. 11. (Chris Keller / Los Angeles Times)

The fire was first reported in Sylmar about 9 p.m. Thursday on the north side of the 210 Freeway, but wind-driven firebrands soared over the 210 and 5 freeways and ignited more dry brush. A 30-acre spot fire broke out west of Balboa Boulevard and pushed westward, officials said.

There are few options for firefighters against a wind-whipped fire with a lot of fuel, Los Angeles firefighter John Ferrer said.

“Because of the wind-driven factor, it creates a more defensive posture for firefighters,” Ferrer said. “We wait until the wind dies down and can deploy adequate resources to contain the flanks of the fire and an early-morning attack on the fire.”

Saddleridge fire burns more than 4,700 acres

The blaze moved so quickly that it jumped into neighborhoods overnight before firefighters and police could warn residents.

In Porter Ranch, a man stared as waves of embers crested against a two-story home abutting a hillside on Sheffield Way and flames lapped at the back of the structure.

“That’s my home,” he said. He had gotten out 15 minutes earlier.

Flames had already reached a second home on the cul-de-sac, which was choked with thick gray smoke, punctured only by the high beams of fleeing cars speeding through the small streets that crisscross the hillsides.

CALIFORNIA

Saddleridge fire: Residents flee flames, worry whether their homes survived

Oct. 11, 2019

Kuriakose Chaz watched flames scale the side of the canyon, thinking about his Porter Ranch home of six years just a few blocks from the houses that by 2:30 a.m. were beginning to be devoured.

“If it goes,” he said, “it goes.”

Chaz, who’d gone to sleep at 10:30 p.m. Thursday, was awakened by a call around midnight from his nephew, who works for Southern California Edison and was monitoring the fire.

His nephew said, “You need to go.”

Chaz watched, dismayed, as flames charred the canyon he often enjoys hiking. Thick brush that had been watered by the winter’s plentiful rains stoked the blaze.

“I’ve watched fires on the news,” Chaz said. “But this hits home. I live here.”

CALIFORNIA

Saddleridge fire approaches Aliso Canyon natural gas facility, site of massive 2015 blowout

Oct. 11, 2019

Cece Merkerson first noticed an orange glow from the living room of her third-story apartment in Porter Ranch about 11:30 p.m. Thursday. She had heard a fire was raging in nearby Granada Hills but figured it was a safe distance away.

“That can’t be that fire,” she thought. “That can’t be it.”

She checked the TV news, but there wasn't an evacuation order for Porter Ranch. To calm her nerves, Merkerson started packing anyway: medication, a small safe with important papers, a change of clothes and a couple of bananas.

Around 2 a.m., Merkerson looked through her window and saw flames. The mandatory evacuation order was issued minutes later.

"I started knocking on all my neighbors' doors because I knew they were sleeping," she said. "I'm banging and banging and I woke up about eight of them — and they all looked at me like I was crazy."

Saddleridge fire: Residents flee flames, worry whether their homes survived

Several major highways were closed because of the blaze, snarling morning traffic across the region, the California Highway Patrol said. The 210 Freeway was shut down in both directions between the 5 and 118 freeways. The 5 Freeway was closed between Roxford Street and Calgrove Boulevard. The 14 Freeway was closed at Newhall Avenue. Authorities have not said when the roads will reopen.

Evacuations have been ordered for Oakridge Estates, Glenoaks, the Foothill area and into neighborhoods in Granada Hills and Porter Ranch. Officials warned that other communities near the fire need to be ready to leave at a moment's notice.

Evacuees included hundreds of teenagers incarcerated at the Barry J. Nidorf Juvenile Hall facility in Sylmar, not far from the fire's edge.

The facility holds 278 teenagers, most of them 15 to 18, along with dozens of facility officers and workers. They all were being relocated to Los Padrinos Juvenile Hall in Downey, said facility spokesman Kerri Webb. It was an hours-long process to move them all.

“It’s very methodical. We have to utilize a lot of security,” Webb said. “Right now, getting everyone out safely is our highest priority.”

CALIFORNIA

Numerous Riverside County homes destroyed by fire; SoCal Edison cuts power to thousands

Oct. 10, 2019

About 1 a.m. Friday, several Sylmar residents stood about three miles from Oakridge Estates, which was under a mandatory evacuation order, watching the fire burn in the mountains beyond.

Iván DeGuzman, 34, said he had packed his car hours before after receiving a text message from a friend alerting him to the fire. He loaded up passports, clothes and some other items.

He recalled how the neighborhood was overwhelmed by smoke and ashes during a massive 2008 fire in Sylmar. He had evacuated then, but said it was still too early to go now.

“We’re waiting for mandatory evacuations,” he said.

Kim Thompson, who lives at the intersection of Sesnon Boulevard and Jolette Avenue in Granada Hills, said she took her dog out at 10 p.m. Thursday and immediately smelled smoke.

After reading about the fire on Twitter and realizing it was a danger,Thompson evacuated her home about midnight, taking just her dog. The flames by then were “bright orange, terrifying to look at,” she said at a strip mall downhill from her neighborhood on Balboa where other displaced residents had gathered to await news.

Later, she admitted, she doubled back to retrieve a bottle of wine. Her neighbors were less willing to leave: “Up here, we’re stubborn. My neighbors are spraying their roofs right now.”

A little after 1 a.m., Thompson heard from a friend that fire crews were allowing two homes on Jolette Avenue to burn to the ground. She thought back to the Aliso Canyon and Sayre fires, which burned to the very edge of her cul-de-sac.

“We’ve been through a lot, but we choose to live here,” she said.

“You’re on edge. You think you get used to it,” Thompson said, the wind whipping eye-stinging smoke and ash through the air, “but you can’t really get used to this.”

CALIFORNIA FIRES

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PG&E power outages bring darkness, stress and debt to California's poor and elderly

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Saddleridge fire: Latest evacuations, school and road closures

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Small-scale habitat fragmentation effects on pollinator behaviour: experimental evidence from the bumblebee *Bombus veteranus* on calcareous grasslands

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Abstract

We examined visiting patterns of pollinators of *Betonica officinalis* L. (Lamiaceae) in experimentally fragmented calcareous grasslands and corresponding control plots at two study sites (Movelier and Nenzlingen) in the north-western Swiss Jura mountains. Fragments (1.5×1.5 m) were isolated by a 5-m wide strip of frequently mown vegetation while the control plots were situated in the adjacent undisturbed vegetation. The most common pollinator, the bumblebee *Bombus veteranus* (Apidae), visited fragments 53.7% less frequently than control plots. Furthermore, a change in foraging behaviour of *Bombus veteranus* was observed. In fragments the bumblebees visited more inflorescences, flew longer total visiting distances and the visiting time per patch tended to be higher than in control plots. The distribution of angles between arrival and departure direction (turning angles) differed from a uniform distribution in fragments but not in control plots. The increased directionality of bumblebee flight might be due to a decrease in floral rewards. Our results show that small-scale habitat fragmentation can affect plant pollination at two levels both relevant for plant fitness. First, lower visitation rates indicate a limitation of pollinators which might result in reduced seed set of the pollinated plant. Second, changes in pollinator behaviour might reduce pollen dispersal among flowers, increase inbreeding and hence reduce genetic variability in populations of this bumblebee pollinated plant.

Keywords: *Betonica officinalis*; *Bombus veteranus*; Bumblebee; Gene flow; Plant–pollination interaction

1. Introduction

Nutrient-poor, calcareous grasslands are among the habitats with the highest species richness in western Europe (Zoller, 1954; Ellenberg, 1982; Willems, 1982). However, industrialisation and changes in agricultural land use since the 1950s caused a dramatic decline of this once common type of grassland, and the remaining remnants are often small, fragmented and isolated (e.g. Willems, 1982; Zoller et al., 1986; Fischer and Stöcklin, 1997). Fragmentation of these natural habitats has especially negative biological consequences for ecosystem functions (Saunders et al., 1991; Kearns et al., 1998), such as plant–pollinator interactions, the subject of the present study.

The ecological importance of pollinators in their communities is crucial (Kearns et al., 1998). The entire structure of biotic communities will be dramatically changed when keystone plant species lose their pollinators. A cascade of changes including a decline in biodiversity may follow (Allen-Wardell et al., 1998; Kearns et al., 1998). Habitat fragmentation can affect pollinator behaviour, population size of animals and plants, and even pollinator morphology (Phillips, 1997; Berwaerts et al., 1998; Thomas et al., 1998; VanDyck and Matthysen, 1999). These chances might in turn influence community structure, population dynamics, trophic levels and genetic diversity in natural ecosystems. Plants experience lower fitness if pollinators are missing or reduced in numbers (e.g. Jennersten, 1988; Pavlik et al., 1993; Fischer and Matthies, 1997; Robertson et al., 1999). Furthermore, habitat fragmentation can change the spatial distribution of plants, which in turn changes foraging patterns of pollinators (Cresswell, 1997). If the distance between plants to be pollinated is too large, pollination is limited (Schmitt, 1983; Klinkhamer et al., 1989) and plant fitness may be reduced due to inbreeding and/or outbreeding depression caused by increased genetic drift (Waser and Price, 1983; Van Teuren et al., 1991; Holsinger, 1993; Percy and Cronk, 1997; Gigord et al., 1999). Thus, a change in pollinator behaviour might strongly affect plant reproductive success and plant fitness.

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There is empirical evidence that habitat fragmentation can influence pollinator populations directly or indirectly, and may cause declines of pollinators (Allen-Wardell et al., 1998). However, little attention has been given to the effect of fragmentation on pollinator behaviour. The aim of this study was to investigate under natural conditions the influence of experimental small-scale fragmentation on the pollinator behaviour of *Bombus veteranus* (Apidae), the most common pollinator of *Betonica officinalis* L. (Lamiaceae), a typical perennial forb in calcareous grasslands of the Swiss Jura mountains.

2. Methods

2.1. Fragmentation experiment and sampling

The study was carried out from 22 July to 7 August 1998 in the experimental habitat fragmentation study site of the University of Basel in the Swiss Jura mountains (Baur and Erhardt, 1995; Baur et al., 1996). The original design, established in spring 1993, consists of three field sites with a total of 12 blocks (Fig. 1) on nutrient-poor, dry calcareous grasslands belonging to the Teucrio-Mesobrometum type (Ellenberg, 1988). In the present study the medium-sized fragments (1.5×1.5 m) and control plots of equal size from six blocks at two sites were used (three blocks at Movelier and three blocks at Nenzlingen). These field sites are situated near Nenzlingen (10 km south of Basel) and near Movelier (5 km north of Delémont).

In each block, fragments were separated by a 5-m wide strip of frequently mown vegetation (6–12 times per year). Corresponding control plots of equal size were mirror-symmetrically arranged and surrounded by undisturbed vegetation (Fig. 1). Because the original control plots varied largely in occurrence of *Betonica officinalis*, we placed control plots in the undisturbed vegetation so as to contain approximately the same number of *Betonica officinalis* inflorescences as in the fragments. Thus, in the surroundings of the control plots numerous other *Betonica officinalis* inflorescences were present, whereas those in the fragments were separated by at least 5 m from other *Betonica officinalis* inflorescences.

In each patch (fragment or control plot) all *Betonica officinalis* inflorescences and open flowers were counted. The positions of all flowering *Betonica officinalis* inflorescences were mapped in 36 cells measuring 25×25 cm. Pollinators were observed in each patch for 20 min on three separate days. We recorded the visitation pattern of every flower visitor entering the plot during the survey. We measured for each insect the visiting distances between successively visited inflorescences, the total flying distance in the patch and the turning angles. Flower visitors that were already in the patch at the beginning of the survey were not considered. Additionally, the duration of the visit in the plot of each flower visitor was assessed using a DAT-recorder. Observations were performed between 10:00 and 16:00 in sunny and warm weather. To avoid any time effect the order of surveys in fragments and their control plots were randomised on each observation day. Fragments and control plots of each site were surveyed on three different days (Nenzlingen on 22 and 30 July and on 8 August 1998, Movelier on 24 July and on 6 and 7 August 1998).

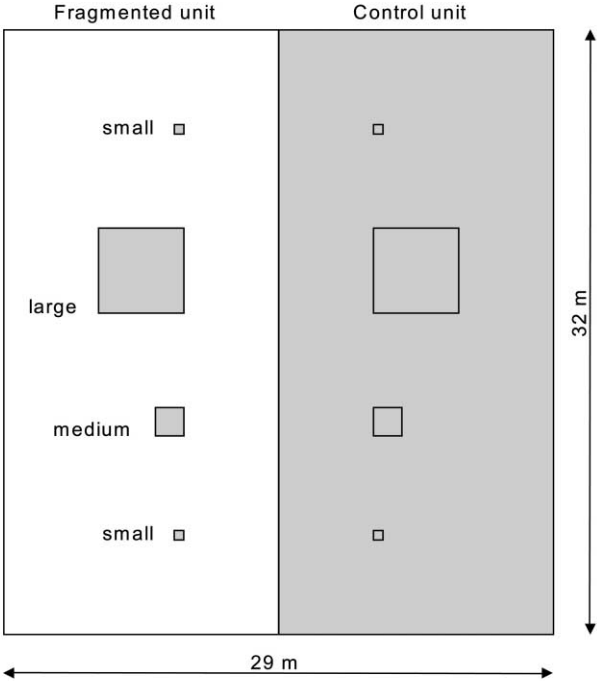

Fig. 1. Experimental layout for one of 12 experimental blocks of 29×32 m established in spring 1993. Each unit contained one large (4.5×4.5 m), one medium (1.5×1.5 m) and two small fragments (0.5×0.5 m), all of them separated by a 5-m wide strip of mown vegetation (white area), as well as the corresponding control plots, which were mirror-symmetrically arranged and surrounded by undisturbed vegetation (grey area).

The distance between nesting sites of *Bombus veteranus*, the most frequent visitor, and the experimental patches could potentially have affected our observations. However, the fact that bumblebees can forage several hundred metres away from their nesting sites (Osborne et al., 1999), and the design of our experiment (random distribution of fragments and control plots) suggest that positions of nesting sites do not affect the results of the present study.

2.2. Data analyses

To compare the number of visits between fragments and control plots a chi-square goodness of fit test with a hypothesised ratio of 1:1 was used for each site (Zar, 1999). We used pooled data from the three survey days for each fragment and control plot.

To prevent spatial pseudoreplication, data from visiting patterns were averaged per fragment or control plot, respectively, for each survey day. To prevent temporal pseudoreplication we used the average of the three survey days per site, thus, resulting in 12 independent replications (six fragments and six control plots). Three-way analyses of variance (ANOVA, type III model, using JMP 3.1, SAS, 1995) with the fixed factors site and treatment and the random factor block nested by site were used to examine effects on the following parameters (patches refer to fragments or control plots):

Percent of visited inflorescences

$$= \frac{\text{Mean of visited inflorescences per bumblebee}}{\text{Total number of inflorescences in patch}}$$

Visiting time per patch related to inflorescence number (= "Visiting time per patch")

$$= \frac{\text{Mean time spent in patch per bumblebee}}{\text{Total number of inflorescences in patch}}$$

Ratio of mean visiting distances

$$= \frac{\begin{array}{l}\text{Mean distance flown between two successively}\\ \text{visited inflorescences}\end{array}}{\begin{array}{l}\text{Mean nearest neighbour distance between}\\ \text{inflorescences}\end{array}}$$

Ratio of total visiting distances

$$= \frac{\begin{array}{l}\text{Total distances between visited inflorescences}\\ \text{in patch per bumblebee}\end{array}}{\begin{array}{l}\text{Total nearest neighbour distances between}\\ \text{inflorescences in patch}\end{array}}$$

As a measure of the pollinators' flight directionality, turning angles between the arrival and departure directions were assessed from visiting patterns of single bumblebees. For data analysis angles were assigned to 18 classes each of 20°. The distributions of angles recorded in fragments and those from the control plots were compared with a uniform distribution using chi-square goodness of fit test (Zar, 1999). Furthermore, a 2×18 contingency table (G-test) was used to compare the distribution of angles in fragments with those in control plots (Zar, 1999).

3. Results

The number of inflorescences per patch as well as the number of open flowers were not affected by the experimental fragmentation but differed between sites (Table 1). Furthermore, the number of open flowers per inflorescence did not differ between sites ($F_{1,4}=0.44$, n.s.) or treatments ($F_{1,5}=0.17$, n.s.).

In total, the visiting pattern of 314 flower visitors was recorded. Among them, 218 belonged to the most common species, *Bombus veteranus*. The remaining flower visitors were other Hymenoptera (34), *Zygaena* spp. (42), other Lepidoptera (12) and Diptera (eight). Individuals of *Bombus veteranus* visited the fragments less frequently (69 individuals) than the control plots (149 individuals; Fig. 2) which means 53.7% fewer visits in the fragments.

Fragmentation significantly influenced the behaviour of the pollinator *Bombus veteranus* (Fig. 3). The percentage of visited inflorescences and the ratio of total visiting distances was significantly higher in fragments than in control plots (Fig. 3A,D). Thus, flying longer distances and especially visiting more inflorescences within a fragment indicate more near-neighbour pollination, which may result in increased inbreeding in pollinated plants in the fragments. Furthermore, the "visiting time per patch" tended to be longer in fragments than in control plots (Fig. 3B), while the ratio of mean visiting distances did not differ between fragments and control plots (Fig. 3C). A significant site effect on

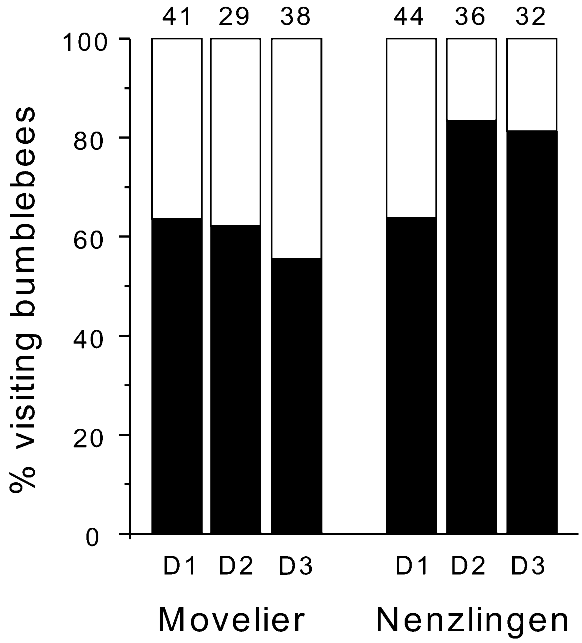

Fig. 2. Percentage of visits of *Bombus veteranus* in fragments (open bars) and corresponding control plots (black bars) at the two different sites, separated per day (D1, D2, D3 = first, second and third observation day, respectively). The numbers above the bar indicate the total number of observed bumblebees at this day. The difference between fragments and control plots was significant for both sites (Movelier: $\chi^2=4.48$, d.f. = 1, $P=0.034$; Nenzlingen: $\chi^2=28.00$, d.f. = 1, $P<0.001$).

Table 1
(a) Mean number (±1 S.E.) of inflorescences and open flowers of *Betonica officinalis* in fragments ($n=3$) and control plots ($n=3$) at the two study sites in Movelier and Nenzlingen. (b) Three-way analyses of variance (ANOVA) for effects of site and fragmentation treatment

(a)

Site	Treatment	Number of inflorescences per patch (2.25 m^2)	Number of open flowers per patch (2.25 m^2)
Movelier	Fragments	9.9±3.3	85.8±36.7
	Control plots	7.4±1.7	64.2±24.5
Nenzlingen	Fragments	22.9±1.3	146.0±8.4
	Control plots	21.7±0.5	176.8±14.5

(b)

	d.f.	SS	*F*	*P*	d.f.	SS	*F*	*P*
Site	1	630.18	35.58	0.004	1	30959.51	15.40	0.017
Treatment	1	17.17	3.87	0.11	1	163.33	0.12	0.75
Block (site)	4	70.84	3.99	0.08	4	8041.43	1.43	0.35
Error	5	22.20			5	7036.28		

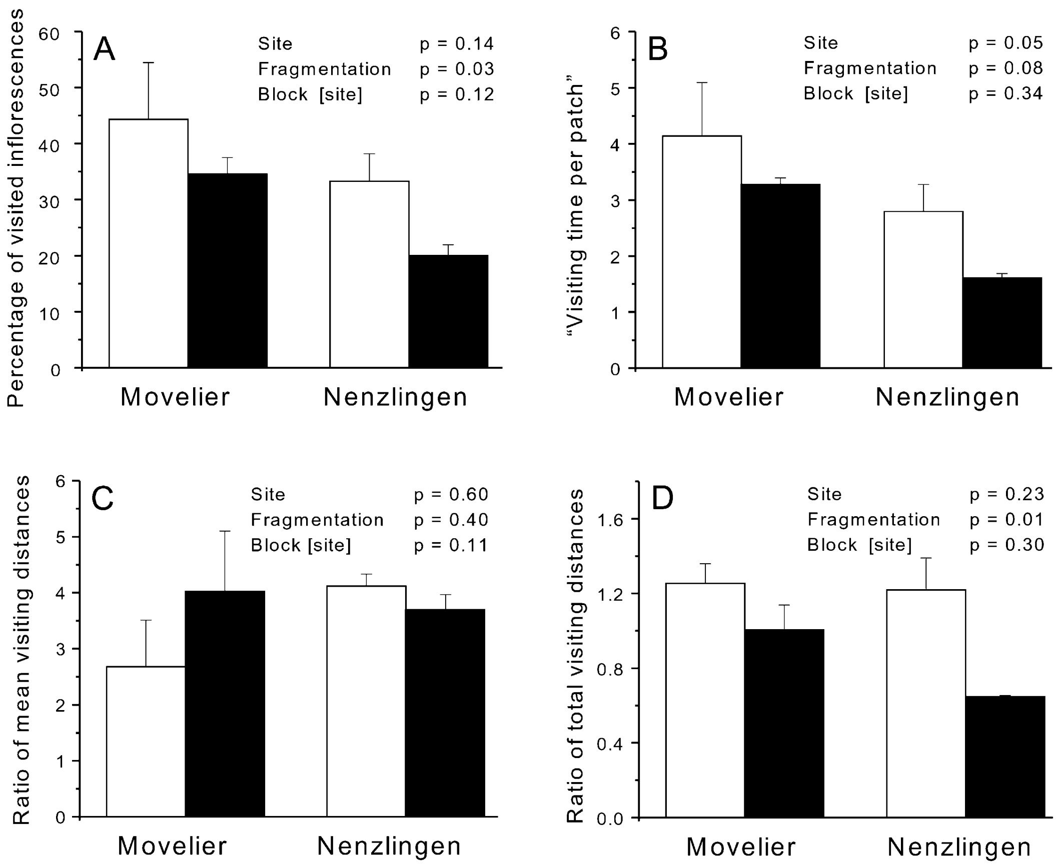

Fig. 3. Effect of habitat fragmentation on the behaviour of the pollinator *Bombus veteranus* visiting *Betonica officinalis* (mean±1 S.E.; open bars = fragments, black bar = control plots) at the sites Movelier and Nenzlingen. (A) percentage of visited inflorescences, (B) visiting time per patch related to inflorescence number ("visiting time per patch"), (C) ratio of mean visiting distances, and (D) ratio of total visiting distances.

the behaviour of *Bombus veteranus* was only found in "visiting time per patch" (Fig. 3B).

The distribution of turning angles of foraging *Bombus veteranus* differed significantly from a uniform distribution in fragments (Fig. 4, $\chi^2=48.28$, d.f. = 17, $P<0.001$), but not in the control plots (Fig. 4, $\chi^2=23.79$, d.f. = 17, $P=0.12$). There is thus a stronger tendency towards directionality in fragments than in control plots. However, a direct comparison of the distributions of turning angles in fragments and control plots revealed no significant difference ($G=14.14$, d.f. = 17, $P=0.66$).

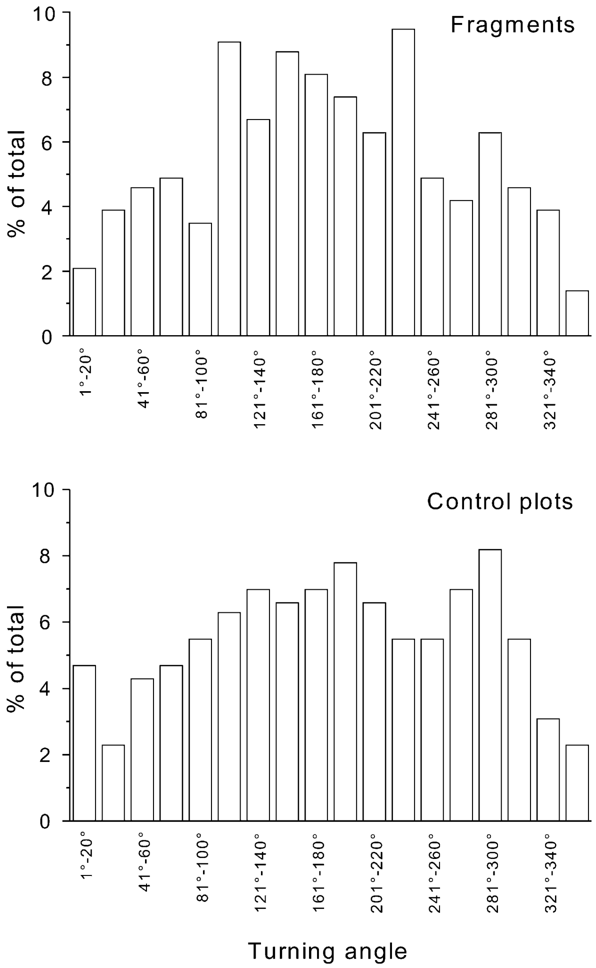

Fig. 4. Distribution of turning angles for *Bombus veteranus* visiting *Betonica officinalis* inflorescences in fragments ($n=285$) and control plots ($n=256$).

4. Discussion

The present study shows that the behaviour of the most common pollinator of *Betonica officinalis*, the bumblebee *Bombus veteranus*, was altered by small-scale fragmentation of calcareous grasslands. Bumblebees visited more inflorescences, flew longer total distances and tended to stay longer in fragments than in control plots (Fig. 3A,B,D). Thus, *Bombus veteranus* preferred to stay within the fragment rather than flying a long distance to reach the next inflorescence outside the fragment. Rasmussen and Brodsgaard (1992) examined visiting patterns of *Bombus lapidarius* in *Lotus corniculatus* patches, which were of different sizes and interspersed with dry areas dominated by mosses, lichens and short grass. Most flights of *Bombus lapidarius* were restricted to single patches (97.4%), although the animals had no difficulty to cross the distance of 10–40 m between patches. Since long distance flying is energetically expensive, the higher visitation rate within patches can be explained by the attempt of pollinators to optimise net energetic gain during foraging (Zimmerman, 1982; Price, 1997). In the present study, fragments were 53.7% less frequently visited than control plots. As a consequence, nectar rewards of inflorescences in fragments might be higher and pollinators might probe more thoroughly because movement decisions are based on the amounts of nectar encountered in flowers (Heinrich, 1979; Cresswell, 1990). However, measurements of nectar samples of *Betonica officinalis* did not support this assumption. The nectar quantity was smaller in fragments than in control plots, whereas the nectar concentration was higher in fragments than in control plots (H.-P. Rusterholz, unpublished data). These differences could be a result of lower soil moisture in fragments than in control plots resulting from frequent mowing of the surroundings (H.-P. Rusterholz, personal communication). In spite of this, bumblebees visiting fragments could have a more economic net energetic gain if they properly probe all available inflorescences in fragments.

The bumblebees' attempt to achieve the highest net energetic gain is confirmed by the observed difference in "visiting time per patch" between the two study sites (Fig. 3B). At Movelier, where there were fewer inflorescences per patch, bumblebees spent more time in a particular patch relatively to the total number of inflorescences, i.e. they visited more intensively all available inflorescences. This finding is supported by other studies in which bumblebees probed fewer flowers per plant and bypassed more plants with increased plant aggregation (e.g. Zimmerman, 1982; Cresswell, 1997). Furthermore, the directionality of foraging movement of bumblebees decreases with increasing plant aggregation (Cresswell, 1997). Additionally, edge plants in isolated patches provoke more reversals of flight than plants in the centre of patches (Rasmussen and Brodsgaard, 1992). Therefore, we assumed that foraging pollinators show less distinct directionality in their flights in fragments, while in the control plots pollinators would rather pass through the patch and, consequently show a directionality in their flight. Directionality in foraging flight decreases revisitation and results in decreased self-pollination, which in turn may affect the genetic structure of the plant population (Cartar and Real, 1997). In the present study bumblebees tended to fly more directly in fragments than in control plots (Fig. 4). A possible explanation could be an adjusted behaviour pattern of foraging strategy. The directionality of flights between inflorescences is random when rewards are high but approaches 180° when rewards are intermediate or poor (Heinrich, 1979; Richards, 1997). Thus, the lower nectar volume of flowers in fragments mentioned earlier might explain the observed tendency towards directionality in fragments.

Most relevant for plant fitness are the lower visitation rates in fragments and the tendency of bumblebees to remain in isolated patches. Pollinator limitation may reduce seed set while the frequent neighbour visits may reduce the exchange of pollen between distant plants. Thus, gene flow is reduced between fragments which may decrease the probability of outcrossing. Indeed, genetic investigations conducted in the same fragmentation experiment revealed that offspring of *Betonica officinalis* had a lower genetic diversity and an increased self-fertilisation rate in fragments (H.P. Rusterholz, personal communication). These findings illustrate general processes in fragmented landscapes, which in turn might lead to an Allee effect followed by the extinction of small plant populations (Allee et al., 1949; Courchamp et al., 1999).

We showed that experimental small-scale fragmentation reduced flower visitation and changed the behaviour of a common pollinator. Other pollinator species might be affected in a similar way. The reproductive success of pollinated plants might be reduced in fragments due to higher geitonogamy and increased rate of inbreeding. However, any extrapolation of the findings to large-scale fragmentation should be made with caution.

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References

Allee, W.C., Emerson, A.E., Park, O., Park, T., Schmidt, K.P., 1949. Principles of Animal Ecology. Saunders, Philadelphia.

Allen-Wardell, G., Bernhardt, P., Bitner, R., Burquez, A., Buchmann, S., Cane, J., Cox, P.A., Dalton, V., Feinsinger, P., Ingram, M., Inouye, D., Jones, C.E., Kennedy, K., Kevan, P., Koopowitz, H., Medellin, R., Medellin-Morales, S., Nabhan, G.P., Pavlik, B., Tepedino, V., Torchio, P., Walker, S., 1998. The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. Conservation Biology 12, 8–17.

Baur, B., Erhardt, A., 1995. Habitat fragmentation and habitat alterations: principle threats to most animal and plant species. Gaia 4, 221–226.

Baur, B., Joshi, J., Schmid, B., Hänggi, A., Borcard, D., Stary, J., Pedroli-Christen, A., Thommen, G.H., Luka, H., Rusterholz, H.-P., Oggier, P., Ledergerber, S., Erhardt, A., 1996. Variation in species richness of plants and diverse groups of invertebrates in three calcareous grasslands of the Swiss Jura mountains. Revue Suisse de Zoologie 103, 801–833.

Berwaerts, K., VanDyck, H., VanDongen, S., Matthysen, E., 1998. Morphological and genetic variation in the speckled wood butterfly (*Pararge aegeria* L.) among differently fragmented landscapes. Netherlands Journal of Zoology 48, 241–253.

Cartar, R.V., Real, L.A., 1997. Habitat structure and animal movement: the behaviour of bumble bees in uniform and random spatial resource distributions. Oecologia 112, 430–434.

Courchamp, F., Clutton-Brock, T., Grenfell, B., 1999. Inverse density dependence and the Allee effect. Trends in Ecology and Evolution 14, 405–410.

Cresswell, J.E., 1990. How and why do nectar-foraging bumblebees initiate movements between inflorescences of wild bergamot *Monarda fistulosa* (Lamiaceae). Oecologia 82, 450–460.

Cresswell, J.E., 1997. Spatial heterogeneity, pollinator behaviour and pollinator-mediated gene flow: bumblebee movements in variously aggregated rows of oil-seed rape. Oikos 78, 546–556.

Ellenberg, H., 1982. Vegetation Mitteleuropas mit den Alpen. Ulmer, Stuttgart.

Ellenberg, H., 1988. Vegetation Ecology of Central Europe. Cambridge University Press, Cambridge.

Fischer, M., Matthies, D., 1997. Mating structure and inbreeding and outbreeding depression in the rare plant *Gentianella germanica* (Gentianaceae). American Journal of Botany 84, 1685–1692.

Fischer, M., Stöcklin, J., 1997. Local extinction of plants in remnants of extensively used calcareous grasslands 1950–1985. Conservation Biology 11, 727–737.

Gigord, L., Picot, F., Shykoff, J.A., 1999. Effects of habitat fragmentation on *Dombeya acutangula* (Sterculiaceae), a native tree on La Reunion (Indian Ocean). Biological Conservation 88, 43–51.

Heinrich, B., 1979. Resource heterogeneity and patterns of movement in foraging bumblebees. Oecologia 40, 235–245.

Holsinger, K.E., 1993. The evolution dynamics of fragmented plant populations. In: Kareiva, P.M., Kingsolver, J.G., Huey, R.B. (Eds.), Biotic Interactions and Global Change. Sinauer Associates Inc, Washington, pp. 198–216.

Jennersten, O., 1988. Pollination in *Dianthus deltoides* (Caryophyllaceae): effects of habitat fragmentation on visitation and seed set. Conservation Biology 2, 359–366.

Kearns, C.A., Inouye, D.W., Waser, N.M., 1998. Endangered mutualisms: the conservation of plant–pollinator interactions. Annual Review of Ecology and Systematics 29, 83–112.

Klinkhamer, P.G.L., de Jong, T.J., de Bruyn, G.J., 1989. Plant size and pollinator visitation in *Cynoglossum officinale*. Oikos 54, 201–204.

Osborne, J.L., Clark, S.J., Morris, R.J., Williams, I.H., Riley, J.R., Smith, A.D., Reynolds, D.R., Edwards, A.S., 1999. A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. Journal of Applied Ecology 36, 519–533.

Pavlik, B.M., Ferguson, N., Nelson, M., 1993. Assessing limitations on the growth of endangered plant populations: 2. Seed production and seed bank dynamics of *Erysimum capitatim* ssp. *howellii*. Biological Conservation 65, 267–278.

Percy, D.M., Cronk, Q.C.B., 1997. Conservation in relation to mating system in *Nesohedyotis arborea* (Rubiaceae), a rare endemic tree from St. Helena. Biological Conservation 80, 135–145.

Phillips, O.L., 1997. The changing ecology of tropical forests. Biodiversity and Conservation 6, 291–311.

Price, P.W., 1997. Insect Ecology. John Wiley & Sons, New York.

Rasmussen, I.R., Brodsgaard, B., 1992. Gene flow inferred from seed dispersal and pollinator behaviour compared to DNA analysis of restriction site variation on patchy population of *Lotus corniculatus* L. Oecologia 278–283.

Richards, A.J., 1997. Plant Breeding Systems. Chapman & Hall, London.

Robertson, A.W., Kelly, D., Ladley, J.J., Sparrow, A.D., 1999. Effects of pollinator loss on endemic New Zealand mistletoes (Loranthaceae). Conservation Biology 13, 499–508.

SAS, 1995. JMP® User's Guide, Version 3.1. Cary, NC, USA.

Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5, 18–32.

Schmitt, J., 1983. Flowering plant density and pollinator visitation in *Senecio*. Oecologia 60, 97–102.

Thomas, C.D., Hill, J.K., Lewis, O.T., 1998. Evolutionary consequences of habitat fragmentation in a localized butterfly. Journal of Animal Ecology 67, 485–497.

VanDyck, H., Matthysen, E., 1999. Habitat fragmentation and insect flight: a changing 'design' in a changing landscape? Trends in Ecology and Evolution 14, 172–174.

Van Teuren, R., Bijlsma, R., Van Delden, W., Ouborg, N.J., 1991. The significance of genetic erosion in the process of extinction. I. Genetic differentiation in *Salvia pratensis* and *Scabiosa columbaria* in relation to population size. Heredity 66, 181–189.

Waser, N.M., Price, M.V., 1983. Optimal and actual outcrossing in plants, and the nature of plant-pollinator interaction. In: Jones, C.E., Little, R.J. (Eds.), Handbook of Experimental Pollination Biology. Van Nostrand Reinhold, New York, pp. 341–359.

Willems, J.H., 1982. Phytosociological and geographical survey of *Mesobromiom* communities in western Europe. Vegetatio 48, 240–277.

Zar, J.H., 1999. Biostatistical Analysis. Prentice Hall International, New Jersey.

Zimmerman, M., 1982. Optimal foraging, plant density and the marginal value theorem. Oecologia 49, 148–153.

Zoller, H., 1954. Die Arten der *Bromus erectus* Wiesen des Schweizer Juras. Veröffentlichung des Geobotanischen Institutes ETH, Stiftung Rübel, Zürich 28, 1–283.

Zoller, H., Wagner, C., Frey, V., 1986. Nutzungsbedingte Veränderungen in Mesobromiom-Halbtrockenrasen in der Region Basel—Vergleich 1950–1980. Abhandlungen 48, 93–108.

Wildfires and Climate Change: California's Energy Future

A Report from Governor Newsom's Strike Force

April 12, 2019

Executive Summary

Climate change has created a new wildfire reality for California. The state’s fire season is now almost year round. More than 25 million acres of California wildlands are classified as under very high or extreme fire threat. Approximately 25 percent of the state’s population – 11 million people – lives in that high-risk area.

Wildfires are not only more frequent but far more devastating. **Fifteen of the 20 most destructive wildfires in the state’s history have occurred since 2000; ten of the most destructive fires have occurred since 2015.** The results are visible to all: lives lost, grave fire damage to homes and communities, rising gas and electricity rates, pressure on the home insurance market, and the threat of insolvency for California’s utilities. The largest investor-owned utility in the state has filed for bankruptcy protection and two other major investor-owned utilities in southern California have had their credit ratings downgraded. Financial experts have opined that these utilities are likely one major fire away from bankruptcy. Making matters worse, this year has all the conditions for devastating fires, with a very wet season leading to high vegetation density. During fire season, that vegetation dries out and becomes fuel.

Since the first days of his administration, the Governor has taken decisive action to strengthen California’s emergency preparedness and response capabilities to mitigate wildfires and build community resilience. In response to instability in the energy sector and to PG&E’s decision to file for bankruptcy, the Governor created a strike force to coordinate the state’s efforts relating to the safety, reliability, and affordability of energy, as well as to continue progress to achieve the state’s climate commitments. As part of these efforts, sixty days ago, the Governor directed the strike force to develop a comprehensive roadmap to address the issues of wildfires, climate change, and the state’s energy sector. That roadmap is attached.

The strike force report sets out steps the state must take to reduce the incidence and severity of wildfires, including the significant wildfire mitigation and resiliency efforts the Governor has already proposed. It renews the state’s commitment to clean energy. It outlines actions to hold the state’s utilities accountable for their behavior and potential changes to stabilize California’s utilities to meet the energy needs of customers and the economy.

It is imperative that utilities not put profits ahead of safety and service. That is why the state has and will continue to advocate in PG&E’s bankruptcy proceeding for fair treatment of fire victims, for California consumers, and for California policies and values.

Preventing and Responding to Catastrophic Wildfires

The report begins by setting out steps that the administration, the CPUC, local communities, and utilities must take to reduce the incidence and severity of wildfires and to step up both community resilience and the state’s response capabilities. To accomplish this, it is critical that the state:

- **Expand fire prevention activity** by improving forest and vegetation management, accelerating fuel reduction projects on both public and private land, training the workforce needed to scale up these projects, investing in new technologies to model and monitor fire risk, and strengthening utility oversight so that they invest more in safety.
- **Make communities more resilient** by considering updating codes that govern defensible space, encouraging cost-effective hardening of homes, strengthening evacuation, encouraging other emergency planning, and improving land use practices to reduce the damage to life and property from wildfires.
- **Invest in fire suppression and response** by investing in new fire engines and aircraft, re-deploying National Guard personnel from the border to support fire suppression initiatives, purchasing detection cameras to provide advanced data to firefighters, and investing in a statewide mutual aid system to pre-position resources in high-risk areas.
- **Call on the Federal Government to Better Manage Federal Forest Land.** As the owner of 57 percent of California's forestland, the federal government must also do its fair share to reduce fire risk. Specifically, the Governor has joined the governors of Washington and Oregon to call for the federal government to double the investment in managing federal forestlands in our states due to the high risk of wildfires.

Renewing California's Commitment to Clean Energy

Given that climate change is a core driver of heightened wildfire risk, California must continue its transition to clean energy. California has established ambitious greenhouse gas reduction targets and the utility sector has been critical to the significant progress our state has made. But, an unstable energy market presents new risks, and temperatures keep rising. Any solution must adapt to the changing market landscape while maintaining the state's commitment to mitigating climate change. To do this, the state should consider:

- **Evaluating state-level resource backstop options** to reduce gaps and inefficiencies that can result from an increasingly fragmented energy market – including the option of creating a state power procurement entity.
- **Increasing transparency and reliability protections for customers** by establishing standards to make energy provider information more transparent and facilitate statewide planning.

Allocating Responsibility for Wildfire Costs

An honest assessment of the realities of current and future climate change tells us that no matter how committed we are to preventing and fighting fires and to reducing carbon emissions over the long-term, the state will experience further fire damage in the coming years. If we continue on our current legal and regulatory path, we will get similar results – more deadly and destructive fires that put utilities near insolvency. That is unacceptable for fire victims and utility customers and is incompatible with an economy that requires safe, reliable, and affordable power. Any real plan must allocate costs resulting from wildfires in a manner that shares the burden broadly among stakeholders, including utilities (ratepayers and investors), insurance companies, local governments, and attorneys. Taxpayers have substantially increased their contribution to mitigating fire risk and fighting fires when they ignite.

Any successful approach for allocating responsibility for wildfire costs should be based on the following principles: (1) maintaining safe and affordable power, (2) holding utilities accountable to prioritize safety, (3) treating wildfire victims fairly, (4) requiring equitable stakeholder contributions, (5) reducing overall costs from wildfire damage, (6) promoting California's clean energy goals, and (7) recognizing the contribution of California taxpayers.

The strike force has identified the following three concepts for evaluation against these principles:

- A **liquidity-only fund** that would provide liquidity for utilities to pay wildfire damage claims pending CPUC determination of cost recovery potentially coupled with modification of cost recovery standards.
- Adopting a **fault-based standard** that would modify California's strict liability standard to one based on fault to balance the need for public improvements with private harm to individuals.
- Creation of a **catastrophic wildfire fund** coupled with a revised cost recovery standard to spread the cost of catastrophic wildfires more broadly among stakeholders.

These concepts should be publicly debated, as each has impacts, tradeoffs, and consequences that must be addressed. Some concepts rely on voluntary contributions from utility investors, who in exchange will demand more clarity in the regulatory standard for cost recovery from ratepayers.

The choices are difficult, the future is uncertain and the solutions are imperfect. But legislative action is necessary for the stability of the state's energy market to meet the needs of Californians, and to achieve the state's clean energy goals.

Under the status quo, all parties lose – wildfire victims, energy consumers, and Californians committed to addressing climate change. Victims face a great deal of uncertainty and diminished ability to be compensated for their losses and harm. Customers face rising rates and instability. California's ability to achieve its climate goals is frustrated. Utility vendors and employees face uncertainty and likely significant losses. The bottom line is that utilities either in or on the verge of bankruptcy are not good for Californians, for economic growth, or for the state's future.

Strengthening Utility Market Regulation

Utilities must be active participants in the quest for safe, reliable, and affordable power. This report recommends strengthening utility regulation by reforming the California Public Utilities Commission (CPUC) to:

- **Expand safety expertise** by improving the CPUC's ability to review wildfire mitigation plans, conduct inspections and audits, and enforce safety standards at investor-owned utilities.
- **Clarify cost recovery standards** by setting clear guidelines in statute for when the CPUC can pass on the costs of claims from wildfire damage to ratepayers.
- **Improve decision-making** by overhauling procedures, delegating more decisions to technical staff so that judges and commissioners focus on core questions of rate-setting, and improving enforcement.
- **Review high-risk industry regulatory models** and explore options for incorporating the latest climate impact research, in concert with the Governor's Office of Planning & Research, as well as academic and industry experts in risk reduction.

Holding PG&E Accountable for Safety

PG&E is a textbook example of what happens when a utility does not invest in safety after numerous deadly reminders to do so over many years. Even today, PG&E is taking advantage of the bankruptcy process to promote the interests of investors over fire victims and other stakeholders. California will advocate for fair treatment of victims and employees, as well as to uphold the state's clean energy commitments in the bankruptcy process. The state will:

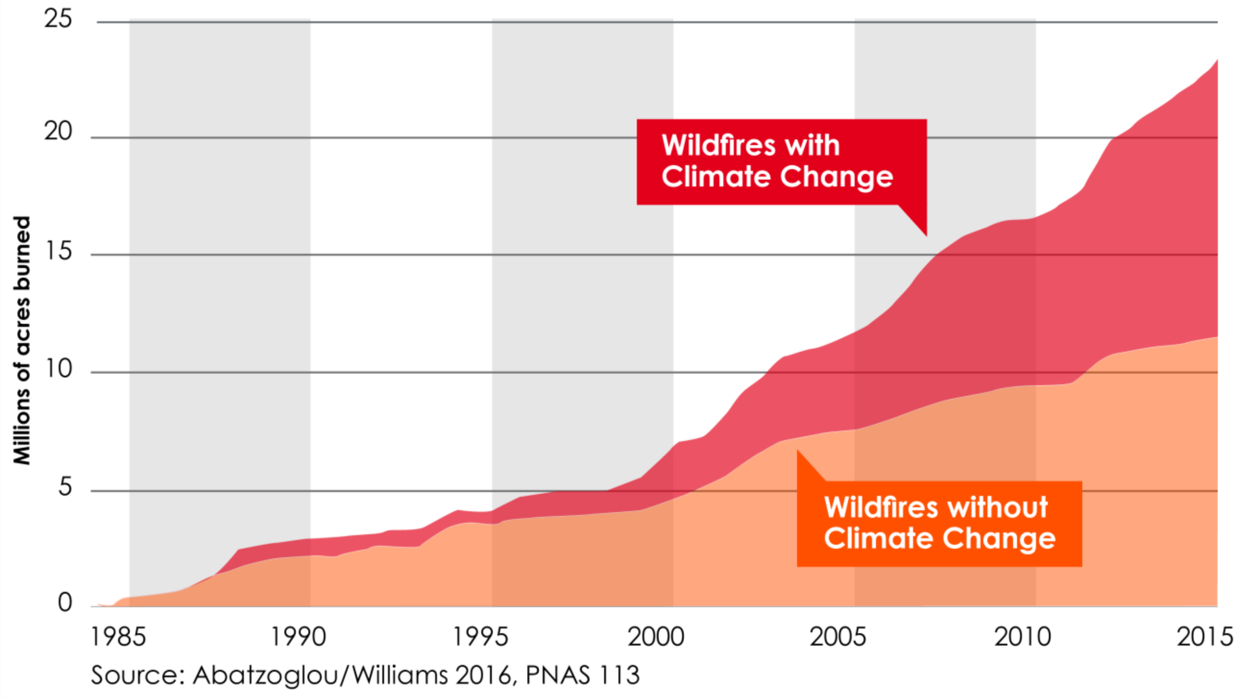
- **Monitor – and intervene – in the bankruptcy proceedings** to protect California's interests. PG&E is a private entity, but its misconduct has had grave consequences for the state and its people.
- **Evaluate options to satisfy wildfire claims** from the last two years so fire victims are treated fairly.
- **Demand that a reorganized PG&E serve the public interest**. After years of mismanagement and safety failures, no options can be taken off the table to reform PG&E, including municipalization of all or a portion of PG&E's operations; division of PG&E's service territories into smaller, regional markets; refocusing PG&E's operations on transmission and distribution; or reorganization of PG&E as a new company structured to meet its obligations to California.

The status quo is unsustainable. A better future is possible – one grounded in clear rules, effective regulation, and a new emphasis on safety so every Californian can access safe, reliable, affordable power. As the climate changes and risks rise, California must once more lead the way.

Introduction

California faces a dramatic increase in the number and severity of wildfires. Fifteen of the 20 most destructive wildfires in the state's history have occurred since 2000; ten of the most destructive fires have occurred since 2015.[1] While wildfires are a natural part of California's ecology, the fire season is getting longer every year—with most counties now experiencing fire season from mid-May to mid-December and several counties facing fire danger year-round.[2] Warmer temperatures, variable snowpack, and earlier snowmelt caused by climate change make for longer and more intense dry seasons, leaving forests more susceptible to severe fire.

Figure-01[3]



Source: Abatzoglou/Williams 2016, PNAS 113

At the same time that our climate is changing and fueling the devastating force of wildfires, increased development in the wildland-urban interface (WUI) has placed more

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[1] *See generally*, CAL FIRE, *Top 20 Most Destructive California Wildfires*, (Mar. 2019), http://www.fire.ca.gov/communications/downloads/fact_sheets/Top20_Destruction.pdf) (last visited Apr. 10, 2019) ("Top 20 Most Destructive California Wildfires").

[2] *See generally*, CAL FIRE, 2018 Fire Season Incident Information, http://cdfdata.fire.ca.gov/incidents/incidents_seasondeclarations?year=2018 (last visited Apr. 10, 2019).

[3] Eberhard Faust & Markus Steuer, CLIMATE CHANGE INCREASES WILDFIRE RISK IN CALIFORNIA | MUNICH RE MUNICHRE.COM (2019), https://www.munichre.com/topics-online/en/climate-change-and-natural-disasters/climate-change/climate-change-has-increased-wildfire-risk.html (last visited Apr 11, 2019) ("Climate Changes Increases Wildfire Risk").

residents in the potential path of destruction. Today, approximately 25 percent of the state's population (over 11 million people) lives in high fire-risk areas, including the WUI.[4]

The combination of more powerful wildfires and more Californians living in their paths has resulted in enormous, incomprehensible loss. Last year, 85 people died in the Camp Fire alone and 19,000 homes and other structures were damaged or destroyed.[5] According to data from Butte County, more than 60 percent of those victims were over 60 years old.[6] Paradise and other towns were devastated. The Camp Fire was only one of approximately 7,600 wildfires in 2018. Damage estimates for the 2018 wildfire season are staggering, with insured losses alone exceeding $12 billion.[7] Thousands of Californians who lost their homes, and their livelihoods in these fires, are still without permanent homes and struggling to rebuild their lives.

The damages caused by wildfires are unsustainable for the directly impacted victims, for the state, which is spending hundreds of millions of dollars to respond, and for local communities trying to rebuild. In response to climate change and heightened wildfire threat, California is expanding resilience efforts through increased investments in fire mitigation and response, community hardening, and emergency preparedness.

California's electric utilities must be part of the solution to this problem. In the past four years, equipment owned by California's three largest investor-owned utilities sparked more than 2,000 fires.[8] Utility-caused fires tend to spread quickly and be among the most destructive. Hundreds of thousands of miles of electrical transmission and distribution lines snake across the California landscape, often igniting fires during extreme wind events and in remote areas, making early detection and fire suppression extremely challenging. Longer fire seasons make utility-caused fires even more likely. Hardening the electrical grid is thus a critical component to overall wildfire risk management.[9] Our utilities—public and private—must make needed investments to reduce the risk of utility-ignited fires and, with the new reality of climate change, must do so now.

At the same time, the current system for allocating costs associated with catastrophic wildfires—often caused by utility infrastructure, but exacerbated by drought, climate change, land-use policies, and a lack of forest management—is untenable both for

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[4] Leventhal Center for Advanced Urbanism, *Cataloguing the Interface: Wildfire and Urban Development in California,* (Spring 2018), http://lcau.mit.edu/project/cataloguing-interface-wildfire-and-urban-development-california (last visited Apr. 10, 2019).

[4] Top 20 Most Destructive California Wildfires.

[5] Cal Fire, *Top 20.*

[6] *Los Angeles Times, Many victims of California's worst wildfire were elderly and died in or near their homes, new data show,* (Dec. 13, 2018) (archived from the original on Dec. 14, 2018).

[7] Cal. Dep't. Insur., *California Department of Insurance Insured Losses From The 2018 California Wildfires*, (Jan., 28, 2019), http://www.insurance.ca.gov/0400-news/0100-press-releases/2019/upload/nr14-2019Insured-Losses-2018-Wildfires.pdf (last visited Apr. 10, 2019).

[8] *Carolyn Kousky, et. al., Wildfire Costs In California: The Role of Electric Utilities* Wharton Risk Management and Decision Processes Center (Sept. 2018), riskcenter.wharton.upenn.edu/wp-content/uploads/2018/08/Wildfire-Cost-in-CA-Role-of-Utilities-1.pdf (last visited Apr. 10, 2019).

[9] Measures commonly used to harden the electrical grid include using insulated electrical lines in high-risk areas, replacing wood poles with steel, installing specialized monitoring equipment, and using new technologies that can reduce sparks or undergrounding lines when necessary in extreme high-fire areas.

utility customers and for our economy. Multi-billion dollar wildfire liabilities over the last several years have crippled the financial health of our privately and publicly owned electric utilities. Pacific Gas & Electric Company (PG&E) filed for bankruptcy in the face of massive potential liability for wildfire damages. Other investor-owned and public utilities have experienced recent credit ratings downgrades, with San Diego Gas & Electric (SDG&E) and Southern California Edison Company (SCE) now precipitously hovering just above junk status. Utilities rely on credit to finance ongoing infrastructure investments, including fire mitigation. As utilities' credit ratings deteriorate, their borrowing costs increase and those costs for capital necessary to make essential safety improvements are passed directly tto customers. These downgrades, and the prospect of additional utility bankruptcy filings, directly impact Californians' access to safe, reliable and affordable electricity.

In his State of the State Address, the Governor directed a strike force to develop a comprehensive strategy, within 60 days, to address the destabilizing effect of catastrophic wildfires on the state's electric utilities. He charged the strike force with developing a strategy to ensure California's "continued access to safe affordable power" and to "seek justice for fire victims, fairness for employees and protection for consumers."[10]

As the Governor stated, the crisis confronting California's electric utilities comes "at a time when the entire energy market is evolving" and is exacerbated by "regulations and insurance practices created decades ago [that] didn't anticipate these changes." The Governor recognized the need to "map out longer-term strategies, not just for the utilities' future, but for California's future, to ensure that the cost of climate change doesn't fall on those least able to afford it."

The Governor directed his strike force to develop a comprehensive strategy that achieves the following objectives:

1. Assure access to safe, reliable and affordable power for all Californians.
2. Reduce the severity of wildfires through continued investments in fire mitigation, vegetation management and other strategies to reduce fuels.
3. Develop and implement technologies to more quickly identify and respond to wildfires.
4. Reduce the number of utility-sparked wildfires through smart investments in increased safety, prevention, grid-hardening, and vegetation management around electrical lines.
5. Facilitate fair and prompt treatment for wildfire victims and allocate the burden of wildfire damage responsibly and fairly across all stakeholders.
6. Ensure that California continues to make progress toward its clean energy goals.

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[10] OFFICE OF GOV. GAVIN NEWSOM, *Governor Newsom Delivers State of the State Address*, (Feb. 12, 2019), https://www.gov.ca.gov/2019/02/12/state-of-the-state-address/ (last visited Apr. 10, 2019).

7. Provide sufficient certainty to investors and credit ratings agencies to avoid downgrades of utilities that could cause further bankruptcies and/or drive up borrowing costs, each of which raises prices for utility customers.
8. Hold utilities accountable for improving safety and preventing wildfires and for damages if their misconduct causes a wildfire.
9. Avoid a band-aid approach and instead set a path for the energy market of the future.
10. PG&E serves 40 percent of California electricity customers and has an egregious safety record. The state must hold PG&E accountable and demand systemic reforms and a commitment to safety.

This Report provides a roadmap to confront the challenges of catastrophic wildfires:

Part 1: Catastrophic Wildfire Prevention and Emergency Response

Part 2: Mitigating Climate Change through Clean Energy Policies

Part 3: Fair Allocation of Catastrophic Wildfire Damages

Part 4: A More Effective CPUC with the Tools to Manage a Changing Utility Market

Part 5: Holding PG&E Accountable & Building a Utility that Prioritizes Safety

It will take a comprehensive approach to mitigate and prepare for wildfires, as well as to advance our climate goals. That said, the most vexing public policy challenge addressed in this Report is the equitable distribution of wildfire liability. The Report sets forth three concepts to address this central question--the imminent wildfire liability issues facing California's utilities--each as described further in Part 3:

- **Concept 1:** Liquidity-Only Fund. This concept would create a fund to provide liquidity for utilities to pay wildfire damage claims pending CPUC determination of whether or not those claims are appropriate for cost recovery and may be coupled with modification of cost recovery standards.
- **Concept 2:** Changing Strict Liability to a Fault-Based Standard. This concept would involve modification of California's strict liability standard under inverse condemnation to one based on fault to balance the need for public improvements with private harm to individuals.
- **Concept 3:** Wildfire Fund. This concept would create a wildfire fund coupled with a revised cost recovery standard to spread the cost of catastrophic wildfires more broadly among stakeholders.

California needs to think creatively to find new ways to apportion the cost of catastrophic wildfires—ones that treat victims fairly and compassionately, that are sustainable for consumers, and that spread the burden equitably.

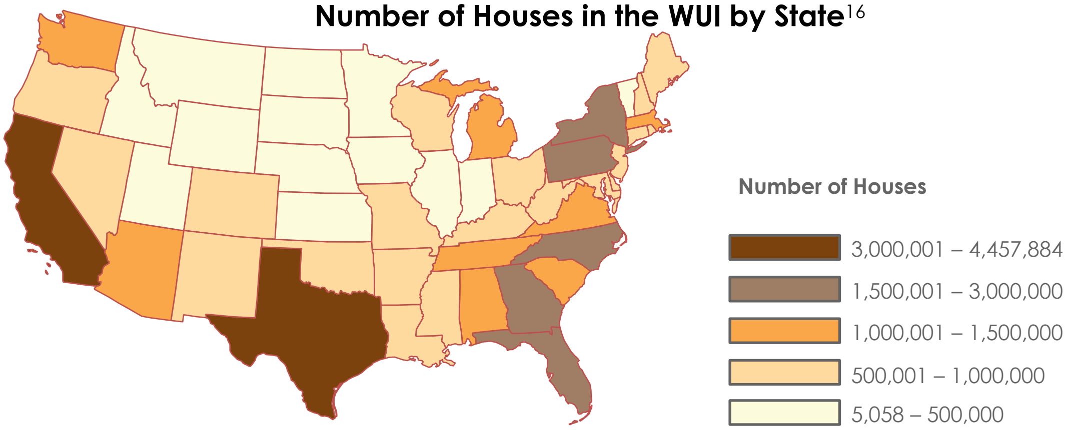
Part 1: Catastrophic Wildfire Prevention and Response

Catastrophic wildfires pose an urgent threat to lives, property, and resources in California. The 2017 and 2018 wildfire seasons were the most destructive in California's history.[11] More than 9,000 wildfires ignited across California in 2017 and 7,571 wildfires ignited in 2018, burning more than 2.8 million acres combined.[12] These fires caused the loss of 139 lives and destroyed tens of thousands of homes and businesses.[13] They also poisoned the air across vast swaths of the state and harmed public health.[14] Additionally, catastrophic wildfires compounded the challenge of reducing our greenhouse gas emissions by emitting millions of carbon particles into the air.[15]

Climate change, widespread tree mortality, weak utility infrastructure, and the proliferation of homes in the WUI magnify the wildfire threat and place substantially more people and property at risk than ever before.

Today, as illustrated in Figure-02 below, California's WUI is home to approximately 4.5 million homes and 11 million people.

Figure-02
Number of Houses in the WUI by State[16]



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[11] CAL FIRE, Incident Information as of Jan. 24, 2018, http://cdfdata.fire.ca.gov/incidents/incidents_stats?year=2017 (last visited Apr. 10, 2019).

[12] Id.

[13] CAL FIRE, *Top 20 Most Destructive California Wildfires,* (Mar. 14, 2019), http://www.fire.ca.gov/communications/downloads/fact_sheets/Top20_Destruction.pdf (last visited Apr. 10, 2019); CAL FIRE, *Top 20 Deadliest California Wildfires,* (Feb. 19, 2019), http://calfire.ca.gov/communications/downloads/fact_sheets/Top20_Deadliest.pdf (last visited Apr. 10, 2019); CAL FIRE, *Top 20 Largest California Wildfires,* (Mar. 14, 2019), http://www.fire.ca.gov/communications/downloads/fact_sheets/Top20_Acres.pdf (last visited Apr. 10, 2019).

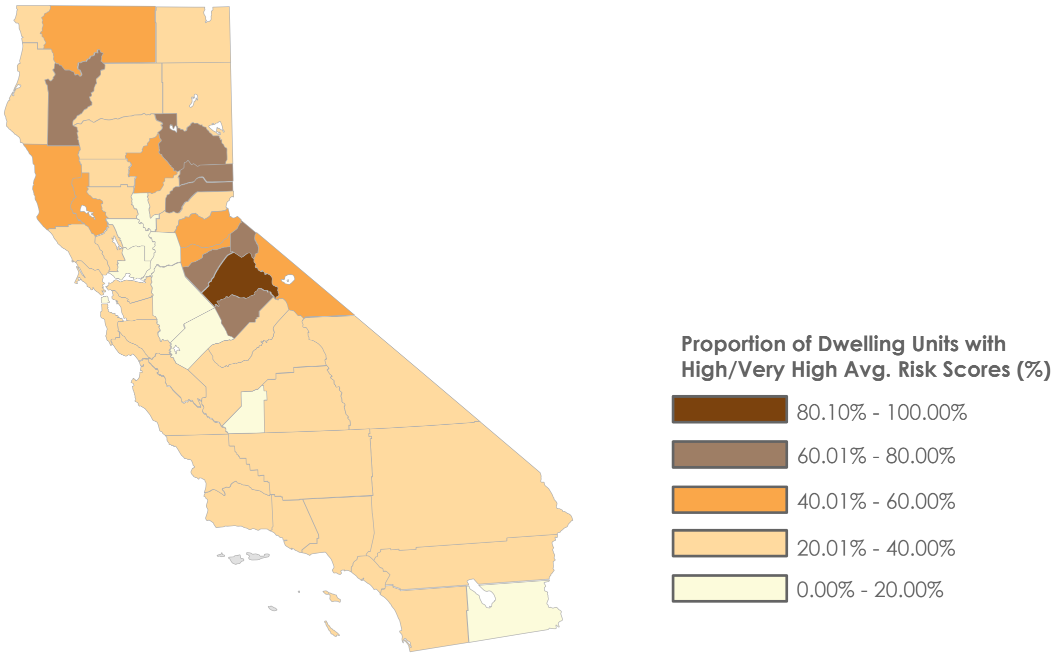
[14] STATE OF CALIFORNIA GOVERNOR'S OFFICE OF PLANNING AND RESEARCH, et al., *California's Fourth Climate Change Assessment: Statewide Summary Report* at 38, http://www.climateassessment.ca.gov/state/docs/20190116-StatewideSummary.pdf) (last visited Apr. 10, 2019).

[15] CALIFORNIA DEPARTMENT OF INSURANCE, *New Analysis Shows 2018 California Wildfires Emitted as Much Carbon Dioxide as an Entire Year's Worth of Electricity* (Nov. 30, 2018), https://www.doi.gov/pressreleases/new-analysis-shows-2018-california-wildfires-emitted-much-carbon-dioxide-entire-years) (last visited Apr. 10, 2019) ("Fourth Climate Assessment").

[16] CAL. DEP'T. INSUR., *The Availability and Affordability of Coverage for Wildfire Loss in Residential Property Insurance in the Wildland-Urban Interface and Other High-Risk Areas of California: CDI Summary and Proposed Solutions,* (Dec. 2017), http://www.insurance.ca.gov/0400-news/0100-press-releases/2018/upload/nr002-2018AvailabilityandAffordabilityofWildfireCoverage.pdf (last visited Apr. 10, 2019).

More than 25 million acres of California wildlands are now classified as under very high or extreme fire threat, extending that risk to over half the state--a high-risk area that will likely grow over time.[17] Decades of fire suppression have disrupted natural fire cycles and added to increased wildfire risk.

Figure-03
Proportion of Dwelling Units with High / Very High Average Risk Scores[18]



The state's major study on climate impacts, the Fourth Climate Assessment, projects that California's wildfire burn area likely will increase by 77 percent by the end of the century.[19] The growing risk of catastrophic wildfires has created an imperative for the state to act urgently and swiftly to expand preemptive fire prevention and bolster wildfire response efforts to help protect vulnerable communities and reduce the severity of wildfires in our state.

All levels of government, communities, utilities, and residents must share in this responsibility in order to better defend California from this devastating threat.

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[17] *See* California Department of Forestry and Fire Protection, *Community Wildfire Prevention & Mitigation Report* (Feb. 22, 2019), http://www.fire.ca.gov/downloads/45-Day%20Report-FINAL.pdf (last visited Apr. 10, 2019).

[18] Ibid.

[19] Fourth Climate Assessment at 9.

Wildfire Reduction and Mitigation Action Plan

Recognizing the need for urgent action, the Newsom administration has placed a high priority on fire prevention and recovery measures, as well as on identifying ways the state can become more resilient in the face of future fires.

On January 9, the Governor issued Executive Order N-05-19, directing CAL FIRE to recommend immediate, medium and long-term actions to help prevent destructive wildfires. With an emphasis on taking immediate actions to protect vulnerable populations, and recognizing a backlog in fuels management, the Executive Order called for a strategic approach to focus actions on California's most vulnerable communities to realize the greatest returns on reducing risk to life and property in the most fire-prone areas of the state.

To further augment fire prevention, the Governor signed a General Order in February rescinding previous authorization for California National Guard operations at the U.S.-Mexico border and redeploying personnel to prepare for the upcoming fire season by supporting CAL FIRE in fire prevention and fire suppression efforts.

The state needs to continue to build on this work with a focus on four specific areas:

11. General Prevention and Fire Suppression
12. Building Safer Utilities
13. Emergency Response
14. Land Use, Building Codes and Community Resilience

General Prevention and Fire Suppression

In response to Executive Order N-05-19, CAL FIRE released the Community Wildfire Prevention and Mitigation Report (CAL FIRE Report) on March 5. The CAL FIRE Report outlined a suite of actions to substantially reduce wildfire risk to 200 of California's most vulnerable communities this fire season.

On March 22, the Governor, citing the extreme peril posed by wildfire risk, issued an Emergency Proclamation directing CAL FIRE to immediately implement 35 emergency projects identified to protect lives and property. CAL FIRE will utilize existing funding totaling $30 million from the Forest Health and Fire Prevention Program to immediately execute the priority fuel reduction projects.

The proclamation suspends certain requirements and regulations. To ensure environmental protection, CAL FIRE requested input from regulatory agencies, and will employ a set of best management practices designed to identify and avoid sensitive natural and archaeological resources.

As discussed below, the state has numerous new initiatives to prevent and suppress fires.

Improving Vegetation Management and Forest Health

After decades of disinvestment, the state has committed hundreds of millions of dollars in recent years to improve the health and resiliency of the state's forests.
Despite these increases, much work remains to be done. Over the next five years, the state will commit over $1 billion for critical fuel reduction projects, to support prescribed fire crews, forest thinning, and other forest health projects. In addition, the Governor redeployed the National Guard to support fire prevention efforts and is proposing to expand the California Conservation Corps to focus on forest management.

Since 2010, California has nearly doubled the number of acres treated annually by fuel reduction, and has tripled the number of acres treated by prescribed burning. However, these efforts—less than 33,000 treated acres in 2017-18—are dwarfed by the number of acres that require attention. California's Forest Carbon Plan sets a goal of treating 500,000 acres of private land every year.

As the owner of 57 percent of California's forestland, the federal government must do its fair share to reduce fire risk. Specifically, the Governor has joined the governors of Washington and Oregon to call for the federal government to double the investment in managing federal forestlands in our states due to the high-risk of wildfires.[20]

Support for Regional Projects

In March 2019, the California Natural Resources Agency and Department of Conservation announced the award of $20 million in block grants for regional projects to improve forest health and increase fire resiliency. The Regional Forest and Fire Capacity Program helps communities prioritize, develop and implement projects that strengthen fire resiliency.

Suppression

In recent years, the state has added additional year-round fire engines and firefighters to address longer, more severe fire seasons. The state has also launched a major initiative to replace Vietnam War-era helicopters with new state-of-the-art helicopters with enhanced firefighting capabilities. The Governor's Budget proposes to further expand the state's firefighting surge capacity by adding additional crews and engines. The Budget also includes funding to operate C-130 federal air-tankers.

To spur engagement from innovators in fire safety technologies and more effectively fight fires, Governor Newsom signed Executive Order N-04-19 to modernize the state contracting process for goods and technology systems. The "Innovation Procurement Sprint" will enable CAL FIRE to identify solutions to more effectively detect wildfire starts and predict the path of wildfires.

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[20] Letter from Gov. Gavin Newsom to Pres. Donald J. Trump (Jan. 8, 2019), https://www.gov.ca.gov/wp-content/uploads/2019/01/1.8.19-Joint-Letter.pdf

Figure-04
Additional Recommendations on Prevention[21]

Implement Additional Recommendations from the Community Wildfire Prevention and Mitigation Report: The strike force recommends that the following additional actions from the CAL FIRE Report be considered and, when appropriate, expedited.

A. Create Incentives for Fuel Reduction on Private Lands

- Small non-industrial private landowners make up approximately 25 percent of California's forestland owners and managers, almost twice as much as private industrial forestlands. These private landowners may not have the resources to actively manage their forests and are subject to the same fire risk as other Californians.
- The Board of Forestry and Fire Protection should consider changes in regulations, through an emergency rule-making process as needed, to encourage private landowners to engage in fuel reduction projects.

B. Develop Methodology to Better Assess At-Risk Communities

- The methodology used to identify priority projects provides a robust assessment of near-term projects that can be implemented before the 2019 fire season. This methodology should serve as the basis for ongoing assessment methods to evaluate short- and long-term wildfire risk reduction strategies across the state, with specific attention to identifying vulnerable communities noting that long-term planning and decision-making efforts to reduce wildfire risk require consideration of additional factors, including more robust integration of climate risk factors into fire vulnerability assessments.
- The Forest Management Task Force should establish an interagency team with experience in spatial analysis, technology support, environmental management, public health, climate change, and social vulnerability to develop the methodology enhancements needed to inform the long-term planning needs of both state and local agencies.

C. Jumpstart Workforce Development for Forestry and Fuel Work

- The California Natural Resources Agency should identify specific opportunities to develop and encourage workforce training programs.
- The goal should be to increase the number of properly trained and compensated personnel, with an emphasis on providing opportunities for local residents, available to perform fuel reduction and forest management and restoration work in the private sector. These training programs should be implemented before the end of 2019.

D. Develop a Mobile Data Collection Tool for Project Reporting

- The California Natural Resources Agency should procure a mobile fuel reduction data collection application to be used by all land management departments and agencies to increase accuracy and ease of data collection in the field.

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[21] *See* CALIFORNIA DEPARTMENT OF FORESTRY AND FIRE PROTECTION, *Community Wildfire Prevention & Mitigation Report* (Feb. 22, 2019), http://www.fire.ca.gov/downloads/45-Day%20Report-FINAL.pdf (last visited Apr. 10, 2019.

E. Develop a Scientific Research Plan for Wildfire Management and Mitigation, with Funding Recommendation

- The Forest Management Task Force should develop a research plan with prioritized funding.
- Topics that should be considered include:
    - Leverage the Governor's Request for Innovative Ideas (RFI2).
    - Best management practices in the face of a changing climate and developing an understanding of forest health and resilience.
    - Use of LIDAR, satellite, and other imagery and elevation data collection, processing and analysis for incorporation into state management plans and emergency response.
    - Funding for collaborative research to address the full range of wildfire-related topics. Important research investments could include both basic and applied research as well as social science to better understand social vulnerability, human behavior, land use, and policies that support resilience in communities that coexist with fire and mitigate impacts on life and property.
    - Research and development on new WUI building test standards in future research programs including the use of damage inspection reports from recent fires.

F. Develop Models and Best Management Practices for Evacuation Planning

- CAL FIRE and the Governor's Office of Emergency Services (Cal OES) and the Standardized Emergency Management System Advisory Committee should develop robust local evacuation planning models for high or very high Fire Hazard Severity Zones based upon best practices from within California.

Explore Public Private Partnerships and Capital Investment in Forest Waste Management Businesses: Public-private partnerships that find secondary uses for forest waste and increase fuel reduction can be a constructive part of the solution. Fostering innovation and entrepreneurship, these could include biomass facilities, especially those that use the energy on-site or as an "alternate fuel" for electric vehicles, cross-laminated timber using beetle kill wood, wood chips or pellets, or composting practices for soil restoration.

Expanding small scale businesses around forest waste, like micro-mills or carpentry using "Alpine Blue" (beetle kill) wood, will help scale-up forest treatment on small, private land. The strike force recommends that the Natural Resources Agency explore how best to facilitate these types of partnerships, recognizing the critical role they play in both forest management and community economic development.

Building Safer Utilities

The state's most destructive wildfires have been sparked by utilities. Electrical fires tend to ignite during extreme wind events in remote areas with limited access for first responders. To reduce the overall risk of catastrophic wildfires for vulnerable communities, public and private utilities must make needed investments in grid hardening, vegetation management, and fire detection technologies.

Current Process for Utility Safety Investment

Regulatory review of safety investments follows the same general approach as discussed in Part 4 of this Report. Historically, this meant that investment in fire safety and mitigation was driven largely by the utilities. The California Public Utilities Commission (CPUC) adopted safety regulations for overhead electrical systems in Rule 35 of CPUC General Order 95. Utilities were required to comply with those regulations but set their own priorities for safety investment.

This largely utility-defined fire mitigation program resulted in inconsistencies in investment among the state's investor-owned utilities. SDG&E engaged in a robust fire mitigation and safety program after experiencing devastating fires in its service territory in 2007 and has become a recognized leader in wildfire safety.

More recently, SCE implemented a wildfire safety program designed to mitigate the challenges of wildfires, including the development of operational practices and inspections, vegetation management activities, and community outreach.

PG&E has begun to implement wildfire safety measures, but its efforts lag behind the other IOUs, which is particularly troubling given that it serves 40 percent of California's utility customers and many counties in high-risk areas.

CPUC and Wildfire Mitigation Plans

As the scale of utility-sparked wildfires increased, the CPUC, through statutory changes and on its own initiative, increased oversight of utility wildfire mitigation efforts. Each IOU is now required to prepare and submit a wildfire mitigation plan (WMP) annually to the CPUC for review and approval.[22] The CPUC, in consultation with CAL FIRE, will evaluate the WMPs.[23] As part of this process, the CPUC held a public workshop and two days of technical workshops on wildfire mitigation. A comparison of the WMPs submitted by PG&E, SCE and SDG&E is attached as Annex A to this Report. The CPUC expects to approve the WMPs in May 2019 and thereafter oversee compliance with the WMPs. The CPUC intends to develop and refine the content of and process for review and implementation of wildfire mitigation plans to be filed in future years.

While substantial efforts are underway to build safer utilities, the strike force has identified areas for immediate improvement.

Recommendations

Establish a More Rigorous WMP Process: The WMP requirements should be revised to include a section on long-term fire management and a process to ensure faster compliance with the proposed plan. WMPs should also include specific performance-based risk mitigation metrics that are independently and scientifically verified as well as

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[22] Cal. P.U.C. § 8386.

[23] The IOUs that are required to submit WMPs are PG&E, SCE, SDG&E, Liberty Utilities/CalPeco Electric, Bear Valley Electric Service, and Pacific Power.

cost-effective. Further, to hold IOUs accountable, California should consider putting in place an auditing system tied to financial incentives.

- **Safety Incentives:** Consider other CPUC reforms to better align IOU incentives with safety, including:
    - Adjust the allowed return on equity (ROE) based on wildfire safety performance
    - Align compensation and stock options of executives with wildfire safety performance
    - Make Board composition contingent on wildfire safety performance
    - Require Board-level reporting to CPUC on wildfire safety issues
- **Invest in Technology and Innovation:** New technologies, including weather stations, drones, and artificial intelligence have tremendous potential as tools to more effectively prevent, detect and respond to wildfires. The CPUC convened the state's first Wildfire Technology Innovation Summit in March 2019 to gather national and international thought leaders and practitioners from state and local governments, academia, industry and other areas to inform and collaborate as to innovative technological solutions to wildfire risk, including:
    - Statewide deployment of weather stations and cameras paired with meteorology and fire behavior modeling
    - Artificial Intelligence-based visual recognition technology to analyze satellite imagery to determine fuel conditions and vegetation risks in proximity to utility lines
    - Fire modeling tools to support all fire departments and emergency responders across the state
    - Machine learning and automation inspections for increased safety assurance and regulatory compliance
    - Widespread adoption of aerial patrols, LIDAR and advanced imaging for vegetation management and utility infrastructure inspections
- **Update Models to Reflect Climate Change:** Climate change has rendered many assumptions about California's climate outdated. Historical records for humidity, wind, rain, and temperature are regularly broken. CPUC regulations—such as General Order 95 governing electrical lines—are premised on historical climate trends which may no longer be accurate. The state should work with experts to update their models on climate change, using the existing Adaptation Clearinghouse and Climate Assessment process as a central location for data, maps, and information. The state should also facilitate cross-learning with utilities, which often make capital investments in physical infrastructure over decades.
- **More Cost-Effective Financing for Wildfire Mitigation Safety Investments:** A critical element of mitigating utility-sparked wildfires is substantial and immediate investment in electrical grid safety. The state may be able to mitigate the rate impact of this investment by offering a lower cost financing alternative through a dedicated rate

stream. Where IOUs fall behind on making needed investments, a reduced return on equity for this deferred maintenance can further reduce ratepayer impact.

Emergency Response

In a matter of hours, 52,000 people from rural Paradise and surrounding communities evacuated onto roads built for a fraction of that capacity and converged on Chico, overwhelming the recovery system. The scale and speed of catastrophic, wind-driven wildfires, like the Camp Fire, incapacitate existing emergency response systems, local infrastructure and planned recovery efforts. Many California communities designed their fire emergency response and recovery systems decades ago, using old technology and outdated fire modelling. A clear overhaul of the California emergency response systems and the underlying infrastructure is needed.

The lack of broadband in rural communities and access to cell service make it difficult to communicate clear emergency evacuation orders to residents or locate residents who are in trouble. Roads in rural counties were often designed around old gold-rush tracks that were not designed to accommodate the number of residents using those roads, the ability of emergency vehicles to access the roads, or the need for defensible space. Evacuation plans assume that residents can evacuate and do not identify safe havens and shelter-in-place options for residents.

The state should partner with local government to encourage updates to local emergency plans, to increase resident awareness of those plans, and to otherwise improve emergency prevention and response efforts. Further, the state should encourage local governments to adopt recently issued guidelines to improve communications during an emergency.

On February 13, the Governor signed AB 72 (Assembly Committee on Budget, Chapter 1, Statutes of 2019), which appropriated $50 million for an emergency preparedness campaign focused primarily on California's most vulnerable populations, including the elderly, disabled, and those in disadvantaged communities. The California for All Emergency Preparedness Campaign—a joint initiative between California Volunteers and Cal OES—will augment the efforts of first responders by ensuring at least one million of the most vulnerable Californians are connected to culturally and linguistically competent support.

The Emergency Preparedness Campaign will provide:

- $24.25 million in grants to community-based organizations across the state to prepare residents for natural disasters through education and other resources designed to bolster resiliency.
- $12.6 million to support community efforts to build resiliency and respond to disasters by dispatching expert disaster teams to key regions and expanding citizen emergency response teams (CERT).
- $13.15 million to assist community groups in the development of a linguistically and culturally appropriate public awareness and outreach campaign, directed specifically at the most vulnerable California communities.

Recommendations

- **Governor's Emergency Preparedness Summit:** By the end of June 2019, Cal OES, in partnership with the League of California Cities and the California State Association of Counties, will convene first responders, government agencies, local governments, community residents, and technical experts to develop plans for the state's emergency preparedness. The summit will highlight best practices of local communities, share resources that have worked around the world, and develop the networks necessary for ongoing preparedness improvements.
- **Develop Models and Best Management Practices for Evacuation Planning:**_Cal OES, in collaboration with CAL FIRE, the Standardized Emergency Management System Advisory Committee, and local governments should develop evacuation planning models for high or very high Fire Hazard Severity Zones based upon best practices. These models can be a tool for local governments to use when developing location specific evacuation plans. Cal OES should consider how adoption of these models can be incorporated into County Operational Area plans of jurisdictions that also receive FEMA program grant dollars.
- **Develop Methodology to Better Assess Communities At-Risk:** The Forest Management Task Force should establish an interagency team with experience in spatial analysis, technology support, environmental management, public health, climate change, and social vulnerability to develop methodology improvements to inform the long-term planning needs of both state and local agencies.

Land Use, Building Codes, and Community Resilience

According to the Fourth Climate Assessment, the average area burned statewide will increase by an estimated 77 percent by 2100. At the same time, the housing affordability crisis is forcing more Californians to move farther from urban areas, and often into high-risk areas. An additional outcome of these land use patterns is the year-by-year increase in driving, or "vehicle miles traveled" (VMT), which in turn increases carbon emissions and vehicle pollution across the states. California's housing affordability crisis is increasingly fueling the dangers of climate change and wildfire. Reducing fire risk to these areas will require changes in how higher-risk areas are designed, planned, built, served by utilities, and allowed to grow, and will require people across the state to participate in the solution.

The Governor has made housing production and affordability a key priority. California already has strong standards to reduce VMT. The strike force recommends that at the state and regional level, governments and planners incorporate CAL FIRE's fire risk projections and the fire projection information in the Adaptation Clearinghouse and Fourth Climate Assessment into short-term and long-term planning, and begin to de-prioritize new development in areas of the most extreme fire risk. In turn, more urban and lower-risk regions in the state must prioritize increasing infill development and overall housing production.

California has made progress in developing and adopting stringent wildland building codes. Since 2008, new construction in California's wildlands must use ember-resistant building materials. For homes built before the 2008 standards, CAL FIRE is working to develop a list of low-cost retrofit steps homeowners can take. In addition, the Office of the State Fire Marshal (OSFM) maintains an advisory committee of fire and building officials that continuously considers building code updates to improve fire safety. Most recently, OSFM advanced building code changes including sealing of garage door gaps, sealing skylights and safety improvements to outbuildings.

Developing new housing in Very High Fire Hazard Severity Zones presents challenges. Since 2015, CAL FIRE has assisted local governments in land use planning. CAL FIRE is working to identify subdivisions at significant fire risk without secondary evacuation routes and to make recommendations to improve access.

Homeowners are encouraged to actively maintain defensible space, which is defined as a minimum 100-foot area around a home. Maintenance is an ongoing task. California inspected more than 217,600 homes for defensible space compliance in 2017-2018 alone.

It is critical that roads and other infrastructure be more fire defensible and evacuation ready for the populations in the WUI. All levels of government must establish clear contingency plans with local communities to identify and create temporary refuge areas and shelter-in-place procedures to help fire evacuees survive when unable to escape a wildfire.

Cal OES, in coordination with local communities and the Standardized Emergency Management System Advisory Committee, should consider developing local evacuation planning models for high or very high fire hazard severity zones based on best practices in California.

Recommendations

- **Prioritize Building In Less Fire-Prone Areas:** The strike force recommends that at the regional level, governments and planners incorporate CAL FIRE's fire risk projections and the fire projection information in the Adaptation Clearinghouse and Fourth Climate Assessment into short- and long-term planning, and consider how to encourage more urban and lower-risk regions in the state to provide an alternative for those otherwise shut out of the state's housing market.
- **Local General Planning:** The strike force recommends that the safety element of local general plans be strengthened in high-risk areas, specifically for local governments to include fire risk projections into general and specific plans, including through zoning and design standards. Additionally, OPR should prioritize providing technical assistance support to these communities, many of which are rural and lack planning resources.
- **Cost-Effective Home Retrofits**: While California has stringent building standards and requirements for defensible space, the intensity of the wildfire threat in California now warrants higher levels of fortitude.
    - CAL FIRE should consider options to encourage cost-effective home hardening to create fire resistant structures within the WUI and with a focus on vulnerable communities.

  - The Forest Management Task Force should work with the Department of Insurance to seek input from the insurance industry on potential rebates or incentives for homeowners.
  - CAL FIRE and the Department of Housing and Community Development should develop a list of low-cost retrofits that provide comprehensive fire risk reduction to protect structures from fires spreading from adjacent structures or vegetation and to prevent vegetation from spreading fires to adjacent structures.
  - Consideration should be given to implementing a funding mechanism to assist individuals with cost-effective home retrofits. The model used by the California Earthquake Authority provides an example of such a mechanism.
- **Defensible Space and Forest and Rangeland Protection:** Compliance and enforcement is key to ensure that defensible space standards are met. CAL FIRE should review and make recommendations to increase defensible space.

Part 2: Mitigating Climate Change through Clean Energy Policies

California's recent experience with catastrophic wildfires confirms the critical importance of climate change mitigation efforts. As discussed in Part 1 of this report, the devastating impacts of climate change, predicted for years, are now a reality. As the state moves quickly to respond to these impacts and become more resilient, we must remain focused on addressing climate change through clean energy policy.

The state's IOUs have played a significant role in moving California away from fossil fuels—from enabling the renewable energy markets to mature with continuing decreasing costs to carrying out energy efficiency mandates and demand response and storage programs. While other retail providers have entered the energy market and helped advance clean energy, IOUs still play a critical role in the state's efforts to address climate change. To continue the state's progress in reducing greenhouse gas emissions in the energy sector, California needs investment-worthy IOUs.

California's efforts to mitigate and adapt to climate change must remain an overarching priority for the state and for the IOUs. Action must be taken to facilitate progress toward a 100 percent clean energy grid. We also must ensure that the state's current system of oversight keeps up with the evolving energy market so that reliability, affordability, and continued progress toward California's climate goals is not compromised.

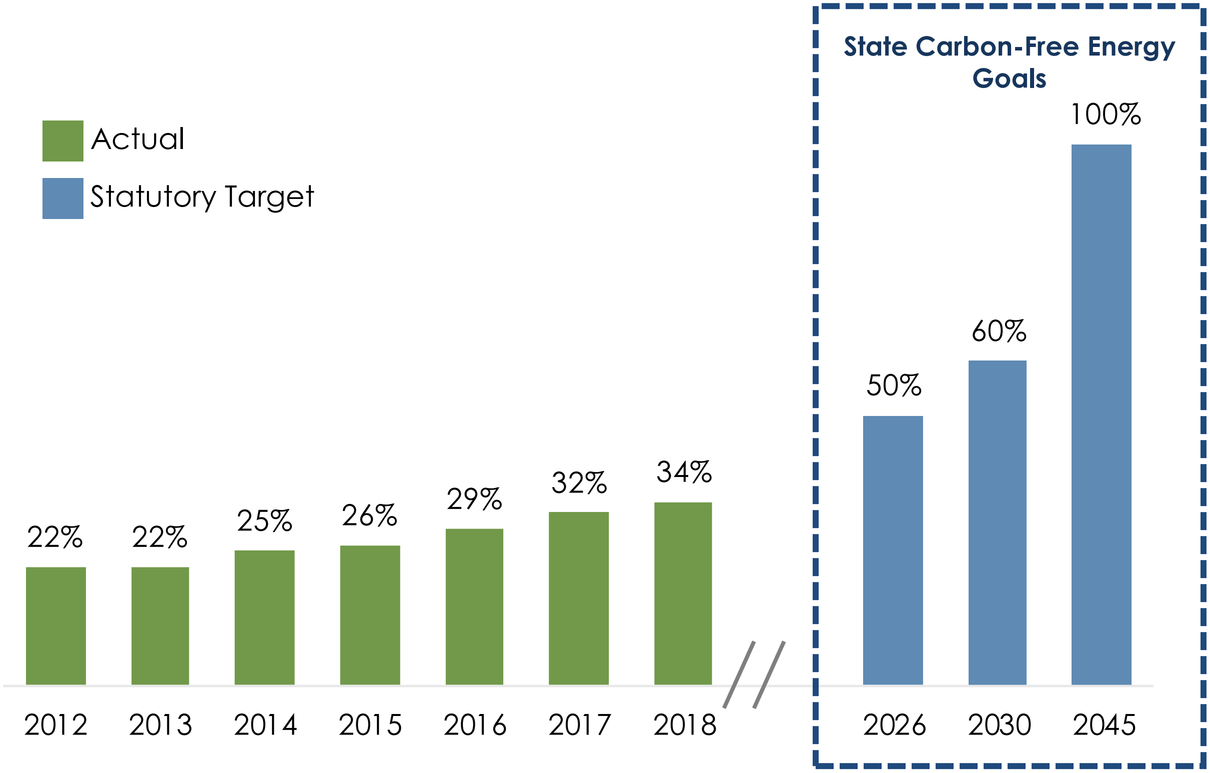
While working to increase carbon-free energy resources, utilities are also improving wildfire prevention and safety planning practices. Investments in safety at a level necessary to stay ahead of volatile climate conditions come at a cost, and this cost is being incurred at a time when maintaining low electricity rates is vital to meeting California's climate goals, as the next steps in carbon reduction involve electrifying the transportation and building sectors of the economy.

Safety investments have many benefits. A modern transmission and distribution system will create high-quality jobs and long-term economic stability, in addition to making us more resilient to the impacts of climate change and protecting the millions of residents living in fire-prone areas.

Renewable Energy Development

California has made extraordinary progress in meeting its energy sector climate goals. The state is a leader in replacing conventional forms of electric generation with cleaner sources using wind, solar, and other renewable resources instead of fossil fuels. Currently approximately 34 percent of retail electric sales are served by renewable resources and over 55 percent of sales are covered by carbon-free resources, including hydroelectric and nuclear energy. Figure-05 illustrates the progress toward renewable and carbon-free energy development.

Figure-05



California's renewable energy industry is a powerful economic force in the state. Wind and solar energy projects brought over $70 billion in capital investments to California, establishing the state as a leader in renewable generation and spurring broader innovations.[24] Future electrification of buildings and transportation offers even more benefits, as those sectors represent the most cost-effective opportunities to decarbonize.[25]

Over $22 billion in clean technology venture capital funding was invested in California from 2007 to 2017.[26] One 2015 study shows that from 2003-2014, approximately 52,000 jobs were created in California due to the construction of renewable energy facilities.[27] The construction of those facilities also created and facilitated a number of indirect jobs and opportunities. In total, approximately 130,000 jobs were created. The study also projected that increasing California's renewable portfolio standard to 50 percent could

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[24] AMERICAN WIND ENERGY ASSOCIATION, *Wind Energy in California,* https://www.awea.org/Awea/media/Resources/StateFactSheets/California.pdf (last visited Apr. 10, 2019); SOLAR ENERGY INDUSTRIES ASSOCIATION, *Solar State By State,* https://www.seia.org/states-map (last visited Apr. 10, 2019).

[25] California Energy Commission, *Deep Decarbonization in a High Renewables Future,* (June 2018), https://www.ethree.com/wp-content/uploads/2018/06/Deep_Decarbonization_in_a_High_Renewables_Future_CEC-500-2018-012-1.pdf (last visited Apr. 10, 2019).

[26] NEXT 10, 2018 California Green Innovation Index (10th Ed.), (2016) (https://www.next10.org/sites/default/files/2018-ca-green-innovation-index.pdf (last visited Apr. 10, 2019).

[27] UC BERKELEY LABOR CENTR., INST. FOR RESEARCH ON LABOR AND EMPLOY'T., *Job Impacts of California's Existing and Proposed Renewables Portfolio Standard*, (Aug. 2015), laborcenter.berkeley.edu/pdf/2015/job-impacts-ca-rps.pdf (last visited Apr. 10, 2019).

create an additional 354,000 to 429,000 direct jobs from the construction of new renewable generation, and hundreds of thousands of indirect jobs and opportunities.

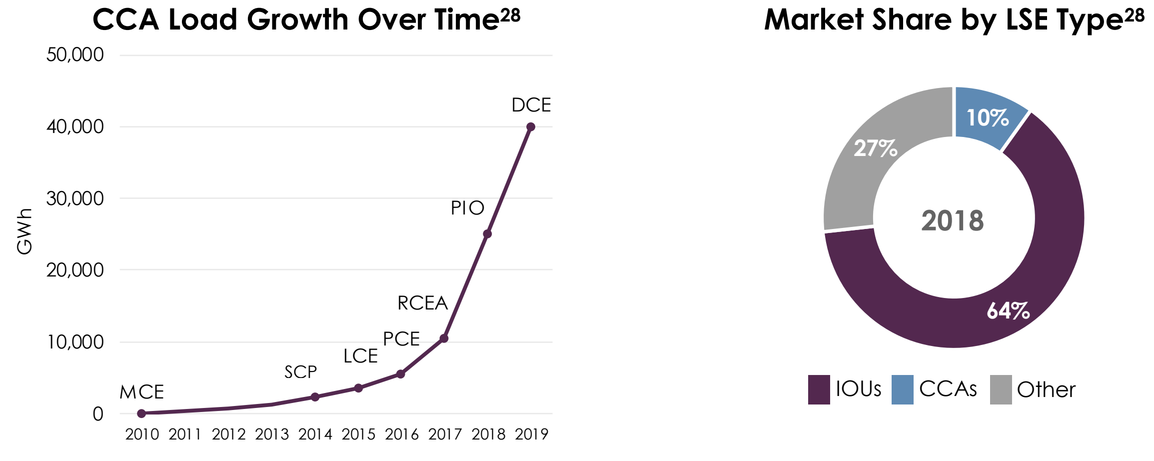
Today, we have both a challenge and an opportunity: a challenge to continue progress toward 100 percent carbon-free energy generation and an opportunity to transform the state's economy. During this transition period, we need to make sure we have effective tools and protections to manage costs to consumers, ensure reliability, and reduce risks.

Challenges in the Evolving Electric Sector

Maintaining Reliability with Less Centralized Control

As more IOU customers install rooftop solar and storage, migrate to community choice aggregators (CCAs) and purchase energy from energy service providers (ESPs), IOUs are focusing on providing electric transmission and distribution service. New CCAs and ESPs are entering the market, acquiring energy in the wholesale market from electric generating companies, and selling energy to customers at retail. As a result, IOUs increasingly are becoming "poles and wires"--companies that are responsible for constructing, maintaining, and operating the facilities over which electric energy is delivered to customers. Figure-06 illustrates the CCA load growth over time.

Figure-06



CCA Load Growth Over Time[28]

Market Share by LSE Type[28]

MCE: MCE Clean Energy
SCP: Sonoma Clean Power
LCE: Lancaster Choice Energy
RCEA: Redwood Coast Energy
PIO: Pioneer Community Energy
DCE: Dessert Community Energy

Between rooftop solar, Community Choice Aggregators (CCAs) and Direct Access providers (ESPs), as much as 85% of Investor Owned Utility (IOU) retail electric load will be effectively unbundled and served by a non-IOU source or provider by the middle of the 2020s".

The IOUs delivery electricity and perform other important functions, such as metering and billing (including collecting fees from consumers to fund certain public-interest programs). CCAs typically do not have credit ratings which can limit their ability to

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[28] See UCLA Luskin Center for Innovation's The Growth in Community Choice Aggregation, dated July 2018. CCA annual load data from each CCA's respective implementation plan. "Other" category represents the difference between the California Energy Commission's statewide load estimation and the IOU and CCA loads.

obtain the financing necessary to enter into long-term contracts at the scale needed to achieve a zero-carbon grid by 2045 and to meet Resource Adequacy (RA) requirements.

Meeting Provider of Last Resort (POLR) Obligations

Customers who choose not to obtain retail service from a CCA or an ESP, or who may be subject to a failure by a CCA or ESP to provide service, currently are protected by the requirement that an IOU must step in to provide energy under the IOUs' POLR obligation.[29] If IOUs become primarily "poles and wires" businesses, it raises the question as to whether the IOUs should continue to provide POLR service or whether another entity should assume this responsibility.

Avoiding Significant Rate Increases and Addressing the Need for Investment

Major investments will be needed in the electric transmission and distribution system in California to make the system less susceptible to wildfires, to otherwise modernize it, and to accommodate changes in generation and demand. It will be important to have financially strong utilities so they can attract the capital necessary to make these investments at low rates (since the cost of capital is passed along to consumers). Keeping capital costs down is particularly important in light of potential increases in other costs, including the cost of large wildfire liabilities.

Continuing Progress in Reducing Certain Carbon Emissions

As shown in Figure-07 below, California has made significant progress in reducing carbon emissions. In the energy sector, the IOUs have been instrumental in reducing carbon emissions. Their long-term contracts for renewable energy resources have driven prices down as new technologies have been deployed at commercial scale. Some CCAs have more aggressive renewable targets than the IOUs, and benefit from the early IOU renewables projects because they are benefitting from today's lower solar and wind energy prices. New CCAs are required to collect an adjustment charge from their customers to reflect the cost of older, long-term contracts that IOUs entered into on their behalf.

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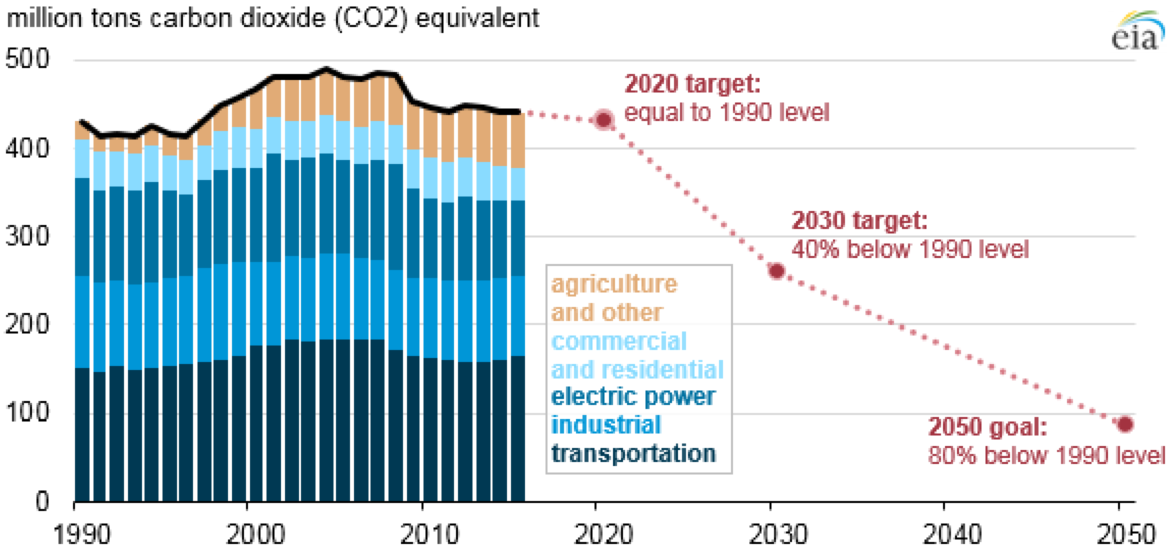
[29] The IOUs have a duty to provide distribution service on a non-discriminatory basis to the customers in their service territory. This currently includes the POLR obligation to sell energy at retail to those customers who opt out of obtaining service from a CCA. This POLR obligation also would extend to any situation in which a CCA or ESP were to cease providing service for some reason such as in the case of a bankruptcy.

Figure-07
California Greenhouse Gas Emissions by Sector[30]



Distributed Resources

California utilities provide a means to implement various Distributed Energy Resources (DER) initiatives throughout the state.[31] California has experienced phenomenal growth in electric generation by customers on a distributed basis (in contrast to obtaining energy from large, central generating stations), particularly in the form of rooftop solar generation. In the future, it is expected that more customers will install battery storage on a distributed basis.

Many of these programs grew as a result of state mandates carried out by IOUs. Few of the programs (with the notable exception of net energy metering) directly involve CCAs, ESPs or publicly-owned utilities (POUs). Additionally, the California Independent System Operator (CAISO) has developed an innovative mechanism to allow distributed resources to join together and bid into the wholesale market, providing revenue for distributed resources as well as a benefit to the electrical system. Distributed resources, however, contribute to the fragmentation of the energy supply, and need to be managed to ensure they continue to benefit the electricity system.

Adapting to Intermittent Electric Generation

Today, almost two-thirds of California's renewable energy generation capacity is from intermittent sources such as wind and solar. The output from these sources vary

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[30] *See* U.S. Energy Information Administration, based on California Air Resources Board data.

[31] Those initiatives include (i) providing rebates to customers that install self-generation facilities or storage; (ii) these are funded by a charge that the IOUs collect from their consumers; mandating that IOUs (and to a lesser extent CCAs and POUs) directly procure battery storage technologies that connect at the distribution grid level; and (iii) developing pilot projects to test the ability of DER to offset the need to build new distribution lines; and developing programs within the RPS that target distributed solar resources.

depending on the weather, season, and time of day. This imposes challenges on electric grid operations. Generation output from wind and solar sources is not controlled by the grid operator and can increase or decline rapidly, which requires adjustments in generation from other sources (or adjustments in demand) to keep supply in balance with demand. In particular, large amounts of low-cost solar electric generation during the middle of the day has created a situation where on some days there can be an overproduction of electricity and on many days generation from other sources must ramp up rapidly in the afternoon.

Overproduction can be a good problem to have since that energy, coupled with the right policies, can be harnessed to electrify other parts of the economy, such as transportation and buildings. A diverse portfolio of renewable resources and policies, including time-of-use rates, demand response programs, storage, energy efficiency, increased regional coordination, and electric vehicle charging, will continue to be critical to reduce the need for the carbon-intensive resources generally used to meet the afternoon ramp and overnight demand.

Reliability

Several factors, including flat demand for electricity and growth in renewable energy generation, have contributed to substantial retirements of fossil-fueled electric generation (mainly natural gas). Stricter environmental standards have accelerated this trend. Yet flexible resources continue to be needed in the near term to quickly ramp up as solar generation resources go off-line or load increases, and during extended cloudy periods. Over the long-term, it will be critical to ensure that cost-effective clean energy resources are available for reliability and other grid services.

Resource Adequacy Requirements

California has responded to energy shortages in the past by requiring that load-serving entities (LSEs) contract to purchase sufficient electric generation (or distributed resources or storage) to meet their forecasted peak demand plus a pre-set reserve margin. Several factors caused some LSEs to experience difficulty meeting their RA requirements.[32] Some LSEs have had to obtain temporary waivers from the CPUC and others have been penalized. Additionally, IOUs have taken on procurement of some resources needed for reliability that other LSEs may not want to procure. In some cases, the CPUC required IOUs to enter into long-term contracts needed for reliability, including contracts for battery storage. This option is less effective as IOUs have fewer and fewer retail customers.

Maintaining Public Purpose Programs; Promoting Energy Efficiency and Demand Response.

California has been a leader in energy efficiency, with electricity use per capita remaining virtually flat over the past four decades despite substantial economic growth

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[32] Challenges in the RA market include (i) a growing number of LSE competing to buy the same existing resources, (ii) a shrinking pool of resources LSE can procure as the planned retirement dates of older natural gas plants approach, and (iii) the inability/unwillingness of LSEs to enter into long-term contracts for some needed resources.

during that period.[33] The state has had success with programs that align the incentives of utilities and consumers in using less energy, including programs providing financial incentives or rebates, incorporating efficiency requirements in various codes and standards, and providing education and technical assistance.

Demand response programs, which provide incentives for customers to adjust their consumption during certain periods, have also been successful. Similarly, time-of-use rates provide incentives for customers to adjust their energy use to optimize renewable resources. New demand response programs are being developed that can increase loads at times when there is an abundance of solar generation.

California has relied on the IOUs to implement public-purpose programs to fund energy efficiency and demand response, as well as reducing rates for low-income customers and renewable energy incentives. If the IOUs become "poles and wires" companies, it will be important to ensure that this change does not threaten these public-purpose programs.

Electric Vehicle Integration

A critical component of California's efforts to meet its goals to reduce carbon emissions is to replace vehicles that use gasoline or diesel fuel with electric vehicles or hydrogen vehicles. The CPUC and other agencies in California support this effort by promoting deployment of charging stations, providing rate incentives (encouraging charging at off-peak hours), and other programs. Growth in vehicle electrification will result in increases in electric consumption over time and further increase the dependence of Californians on the electrical grid and the utilities that own and operate it. Over half of California's greenhouse gas emissions are from the transportation sector. Thus, the success of transportation electrification programs is essential to meeting the state's climate goals, and will depend on electricity being clean and available, and a less expensive option to fuel vehicles than gasoline. This provides one justification, among many, for efforts to minimize increases to electric rates. Figure-08 illustrates the California vehicle forecast.

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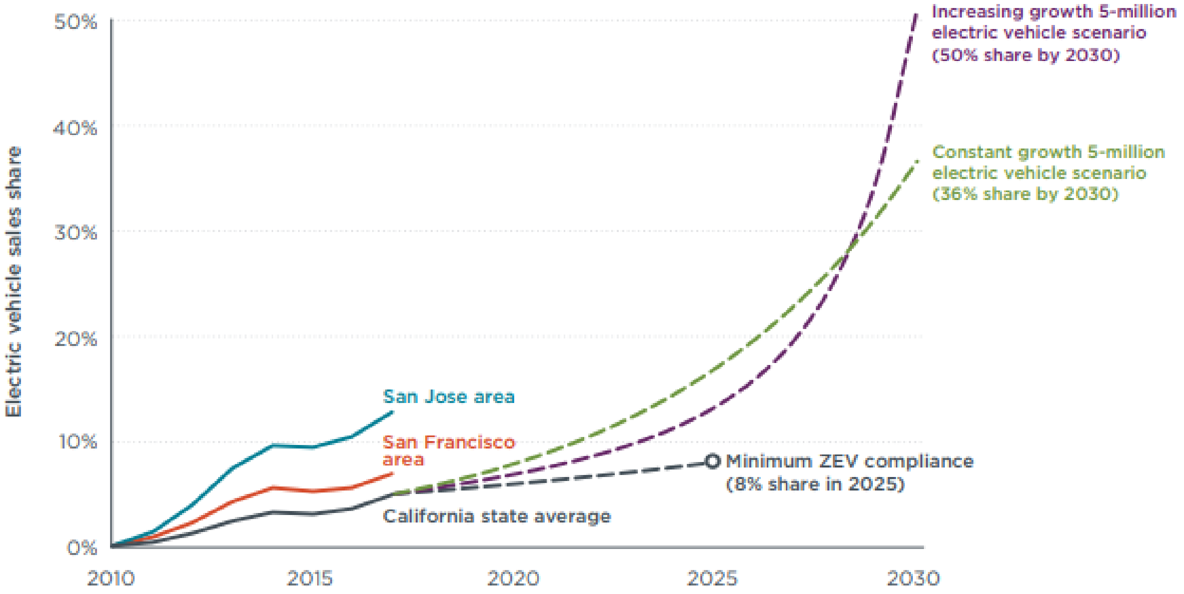
[33] Energy efficiency helps to reduce the need for electric generation, including from sources that emit carbon and other greenhouse gases. Targeted energy efficiency, as well as programs such as demand response and time-of-use pricing, to reduce energy use at periods of high prices or demand, contributes to a more reliable electric grid with less need for physical improvements to the grid.

Figure-08
California Electric Vehicle Adoption Forecast[34]



Recommendations

- **Evaluate Resource Adequacy Back-Stop Options Through the Legislative Process***:* Procurement by the IOUs, under supervision by the CPUC, has been effective over time. But as the state transitions to more LSEs, gaps and inefficiencies could emerge. To manage this transition, new procurement support models, including a new state procurement entity that could enter into long-term contracts, provide credit support or otherwise facilitate purchases of electric energy, should be explored. Procurement support could have a number of benefits, including providing back stop resource adequacy procurement and ancillary services needed to support reliability. To maintain cost-effectiveness and achieve rate benefits, it will be important to continue to focus on procurement through integrated resource planning or a similar framework. In addition, the POLR obligation discussed above and the responsibility for implementing public purpose programs could also be examined.
- **Increase Transparency for Load-Serving Entities and State Coordination of Procurement:** Customers in California should have access to complete and accurate information about the energy they are procuring, regardless of whether the procurement is from an IOU, POU, CCA, or ESP. This should include transparent information about prices, compliance with resource adequacy requirements, and the sources of energy being procured (including reliance on renewable energy sources). To the extent that customers have a choice regarding their retail electric provider, transparency is required so that they are able to make informed choices. Of course, transparency also is required for the appropriate government agencies to

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[34] *See* International Council on Clean Transportation, May 2018 Briefing.

ensure compliance with applicable RPS, resource adequacy, and other requirements. Additionally, new programs or legislation may be needed for coordination of purchasing by CCAs and ESPs to ensure they continue to meet California's standards for integrated resource planning, resource adequacy, clean energy progress, consumer protection, and hedging risk.

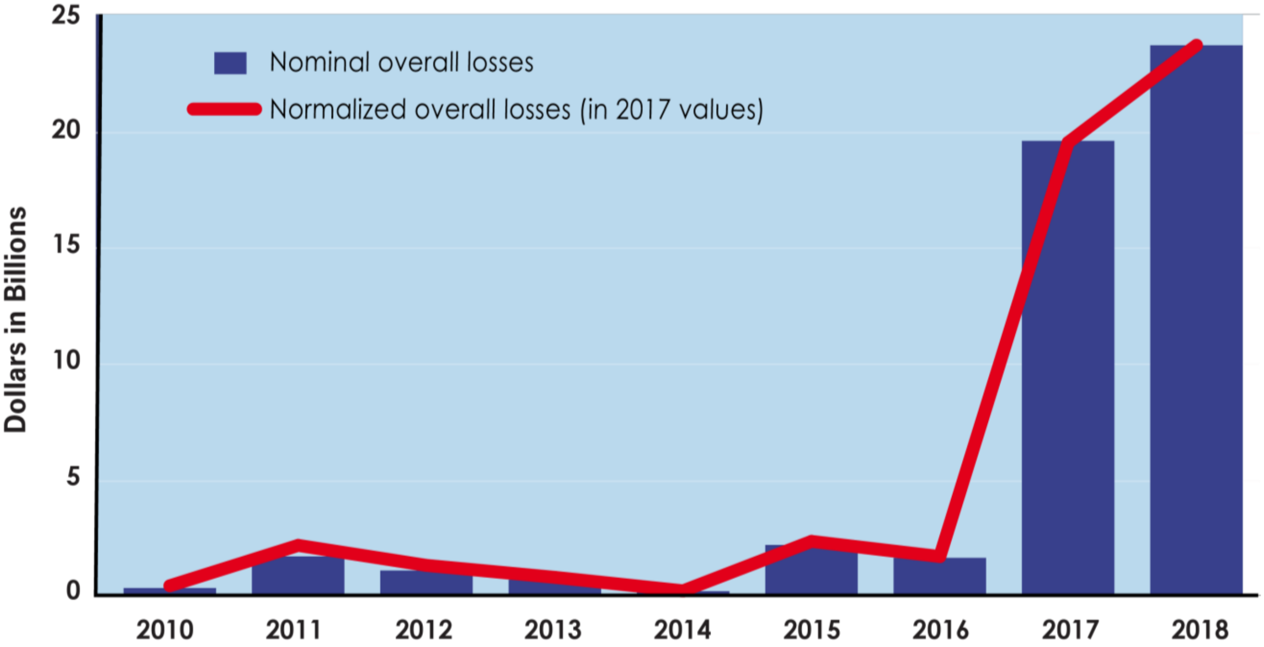
- **Addressing Variability in Generation and Consumption:** Addressing variability in electric generation and consumption will require efforts on a number of fronts. The afternoon ramp—the period when solar and wind energy decline and demand goes up—is increasing. Traditionally, flexible resources, such as natural gas-fired generators, have been used to provide a reserve margin, to ensure that generation and consumption stay in balance, and to provide other ancillary services needed for reliability. In the near term, a limited number of natural gas resources are still needed. In the longer term, more innovative solutions will be required. Further progress in time-of-use rates, demand response programs, storage, energy efficiency, increased regional coordination, and electric vehicle charging can help to ensure that demand at any given moment is at a level that can be accommodated by the amount of available electric generation. Proper infrastructure and incentives can be developed to facilitate and encourage integration of electric vehicles into the electric system in a manner that can enhance reliability and reduce costs. The strike force recommends that the CPUC use its Integrated Resource Planning process and other related proceedings to address these issues.

Part 3: Fair Allocation of Catastrophic Wildfire Damages

Climate change, forest management practices, and real estate development patterns in the WUI have dramatically increased the risk and magnitude of wildfire damage. All stakeholders, public and private, must invest in mitigation, suppression and emergency response to reduce the incidence of catastrophic fire and to protect lives and property. At the same time, communities need electricity—including communities in remote, high fire-risk areas. As long as electrical lines run through tinder-dry forests, California can mitigate but not eliminate utility-sparked fires. California also must support wildfire victims and communities as they work to rebuild. These often competing imperatives require a new policy framework to responsibly and fairly allocate the cost of wildfire damage in an era of climate change. No single stakeholder created this crisis, and no single stakeholder should bear its full cost.

Developing workable solutions to equitably share the burden of compensating victims for wildfire damages is made more challenging by uncertainty regarding the future effects of climate change and the efficacy of mitigation efforts. The staggering wildfire damages of 2017 and 2018 highlight the potential severity of wildfires in the future.

Figure-09
Wildfire Damages[35]



We do not know whether this magnitude of damage is a new normal, or if recent years were aberrational. Experts consulted by the strike force believe climate change, development patterns, deferred utility equipment maintenance, and other factors suggest much heightened risk going forward but predicting how much risk and how

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[35] Climate Changes Increases Wildfire Risk

consistently is more difficult. There is also uncertainty about the level of success we can expect in reducing the frequency and severity of wildfires.

Another challenge to a durable solution is that liability for wildfires ignited by utility equipment is governed by California's inverse condemnation law, which holds a utility strictly liable for wildfire damages if the utility's equipment ignites a wildfire, even if the utility's design and maintenance of infrastructure were not unreasonable or negligent. While a utility faces strict liability for all damages caused by its equipment, it can recover those costs through rates only by proving to the CPUC that its conduct was prudent. This regime—strict liability for wildfire damage coupled with uncertain ability to recover those damages in rates—increases the risk of bankrupt utilities, which in turn drives up costs for consumers, threatens fair recoveries for fire victims, undermines the state's ability to mitigate and adapt to climate change, and creates uncertainty for utility employees and contractors.

Under the status quo, all parties lose – wildfire victims, energy consumers, and Californians committed to addressing climate change. Victims face a great deal of uncertainty and diminished ability to be compensated for their losses and harm. Customers face rising rates and instability. California's ability to achieve its climate goals is frustrated. Utility vendors and employees face uncertainty and likely significant losses. Bottom line --- utilities in or on the verge of bankruptcy are not good for Californians, for economic growth or for the state's future.

Strike Force Deliberations

The strike force has identified and intensively researched several approaches to address wildfire liabilities. Each of the approaches evaluated by the strike force has benefits and tradeoffs.

Much work remains to be done to evaluate these concepts and determine which alternative or combination of alternatives will best support safe, reliable, and affordable energy for Californians, further clean energy goals, and enable fair treatment for wildfire victims. The strike force recommends that the Commission on Catastrophic Wildfire Cost and Recovery (SB 901 Commission) jointly appointed by the Governor and the Legislature, evaluate these concepts and report back to the Governor and the Legislature on its findings.

Principles Underlying a New Approach to Stabilizing and Sharing Costs

California's approach to wildfire mitigation must be grounded in principles that further the imperative to provide safe, reliable, and affordable power on a sustainable basis. To that end, the strike force has identified the following principles against which any proposal must be measured:

1. *Maintaining Safe, Reliable, and Affordable Power.* California residents and businesses require a safe and reliable electrical system, the achievement of which requires ongoing investment in new equipment, systems, and workforce. At the same time, steep rate increases would have adverse consequences for consumers, businesses, and California's climate goals. Thus, rate increases must be mitigated.

2. *Hold Utilities Accountable to Prioritize Safety.* Any changes in the liability rules should provide incentives for utilities and their management to prioritize and invest in safety and impose penalties for failure to do so. Any changes also must continue to hold a utility's shareholders—not its customers—responsible for failures to operate safely.
3. *Treat Wildfire Victims Fairly*. California wildfire victims deserve fair disposition of their claims so that they can move forward with their lives.
4. *Require Equitable Stakeholder Contributions*. The burdens of wildfire damages brought on by climate change are too great to be borne by any one stakeholder. A fair distribution of the burden requires utilities (ratepayers and investors), insurance companies, local governments, and attorneys representing victims to contribute.
5. *Reduce Overall Costs.* We must reduce wildfire damages as well as the financial claims that arise from them. This means prioritizing and paying for safety. It also means structuring the process by which claims are made and paid to assure the highest proportion of resources to pay for the actual losses victims suffer. And it means not creating a "free rider" problem or creating incentives for people not to act responsibly (e.g. by not properly insuring property against the risk of fire damages).
6. *Promote California's Clean Energy Goals.* Any solution must be consistent with California's long-term climate and clean energy goals and minimize the risk that wildfire liabilities will prevent utilities from having the resources to advance those goals, both in the near-term and over time.
7. *Recognize the Contribution of Taxpayers.* As described elsewhere, taxpayers have substantially increased their contribution to mitigating fire risk and fighting fires when they ignite. Any consideration of a fair burden of costs must recognize the substantial contribution the state and its taxpayers have already made and are continuing to make.

Current Framework for Allocating Costs of Utility-Caused Wildfires

In California, when a utility's equipment causes a wildfire, the utility may be held liable to pay for damages through (1) inverse condemnation lawsuits for property damages[36] brought by property owners or insurance companies (which seek compensation for payments they make to insured property owners); (2) tort lawsuits by a harmed party; and/or (3) recovery of fire suppression costs from third parties.[37] California's application

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[36] Inverse condemnation is limited to property damage caused by utility equipment, so not all utility wildfire liabilities are actionable under inverse condemnation. For example, wildfire liabilities caused by a utility company employee, rather than utility equipment, are not recoverable under inverse condemnation. In practice, litigation pursuing subrogation recovery will include multiple liability theories, including inverse condemnation, some of which apply a strict liability standard and some of which apply other standards, such as negligence.

[37] When a utility is found to be a cause of a wildfire, the utility can be required to pay for three primary types of losses: (i) property damage and damages for personal injury, death, and related impacts, (ii) suppression expenditures incurred by government entities, including Cal FIRE and the United States Forest Service, and (iii) other economic and natural resource damages. The first two categories are direct costs (e.g. damage to structures, fire-fighting expenditures, injury and mortality) and are well defined, whereas the third category represents indirect damages (e.g. business interruption, temporary housing costs).

of inverse condemnation to utilities places 100 percent of the cost of wildfire property damage on a utility if its equipment caused the fire—regardless of fault and without consideration of the contributing role of climate change, forest management, land-use policies and other factors.

California is unique in extending the concept of inverse condemnation to IOUs.[38] Nonetheless, California courts have reasoned that "the nature of the California regulatory scheme demonstrates that the state generally expects a public utility to conduct its affairs more like a governmental entity than a private corporation."[39] The primary purpose of inverse condemnation is to spread costs to relieve individuals from bearing a disproportionate share of the economic burden of a governmental action.

Inverse condemnation claims have two unique features that create challenges for California's IOUs:

1. *Fault is Irrelevant.* In an inverse condemnation claim, the plaintiff need not allege or prove that the utility behaved unreasonably or negligently. An entity may be held strictly liable for damages so long as the plaintiff proves that the utility was a substantial cause of such damage--even if it was only one of several concurrent causes.
2. *Attorney's Fees and Expenses are Part of the Claim.* The California Code of Civil Procedure provides that in any inverse condemnation proceeding the plaintiff is entitled to recover the reasonable costs, disbursements, and expenses, including reasonable attorney's fees and expert costs.[40] These costs can be substantial.

The combination of strict liability and statutory attorney's fees exposes California utilities to significant potential liabilities.

Insurance companies play an important role in the practical application of inverse condemnation to utilities in California. Insurance companies write insurance and collect premiums to cover property owners for fire losses. In the event of a fire, the insurance company pays an insured property owner's claim and absorbs the loss. If the fire was ignited by a utility's equipment, the insurance company seeks reimbursement from the utility for the damage claim it paid to homeowners, typically through an inverse

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[38] Only Florida and Alabama have applied the doctrine of inverse condemnation to utility companies and only Alabama has extended the doctrine to privately-owned utilities. Similar to California, under Alabama law, a non-governmental entity can be subject to a claim for inverse condemnation. As such, in Schultz v. SE. Supply Header, LLC, No. CA 09-0055-KD-C, 2009 WL 3075671 (S.D. Ala. Aug. 20, 2009), the property owners' claim for inverse condemnation against the private utility company did not fail by virtue of the utility company's non-governmental status. In that case, the property owners gave the utility company a permanent easement to their property for the installation of a natural gas pipeline to run underground, but in the process of construction, the utility company flooded the property and caused the property owners' septic system to malfunction, reducing the property to a swamp. Since the utility company was expressly authorized to exercise the power of eminent domain for installation of the natural gas pipelines, the property owners could avail themselves of the remedy of inverse condemnation for damage of the property by the company.

[39] *Barham v. Southern California Edison Company*, 74 Cal. App. 4th 744, 753 (1999).

[40] CA Civ. Pro. Code § 1036 (2017).

condemnation claim.[41] These claims from the insurance company are known as subrogation claims.[42]

Cost Recovery and Wildfire Damages

While a public utility found liable under inverse condemnation spreads the costs by using its rate-setting power to pass the costs to customers, investor-owned utilities can recover inverse condemnation damages in rates only if the CPUC separately determines that they may do so. California law requires that any rates charged by a utility must be "just and reasonable". [43] A utility may pass through and recover non-routine costs as a result of third-party litigation or inverse condemnation only if the IOU demonstrates to the CPUC that it acted reasonably and prudently (i.e., met a "prudent manager" standard).[44]

To meet this prudent manager standard in the context of extraordinary wildfire expenses, the CPUC requires that a utility affirmatively prove that it: (1) behaved reasonably and prudently in managing its facilities before and during the fire and (2) behaved reasonably and prudently in settling any litigation claims, if applicable. The CPUC has wide latitude as to the applicable evidentiary standard—typically applying a preponderance of the evidence standard—which generally requires evidence that "when weighed with that opposed to it, has more convincing force and greater probability of truth."[45]

Recent Application of Utility Wildfire Cost Recovery Standards

In October 2007, three large wildfires occurred in the service area of SDG&E. The ignition of those fires was attributed to the company's equipment. After 7 years of litigation, SDG&E settled legal claims for $2.4 billion in costs and legal fees to resolve third-party damages arising from the fires. After collecting from other responsible parties and under liability insurance policies, SDG&E sought recovery from ratepayers for the remaining

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[41] Inverse condemnation is limited to property damage caused by utility equipment, so not all utility wildfire liabilities are actionable under inverse condemnation. For example, wildfire liabilities caused by a utility company employee, rather than utility equipment, are not recoverable under inverse condemnation. In practice, litigation pursuing subrogation recovery will include multiple liability theories, including inverse condemnation, some of which apply a strict liability standard and some of which apply other standards, such as negligence.

[42] Generally, insurance company subrogation recoveries are not 100 percent reimbursement for claims paid to property owners. Limited public information suggests that subrogation settlements equal about 50 percent of the claim. Specifically, SCE's general auditor stated that wildfire subrogation claims have in the past settled at "historical levels" of "around 50 percent" at a meeting of the Commission on Catastrophic Wildfire Cost and Recovery on April 3, 2019.

[43] CAL. P.U.C § 451.

[44] The prudent manager standard means that "at a particular time any of the practices, methods, and acts engaged in by a utility follow the exercise of reasonable judgment in light of facts known or which should have been known at the time the decision was made." The prudent manager standard is a standard of care that demonstrates all actions were well planned and properly supervised and all necessary records are retained. See *See In re: San Diego Gas & Electric Co.*, Order Denying Application for Decision 17-11-033 at p.5 (Cal. Pu. Util. Comm'n) (Nov. 30, 2017).

[45] Decision Implementing a Safety Enhancement Plan and Approval Process, Decision 14-06-007 [D.14-06-007]

$379 million in damages it had paid. In October 2017, the CPUC denied SDG&E's request, ruling that the utility had not met required standards of prudency.[46]

The CPUC decision in the San Diego case was the first time a utility had incurred costs that exceeded its insurance coverage. The decision raised concerns in the capital markets that investors in California utilities were more exposed to wildfire liabilities than previously thought.

In late 2017, shortly after the CPUC's decision in the San Diego fires, California suffered one of its worst wildfire seasons on record. Combined, these events created uncertainty in the capital markets regarding the safety of investing in California utilities.

Senate Bill 901 (Dodd, Chapter 626, Statutes of 2018) (SB 901)

After the utility market destabilization, California enacted SB 901, which requires the CPUC to consider "conduct of the electric grid and relevant information submitted into the commission record" when determining whether a utility is permitted to recover costs related to wildfires. The statute outlines 12 categories of information for consideration, which are set forth on Annex B. SB 901 also incorporated a "stress test" that provided the CPUC additional flexibility to allow utilities to recover their costs in respect of wildfire liabilities from ratepayers where the denial of cost recovery could negatively impact the IOUs' financial condition.

In a cost recovery action, the CPUC must first find that utility equipment ignited the wildfire. Then the CPUC must determine whether the utility acted prudently both in the behavior causing the wildfire and in the settlement of any claims. If it acted prudently, the utility may recover the costs by charging higher rates to customers. If it did not act prudently, the utility would be required to bear those costs itself, in effect by reducing the returns paid to its equity investors. SB 901 attempted to provide the CPUC guidance on application of the cost recovery rules that would create more certainty around cost recovery.

After passage of SB 901, the credit rating agencies (Moody's, Standard & Poor's and Fitch) immediately began to downgrade California's three large IOUs, opining that the measure failed to adequately address the risks to the utilities' financial health posed by inverse condemnation. Two months later, the Camp Fire occurred. Two months after that, PG&E stated its intention to seek chapter 11 bankruptcy protection.

The rating agencies followed with an additional series of downgrades that now leave SCE and SDG&E with close to non-investment grade ratings.

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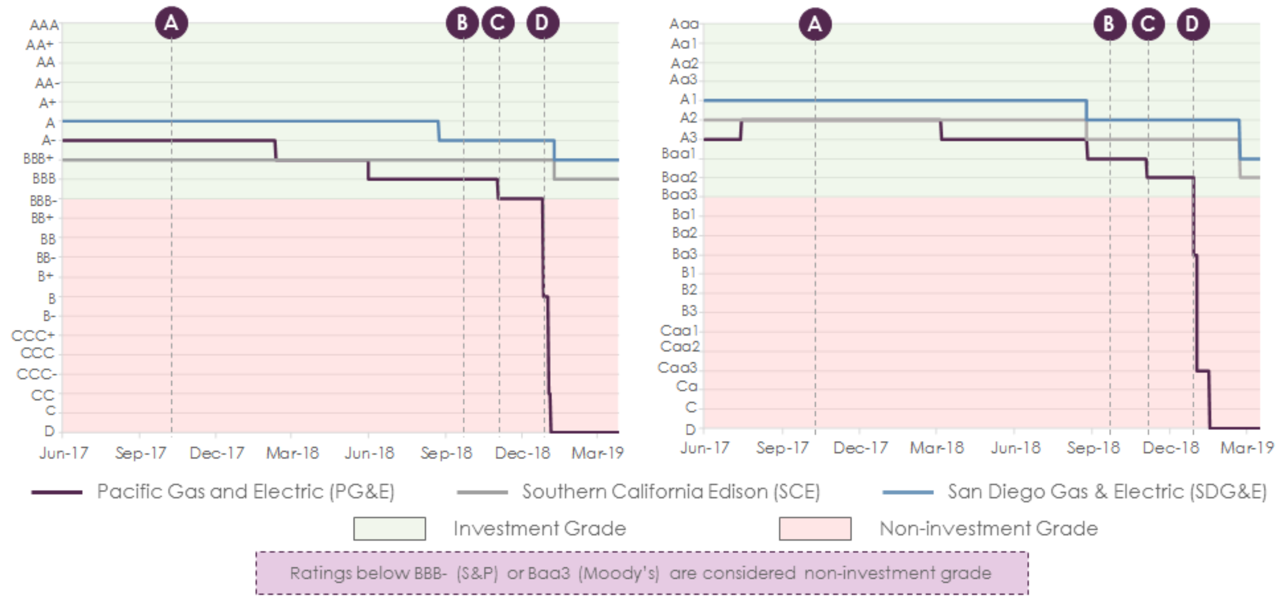
[46] See Order Denying Application [D. 17-11-033] (Cal. Pu. Util. Comm'n) (Nov. 30, 2017); Order Denying Rehearing of Decision (D.) 17-11-033 [D. 18-07-025] (Cal. Pub. Util. Comm'n) (July 12, 2018); Order Denying Writ for Review, No. D074417, Cal. Ct. of Appeal, 4th District, Div. 1 (Nov. 13, 2018)

Figure-10

Increasing wildfire risk coupled with uncertainty surrounding cost recovery for wildfire liabilities has resulted in credit ratings downgrades for all California IOUs



Ⓐ **October, 2017** – Tubbs Fire, the second most destructive wildfire in California history, burns 36,810 acres

Ⓑ **September 24, 2018** – Former Governor Jerry Brown signs SB 901 as an attempt to address outstanding wildfire liabilities

Ⓒ **November, 2018** – Camp Fire, the most destructive wildfire in California history, burns 153,336 acres

Ⓓ **January 14, 2019** – PG&E announces its intent to file for bankruptcy, providing the required 15 day advance notice to their employees

Source: Moody's and S&P.

Ratings downgrades increase utilities' cost of capital (including capital raised for investment in fire mitigation and safety) and those additional costs are generally passed on to consumers.

The capital markets concluded that too much uncertainty regarding cost recovery remained following passage of SB 901. Their key concerns were that it left the CPUC with extensive discretion to determine whether catastrophic wildfire damages could be passed through to the ratepayers.[47] In addition, investors raised concerns that SB 901 did not address the significant time period between the occurrence of a catastrophic wildfire, the payment of damages arising from that wildfire, and the CPUC's final

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[47] California's cost recovery process contrasts with the framework employed for federally-regulated transmission rates by the Federal Energy Regulatory Commission (FERC). Pursuant to section 205 of the Federal Power Act (FPA), public utility rates for transmission services in interstate commerce must be "just and reasonable," which includes a requirement that the utility is prudent in incurring costs. This statutory standard is similar to the standard in the California Public Utilities Code, however, FERC applies the standard differently than the CPUC applies its similar statutory standard. In practice, FERC generally presumes that a utility's expenditures have been prudent unless a third party raises a formal complaint that casts a serious doubt on the utility's prudency, in which case the utility has the burden to prove that its conduct and expenditures were prudent. FERC will consider a utility's conduct prudent if the utility acted as any other reasonable utility in its position would have acted, given the same circumstances and the same facts known to the company at the time. FERC precedent in evaluating the prudency standard affords considerable latitude as FERC, in reviewing a decision, does not look for a single correct result or require the evaluation of every possible alternative. Thus, the FERC standard is far more predictable.

determination of whether those payments can be recovered in rates. Under current timelines, a utility does not file an application for cost recovery until after it resolves all litigated claims, which in the case of San Diego took more than seven years from the time of the fires. The CPUC's cost recovery process can take 18 months to two years. This time lag creates financial stress on a utility which may need to raise additional capital to pay billions of dollars of wildfire claims without knowing whether it will be able to recover the costs of that capital in future rate increases. This can lead to lower credit ratings, higher borrowing costs and, therefore, higher rates paid by utility customers. Ultimately, as we have seen with PG&E, it can lead a utility to seek protection under the federal bankruptcy laws.

Consideration of Insurance Impacts

Before discussing potential concepts, it is important to consider the current impact of climate change and catastrophic wildfire damage on the availability and affordability of insurance and the risk that any proposed changes to liability for wildfire damage could exacerbate those impacts.

Insurance pricing and availability is responsive to a very basic principle: as risk increases, the cost of insurance increases and the availability of insurance coverage decreases. With record high losses from catastrophic wildfires, insurers are responding by filing for rate increases and retrenching their coverage eligibility standards. According to the California Department of Insurance (CDI), many regions of the state face insurance availability and affordability constraints. This is evidenced by increasing non-renewals and significant insurance premium increases in the areas of the state affected by wildfires. Investments that increase resiliency to climate-related catastrophes will add stability to insurance options. Without affordable insurance, regions throughout the state will find homes decreasing in value.

Current Trends in Insurance Availability and Affordability

Insurance rates are principally based on recent loss experience. According to CDI, in California, the loss experience resulting from catastrophes is not loaded directly into the rates but instead placed in a catastrophe load that is an average of at least 20 years of catastrophe experience. Despite that fact, rates are beginning to increase.

According to the CDI:

- Carriers have submitted applications to CDI for over 100 rate increases for homeowners insurance in the last two years, more than double the filings in the previous two years;
- Homeowners in areas with heightened wildfire risk are receiving double-digit rate increases;

- There has been a significant uptick in policy counts at the California Fair Access to Insurance Requirements Plan (FAIR Plan)[48] for homes located in areas of high wildfire risk, by 50 percent in the last five years (from 22,000 policies for homes with wildfire risk exposures to 33,000 such policies), although the FAIR Plan only insures about 130,000 homes in total out of approximately 13 million residences in the state;
- The number of homeowners who have purchased insurance from surplus lines insurers has also increased, though the total remains fewer than 60,000 statewide. Surplus lines coverage is available only to consumers who cannot find coverage with an admitted insurer. The rates are not regulated nor is the coverage backed by the California Insurance Guarantee Association; and
- Consumer complaints about non-renewals in high risk counties have also doubled in the last two years.

According to CDI, the overall number of adverse actions that are reflected in available data are relatively low compared to the California homeowners' insurance market as a whole. After two consecutive years of massive homeowners insurance loss ratios of insurers—201 percent in 2017 and 170 percent in 2018–there is a sense of urgency about the decreasing availability and affordability in 2019, especially for regions with high wildfire risk.

The strike force recommends that the Governor and Legislature, in consultation with the Insurance Commissioner, consider the following:

- Should all insurers be obligated to offer insurance to homeowners living in the WUI if the insured conducts specific wildfire mitigation?
- Should all insurers be obligated to offer reduced rates for those homeowners and communities that implement prescribed wildfire mitigation measures?
- Should insurers be obligated to offer consumers who are ineligible for a homeowners' policy either a "difference in conditions" policy or a "premises liability policy" as complementary coverage for a FAIR Plan fire policy?
- The California Insurance Guarantee Association policy limits have not been increased for at least two decades. Is it time to increase the current limit of $500,000 to recognize current construction costs?

Concepts for a Solution

The strike force heard from experts and stakeholders about alternative approaches. Based on this input, research and evaluation of the strengths and weaknesses of alternative approaches, we identified three concepts for consideration:

- **Concept 1:** Liquidity-Only Fund. This concept would create a fund to provide liquidity for utilities to pay wildfire damage claims pending CPUC determination of

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[48] The FAIR Plan was created in July 1968 as an insurance pool established to assure the availability of basic property insurance to people who own insurable property in the State of California and who, beyond their control, have been unable to obtain insurance in the voluntary insurance market. *See* https://www.cfpnet.com.

whether or not those claims are appropriate for cost recovery and may be coupled with modification of cost recovery standards.

- **Concept 2:** Changing Strict Liability to a Fault-Based Standard. This concept would involve modification of California's strict liability standard under inverse condemnation to one based on fault to balance the need for public improvements with private harm to individuals.
- **Concept 3:** Wildfire Fund. This concept would create a wildfire fund coupled with a revised cost recovery standard to spread the cost of catastrophic wildfires more broadly among stakeholders.

Given the inherent uncertainty we face and the number of foundational policy questions that must be addressed, the strike force recommends that the Commission on Catastrophic Wildfire Cost and Recovery, the Legislature, and the Governor's strike force continue working over the next two months to develop a solution for consideration by the Governor and the Legislature that most effectively addresses wildfire liability consistent with the principles that the strike force has outlined.

Each of the three concepts requires statutory changes to clarify the prudent manager standard and the requisite burden of proof related to when an IOU is permitted to recover costs and expenses of wildfires from its customers. To achieve a result that meets the principles outlined in this Report, utilities will have to make significant contributions to the benefit of ratepayers.

Concepts 1 and 3 rely on voluntary contributions from utility investors to different extents. The larger the contribution required, the more clarity utility investors will demand in the regulatory standard for cost recovery from ratepayers.

Concept 1: Liquidity-Only Fund

The liquidity-only fund involves a modest modification to the current SB 901 framework to address the delay between when a utility pays wildfire claims and when the CPUC makes its rate recovery determination. This concept would create a fund to provide bridge financing for utilities to pay wildfire liability claims pending the CPUC's decision on cost recovery under a modified standard. The liquidity-only fund does not reduce the burden on utility customers or re-distribute the costs of wildfires among stakeholders. As such, it does not address certain principles set forth above. In combination with changes to the CPUC cost recovery process, a liquidity-only fund could stabilize the credit ratings of utilities.

The liquidity-only fund could be capitalized by utility investors and ratepayers, potentially through a continuation and securitization of the Department of Water Resources (DWR) charge implemented during the power crisis in 2001 and expected to be fully repaid before the end of 2020. All or a portion of that securitization charge could be extended and dedicated to the liquidity-only fund.

The fund would then be available to provide funds for utilities to pay claims after a determination of cause and before a determination of cost recovery. When the CPUC makes a cost recovery determination, the fund then works as follows:

- If the CPUC determines that the utility met the cost recovery standard and therefore can recover the costs in rates, then the utility would charge the ratepayers and reimburse the fund for the amounts drawn.
- If the CPUC determines that the utility did not meet the cost recovery standard and therefore cannot recover costs in rates, then the utility would be required to repay the amounts drawn from the fund such that ratepayers would not bear the cost of such amounts.

This concept does not shield utility customers from uncapped liability for wildfire damages. In fact, if cost recovery changes increase the certainty that utilities can recover damages from their customers, ratepayers will pay more.

Further Research.

Several questions and policy considerations must be addressed to evaluate the liquidity-only fund and the impact it would have on reducing and socializing costs, and its ultimate impact on consumers:

- Can the fund provide sufficient liquidity to pay claims in a timely manner while allowing the CPUC to evaluate wildfires?
- Can this concept, in combination with necessary changes in the CPUC rate recovery process, provide enough certainty to the capital markets to stabilize ratings and the perception of a utility's credit quality?
- How durable can the liquidity fund be while the utilities address their safety deficiencies?
- How much can we expect from this simplified solution if we don't address the factors that turn massive wildfires into massive damage claims?
- What does this option mean for rates and affordability?
- What shareholder contribution, if any, would be required to capitalize the fund?

Concept 2: Changing Strict Liability to a Fault-Based Standard

A second concept is to change California's strict liability standard to one based on fault. Applying a fault-based standard—utilities pay for damage if caused by their misconduct—would balance the need for public improvements (i.e. an electrical distribution system) with the private harm to individuals occasioned by those improvements. This change would impact only claims for property damage, since California already applies a negligence standard to personal injury, wrongful death, and other tort claims.

Moving to a fault-based standard would shift the risk of property loss to insurance companies and uninsured or underinsured property owners in cases where the utility was not a bad actor. Where the utility acted negligently, recklessly, or with intentional misconduct, it would still be responsible for paying damages, including possible punitive damages.

As with Concepts 1 and 3, a solution that changed to a fault-based liability standard would be accompanied with modifications to clarify the prudent manager standard and the requisite burden of proof related to when an IOU is permitted to recover costs and expenses of wildfires from its consumers.

Shifting more of the direct financial burden of wildfires to insurance companies may also affect the cost and availability of property insurance in the WUI. Whether a reform of inverse condemnation would affect the cost and availability of insurance is unclear. If such an impact occurred, a variety of policy responses might be considered, including creating a catastrophic pooled insurance fund or reforms to the FAIR Plan, which provides last-resort fire insurance when homeowners or dwelling coverage is unavailable in the voluntary market of admitted insurers.[49] Admitted insurers are obligated to share in any losses suffered by the FAIR Plan.

Further Research.

Several questions and policy considerations must be addressed to evaluate the impact moving to a fault-based system would have on reducing and spreading costs, and its ultimate impact on consumers:

- How much would moving to a fault-based system reduce the settlements that utilities pay for wildfire claims?
- Would availability and affordability of property insurance in the state, particularly in the WUI be affected? If so, are there policy options to mitigate that impact?
- Would this approach yield certainty in the needed timeline given the potential legal risks and challenges?

Concept 3: Wildfire Fund

A third concept is to establish a well-capitalized wildfire fund that would create a buffer to absorb a significant portion of the wildfire liability costs that might otherwise be passed on to ratepayers under existing law and regulation while providing time for mitigation efforts to be advanced. The wildfire fund would also provide the utilities a source of immediate funding for the claims asserted against them for catastrophic wildfire damages and ensures prompt payment of those claims.

This concept could accomplish each of these objectives if utility shareholders were prepared to make a substantial contribution to the fund's claims-paying resources and if insurers were willing to accept a cap on their subrogation claims (their claims for reimbursement from the utilities of the payments to their insurance policyholders). If the wildfire fund is not sufficiently capitalized and/or the other stakeholders are not willing to

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[49] The Commission on Catastrophic Wildfire Cost and Recovery is tasked with, among other matters, evaluating the impact of wildfire damage on insurance availability and affordability. The Commission is expected to deliver its report by July 1.

compromise their claims, then the wildfire fund will be exhausted more quickly and ratepayers will be responsible for costs thereafter.

The CPUC would retain jurisdiction to impose penalties on utilities that fail to prudently manage their wildfire risks, and those penalties would be paid to the fund to enhance its claims paying resources. Like the liquidity-only fund, an extended DWR charge could be dedicated to support the claims paying resources of the wildfire fund.

The following are reasonable elements of a wildfire fund that, depending on additional research, analysis, and development, may warrant consideration in the future.

3. **Pooled Capital:** The wildfire fund would include pooled capital from all IOUs including each of SDG&E, SCE and PG&E and be accessible by each of those utilities to pay catastrophic wildfire claims. Municipally owned utilities may participate at their option.
4. **Only Catastrophic Fires:** The fund would be limited to paying claims of utility-caused catastrophic wildfire liabilities only (as such fires would be defined in legislation establishing the fund). Smaller utility-caused fires and the first-dollar costs of catastrophic wildfires would be paid by a utility's commercial liability insurance policy and/or self-insurance reserve.
5. **Claims Administration Trust.** A wildfire fund could use a trust for the administration of claims. The trust could pay all subrogation claims to insurance companies and reimburse utilities for the costs of judgments on or settlements of uninsured and underinsured victims' claims. All insurance companies writing insurance in the state could be required to agree that subrogation claims arising out of catastrophic wildfire claims will be asserted against the trust. A potentially valuable feature of the wildfire fund could be that subrogation claims will receive settlements at a stated percentage of the validated amount of their claim. Utilities could be responsible for litigating or settling claims brought by uninsured and underinsured victims. They could then seek reimbursement from the trust for the settlement amounts or final judgments. The reimbursement process could provide incentives for the utilities to settle promptly with victims, while also ensuring that they settle for fair, but not excessive, amounts.
6. **Automatic Access to the Fund.** A utility could seek to pay wildfire claims from the fund upon determination that the fire was a catastrophic utility-caused wildfire without pre-determination by the CPUC whether or not the utility acted prudently, reasonably, or without negligence.
7. **Penalties to Discourage Behavior by Fund Participants that Violates Regulatory Requirements or is Imprudent:** Regulatory reforms could incorporate penalties that would create disincentives for negligent or unreasonable behavior by fund participants. Penalties could be paid into the fund to further extend claims paying capacity.

Further Research.

- How large would the fund need to be to be durable over the anticipated period of time necessary for utilities to make material progress in containing catastrophic wildfire risk?
- How can we design a fund that provides the proper incentives for utilities to invest in prevention to reduce wildfire damages and claims and for property owners to protect themselves by purchasing adequate insurance?
- After emerging from bankruptcy and providing for adequate compensation to its pre-petition wildfire victims, how will PG&E raise the necessary capital to make its contribution to the fund?
- How much time will it take to form and capitalize a wildfire fund? How should liability for wildfires that may occur in 2019 prior to the fund's formation be treated? Can the fund be established before PG&E emerges from bankruptcy?
- Capping subrogation claims moves the upper range of risk from the utility to the insurers, who will pass it on to customers. What would be the long-term impact on the availability of insurance?
- Would the subrogation cap apply to both property claims and casualty claims, which are different rights under the law?
- Should insurers or insureds contribute to fund capitalization?

Part 4: A More Effective CPUC with the Tools to Manage a Changing Utility Market

California's changing energy market and the need to mitigate and adapt to climate change require a state utility regulator that is effective in today's reality.

The CPUC has a long history as a regulator of rates. It manages complex, participatory, and time-consuming proceedings to set energy rates for the state's utilities. Its structure and deliberative processes flow from the California Constitution, which authorizes the CPUC to fix rates and charges and allows utilities to raise rates or charges if justified.[50] The CPUC has an imperative to balance the financial health of utilities and the need to keep rates as low as possible.

The current structure of the CPUC does not align with California's need for a regulator that can effectively address wildfire safety and can be nimble in today's changing energy market. The CPUC has assumed a greater role in safety regulation, as well as in protecting consumers. However, its structure has not fundamentally changed. Further, its other obligations, including regulation of some transportation industries, telecommunications, and other industries has grown as the demands on the Commission as the state's regulator of utilities have increased and become more complicated.

The Commission needs to strengthen its efforts as an evaluator of risk reduction and as a key line of defense to prevent wildfires caused by utility infrastructure. It must also be more nimble and provide necessary certainty more quickly than it does today in light of the changing energy market and heightened fire risk. Implementing a comprehensive strategy to improve safety, keep costs down and reach California's clean energy goals requires a regulator that applies and enforces regulation in a predictable, timely, and fair way.

The Current CPUC Process

The CPUC has three primary roles: quasi-legislative, rate-setting, and adjudicatory disputes. Under current law and practice, the CPUC uses different processes depending on the role it is performing. All types of proceedings are record based and governed by either an Assigned Commissioner or an Administrative Law Judge (ALJ). All involve extensive consultation and public input.

The CPUC typically addresses policy issues and capital expenditures in separate proceedings. For example, the issue of wildfire mitigation is being handled in two separate proceedings in front of the CPUC--one specific to the WMPs and the second as part of the general rate case (GRC). As wildfires become more frequent and larger, and as the state's energy market changes, the CPUC needs a decision-making process that is responsive to these developments.

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[50] Article XII Public Utilities, CAL. CONS. [SECTION 1 - SEC. 9].

IOUs file GRCs with the CPUC every three years for prospective costs. Between GRC proceedings, the IOUs often file for approval for recovery of unexpected costs incurred. Except for certain minor matters, a highly structured legal process applies to decisions on these filings. The process insures that the filing party and opposing parties have an ability to be heard, including by submitting pleadings and testimony. The testimony and filings are important because the Commission must base its decisions on evidence in the record. The process provides other parties the ability to present views that are contrary to those of the IOUs. While it has value, the existing process can be time-consuming.[51]

If the Assigned Commissioner is not the presiding officer, the statutory structure of the CPUC's decision-making process often leaves ALJs with more control over the timing of the process than the Commissioners. That can lead to delays in proceedings even when the Commissioners wish to prioritize the decision-making.

In its rate-setting mode, the CPUC faces a difficult balancing act. On the one hand, the CPUC wants the IOUs to make appropriate investments and expenditures so they can provide safe and reliable service to their customers. On the other hand, an IOU's only source of income is its customers. Consumers have an interest in avoiding unnecessary costs and investments and keeping borrowing costs down. IOUs operate their business by collecting a return on investment, but the investments and the return are closely regulated by the CPUC. When the IOUs are financially healthy, utility customers benefit from lower cost of capital. When utilities are financially unhealthy, the inverse occurs as evidenced today in the case of PG&E.

In rate-setting and cost recovery cases, the burden falls on the utility to prove that its requests or its past actions were reasonable or prudent. In some instances, the utility may face difficulty proving that past actions meet this burden, which can create financial uncertainty for the utility. To avoid this, utilities may elect not to make expenditures unless the cost recovery was pre-approved by the CPUC.

The CPUC sometimes is tasked with new responsibilities that fall outside its traditional function of ensuring that rates are just and reasonable. After the San Bruno and Aliso Canyon events, safety has become a much more significant issue for the CPUC. The recent expansion of the Commission's role into reviewing WMPs under SB 901, as described above, is a further example of the CPUC's expanded role.

The CPUC's statutory and Constitutional responsibilities go beyond the rate-making cases. In developing and overseeing clean energy programs and in its role in

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[51] As an example, SCE filed its most recent GRC on September 1, 2016, and it is still pending today, more than 2 years later. *See In re: San Diego Gas & Electric Co.*, Test Year 2018 General Rate Case Application of So. Cal. Edison Co A 16-09-001 (Cal. Pu. Util. Comm'n) (Sept. 1, 2016); When SDG&E filed to recover its third-party damage claims in connection with its 2007 wildfires, it took 2 years for the CPUC to issue its decision denying recovery, and it took 6 months for the CPUC to issue its rehearing order after SDG&E filed its rehearing request. *See* Application of San Diego Gas & Elec. Co. (U 902 E) for Authorization to Recover Costs Related to the 2007 Southern California Wildfires Recorded in the Wildfire Expense Memorandum Account, *In re: San Diego Gas & Electric Co.*, Decision Denying Application, A 17-11-033 (Cal. Pu. Util. Comm'n) (Dec. 6, 2017); *In re: San Diego Gas & Electric Co.*, Order Denying Rehearing of Decision 17-11-033 (Cal. Pu. Util. Comm'n) (Jul. 13, 2018).

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developing and enforcing safety regulations, the CPUC can also be a policy-setting body and a quasi-judicial body. At times, the ALJ-led process the CPUC utilizes does not lend itself to public accessibility or speedy development of new policies. This may contrast with the public's expectation that the Commissioners be the ultimate decision makers who should be held accountable for the timing of developing new rules and programs.

While there is merit in existing CPUC processes, the lack of flexibility and inefficiency frustrates the ability of the CPUC to effectively regulate utilities in a way that best meets the needs of Californians from a safety and financial standpoint. To more effectively meet the state's needs in today's environment, the CPUC must be reformed. The recommendations set forth below represent near-term steps that can be taken to improve CPUC efficiency and effectiveness. Longer-term, the state should evaluate a more comprehensive overhaul of the CPUC in an effort to better serve the changing needs of California.

Recommendations

- **Expand Safety Expertise:** Provide resources to the CPUC for meaningful review of WMPs or alternatively create a wildfire safety division in another agency. The CPUC must—on a priority basis—develop appropriate processes and expertise to handle matters involving safety. This should cover the CPUC's responsibilities for setting safety standards, conducting inspections and audits, and enforcing the standards. A good starting point would be to look at safety-related programs used by regulators in other industry sectors that involve high risks to property and human health and safety, such as the nuclear, aviation, and refinery industries. While the 2016 reforms made a small step toward an increased focus on safety, more is needed. Building the CPUC's capabilities related to safety may require organizational changes, budget increases, and a concerted effort to hire, contract for, or obtain through cooperative efforts with other agencies, the expertise needed to handle these new responsibilities. If experts are not available, then the CPUC should consider entering into grants or contracts with universities or consulting firms that could conduct research and develop standards and training programs to create the necessary expertise.
- **Overhaul Decision-Making Processes.** The CPUC should overhaul and reform its procedures to implement safety related initiatives and requirements more efficiently. Given the potentially large financial implications of such determinations as related to wildfire-related costs, it is particularly important that the CPUC put in place a process that is both timely and fair, while maintaining public input and transparency as appropriate. To achieve this goal, the strike force recommends that the Legislature consider directing the CPUC to do the following:
  - Streamline procedural designations for simpler cases. Many proceedings that could be quasi-legislative are currently subject to full rate-setting procedures.
  - Increase authority to delegate lower-level decisions to technical staff to free up time for administrative law judges and commissioners to focus on traditional rate-setting matters.
  - Eliminate unnecessary steps in proceedings and provide Commissioners with discretion to shorten timelines.

    - Streamline enforcement procedures and increase enforcement authority, including delegating more enforcement authority to the Commission's safety division staff.

- **Review of High-Risk Industry Regulatory Models.** The Governor's Office of Planning and Research, in consultation with experts from academia, industry, and other research institutions, should review models of agencies that regulate high-risk industries, such as nuclear power and refineries, and summarize best practices that could be applied to the CPUC. These practices could include structural or procedural models and necessary expertise.
- **Industry Best Practices.** The CPUC should develop and adopt industry best practices for utilities as a resource. It should regularly monitor and update those practices to reflect learning, changing technology, and the latest assessment of climate change.

Part 5: Holding PG&E Accountable and Building a Utility that Prioritizes Safety

On January 29, PG&E filed voluntary chapter 11 petitions in the United States Bankruptcy Court for the Northern District of California--PG&E's second bankruptcy filing in the last 18 years.[52] PG&E attributed its chapter 11 filing to claims resulting from the 2018 wildfires, including the Camp Fire which PG&E has since stated was likely ignited by its equipment.[53] PG&E justified the filing, in part, by citing the need to provide fair compensation for fire victims. Yet consistent with its historic culture, PG&E failed to honor scheduled settlement payments to victims of the Butte Fire in the days leading up to its bankruptcy. PG&E's willingness to use the bankruptcy process to the advantage of its investors, and at the expense of Californians, cannot be repeated.

PG&E's decision to voluntarily seek the protection of a chapter 11 bankruptcy court punctuates more than two decades of mismanagement, misconduct, and failed efforts to improve its safety culture. Prior to its filing, PG&E already was on criminal probation, having been convicted of five felony counts for safety violations in connection with the San Bruno gas explosion in 2010. That explosion resulted in eight deaths, approximately 58 injuries and 38 homes destroyed.[54] PG&E was also convicted of obstruction of justice, fined over $4.6 million, and sentenced to substantial community service as a result of the same incident.

In addition to the incidents described above, PG&E has been investigated in connection with or settled claims related to numerous wildfires and explosions in the last 25 years including:

- The Trauner Fire (1994)
- The Pendola Fire (1999)
- The Sims Fire (2004)
- Fred's Fire (2004)
- The Rancho Codova gas explosion (2008)
- The 2009 San Francisco electrical explosion
- The 2014 Carmel gas explosion
- The Butte Fire (2015)
- Numerous electrical and substation fires (*e.g.* 1996, 1999, 2003).

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[52] PG&E previously filed for bankruptcy in 2001 in an effort to undermine the jurisdiction of the CPUC. That multi-year bankruptcy resulted in substantial rate increases for PG&E customers.

[53] PG&E, *PG&E Publicly Releases Supplemental Report on Electric Incidents Near the Camp Fire," the Camp Fire*, (Dec. 11, 2018) https://www.pge.com/en/about/newsroom/newsdetails/index.page?title=20181211_pge_publicly_releases_supplemental_report_on_electric_incidents_near_the_camp_fire (last visited Apr. 10, 2019).

[54] *See* CAL. PUB. UTILITIES COMM., *The San Bruno Catastrophe and Its Aftermath*, (May 2012), https://www.in.gov/iurc/files/Zeller_-_San_Bruno_Catastrophe_Aftermath.pdf (last visited Apr. 10, 2019).

Despite repeated assurances from management that the company would change, PG&E has failed to implement the fundamental management and cultural reforms to prioritize safety and reliable service.

Californians deserve better, and we will demand better. The state simply will not accept a situation where 40 percent of Californians are served by a company that cannot be trusted to provide safe and affordable power. PG&E must be radically restructured and transformed into a responsible and accountable utility.

PG&E's bankruptcy proceedings will have direct and profound impacts on the people of California. The state must participate in the proceedings to protect its interests, including those of wildfire victims who have claims against the company that must be resolved fairly and equitably, PG&E employees who are vital to maintain energy delivery and protect the safety of communities, and the company's customers who deserve clean, safe, reliable, and affordable energy. We expect and demand that PG&E will, as it is obligated to do, comply with state law, including CPUC safety directives and renewable energy mandates.

Recommendations

PG&E's stakeholders have the primary responsibility for filing a plan of reorganization or otherwise formulating an exit from chapter 11. For a plan of reorganization to be confirmed in the bankruptcy proceedings, it must meet the criteria set forth in the Bankruptcy Code, including that the plan be feasible and that PG&E be in compliance with law. To meet those standards, PG&E will have to demonstrate that it has sufficient funds available to make fund distributions provided under the plan and comply with its WMP and demonstrate that is in compliance with state and federal laws, rules and regulations, including laws and regulations related to clean energy. Given the importance of PG&E to California, the state must work to assure that any resolution of that proceeding achieves the near, medium and long-term goals of the state and its people over opportunistic investors.

The strike force recommends that the state actively monitor and evaluate the PG&E bankruptcy proceeding to assure that the state's interests are being protected. Where appropriate and necessary, the state should participate in the bankruptcy proceedings and be heard on particular issues of interest to California. The strike force specifically recommends the following:

- **Evaluate Any Proposals to Satisfy 2017-2018 Wildfire Claims.** PG&E must satisfy the claims against it from the 2017-2018 wildfires. To that end, the state should evaluate the structure and amount of any trust or other mechanism to satisfy those claims to assure victims are fully and fairly treated. In addition, the state must evaluate any plan of reorganization to assess whether provisions of that plan could disadvantage existing and future wildfire victims.
- **Assure that PG&E Treats Its Employees Fairly.** PG&E's employees are a critical part of the future of the company and must be treated fairly in the bankruptcy proceeding. The state should monitor the bankruptcy proceedings to assure that employees are treated fairly.

- **Require that PG&E's Investors Contribute to a Solution.** Part 3 of this report identified certain conceptual approaches to the wildfire liability framework applicable to IOUs. While PG&E would be a beneficiary of any of those constructs, PG&E's investors must contribute to any solution adopted by the state to address wildfire liabilities in a way that benefits consumers. Those contributions could take a variety of forms, including investing in wildfire mitigation and safety or providing funding for other solutions.
- **Require PG&E Meet Conditions to Participate in Changes to the Wildfire Liability Structure for IOUs.** PG&E must meet conditions to participate in any approach to address wildfire liabilities, including fully remaking its corporate and safety culture and prioritizing governance that recognizes the public trust placed in PG&E.
- **Assure That PG&E Meets Its Obligations to Decommission Diablo Canyon.** PG&E must move forward with plans to safely and expeditiously decommission the Diablo Canyon Nuclear Power Plant. Trust funds and other moneys collected by consumers must not be diverted from that effort and additional funds must be provided by PG&E as needed. The state should evaluate the filings in the PG&E bankruptcy proceeding including the plan to assure that such filings require PG&E to meet its obligations with regard to Diablo Canyon.
- **Evaluate the Impact of PG&E Bankruptcy on Clean Energy Goals**. PG&E is party to numerous power purchase agreements that could be impacted by the chapter 11. The state should evaluate the impact of any decisions made by PG&E in its chapter 11 with regard to those agreements in light of California's clean energy goals.
- **Assure Plan is Compliant with Law and Feasible.** The state should evaluate any plan of reorganization to assure that the emerging company will be in compliance with law and that the plan will be feasible.
- **Continue Appropriate Regulatory Oversight.** Although PG&E is in chapter 11, the CPUC also has a substantial say in the future of PG&E (as it does for all IOUs). For example, the CPUC has the power to review PG&E's WMP and its compliance with that plan, as well as to review PG&E's safety culture assessment. The CPUC also has the authority to impose substantial penalties on PG&E for failure to comply with applicable regulations. Moreover, through the rate-setting function, the CPUC may provide incentives for PG&E to make prudent expenditures on, and investments in, safety. This can include actions, such as adjusting the allowed return on equity, that directly affect investors and management. The CPUC should continue to provide appropriate regulatory oversight.

While regrettable, the company's chapter 11 filing offers an opportunity to build a new, responsible, and accountable utility for Northern California.

Given the long history of safety failures and the critical interests at stake, the state can take no options off the table, including municipalization of all or a portion of PG&E's operations; division of PG&E's service territories into smaller, regional markets; refocusing PG&E's operations on transmission and distribution; or reorganization of PG&E as a new company structured to meet its obligations to California..

Conclusion

Catastrophic wildfires present tremendous challenges for California. The Governor's strike force makes numerous recommendations throughout this report to address those challenges. The strike force recommended immediate next steps are below.

Figure-11

Next Steps	
Catastrophic Wildfire Prevention and Response	✓ Publicize the Ready, Set, Go app – Wildfire prevention depends on each of us. To help educate property owners and residents in areas most at risk, CALFIRE has developed an app called "Ready, Set, Go!" that breaks down actions needed to be ready for wildfire. CALFIRE should work with leaders in vulnerable communities on outreach and provide technical assistance. Every Californian should download the Ready Set Go App.
	✓ Monitor and assess mitigation efforts – CALFIRE is pursuing a number of aggressive wildfire mitigation efforts, including distributing local community grants for mitigation. Metrics will be developed to measure the effectiveness of these programs and the community reach for local grant recipients.
	✓ Convene Governor's 2019 Emergency Preparedness Summit – The Governor's Office of Emergency Services will, by June 2019, convene first responders, government agencies, local governments, community residents, and technical experts to develop plans for the state's emergency preparedness. The summit will highlight best practices of local communities, share resources that have worked, and develop the networks necessary for ongoing preparedness improvements.
	✓ Prepare for state response to utilities reducing fire risks – Utilities are reportedly considering expanded de-energization of specific areas during high-risk periods to reduce the risk of wildfires. OES and the CPUC will lead an effort to assess utility plans to de-energize and will work with utilities, local governments, first responders, critical providers, businesses and residents to manage the potential of de-energization.
	✓ Implement emergency preparedness campaign and continue to pursue necessary resources for wildfire prevention and response.
Mitigating Climate Change through Clean Energy Policies	✓ Work with the Legislature, Cal ISO, and the CPUC on a legislative and regulatory agenda to ensure that California simultaneously addresses the impacts of climate change, including increased wildfires, and the root causes of climate change. Such work must include review of emissions from the electricity and transportation sectors. We must plan for a multi-year reform agenda, working in collaboration with the Legislature.

	✓ Convene academics, private foundations, stakeholders, and government to assist in the development of a multi-year agenda to ensure that California simultaneously addresses the impacts of climate change.
Fair Allocation of Catastrophic Wildfire Damage	✓ Significant policy development work, legal analysis, and financial simulations have all informed the liability concepts included in the report. However, additional analysis is needed. Request the SB 901 commission to review and analyze major liability concepts presented in report and solicit public comment regarding the different options.
	✓ Direct the Governor's Strike Force to continue its work developing these options for consideration by the Governor and the Legislature by no later than this summer.
	✓ Request the Department of Insurance to monitor, study, and issue recommendations to maintain an accessible and affordable insurance market throughout the state.
Increasing Capacity of the CPUC with the Tools to Effectively Manage a Changing Utility Market	✓ Focus on building internal CPUC capacity to evaluate and help strengthen the IOU's wildfire mitigation plans immediately.
	✓ Direct the CPUC to immediately assess regulatory and legislative changes to make their proceedings more expeditious. Identify and draft regulations and legislation needed to expedite their administrative proceedings. Such proposals should be reviewed with stakeholders and pursued as soon as possible.
Holding PG&E Accountable by Building a Utility that Prioritizes Safety	✓ Push for Safety Changes. The CPUC should continue to provide appropriate regulatory oversight on utility safety. The CPUC has the power to review PG&E's wildfire mitigation plan and its compliance with that plan, as well as to review PG&E's safety culture assessment. The CPUC also has the authority to impose substantial penalties on PG&E for failure to comply with applicable regulations. These tools should be actively used to help create the safest utility possible.
	✓ Actively Monitor and Appear in the Bankruptcy Proceedings. The state will actively monitor the PG&E bankruptcy proceedings to assure that California's interests are being protected. Where appropriate and necessary, the state will participate in the bankruptcy proceedings and be heard on particular issues of interest to California, including fair treatment of fire victims and employees, issues relating to safety, and factors affecting the state's progress to achieve climate commitments.
	✓ Require PG&E's investors to contribute to any solution adopted by the state to address wildfire victim claims. Those contributions could take a variety of forms including investing in wildfire mitigation and safety or providing funding for the wildfire fund.

Wildfires have always plagued California. Climate change has made--and will continue to make--the fires hotter, bigger, more frequent, and more destructive. The costs of these fires is unbearable. The loss of human life, property, economic opportunities, community life, exacerbated by the costs to rebuild communities – cannot be sustained.

Yet, we know we cannot avoid all fire risks. This level of disaster touches every Californian. All Californians must share in the responsibility to mitigate wildfires. Paying for the costs of wildfires is also a problem that requires shared responsibility and shared sacrifice. All stakeholders must come together to address the cumulative liability of uncontrolled fires. The status quo is not an option. Doing nothing is unacceptable.

Annex A

Comparison of Wildfire Mitigation Plans

Estimated 2019 Costs ($ in millions)

PG&E	SCE	SDG&E
O&M: $849	O&M: $507	O&M: $24
Capital: $1,623	Capital: $1,027	Capital: $178
Total: $2,472	**Total: $1,535**	**Total: $202**

Plan Priorities

PG&E	SCE	SDG&E
• Vegetation Management & Enhanced Inspections • Wildfire Response • System Hardening • Situational Monitoring • Operational Practices (*e.g.*, de-energization) • Tech Research / Development	• Ignition Reduction in High-Risk Areas • Fire Suppression • System Hardening • Communication	• Ignition Reduction in High-Risk Areas • Fire Suppression • Wildfire safety and recovery

High-Risk Exposure (% of Service Territory)

PG&E	SCE	SDG&E
52%	35%	54%[55]

System Hardening (Est. 2019 % of Circuit Miles Hardened in High-Risk Threat District)

PG&E	SCE	SDG&E
0.6%	0.5%	N/A[56]

Vegetation Management (Est. 2019 removals / % of total trees)

PG&E	SCE	SDG&E
375,000 trees *(0.375%)*	7,500 trees *(0.500%)*	9,000 trees *(1.935%)*

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[55] Percentage of SDG&E's overhead circuit miles that reside in High Fire Threat Districts. Percentage of Service Territory figures were not available.

[56] SDG&E uses an execution metric which expects that 90-100 percent of its system will be hardened by the end of 2019. This includes system miles hardened and percentage of poles replaced

Weather Stations in High-Risk Threat District

PG&E	SCE	SDG&E
2019 Install: 400 *(1.10 per 100 mi^2)*	2019 Install: 315 *(1.70 per 100 mi^2)*	N/A
Cumulative: 600 *(1.65 per 100 mi^2)*	Cumulative[57]: 440 *(2.38 per 100 mi^2)*	Cumulative: 175 *(6.21 per 100 mi^2)*

Cameras in High-Risk Threat District

PG&E	SCE	SDG&E
2019 Install: 71 *(0.20 per 100 mi^2)*	2019 Install: 62 *(0.34 per 100 mi^2)*	N/A
Cumulative: 79 *(0.22 per 100 mi^2)*	Cumulative[58]: 160 *(0.87 per 100 mi^2)*	Cumulative: 107 *(3.79 per 100 mi^2)*

De-Energization

PG&E	SCE	SDG&E
• PG&E has implemented the Wildlife Reclosing Disable program to manage circuit breakers if necessary • PG&E targets an increase in its Public Safety Power Shutoff program from ~7,000 mi of lines to ~25,000 mi of lines in 2019	• SCE has broadly outlined its plans to install additional remote automatic reclosers • SCE will conduct Public Safety Power Shutoffs based on the judgement of the incident management team and has a contingency operating plan in place	• SDG&E has deployed overhead distribution reclosers focusing on High-Risk Threat Districts • To determine whether to employ a Power Shutoff, SDG&E considers multiple variables such as weather conditions, vegetation, field observations, flying debris, expected duration of conditions and location of existing fires/wildfire activity

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[57] Weather stations reflect 2018 + 2019E installations.

[58] Cameras reflect 2018-2020E installations.

Annex B

SB 901 Factors

1. The nature and severity of the conduct of the electric grid and its officers, employees, contractors, and other entities with which the electric grid forms a contractual relationship, including systemic corporate defects.
2. Whether the electric grid disregarded indicators of wildfire risk.
3. Whether the electric grid failed to design its assets in a reasonable manner.
4. Whether the electric grid failed to operate its assets in a reasonable manner.
5. Whether the electric grid failed to maintain its assets in a reasonable manner.
6. Whether the electric grid's practices to monitor, predict, and anticipate wildfires, and to operate its facilities in a reasonable manner based on information gained from its monitoring and predicting of wildfires, were reasonable.
7. The extent to which the costs and expenses were in part caused by circumstances beyond the electric grid's control.
8. Whether extreme climate conditions at the location of the wildfire's ignition, including humidity, temperature, or winds occurring during the wildfire, contributed to the fire's ignition or exacerbated the extent of the damages. The electric grid shall provide the CPUC with specific evidence and data demonstrating the impact of climate conditions on the severity of the wildfire.
9. The electric grid's compliance with regulations, laws, CPUC orders, and its wildfire mitigation plans prepared pursuant to Section 8386 of the PUC, including its history of compliance.
10. Official findings of state, local, or federal government offices summarizing statutory, regulatory, or ordinance violations by any actor that contributed to the extent of the damages.
11. Whether the costs and expenses were caused by a single violation or multiple violations of relevant rules.
12. Other factors the CPUC finds necessary to evaluate the reasonableness of the costs and expenses, including factors traditionally relied upon by the CPUC in its decisions.

NATIONAL

California Firefighters Battle Exhaustion

August 8, 2018 · 5:19 AM ET
Heard on Morning Edition

Firefighters continue to battle blazes in California. NPR's David Greene talks with Ventura County Fire Captain Steve Kaufmann about how crews are holding up.

DAVID GREENE, HOST:

Wildfires raging here in the state of California have now burned some 600,000 acres. And this includes the so-called Mendocino Complex, which is now officially the largest wildfire in California history. Earlier, I spoke to Steve Kaufmann. He's a fire captain in Ventura County. He joined me from Mendocino County and the community of Ukiah. He told me how people are doing in one of the many shelters in the area that have filled up with hundreds of evacuees.

STEVE KAUFMANN: Some of them, it's been up to a week now. And just, you know, trying to explain why we still have them out of their home and in the evacuation shelter, that's probably the most vivid memory that I have of this fire.

GREENE: Are these families you're talking to - I mean, how are they getting by? Are they getting the food and support they need?

KAUFMANN: They are getting along fairly well. The Red Cross takes very good care of them and provides them, you know, a place to sleep, a shelter, meals. They try to, you know, accommodate most of their needs. In these shelters - not only do they have the family in the shelters, but a lot of the shelters are accommodating the family pets. And there's a whole variety of family pets that are in the shelters from bunny rabbits to dogs, cats, birds, stuff like that.

GREENE: I guess having your pets around might be one sort of memory of what it's like to be home and give you a sense of being home.

Captain, can I just ask you - I know that in one of these fires in California - the Carr Fire, not the one you're fighting - two firefighters were killed. How much does knowing that loom over the work you're doing?

KAUFMANN: Well, I mean, it definitely affects our firefighters. And we think about that every single day. And even at the camps that we don't have firefighter fatalities at, there are little, you know, memorials that the firefighters will go and sign to send up to the Carr Fire or the Ferguson Fire or any other fire that we have a firefighter fatality. It definitely - yeah, we think about it. And, you know, our families back home think about it. And you can tell when they're calling you, and they're concerned about you. And they want to know, you know, what your status is. And they, you know, want that daily check-in. It's definitely something that we think about. It weighs heavy on our hearts.

GREENE: Who are you checking in with? Who's calling you to make sure you're doing OK out there?

KAUFMANN: Actually, my parents. I make sure I check in with them and let them know when I get there and how things are going. And yeah, they're definitely concerned.

GREENE: The governor of California, Jerry Brown, suggested that this just is going to become a way of life in California, these types of fires. And I know there have been some reports that suicide rates have been going up among firefighters with all of these blazes, with the limited resources. Does that surprise you? And are you feeling pressures that are getting worse in this line of work?

KAUFMANN: You know, I don't know that I personally am feeling pressures. I know that - you know, I've heard those statistics. And I know that we're, you know, really trying to reach out. And the firefighter community is a tight-knit community. And one of the things - I don't like speaking on behalf of other people very often, but one of the things I do feel comfortable telling you is that for firefighters, this isn't a job for us. This is truly a passion or a calling. And so we take what we do every single day very seriously. And so when I go up to a community like this - there's going to be 3,900 firefighters on the Mendocino Complex. For all intents and purposes, we're the Mendocino and Lake County firefighters as long as we're here.

GREENE: Steve Kaufmann is a fire captain in Ventura County. But as he says, he feels like he's part of the fire community where he is fighting now in Mendocino County.

Captain Kaufmann, thank you so much.

KAUFMANN: Thank you, David.

Best Management Practices for Mitigating the Effects of Roads on Amphibian and Reptile Species at Risk in Ontario

April 2016

Written by Kari Gunson, David Seburn, Julia Kintsch and Joe Crowley

ontario.ca/speciesatrisk

Ontario

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Cover photo provided by Joe Crowley

TABLE OF CONTENTS

1 INTRODUCTION

1.1 Purpose

The purpose of the Ontario Ministry of Natural Resources and Forestry (OMNRF) Best Management Practices for Mitigating the Effects of Roads on Amphibian and Reptile Species at Risk in Ontario (hereafter referred to as the best management practice (BMP) document) is to provide information on designing, implementing and monitoring mitigation measures to restore connectivity and reduce road mortality for species at risk (SAR) amphibians and reptiles. This information will assist in providing information on mitigation planning for amphibians and reptiles at risk in Ontario in order to meet the requirements of the *Endangered Species Act, 2007* (ESA) or its associated regulations. The intended audience includes planning authorities (local or provincial government), individuals applying ESA requirements on the landscape, consultants working on their behalf and conservation organizations involved in the planning and design of impact mitigation for all new roads and road rehabilitation (improvement) projects.

The focus of this BMP document is on crossing structures and fencing. While there is no singular solution for mitigating road effects on amphibians and reptiles, this document offers information for developing site-specific mitigation based on best practices and findings from current peer-reviewed and grey literature (e.g., websites and conference proceedings), government documents, academic theses and personal communication surveys with experts in road ecology and other areas of relevance (e.g., engineering, species biology). When knowledge gaps were identified, the recommendations are based on the best available information and expert opinion, as well as logical interpretation from species-specific needs and life-history traits.

This document presents current information as of the date of publication and is meant to be updated through time as improved information becomes available. If you are interested in providing pertinent information for consideration in updates of this document, please email esapermits@ontario.ca.

1.2 Endangered Species Act, 2007 (ESA)

The ESA provides the legislative framework for the protection of species at risk in Ontario. Section 9 of the ESA includes prohibitions against activities such as killing, harming, harassing, capturing or taking a living member of a species that is listed as extirpated, endangered or threatened on the Species at Risk in Ontario (SARO) List. Section 10 of the ESA includes prohibitions against damage or destruction of the habitat of an endangered or threatened species.

The ESA contains provisions that enable the Minister to issue permits and enter into agreements to authorize activities that would otherwise be prohibited and Ontario Regulation 242/08 sets out conditional exemptions from prohibitions under the Act for certain activities. For additional information, visit the government website or read the full text of the legislation on e-Laws using the links provided below.

How species at risk are protected:
https://www.ontario.ca/page/how-species-risk-are-protected

Endangered Species Act, 2007 on e-Laws:
http://www.ontario.ca/laws/statute/07e06

Ontario Regulation 242/08 on e-Laws:
http://www.ontario.ca/laws/regulation/080242

1.3 Document Outline

This document is organized into the following sections:

Section 1 (Introduction) provides background information on the threats of roads to amphibian and reptile species and the overall objectives of the document.

Section 2 (The Impacts of Roads) details background information on the impacts of roads on amphibians and reptiles and the need for road mitigation measures.

Section 3 (Mitigation Planning) provides information about considerations for developing a mitigation plan in a landscape context within project planning processes.

Section 4 (Road Mitigation BMPs) addresses design variations and applications of three crossing systems for amphibians and reptiles, in addition to detailed considerations for siting, designing, enhancing and maintaining crossing structure and fencing systems.

Section 5 (Supplementary Measures) provides recommendations about using mitigation measures other than crossing structures and fencing systems to reduce road impacts on amphibians and reptiles. These measures may be used when crossing structures are not required, or as a complement to an effective mitigation plan.

Section 6 (Temporary Mitigation During Road Construction) provides considerations for reducing impacts from construction activities, including timing construction activities to avoid construction-related impacts, and considerations regarding the use of temporary mitigation measures to minimize impacts during construction.

Section 7 (Monitoring) highlights where there are knowledge gaps about effectiveness of mitigation measures for reducing road impacts on amphibians and reptiles. Study design and monitoring techniques for measuring crossing structure and fencing effectiveness, in an adaptive approach, are discussed.

References

Appendix A (SAR Amphibian and Reptile Habitat Use and Movement) provides a general summary of seasonal habitat use, general movement distances within and between habitat and when this occurs for species at risk amphibians and reptiles in Ontario.

Appendix B (Definitions) provides a glossary of terms used throughout the document.

Appendix C (Crossing Structure Summary from Literature) summarizes the findings from the literature-based review that informed the recommendations throughout the document.

Appendix D (Links and Other Resources) contains a list of useful references, which may be cross-referenced when developing a mitigation plan for SAR amphibians and reptiles.

Appendix E (Sample Tunnel Cost Table (2014) contains the cost per metre for round and box tunnels, as well as special installation considerations.

2 IMPACTS OF ROADS

Globally, there are significantly more amphibian and reptile species at risk than either mammals or birds (IUCN 2010). Amphibians and reptiles were the most negatively affected species groups in a meta-analysis using data from 75 studies that quantitatively measured the relationship between roads or traffic and population size (Rytwinski and Fahrig 2012). The threats of roads to amphibian and reptile populations in Ontario are well-documented, and primarily include direct mortality of animals as well as habitat loss, degradation and fragmentation (e.g., Fahrig et al. 1995, Ashley and Robinson 1996, Findlay and Houlahan 1997, Vos and Chardon 1998, Haxton 2000, MacKinnon et al. 2005, Crowley 2006, Seburn 2007, Eigenbrod et al. 2008a, Eberhardt et al. 2013).

In southern Ontario the network of major roads increased from 7000 km to over 35 000 km from 1935 to 1995 (Fenech et al. 2001). Consequently, there is no point in southern Ontario that is further than 1.5 km from a road (Gunson et al. 2012), and remaining natural habitat is isolated into patches. In addition, human population growth is projected to increase by at least 30% over the next 20 years in the Greater Golden Horseshoe, increasing traffic volume and pressure for road expansions and rehabilitation. With properly planned and implemented road ecology solutions, these impacts can be lessened across Ontario.

Monitoring has documented significant levels of road mortality (van Gelder 1973, Rosen and Lowe 1994, Ashley and Robinson 1996, Aresco 2005) and road barrier effects (Andrews and Gibbons 2005) for amphibians and reptiles. Snakes are particularly vulnerable to road mortality because some species immobilize in response to a passing vehicle (Andrews and Gibbons 2005), or may bask on the roadway for thermoregulation (Andrews et al. 2008). Snakes may also avoid crossing roads altogether, which may disrupt normal behaviours, prevent access to key habitats, and lead to reduced genetic diversity (Shine et al. 2004, Rouse et al. 2011, Robson and Blouin-Demers 2013). Road mortality of more than three adult females per year can lead to declines for some long-lived snake populations such as the Gray Ratsnake (Row et al. 2007).

Modelling studies suggest that populations of many turtle species are declining because of the high rates of annual traffic mortality in some areas (Gibbs and Shriver 2002). Turtles are particularly vulnerable to traffic mortality because their life history strategy is characterized by long life spans, delayed maturity (sometimes taking more than 20 years), and very high adult survivorship. As a result even small, but ongoing, increases in adult mortality can lead to population declines (Congdon et al. 1993) and recovery is slow (Brooks et al. 1991). Females are threatened by traffic mortality because of overland movements to nesting areas (Steen et al. 2012) and populations of some species have been found to be male-biased in wetlands in areas with high road density (Marchand and Litvaitis 2004, Steen and Gibbs 2004).

Amphibians are subject to road mortality when migrating to wetland breeding sites and this can range from 19% (Gibbs and Shriver, 2005) to as high as 98% (Hels and Buchwald, 2001) depending on traffic volumes (Bouchard et al. 2009). Road mortality of just 10% of the adult population can lead to population extinctions (Gibbs and Shriver, 2005), resulting in lower species richness and abundance of individuals near roads (e.g., Carr and Fahrig, 2001; Eigenbrod et al., 2008). In addition, Karraker and Gibbs (2011) found road mortality reduced the life expectancy of Spotted Salamanders (*Ambystoma maculatum*) next to roads, and because younger salamanders lay smaller egg masses this also reduced reproductive output. In addition to road mortality, roads also inhibit movements of amphibians (deMaynadier and Hunter 2000) which can potentially restrict gene flow (Marsh et al. 2008).

3 MITIGATION PLANNING

3.1. Project-Level Impact Avoidance and Mitigation

Project planning and design for roads is a stepwise process that begins with defining the study area for new road construction or other major road rehabilitation projects. Meese et al. (2009) identifies the potential impacts of different types of road projects on wildlife species in general (Table 1). The list of project types is not meant to be exhaustive but rather to include major road improvements and rehabilitations within the scope of this document. There are other impacts to SAR during road operations and maintenance activities such as shoulder grading and paving that are not covered in this document. Projects should be designed to avoid impacts whenever possible, and this is best achieved by locating roads to avoid species at risk habitat altogether. When impacts are unavoidable, appropriate authorizations need to be obtained and the necessary mitigation measures incorporated into the project design.

3.2 Project Planning Considerations and Sources of Information

The information in this document outlines considerations for devising and integrating a mitigation plan into the road planning process in situations when avoidance cannot be achieved. New roads or road improvements present opportunities to lessen the impacts on SAR by integrating mitigation measures. These mitigation measures include specialized tunnels for wildlife passage as well as modifying or retrofitting existing drainage crossings for both water and wildlife use.

Table 1: A summary of project types during road improvement and rehabilitation activities, and potential impacts on amphibians and reptiles (adapted from Meese et al. 2009).

Road Activity	Project Type	Impacts on SAR
Road improvement	New road alignment or extension	Bisection of existing habitat and movement routes; genetic isolation of populations; road mortality; habitat loss
Road improvement	Road widening	Increased traffic volumes and road width increase risk of road mortality (Gibbs and Shriver 2002); habitat loss
Road improvements	Creation of median and installation of shoulder barriers	Increased barriers and road corridor width increase risk of road mortality
Road rehabilitation	Culvert or bridge improvements	May provide opportunities or barriers to movement, depending on resulting permeability of structure (Kintsch and Cramer 2011); risk of destroying turtle nests if work is carried out during the nesting period
Road rehabilitation	Improved road pavements	Increased risk of road mortality and disturbance of animals

Implementation of the mitigation plan begins during the construction phase, and particular attention to design details is important for amphibians and reptiles. It is important for all individuals involved in construction projects, including road crews, to be aware of the mitigation measures to be implemented for the project. Oversight by individuals with the greatest understanding of the mitigation measures is imperative to ensure that effective road mitigation solutions are implemented. For example, a fence with a gap or a fence buried improperly can render the mitigation measures ineffective. Quality assurance and adherence to the mitigation specifications needs to be practiced for each project. Routine quality checks to ensure that implementation of mitigation measures is not misinterpreted during construction, and routine maintenance of mitigation measures following construction is required.

Compiling field and geographic information system (GIS) data can support the development of an effective mitigation plan. Standard data compilations include species occurrence data obtained from the MNRF or other sources; these data are best supplemented with additional road survey data and species presence data collected in the project study area using standard survey techniques (see section 7.2.1). In the case of larger road projects, the duration of the environmental assessment (EA) process can last up to ten years, especially if there are time lapses between the preliminary assessment, detail design and construction. This provides opportunities for formal data collection within the project study area that can inform both mitigation planning and assessments of the effectiveness of mitigation.

Georeferenced data that may be available to support project planning and design may include the following:

- Existing and future land use and ownership maps,
- Habitat mapping (e.g., Southern Ontario Land Resource Information System, or Ecological Land Classifications),
- Species at risk occurrence information (Natural Heritage Information Centre),
- Terrain features,
- Natural Heritage Systems, and
- Existing and future road network and other infrastructure (i.e., existing barriers or passageways, including culverts, median and shoulder barriers, and adjacent railroads, local or private roads).

3.3 Recommended Process

The recommended steps for developing a comprehensive mitigation plan for SAR amphibians and reptiles are outlined in Figure 1 and described below.

Step 1: Identify and prioritize sections of roads that will impede connectivity and/or pose mortality risk to amphibians and reptiles using field data collections and additional landscape information (see section 3.4). Defined road impacts and objectives for mitigation will provide the content and scope of the mitigation plan.

Step 2: Design and determine the location of mitigation measures such as crossing structures and fencing by combining ecological data (e.g., species, habitat and landscape information) with engineering data (e.g., geomorphological, hydrological and topographical). This step requires collaboration between the ecological and engineering design team to ensure fluid integration of information into the mitigation plan. For a road rehabilitation project, there may be opportunities to retrofit existing infrastructure. Through careful evaluation, existing bridges and drainage culverts may be used or adapted for amphibians and reptiles (see section 4.1.4).

Step 3: Consider a multi-species perspective to ensure that a strategy for an individual species does not create unintended impacts for other wildlife species. Supplementary measures such as warning signs at fence ends may complement a multi-species strategy (see section 5).

Step 4: Identify temporary mitigation measures. This could include carrying out road construction when animals are not active, timing construction at particular road sections when animal activity is minimal (see section 6.1) and installing temporary mitigation measures (see section 6.2).

Step 5: Develop a monitoring plan for evaluating the effectiveness of the mitigation. Refer to section 7 for information on developing a complete monitoring plan that addresses the uncertainty with respect to mitigation design.

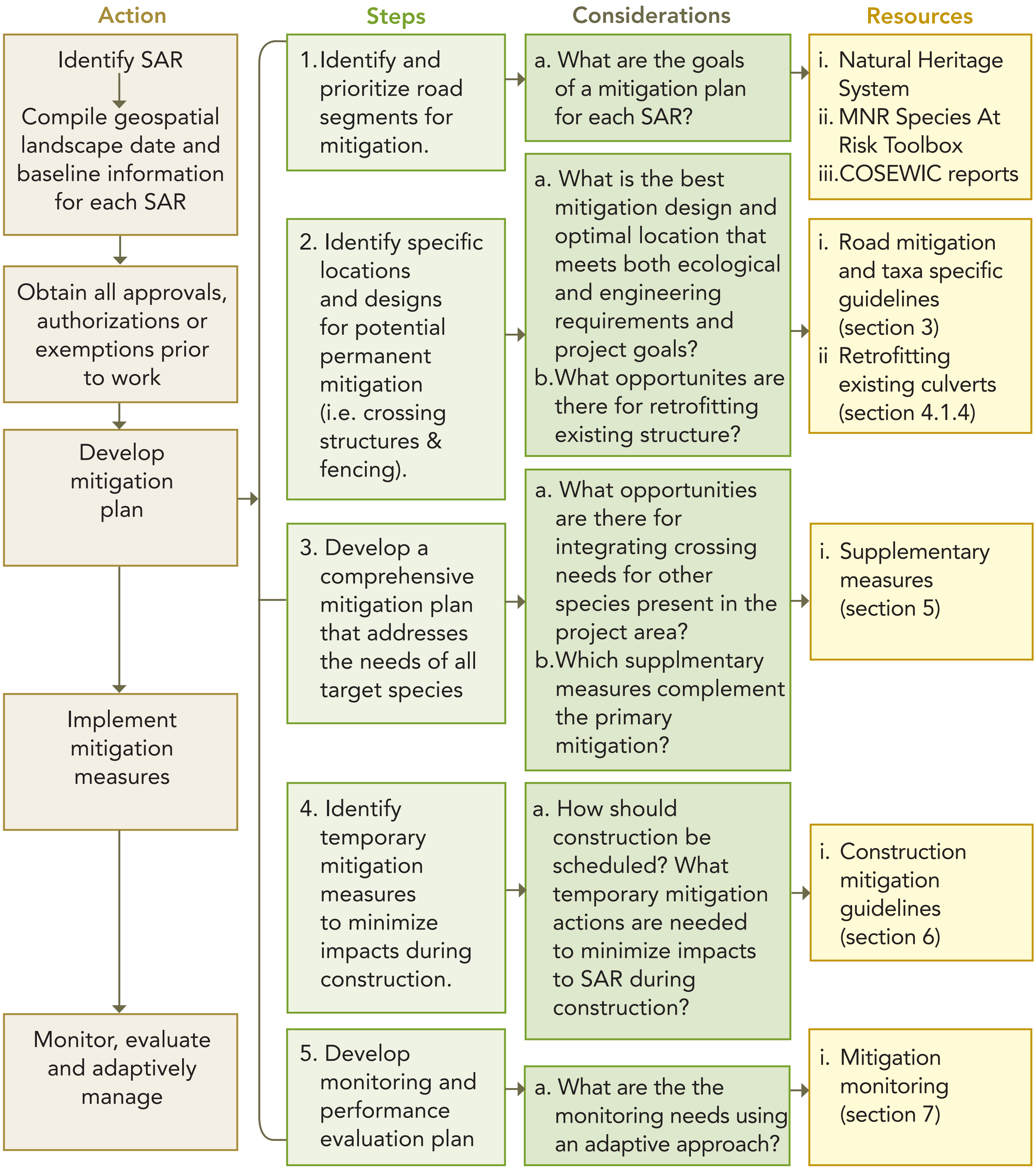

Figure 1: Flowchart summarizing the development of a mitigation plan (individual steps, considerations and supporting resources) within the established authorization processes for major road activities.

3.4 Landscape Considerations

Consideration of the larger landscape context is a vital component of effective mitigation planning for transportation projects because amphibians and reptiles require protection from adverse impacts at both the local and landscape scales (Semlitsch 2008). In other words, animals need to move within habitat patches to access resources (local scale), but also between habitats at different times of year, when habitat becomes inhospitable or to maintain genetic interchange (regional metapopulation scale).

In Ontario, natural heritage systems (NHS) have been developed at a variety of scales. Some are local in scale, while others span multiple jurisdictions, such as the systems in the Greenbelt Plan which span multiple regional municipalities. Natural heritage systems will often include a variety of habitat types including important amphibian and reptile habitat. The natural heritage system identified in the Greenbelt Plan 2005 is an example of a landscape level system approach to cores and linkages for natural heritage conservation. NHS can connect important natural heritage features and areas used by amphibians and reptiles, such as wetlands and upland habitat. Applicable conservation planning efforts, such as NHS, can be refined with taxa specific models for amphibians and reptiles (Gunson et al. 2012) and identified SAR habitat. This information can be used to identify where roads will pose the highest risk for road mortality and isolation of habitat, and should be integrated into early phases of mitigation plan development.

Consideration of the broader landscape context is required because impacts to wildlife are rarely caused by transportation alone (Clevenger 2012). The following landscape level considerations will contribute to the development of a comprehensive mitigation plan:

- Identifying the location of SAR populations and their habitat, including seasonal habitat usage and movement routes (described in Appendix A);
- Identifying connectivity at a regional scale that integrates an ecosystem approach (e.g., natural heritage systems);
- Understanding adjacent land security (i.e., the condition and ownership of land adjacent to a project, and the potential for land-use change); and
- Coordination with other jurisdictions (e.g., municipalities and conservation authorities that own adjacent infrastructure and land).

4 ROAD MITIGATION BMPS

This section provides a summary of BMPs specific to crossing structures and fencing (see sections 4.1 and 4.2). The focus is on the best structural design for all amphibians and reptiles, with species-specific considerations noted when relevant. Following these BMPs, taxa specific (turtles, snakes and lizards, salamanders, frogs and toads; see section 4.1.5) considerations are summarized and supplemented with a rationale section based on a comprehensive literature review. All BMPs are further illustrated and supported with relevant examples, photos, references, and caveats specified throughout. Although SAR amphibians and reptiles found in Ontario are the focus for this document, information also derives from research on related species in other regions for each taxa. This document provides the minimum recommended design specifications (e.g., height, length and width for crossing tunnels and fencing) based on the best available information. All mitigation plans will be subject to trade-offs as presented by engineering, budget, public safety, and site specific constraints.

To date, crossing structures (see section 4.1) combined with fencing (see section 4.2) offer the most effective mitigation of road impacts for amphibians and reptiles by facilitating landscape connectivity and reducing road mortality by excluding animals from the road (Dodd et al. 2004, Aresco 2005). Crossing structures and fencing integrated into road improvement and rehabilitation projects provide the greatest opportunity for creating functional passages, although, in some cases, existing structures may be retrofitted to facilitate wildlife passage (see section 4.1.4). The recommendations herein focus primarily on crossing structure tunnels less than 3 m wide because these structures are typically used for amphibians and reptiles and are available as precast or prefabricated structures. When a tunnel exceeds 25 m in length, a larger structure such as an overpass, multi-span bridge, or viaduct should be considered (see section 4.1.1). Larger structures can be integrated into a multi-species design strategy to increase effectiveness for both large and small species. Multi-species considerations are provided in this document, in addition to approaches for combining mitigation measures to achieve an overall mitigation plan.

4.1. Crossing Structures

Crossing structures can play an integral role in mitigating the impacts of roads on SAR amphibian and reptiles in Ontario. Recommendations regarding the use of different types of crossing structures, design considerations, location and spacing of crossing structures and taxa specific guidelines are provided. The retrofitting of existing drainage culverts and associated considerations are also covered.

In this document, the term tunnel is used to differentiate between crossing structures intended for amphibian and reptile use as opposed to culverts that are designed to transport water under the road. Box tunnels with natural substrate, arch tunnels and round tunnels buried 0.3-0.4 m into the ground are the primary recommended tunnel types because they meet essential criteria, such as providing natural substrate bottoms and a flat crossing surface.

4.1.1 Types of Crossing Structures for Amphibians and Reptilesa

BOX TUNNEL	
• Traditionally used for drainage, but also increasingly being placed and modified specifically for amphibian and reptile passage. • Tunnels up to 3 m wide or high typically made from precast concrete (Photo 1). • Maximum recommended tunnel length of 25 m. • Variations include open-top (Photo 2) or open-grate (Photo 3), open-bottom (Photos 4) or variations of these (Photos 5 - 7). • Straight walls may be perceived by target species as increased openness. • Provide more cross sectional area or openness than round or elliptical culverts with the same width.	
STRUCTURAL VARIATIONS	**OPEN-TOP** • Achieved with slots or grooves along the top (Photo 2), or open-grate set upon two concrete footings (Photo 5). • Allows for more consistent ambient conditions, including moisture, light and temperature (Photo 8). • Possible concerns with influx of road debris, pollutants, or traffic noise. • Installation at a downward incline from middle of road to road edge to allow for drainage and natural cleaning of the tunnel.
	OPEN-BOTTOM • Three-sided structures (Photo 4). • Allows natural substrate conditions to be retained (e.g., streambed or grass floor) (Photo 9).
APPLICATION	• A smaller sized open-top tunnel may increase crossing success or provide microhabitat conditions equivalent to the openness created by larger tunnels. • Open-top grate tunnels have previously been used on low-use cottage roads or roads in protected areas (e.g., Wild Rice Trail, Algonquin Provincial Park, Killbear Provincial Park (Photos 5 and 6)). • For divided highways with two structures that end in the median, tunnels should be connected with a fence (Photo 10). • Headwalls may be used at entrance to shorten length of structure or for a seamless join to a concrete guide wall (Photo 11). • For box culverts, the tunnel floor should be buried with natural substrate and cover objects (Photos 12 and 13). • An open-top in the road shoulder and a closed-top along the road pavement may be more suitable for high volume roads (Photo 7).

BOX TUNNEL	
ENGINEERING CONSIDERATIONS	● Open-top tunnels must be at grade with road surface. ● Design variations may require special design drawings if not prefabricated. ● Size of tunnel must fit within the vertical road profile so that top load is adequate for structural stability.
MAINTENANCE CONSIDERATIONS	● Smaller tunnels will be more difficult to keep clear of debris. ● Open-top tunnels may have to be periodically flushed with water (e.g., with a fire hose) to clean build-up of road pollutants. ● Larger structures allow better maintenance accessibility while having relatively minor cost increases relative to cost of road project. ● Open-top tunnels are thought to interfere with snow removal; however, this has not been the case in other tunnel installations in cold countries and the top of the tunnel wears away with the road surface (see review in Langton 2014). ● Natural substrate and other cover objects must be maintained.
COST (relative material comparison in 2014)	● Costs/m vary from CAN $800.00 for prefabricated open-top ACO tunnel (0.5 m x 0.5 m) to CAN $3,000 for enclosed box tunnel (1.8 m x 1.8 m).

Photo 1. Precast box culvert along highway 69, Ontario. © K. Gunson

Photo 2. Open-top tunnel in Waterton Lakes National Park, Alberta. © K. Gunson

BOX TUNNEL


Photo 3. Open-grate tunnel at Killbear Provincial Park, Ontario. © K. Gunson

Photo 4. Open-bottom tunnel along highway 69, Ontario. © K. Gunson


Photo 5. Open-bottom and open-top grate tunnel at Killbear Provincial Park, Ontario. © K. Gunson

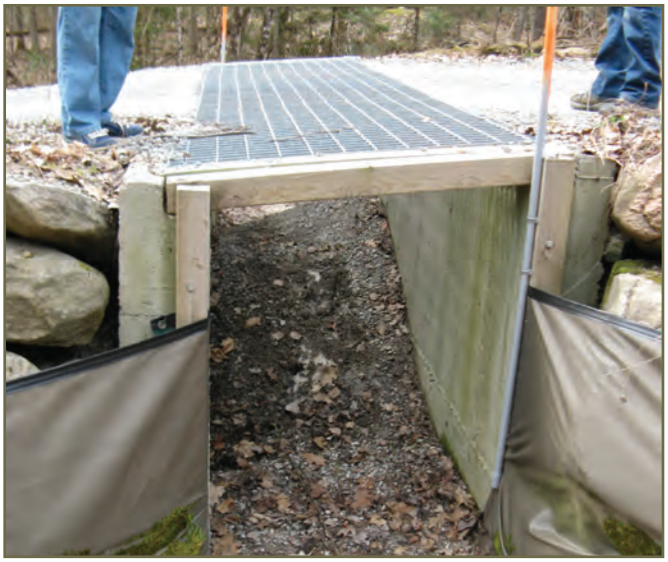
Photo 6 Open-top and open-bottom at Wild Rice Trail, Six Mile Lake. © K. Gunson

BOX TUNNEL

Photo 7. Open- and closed-top variation, Germany. © ACO International

Photo 8. ACO open-top tunnel allowing light into tunnel. © Kari Gunson

Photo 9. Open-bottom box tunnel with natural stream on Trans Canada Highway in Banff National Park, Alberta. © K. Gunson

Photo 10. Box tunnels in median that should be connected with a fence when intended for wildlife passage. © K. Gunson

BOX TUNNEL


Photo 11. Tunnel with headwalls connected to concrete guide fencing in Cuba. © G. Barrett


Photo 12. Adding soil to box tunnel near Ucluelet, B.C. © Barb Beasely


Photo 13. Soil and branches inside tunnel bottom, Ucluelet, B.C. ©Barb Beasley

<table>
<tr><th colspan="2">ARCH/ROUND TUNNEL</th></tr>
<tr><td colspan="2">● Arch tunnels have natural bottoms (Photos 14 and 15) and are recommended for tunnels greater than or equal to 1.5 m diameter (common widths 1.8, 2.4 and 3.0 m).
● Round tunnels work well in aquatic conditions for turtles and semi-aquatic snakes.
● In terrestrial conditions, round tunnels should be filled 0.3-0.4 m with local soil/debris to create a level crossing surface, and it is recommended that the size be increased from the minimum recommendations in section 4.1.5 to compensate for this area that is lost due to infilling.
● Maximum recommended tunnel length of 25 m.
● Terrestrial pathways alongside stream or creek bed are possible with additional structural width.
● Recommended design specifications for arch tunnels are slightly larger than box tunnels to compensate for the loss of openness as a result of tunnel shape.</td></tr>
<tr><td rowspan="2">STRUCTURAL VARIATIONS</td><td>OPEN-TOP
● Slotted open-top (Photos 16 and 17) or vertical skylight risers along the length of the tunnel to provide natural light.</td></tr>
<tr><td>OPEN-BOTTOM
● Achieved by burying round tunnels (0.3 to 0.4 m) to accommodate natural terrestrial floor (Photo 18).</td></tr>
<tr><td>APPLICATION</td><td>● Arch structure may be preassembled and dropped in place or assembled at site (Photo 19).
● Corrugated steel arch or concrete side slabs are placed on footings (Photo 15).</td></tr>
<tr><td>ENGINEERING CONSIDERATIONS</td><td>● Footings required for arch tunnels.
● Buried tunnels may be more suitable when tall footings are required.</td></tr>
<tr><td>MAINTENANCE CONSIDERATIONS</td><td>● Larger structures allow better maintenance accessibility while having minor cost increases relative to cost of road project.
● Natural substrate and other cover objects must be maintained.</td></tr>
<tr><td>COST (relative material comparison in 2014)</td><td>● Costs/m vary from CAN $145.00 for corrugated steel pipe (CSP) (1.2 m) to CAN $990.00 for arch (0.6 m rise; 1.22 m span).
● Costs/m vary from CAN $500.00 for CSP (3.0 m) to $1500.00 for arch (1.45 m rise; 2.99 m span).</td></tr>
</table>

ARCH/ROUND TUNNEL

Photo 14. Arched tunnel allowing natural stream crossing. © D. Seburn

Photo 15. Aluminum arch culvert on metal footings. © K. Williams

Photo 16. Pipe culvert with slotted top installed for Timber Rattlesnakes in Illinois, U.S. © S. Ballard

Photo 17. Zoom-in of open-top pipe culvert at road for Timber Rattlesnakes in Illinois, U.S. © S. Ballard

Photo 18. Buried plastic round culvert allowing terrestrial flat floor in Sweden © K. Gunson

Photo 19. Arch culvert preassembled off site © K. Williams

<table>
<tr><th colspan="2">LARGE UNDERPASS OR WILDLIFE OVERPASS</th></tr>
<tr><td colspan="2">• Larger multi-species crossing structures greater than 3 m wide such as tunnels (Photo 20) and bridges, viaducts or overpasses (Photo 21) that are generally not prefabricated or precast.
• Possible to maintain natural landscape if road is tunneled, (e.g., Herb Gray Parkway in Windsor) or elevated (e.g., viaduct).
• Consider when tunnel length will exceed 25 m.
• Integrated as a multi-species strategy for both large and smaller animals.</td></tr>
<tr><td rowspan="2">STRUCTURAL VARIATIONS</td><td>UNDERPASS
• Designs include crossing structures that are below grade (e.g., tunnel, single or multi-span bridge, arches, and viaducts).
• Larger multi-span bridge, arches and viaducts have opportunity to maintain natural ecosystem and physical properties.
Allows for the integration of dry pathways at creek and river crossings.
• Two structures that open in median allow more openness (Photo 22).</td></tr>
<tr><td>OVERPASS
• Design includes bridge deck spanning over road.
• Requires natural landscape planting strategy and drainage system on top of structure.
• Slope on approach ramps should be minimized for greatest visibility.
• Overpass width has varied from 20 m to > 70 m.</td></tr>
<tr><td>APPLICATION</td><td>• Large structures provide greater opportunity to provide cover objects such as flat rocks, vegetated mounds composed of branches and logs and covered with sod, or rock piles (Photos 23 and 24).
• Design enhancements for amphibians and reptiles include small ponds as ‘stepping-stones’ along or through the length of a structure. Natural or artificial substrate may be used to retain pond water or natural rainfall (Van der Grift et al. 2003; Figure 2).
• For multi-use structures, wildlife and human use should be separated or human use should be mitigated. For example, the Rt. Hon. Herb Gray Parkway, which leads to the international crossing between Ontario and Michigan, incorporates a crossing structure for Butler’s Gartersnake and Eastern Foxsnake into the multi-use trail system to minimize disturbance impacts from recreational trail users.
• Multi-species fencing designs should be used. For example, the Highway 69 fencing combines ¼ inch mesh with 2.4 m high, large animal mesh fence (Photo 25).</td></tr>
</table>

LARGE UNDERPASS OR WILDLIFE OVERPASS	
ENGINEERING CONSIDERATIONS	- Overpass decks can integrate natural footings such as rock cliffs (Photo 26). - Engineering measurements and road design will determine best options for large crossing structure type in the road.
MAINTENANCE CONSIDERATIONS	- Require maintenance checks for initial establishment of vegetation on overpass structures; may require irrigation for pools and vegetation.
COST (relative material comparison in 2014)	- Approximately CAN $7,800 for large concrete box culvert (2.8 m x 3.3 m, Appendix E); range from CAN $2-4 million for installation, design, and materials of wildlife overpass.

LARGE UNDERPASS OR WILDLIFE OVERPASS

Photo 20. 3.4 x 2.4 m concrete box culvert connecting wetland habitat used by turtles on highway 69. © K. Gunson

Photo 21. 30 m wide overpass installed near Sudbury on highway 69. © K. Gunson

LARGE UNDERPASS OR WILDLIFE OVERPASS

Photo 22. 3.4 m x 2.4 m tunnel on Highway 69. © K. Gunson

Photo 23. Brush piles on top of overpass on highway 69. © K. Gunson

Photo 24. Rock and wood piles on top of overpass in Brandenburg, Germany. © K. Gunson

Photo 25. Small animal fence attached to the base of large animal barrier fence. © K. Gunson

Photo 26. Wildlife overpass on highway 69 showing rock footing K. Gunson.

LARGE UNDERPASS OR WILDLIFE OVERPASS

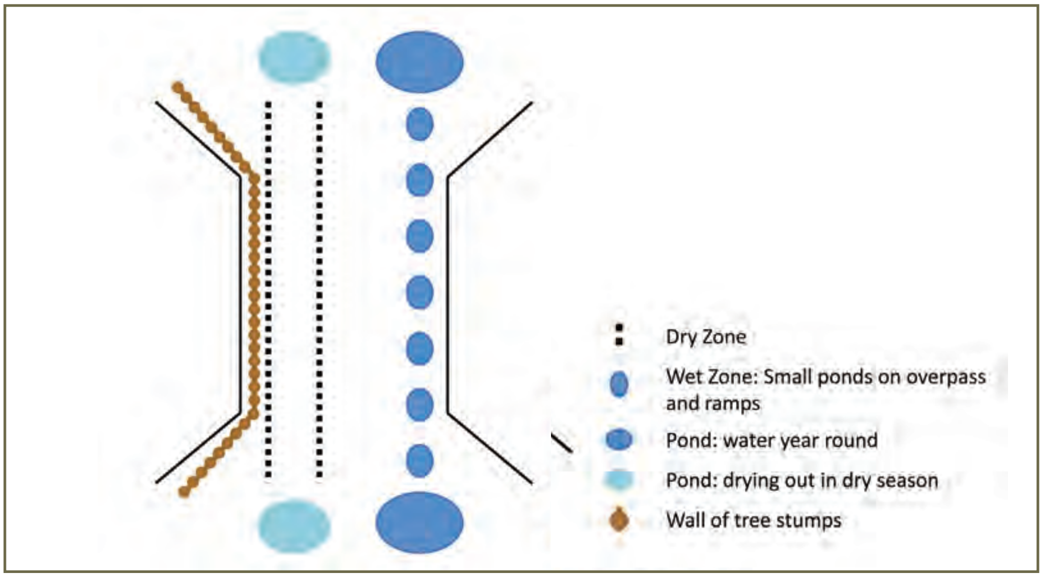

Figure 2: Example of a series of pools created along one side of an overpass (50 m long x 65 m wide). Amphibian passage was at least 1.5 times higher through the wetland zone than the dry zone. Adapted from van der Grift et al. 2009

4.1.2 Crossing Structure Design

Design of effective crossing structures must account for the ecology, behaviour and movement patterns of amphibians and reptiles. For example, amphibians and reptiles possess a number of physiological vulnerabilities that require particular microhabitat conditions when using tunnels to cross roads (Andrews et al. 2008). High skin permeability and vulnerability to water loss necessitates warm and damp conditions in tunnels for amphibians. These microhabitat specializations require additional design modifications (e.g., natural substrate, cover) in and near crossing structures. General recommendations based on the literature and expert opinion for tunnel design (<3 m wide), to facilitate amphibian and reptile use, are outlined below:

Design Specifications

- Refer to minimum design specifications and tunnel types summarized in structural (see section 4.1.1) and taxa recommendations (see section 4.1.5) for each species group; where existing culverts are being replaced, upsize tunnels to at least minimum design specifications and tunnel type.
- Tunnels should be as open as possible to maximize air flow and light inside the tunnel. This may be achieved by designing tunnels with larger (typically wider) openings, using two structures connected with fencing when a median is present (Photo 22), or with an open-top or partial open-top tunnel (Photos 2 and 7).
- Artificial and ambient lighting inside a culvert has been shown to encourage tunnel use by turtles (Yorks et al. 2011) and entry by salamanders (Jackson et al. 2006).
- Generally, larger tunnel dimensions are more effective for amphibians and reptiles. For example, Smith (2003) showed amphibians and reptiles in Florida used tunnels more often that were at least 1.5 m wide and 0.6 m high as compared to smaller tunnels. See section 4.1.5 for additional information on tunnel dimensions for each taxa group.

- In general, the recommended tunnel length for SAR amphibians and reptiles is less than 25 m. There is reduced crossing success as tunnels get longer (e.g.,Yorks et al. 2011) and other jurisdictions suggest tunnels are less effective beyond 20-25 m in length (e.g., British Columbia Ministry of Forests, Lands and Natural Resource Operations 2004).
- In locations where tunnels will be longer than 25 m, consider the following:
- A large underpass (> 3 m) or overpass
- Elevating or tunneling the road
- Using two separate, shorter tunnels under each of the opposing traffic lanes with head walls; ensure the tunnels are connected with appropriate fencing in the median (Photo 22).
- On divided highways, crossing structures should never end in the center median (Photo 27) unless they are connected to other structures through fencing.
- When possible include skylights, or fenced gaps at medians and shoulders (Photos 28 and 29).

Microhabitat and Cover:

- All terrestrial crossings should have a natural substrate that consists of soil, sand, branches and other natural materials on the tunnel floor to increase structure use (Photos 13 and 35). The use of local soil in crossing structures is widely recommended for amphibians (e.g., Jackson 2003, Smith 2003, Schmidt and Zumbach 2008, Amphibian and Reptile Conservation 2009, Beasley 2013). For example, salamanders will cross through tunnels with or without natural substrate, but fewer individuals cross through bare concrete tunnels (Patrick et al. 2010). Considerations for substrates:
- Soils should be from the local area
- Soils that consist of large stones should be avoided
- Sediment baffles such as open plate may be used to 'hold' natural substrate in place (Photo 36).
- Cover objects (flat rocks and/or woody debris) should be placed in larger tunnels along the sides to provide shelter and escape from predators. These cover objects should not block sightlines or impede individuals from crossing straight through the tunnel. Sufficient cover objects (1 large or 2-3 small per 10 m^2) should be present near the entrances to all terrestrial crossing structures to provide shelter and cover. Cover objects should be used for all crossing structures to encourage multi-species use. Retain as much natural vegetation as possible during construction; where needed, additional planting should occur after construction.

Other Design Considerations:

- Terrestrial tunnels should be as level as possible for the entire length of the structure. One exception to this is that open-top tunnels should be installed with the highest point in the middle of the tunnel to allow for drainage and natural cleaning of the tunnel.
- Tunnel entrance bottoms should be at ground-level so animals do not need to 'step up' or 'step down' to enter the structure (Photo 30).
- At terrestrial tunnels, water should be diverted away from the entrances with drainage ditches or sloped excavation (Photo 31).
- If culverts are intended for drainage, or tunnels are large enough, a dry bench placed above the water mark can be integrated into the tunnel, in which case the bench must access dry ground at both entrances to be effective (Photo 32).
- When new highway alignments will bisect provincially significant wetlands and SAR habitat, consider elevating or tunneling the

road (e.g., Rt. Hon. Herb Gray Parkway road mitigation project for Butler's Gartersnake and Eastern Foxsnake).

- When arch tunnels are used at road-stream crossings, terrestrial pathways can be created along the stream by using wider tunnels (Photo 14). This design can better accommodate seasonal high water and flooding events (Lesbarrères and Fahrig 2012).
- When dealing with multi-species issues and variable site conditions, a mixed array of structure types and sizes should be provided along the site (see section 4.1). Structural diversity can compensate for landscape variations, such as land use change, and can also provide an experimental setting to test species-specific crossing preferences (see section 7).

Photo 27. Drainage box tunnel left open in median along highway 69 © K. Gunson

Photo 28. Open grate skylight in median on Terry Fox Extension, Ottawa, Ontario. © D. Seburn

Photo 29. Zoom-in of skylight in median on Terry Fox Extension, Ottawa, Ontario. © D. Seburn

- Aquatic crossing structures should never be fully submerged (e.g., Caverhill et. al. 2011, Photo 37).
- Water in aquatic tunnels should be standing or have low flow rates.
- Many crossing structures are no longer effective due to a lack of maintenance (Iuell et al. 2003). Regular maintenance is required for long-term effectiveness of all tunnels to ensure the microhabitat is intact, passageways are clear of debris, and that suitable substrate remains.

Photo 30. Earth excavated to allow at grade entrance to tunnel. © D. Filip

Photo 31. Water accumulation at tunnel entrance. © K. Gunson

Photo 32. Dry bench in drainage culvert for small animals, could be modified for snakes. © K. Foresman

BOX 1. OPENNESS OR OPENNESS RATIO

Openness Ratio (OR) was first conceived by Reed et al. (1979) as a threshold measure for comparing the relative openness of box culverts for use by Mule Deer (*Odocoileus hemionus*), given their preference for a clear line of site through a structure. This measure has since been extrapolated beyond this original use and applied to a variety of species and structure shapes; see review of OR application to small mammals, deer, and amphibians and reptiles in Gartner Lee and Ecoplans (2009). The ratio is defined as the cross-sectional area of a structure (square metres) divided by the length of the tunnel (metres) ([rise x span] / length). The intent of OR is to provide a measure of the tunnel effect of a structure, which may influence use by various wildlife species.

BOX 1. OPENNESS OR OPENNESS RATIO

The use of OR as a sole measure to inform road mitigation design should be used with caution, especially for amphibians and reptiles, because of the following:

- Cross sectional definition needs to be modified to account for shape.
- OR does not account for the effect that a structure's width versus its rise has on openness and whether this influences wildlife use (Jacobson 2007). For example, once a minimum height has been achieved, wider rather than taller structures may be recommended to enhance openness for some wildlife, such as turtles (Smith 2003) and elk (Kintsch and Cramer 2011).
- Tunnel effectiveness may be improved beyond manipulating structural dimensions by providing natural cover, substrate and light via open-tops into the tunnel design (Woltz et al. 2008, Yorks et al. 2012).
- Openness may be less important for tunnel use when animals become more familiar with new structures then when encountering a structure for the first time (Clevenger et al. 2002).

4.1.3 Crossing Structure Location and Spacing

Species that need to move between different habitats are also particularly susceptible to road mortality and landscape fragmentation by roads. Amphibian and reptile species need to move among breeding sites, summer foraging areas and overwintering sites during their active seasons. When these habitats are not adjacent, animals must move up to several kilometers to find necessary habitat. In areas with high road density, it is likely these movements will cross roads, putting animals at higher risk of road mortality (Gibbs and Shriver 2002, Beaudry et al. 2008).

An effective crossing structure should function as a movement corridor connecting suitable habitat on both sides of a road. Tunnels and fencing are best located where SAR movement paths cross existing and planned roads as determined from field surveys or spatial analyses (see examples in Gunson et al. 2012, Patrick et al. 2012). Examples of predictable movements include an annual spring migration of amphibians from upland forest to breeding ponds (Patrick et al. 2010, Faggyas and Puky 2012, Pagnucco et al. 2012) or an annual snake migration to and from overwintering hibernaculum (e.g., Fortney et al. 2012). Turtles are likely to interact with roads during terrestrial nesting migrations and inter-wetland movements (Gunson et al. 2012).

Amphibians and reptiles have specific microhabitat needs, smaller home ranges and restricted movement capabilities relative to larger fauna (Jochimsen et al. 2004). The following considerations are outlined below to assist with siting the optimal placement and number of crossing structures along a road improvement or rehabilitation project:

- In general, crossing structures should be considered when the road bisects habitat used by the target species (photo 33), when the road is between seasonal habitat used by a species (e.g., wetland and upland forested habitat for Jefferson Salamanders), or when the road bisects a movement corridor (e.g., riparian pathway, hedgerow, or ridge valley). Appendix A provides a general summary of movement distances, home range areas, and habitat used by each species, but more detailed species-specific information should be used to inform mitigation plans.

- When roads bisect large expanses of continuous habitat (e.g., forest), crossing structures should generally be spaced 300 m apart for small animals depending on species, budget, and site-specific engineering and ecological considerations (Carsignol 2005). This is generally applicable to most turtles and snakes; however, Schmidt and Zumbach (2008) recommend that tunnels be spaced no more than 50 m apart for amphibians.
- Species with smaller home ranges usually require crossing structures to be placed closer together and the numbers of crossing structures will depend upon the road length where animals are interacting with the road (preferably measured with road encounter data, see section 7.2.1). The approximate distance between crossing structures can be determined based on the average home range size of the species in question. Another, similar approach is to use the square root of the home range area (Bissonette and Adair 2008).
- Man-made features (e.g., ditches, retaining walls) in the right-of-way may influence species movement and access to crossing structures (Gartner Lee and Ecoplans 2009).
- Likely crossing locations for turtle and amphibian SAR are where aquatic features and wetlands intersect with roads (Photo 34).
- Hydraulic and engineering information should be used to determine the amount of water and flow through the tunnel and whether this is appropriate for the target species. Refer to taxa specific BMPs for aquatic and terrestrial crossing types in section 4.1.5, in addition to site-specific conditions measured in the field.
- Vertical alignment and location of the tunnel should be based on environmental conditions at the site, such as water level. For example, terrestrial tunnels should be above high water marks defined by wetlands and riparian corridors.
- Integrate crossing structures with the natural landscape. For example, take advantage of valleys for crossings under roads and incorporating fencing into natural landscape features, such as existing steep rock faces.

Photo 33. Road bisecting open water wetlands, Victoria Street, Whitby, Ontario. © K. Gunson.

Photo 34. Where drainage meets road would be likely location for tunnel for SAR amphibians and reptiles. © K. Gunson.

Photo 35. Turtle using open-grate tunnel with natural substrate at bottom© A. Mui

Photo 36. Tunnel structure with sediment baffles at bottom © B. Steinberg

4.1.4 Retrofitting Existing Drainage Culverts

Historically, culverts have been used to convey water under roads, and these structures have also been used by some species of amphibians and reptiles (e.g., Caverhill et al. 2011). Road improvement and rehabilitation projects provide opportunities to retrofit or enhance existing drainage culverts to facilitate use by amphibians and reptiles. When replacing a culvert, consider implementing a tunnel-fencing system with specifications for the target species (see section 4.1.5). In some cases, existing drainage culverts may already be sited and designed correctly for use by the target species and may only require guide fencing to facilitate crossing use and reduce road mortality (Caverhill et al. 2011). A formal evaluation of existing wildlife crossing structures for wildlife passage for the intended species is recommended (Kintsch and Cramer 2011, Central Lake Ontario Conservation Authority 2015).

Photo 37. Large 1.8 m drainage culvert partially filled with standing water allows light into tunnel, Highway 24, Aurora, Ontario. © K. Gunson

4.1.5 Taxa-specific Recommendations

In addition to the general design considerations for reptiles and amphibians that are outlined in section 4.1.2, the following are specific recommendations that are unique to each taxa group. The following sections focus on the threatened and endangered SAR in each taxa group; however, the information is generally applicable to all other reptile and amphibian species in Ontario. In general, these recommendations make the assumption that as tunnels get longer an increase in width is more important than an increase in height (see Box 1).

The salamander section only addresses the Jefferson Salamander. The Jefferson Salamander is the only SAR salamander that is likely to be affected by road development in Ontario. In Ontario, the Small-mouthed Salamander and the two Dusky Salamanders have extremely small distributions (only a few isolated sites) and are unlikely to be affected by road construction. To date, the Fowler's Toad is the only endangered or threatened frog or toad species in Ontario, so the information in this section is specific to that species.

SPECIFICATIONS FOR TURTLES

Structure type and minimum size based on tunnel length

Tunnel Length	Box Tunnel (w x h)	Arch Tunnel (w x h)	Round Tunnel (diameter)	Overpass
15 m	1.5 x 1.0 m	1.8 x 0.9 m	1.5 m	NA
15-25 m	1.8 x 1.0 m	2.0 x 1.0 m	1.8 m	NA
> 25 m	NA	NA	NA	Yes

ADDITIONAL DESIGN CONSIDERATIONS

- Terrestrial and aquatic structures are suitable for most turtle species; terrestrial crossing structures are not appropriate for Eastern Musk Turtle or the Spiny Softshell, which are highly aquatic and rarely move over terrestrial areas.
- Open and closed top tunnels have been used by turtles; open-top tunnels may increase crossing success.

RATIONALE

- Turtles have used a variety of crossing structures under roads (e.g., Dodd et al. 2004, Aresco 2005, Caverhill et al. 2011)
- Several studies have demonstrated relatively high use of large (>1.5 m width) crossing structures by turtles:
  - A drainage culvert 1.8 m in diameter in Ontario that was approximately half full of water (Caverhill et al. 2011) was used regularly by Blanding's Turtles and was also used by an unknown number of Snapping Turtles
  - Multiple Spotted Turtles were confirmed to cross through a tunnel 1.8 x 1.8 m (Kaye et al. 2005)
  - Aresco (2005) documented over 200 turtle crossings through a 3.5 m diameter drainage culvert

SPECIFICATIONS FOR TURTLES

RATIONALE

  - Wood Turtles continued to use a stream that passed through a culvert that was 3 m in diameter and 26 m long (Parren 2013).
- In a simulated tunnel experiment, more turtles crossed through a tunnel that let in at least 75% ambient light through the top (Yorks et al. 2011).
- Turtles will cross through tunnels 25 m long (Caverhill et al. 2011), although crossing success may be lower as length increases (Yorks et al. 2011).
- Turtles have used closed-top tunnels (e.g., Dodd et al. 2004, Aresco 2005, Kaye et al. 2005, Caverhill et al. 2011) and Wood Turtles (Photo 54) and Snapping Turtles (Whitelock 2014) have crossed through open-top tunnels in Ontario).
- Substrate type may not be as important in terrestrial tunnels for turtles as with other taxa. Blanding's and Spotted Turtles have been documented to cross through tunnels with natural substrates (e.g., Kaye et al. 2005, Caverhill et al. 2011), but in a simulated crossing structure experiment, Painted and Snapping Turtles did not demonstrate a substrate preference (Woltz et al. 2008).

Photo 54. Wood Turtle using open-grate tunnel © A. Mui

SNAKE AND LIZARD SPECIFICATIONS

Structure type and minimum size based on tunnel length

Tunnel Length	Box Tunnel (w x h)	Arch/Round Tunnel (w x h)	Round Tunnel (diameter)	Overpass
15 m	1.0 x 1.0 m	1.5 x 0.75 m	1.0 m	NA
15-25 m	1.5 x 1.0 m	1.8 x 0.9 m	1.5 m	NA
> 25 m	NA	NA	NA	Yes

ADDITIONAL DESIGN CONSIDERATIONS

- Open and closed-top tunnels have been used by snakes; open-top tunnels may increase crossing success.
- Open-top tunnels should not be used for lizards because they may be able to crawl onto the road surface.
- Aquatic tunnels will likely be used by highly aquatic SAR, such as Eastern Ribbonsnake, Queensnake, and Lake Erie Watersnake; however, they are unlikely to be used by other snake and lizard SAR and are not recommended for those species.

RATIONALE

- Snakes (e.g., Taylor and Goldingay 2003, Laidig and Golden 2004, Roberts 2010, Eads 2013) and lizards (e.g., Taylor and Goldingay 2003, Painter and Ingraldi 2007, Arizona Game and Fish 2010) have used a variety of crossing structures under roads. However, compared to other taxa, there is less certainty about crossing structure design preference for snakes and lizards, particularly for the species that occur in Ontario.
- Snakes have crossed through tunnels as small as 0.25 m in diameter (Roberts 2010), but tunnels 1.0 m in diameter had a greater crossing success than smaller tunnels for the Eastern Gartersnake and Eastern Ribbonsnake in an experimental set-up (Eads 2013).
- Both closed-top (Taylor and Goldingay 2003, Laidig and Golden 2004, Roberts 2010, Eads 2013) and open-top (Pagnucco et al. 2011, M. Colley pers. comm.) crossing structures have been used by snakes.
- Open-bottom box tunnels with cross-sectional dimensions of 1.0 x 1.0 m in Killbear Provincial Park were used by many (11) Massasaugas and 2 Eastern Foxsnakes in 2014 (M. Colley pers. comm.).
- Timber Rattlesnakes have crossed through concrete-bottom structures without natural substrate bottoms (Laidig and Golden 2004), but natural substrate or habitat conditions may enhance use (Laidig and Golden 2004; M. Colley pers. comm.).

SALAMANDER SPECIFICATIONS

Structure type and minimum size based on tunnel length

Tunnel Length	Box Tunnel (w x h)	Arch Tunnel (w x h)	Round Tunnel (diameter)	Overpass
15 m	1.0 x 1.0 m	1.5 x 0.75 m	1.0 m	NA
15-25 m	1.5 x 1.0 m	1.8 x 0.9 m	1.5 m	NA
> 25 m	NA	NA	NA	Yes

ADDITIONAL DESIGN CONSIDERATIONS

- Terrestrial tunnels should be used for salamanders; high moisture content and even small pools of standing water may be beneficial but the tunnel should not be flooded with water.
- Open or closed-top tunnels can be effective. Open-top tunnels allow more light into the tunnel and may increase moisture levels; the latter being important in longer tunnels where salamanders are at risk of desiccation. Consequently, open-top tunnels may offer suitable conditions for salamanders even when the dimensions are smaller than those listed above.
- Despite the potential advantages of open-top tunnels, they may result in higher levels of road salt and other pollutants in the tunnel, but these may be washed away with storm events.
- Soils and leaf litter substrates should be used as opposed to larger gravel or stone substrates.
- Mole salamanders make focused migrations to breeding ponds, and it is important to have multiple tunnels where migration paths cross roads. Tunnels for salamanders should not be more than 50 m apart (Schmidt and Zumbach 2008) as salamanders will not follow a fence for long distances (e.g. Pagnucco et al. 2012).

RATIONALE

- The best size of tunnel to encourage crossing by Jefferson Salamanders is not known, although there have been studies of crossing structures used by other salamanders in the same family (mole salamanders), which share similar life history traits.
- All documented use of tunnels by salamanders has been in terrestrial tunnels.
- Both closed-top (Patrick et al. 2010, Beasley 2013, Bain 2014) and open-top (Jackson and Tyning 1989, Allaback and Laabs 2002, Pagnucco et al. 2012) crossing structures have been used by other mole salamanders.
- Rectangular box culverts with local damp soil conditions are recommended for amphibians (see Jackson 2003, Smith 2003, Schmidt and Zumbach 2008, Amphibian and Reptile Conservation 2009, Beasley 2013).

SALAMANDER SPECIFICATIONS

RATIONALE

- Other mole salamanders have crossed through round tunnels as small as 0.25 m in diameter (Bain 2014) and 0.2 m wide; however, salamanders demonstrate hesitancy entering into small tunnels (Jackson 1996) and the percentage of salamanders that successfully cross through small tunnels may be low (e.g., Allaback and Laabs 2002, Pagnucco et al. 2012). Larger tunnels are required to ensure there is space for natural substrate and cover objects. In general, tunnels for amphibians are recommended to be at least 1 x 1 m in size (Schmidt and Zumbach 2008).
- Salamanders will cross through tunnels with or without natural substrate, but fewer individuals cross through bare concrete tunnels (Patrick et al. 2010). Natural soil substrate will retain moisture longer, lessening the risk of salamanders dehydrating or not entering structures.

FROG AND TOAD SPECIFICATIONS

Structure type and minimum size based on tunnel length

Tunnel Length	Box Tunnel (w x h)	Arch Tunnel (w x h)	Round Tunnel (diameter)	Overpass
15 m	1.0 x 1.0 m	1.5 x 0.75 m	1.0 m	NA
15-25 m	1.5 x 1.0 m	1.8 x 0.9 m	1.5 m	NA
> 25 m	NA	NA	NA	Yes

ADDITIONAL DESIGN CONSIDERATIONS

- Terrestrial tunnels should be used for frogs and toads; high moisture content and even small pools of standing water may be beneficial but the tunnel should not be flooded with water.
- Open or closed-top tunnels may be used.
- Open-top tunnels will provide moisture and air flow in the tunnel; however road salt or other pollutants may also enter into the tunnel but are most likely washed away during storm events.
- Soils and leaf litter substrates should be used as opposed to larger gravel or stone substrates.

RATIONALE

- There is no documented information available for crossing structure preferences for Fowler's Toads, however there is literature available for other species of toads and amphibians. Frogs and toads have used a wide variety of crossing structures under roads (reviewed in Schmidt and Zumbach 2008; Puky et al. 2013).
- Wide crossing surfaces with local soil are recommended for amphibians (e.g., Jackson 2003, Smith 2003, Schmidt and Zumbach 2008, Amphibian and Reptile Conservation 2009, Beasley 2013).

FROG AND TOAD SPECIFICATIONS

RATIONALE

- Although toads have been documented to use tunnels <1.0 m wide (e.g., Lesbarrères et al. 2004, Ottburg and van der Grift 2013, Puky et al. 2013, Wind 2014), larger tunnels tend to be more effective (e.g., Puky et al. 2013). There was very high toad crossing rates through tunnels 1.8 m wide (Biolinx (2013).
- Guidelines for road crossing structures in England have been developed for the Common Toad (*Bufo bufo*). These guidelines recommend a rectangular crossing structure at least 1.0 x 0.75 m (w x h) for tunnels up to 20 m long and 1.5 x 1.0 m (w x h) for longer tunnels (Amphibian and Reptile Conservation 2009).
- Both closed-top (Biolinx 2013, Puky et al. 2013, Wind 2014) and open-top (Pagnucco et al. 2012, Ottburg and van der Grift 2013) crossing structures have been used successfully by other toads.

4.2 Fencing for Reptile and Amphibian Crossings

Fencing in conjunction with crossing structures serves two purposes: 1) directing animals towards structure entrances and 2) providing a barrier to exclude animals from the road. Fencing can be used with crossing structures or as a stand-alone measure to prevent mortality along roads where connectivity is not a concern; this may include situations such as when suitable habitat is adjacent to, but not bisected by the road, or where animals are unlikely to cross successfully due to high traffic volumes (Jackson et al. 2015).

The following BMPs are divided into fencing design, placement, and maintenance considerations and are applicable to all amphibian and reptile SAR. For additional best practices for amphibian and reptile exclusion fencing, refer to Reptile and Amphibian Exclusion Fencing: Best Practices (OMNR 2013).

4.2.1 Fence Design

The primary objective of a fence design is to minimize fence breaches because animals that get through a fence can be trapped on the road and killed (e.g., Wilson and Topham 2009). Therefore these BMPs focus on providing recommendations for designing and installing a gap-free, permanent fence. Permanent fencing may have higher initial costs; however, when ongoing maintenance of temporary fencing is considered, permanent fences are less expensive in the long-run. A number of projects have experimented with fencing effectiveness for amphibians and reptiles (e.g., Woltz et al. 2008; Langen 2011; Smith and Noss 2011), and it is important to recognize that new cost-effective designs are continually being engineered and tested, and are strongly encouraged.

Fencing design should consist of a solid durable framework (stakes, posts, and sheeting) that is able to withstand weight and impact from snow removal and effectively exclude the target species. Recommended durable fencing materials include hardware cloth, chain link fencing, concrete barriers, and heavy-duty plastic fencing designed for wildlife (Table 2; Photos 38-44). Light-duty geotextile fence (lifespan up to 1 year; Photo 45), heavy-duty geotextile fence (2-3 years), or wood lath snow fencing (< 3 years), are not recommend for long-term use.

Standard chain link large animal fencing (e.g., 2.5 m high wildlife exclusion fencing with 4" mesh) does not work for many amphibians and reptiles as individuals can pass through the large mesh holes. In locations requiring guide or barrier fencing for both large animals and amphibians and reptiles, additional fencing material, such as hardware cloth at the appropriate height, can be attached to the base of the large animal fencing (Photo 25). When more than one species is targeted for mitigation, fencing height should be the tallest height recommended for all target species.

Table 2: **Summary of fence materials that have been used for long-term projects to exclude amphibians and reptiles from the road and/or guide animals to tunnels. For additional fencing specifications, refer to OMNR 2013.**

Fence Type	Benefits	Drawbacks	Considerations
Hardware mesh cloth (Photos 38 and 39)	Relatively durable; relatively low maintenance; allows drainage; available in rolls.	Susceptible to rust in seasonally wet areas unless heavy gauge wire used.	Use ¼" or smaller gauge to reduce the risk of small snakes getting stuck; requires attachment to post at regular intervals to avoid collapse.
Chain link fence (Photo 40)	Very durable; low maintenance; allows drainage; available in rolls.	Mesh size typically larger than species specifications.	Use buried hardware cloth with recommended mesh at the base of the fence to provide multi-species use for large and small animals (Photo 25); lip extension may increase effectiveness for some species (Photos 39 and 40).
Concrete (Photo 41), corrugated steel (Photo 43), aluminum sheeting (Photo 44), or vinyl walls	Very durable; low maintenance; vertical smooth surfaces prevent climbing.	Inhibits drainage and may cause pooling.	Aluminum sheeting and vinyl walls are less durable than concrete; corrugated steel can be obtained from corrugated steel pipes cut in half and are curved providing lip extension.

Fence Type	Benefits	Drawbacks	Considerations
Prefabricated plastic sheeting fence (Photo 42)	Very durable designs available, e.g., ACO fencing, available in 1 metre sections OR Animex fencing, available in rolls depending on thickness.	Inhibits drainage and may cause pooling.	Back-fill at road-side of fence to provide escape route for animals (Photo 49); fencing best suited for flat dirt terrain such as in drainage ditch (Photo 42); 1 m sections may not be suitable for long fences greater than 1 km.


Photo 38. Animex plastic sheeting made from post-consumer products ©K. Gunson


Photo 39. Hardwire cloth with ¼ inch mesh, wood frame, and top lip © K.Gunson


Photo 40. Chain link guide fencing and lip extension, Terry Fox Extension, Ottawa, Ontario © D. Seburn.


Photo 41. Concrete wall in Aurora, Ontario © K. Gunson

Photo 42. ACO fencing on highway near, Oliver, B.C. © R. Guse

Photo 43. Angled fence for salamanders at Waterton Lakes National Park© K. Gunson

Photo 44. Example of aluminum sheet fencing © K. Gunson

Photo 45. Fence end U design to deter animals following fence line from entering roadway in Haliburton County © K. Gunson

General considerations for fence design are as follows (see Figure 4 for further illustration):

- Steel posts will not break with snow load.
- Posts that are closer together (e.g., between 2-3 metres) will prevent fence sag and collapse during severe weather events and snow removal along roads.
- Stakes or posts should be placed along the road-side of the fence to deter climbing and be buried 30 cm into the ground (OMNR 2013).
- Use of materials that allow drainage at wet sites to avoid pooling at or near a crossing structure (Smith and Noss 2011; Photo 46).
- Mesh size needs to be appropriate for the target species (Photo 47). Refer to Table 3 for species-specific fence types. Many snakes can pass through ½" mesh fencing and some small snakes can even pass through or get stuck in ¼" mesh (Smith and Noss 2011, S. Marks pers. comm. 2014). A mesh size of ¼" or smaller should be used to help reduce the risk of small snakes getting stuck in the fence (Photo 47). The fence should be buried to deter animals from digging; the recommended depth is 10-20 cm where feasible. If rock cannot be avoided, the bottom of the fence can be folded and covered with gravel to hold it in place (Photo 48).
- The fence height should be higher than the high water level in spring.
- For reptiles, the fence should include an overhang lip extended away from the road to deter climbing (Photo 40).
- Backfill on the road-side of the fence can be used as escape ramps to assist trapped animals to climb to the safe side (e.g., ACO wildlife fence; Photo 49).
- Nylon mesh fencing or erosion materials should not be used along the right-of-way as snakes can become entangled and die in this material.
- Fence end treatments can be used to deter amphibians and reptiles from accessing the road at the fence ends:
    - The fence can be extended away from the road in a curved or 90 degree U design (Photo 45; Figure 4) to redirect animals away from the road
    - The fence should extend along the entire habitat and end at a point where habitat types transition (e.g., wetland-forest edge)
    - Rocks or other inhospitable materials at the fence end can help deter movement onto the road.

Photo 46. Pooling at culvert entrance that should be avoided at terrestrial wildlife tunnels © K. Gunson

Photo 47. Snake caught in ½ inch wire mesh; © M. Patrikeev

Photo 48. Fence along rock with gravel used to hold bottom of fence in place © K. Gunson

Photo 49. Backfill along ACO wildlife fence that can provide an escape ramp for animals on the roadside of the fence © V. D'elia

Table 3: **Fence design specifications for SAR reptile and amphibian species are based on OMNR 2013, Woltz et al. 2008 and expert advice.**

Taxonomic Group	Species	Fencing	
		Fence/wall Material	Minimum Height (above ground)
Salamanders, Frogs, Toads	Jefferson Salamander	• Hardware cloth with ¼ " mesh or smaller, concrete, aluminum, prefabricated plastic fence, or vinyl wall. • Salamanders are generally poor climbers (T. Bain pers. comm.) so a small mesh fence will work and also allow some drainage.	30 cm
	Fowler's Toad	• Solid, permanent material (e.g., cement, plastic panels), or hardware cloth with ¼" mesh or smaller. • Avoid using netted fencing because they can climb (Smith and Noss 2011).	50 cm
Lizards	Five-Lined Skink	• Aluminum flashing; skinks can easily climb most other fencing materials.	50 cm

Taxonomic Group	Species	Fencing	
		Fence/wall Material	Minimum Height (above ground)
Snakes	Eastern Foxsnake, Gray Ratsnake	- Concrete, aluminum, or vinyl wall.	200 cm
	Blue Racer, Milksnake	- Hardware cloth (¼″ mesh or smaller), concrete, aluminum or vinyl walls.	100 cm
	All other snake species	- Hardware cloth (¼″ mesh or smaller), concrete, aluminum or vinyl walls.	60 cm
Turtles	All species	- Hardware cloth, chain link fence (½″ mesh or smaller), concrete, aluminum, vinyl wall, or prefabricated plastic wildlife fence - Combining chain link and hardware cloth will be effective for adults, juveniles, and hatchlings. - When fencing is used for both turtles and snakes, mesh size larger than ¼″ is discouraged as snakes can become entrapped.	60 cm

4.2.2 Fence Placement

Right-of-way considerations:

- Fencing should be placed as far as possible from the road edge to minimize impacts from snow removal, mowing or other road-side maintenance practices.
- Fencing cannot interfere with road interchanges or driveway access.
- Permissions and permits must be obtained from the road authority.
- When the fence will extend beyond the right-of-way, permission must be obtained from property owners, or in the case of Crown land, from the Ministry of Natural Resources and Forestry.

Fence Length and Placement:

Fence length depends on the species' movement abilities as well as the interface of the surrounding habitat with the road. Spatial analyses of where species are found on the road, in the road shoulder and in the road verge can help determine how much fencing is required and where it should be placed (Gunson and Teixeira 2015). However, when roads bisect continuous expanses of SAR habitat, fencing is often required along the entire stretch of a road to prevent mortality. The following should be considered when evaluating fence and crossing structure placement:

- Data collected from field and on-road surveys, expert opinion and other sources such as the NHIC to understand species presence, habitat use, and movements in relation to the road (see Appendix A).
- Maximum and mean movement distances of the target species should be used to inform fencing length. For example, salamanders generally will not move distances greater than a couple hundred metres, while turtles and snakes may move several kilometers (see Appendix A). Some species will move considerable distances along the fence and access the road at the fence ends; this can only be avoided if the fence is longer than the distances that the species will move.
- Gullies, uneven terrain and solid rock areas should be avoided when possible; if rocky areas cannot be avoided, gravel can be used to hold fence in place (Photo 50).
- When multiple crossing structures are used, fencing should span between structures (and angle away from the tunnel opening in a ‘V’ pattern: Photo 43 and Figure 4).
- To be effective, fencing must connect to the tunnel entrances without gaps (Photo 51) or go over top of the tunnel (Photo 52) in a ‘V’ pattern (Photo 53; Figure 3).

Photo 50. Fence with gap at bottom due to erosion from water draining under fence © K. Gunson

Photo 51. Fence tying into tunnel at Rice Lake Trail, Note shadecloth not recommended for permanent fencing © K. Gunson

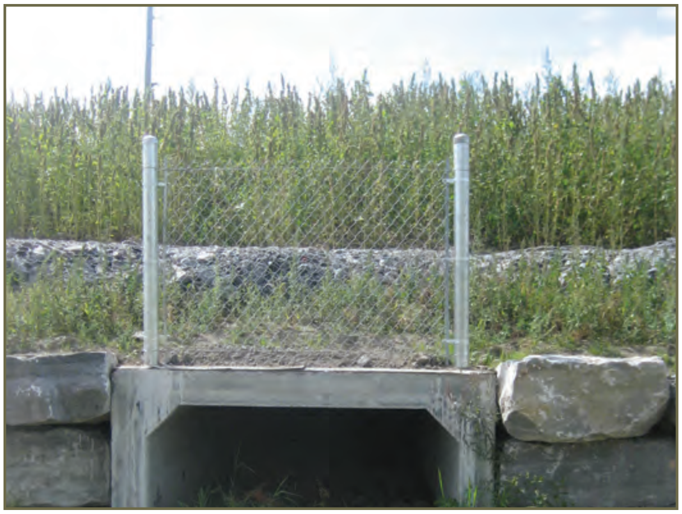

Photo 52. Fencing above tunnel, Terry Fox Drive extension © K. Gunson

Photo 53. Fencing approaching tunnel entrance in a 'V' pattern © K. Gunson

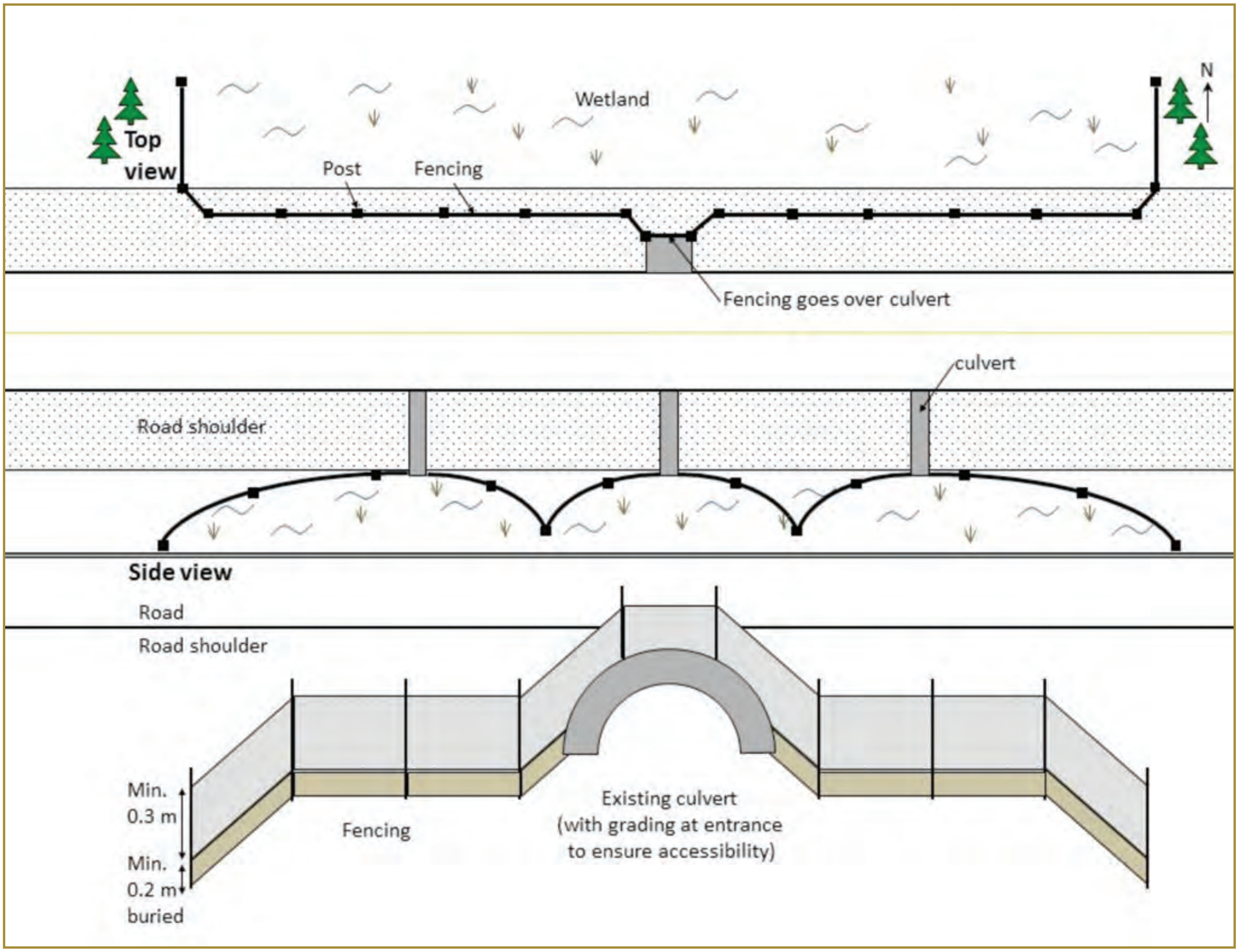

Figure 3. **Top view and side view of fencing design and siting options along the right-of-way. Figure adapted from Nature Conservancy Canada schematic.**

4.2.3 Fence Maintenance

All fencing requires routine survey checks and subsequent maintenance repairs and this should be planned and budgeted for. The frequency of maintenance checks and repairs will vary with the durability of the fence. After snowmelt, a thorough survey and follow-up fence repairs are essential prior to animals emerging from hibernation. The following are recommended considerations for fence maintenance:

- Woody vegetation, leaves, thick grasses, and other debris that pile up along fence may provide a `ladder` or puncture the fence allowing animals access to the road. Regular maintenance is required to clear vegetation from all fences.
- Fences should be marked with long posts and flagging tape to warn maintenance crews about its presence, especially where mowing will occur.
- Routine fence surveys should be done using a checklist approach to identify where repairs are required, including a description of the damage and the location. Checklist items should include that the fence has not collapsed, fence is still in the ground, fence abuts crossing tunnels, vegetation is not near the fence, and that there are no holes in the fence. Repair crews need to fix the fence in a timely manner to minimize fence breaches during the active season for amphibians and reptiles.

5 SUPPLEMENTARY MEASURES

Specifically designed crossing structures, combined with fencing, are the most effective mitigation strategy to reduce road mortality and enhance habitat connectivity (Dodd et al. 2004, Aresco 2005); however supplementary mitigation measures may be used in association with crossing structures and fencing (i.e., installing signage or reduced speed zones at fence ends). In addition, supplementary measures may be used as temporary measures during construction, or prior to road upgrade and rehabilitation projects, or on existing roads where there would otherwise be no mitigation. The effectiveness of some of these strategies at reducing road mortality and improving connectivity is difficult to measure and largely unknown; therefore implementation of these measures should proceed with caution using an adaptive management approach.

This section classifies each measure as those that influence driver behaviour, and those that influence wildlife movement as defined by Huijser et al. 2007. The following list of measures is not exhaustive, but instead summarizes what has been used in Ontario and elsewhere, with specific consideration for how each strategy may be applied to amphibians and reptiles.

5.1 Influencing Driver Behaviour

The strategies outlined in this section have relatively low effectiveness when used in isolation and several of these approaches should be used concurrently whenever possible. For example, a good strategy may include a reduced speed limit, traffic calming measures to reinforce the low speed limit, high quality signage to warn drivers, and a public education program to help drivers understand the measures that have been put in place.

With the exception of road closures, strategies that influence driver behavior rarely result in a significant reduction in road mortality. This is in part because, despite these measures, many reptiles and amphibians are small and difficult to see and/or avoid. Further, Ashley et al. (2007) found that approximately 2.7% of drivers intentionally ran over reptiles, and such behavior severely limits the success of these strategies.

Reduced speed zones allow drivers more time to react to an animal on the road, and subsequently safely avoid a collision. They have been implemented in Banff National Park to reduce collisions with larger wildlife, such as Grizzly bears (Banff National Park, unpublished data 2011-2014). Speed limits may be reduced seasonally and/or at specified times of day. This methodology is only suitable for amphibians and reptiles on low volume roads or roads in protected areas. A reduced speed zone is typically combined with a public awareness strategy and/or signage to educate motorists about the need to minimize road mortality for amphibians and reptiles. Enforcement or traffic calming mechanisms (see below) are usually necessary for the effective implementation of lower speed limits. This strategy can have a high cost given the need for regular enforcement.

Seasonal road closures offer an effective mechanism for reducing road mortality by eliminating vehicles from a road. Although this is a very effective solution, such closures are typically only feasible for a few days per year and they must be timed precisely to coincide with amphibian and reptile migrations. This method is most easily implemented in protected areas, on low volume roads where access to residences or businesses is minimal, or on roads where alternate access exists. A good example is King Road on the Niagara escarpment (Photo 55), where a seasonal road closure has been implemented for several years for the endangered Jefferson Salamander. Salamanders typically move across a defined road segment within a 2-3 week time period in early spring during a warm, rainy period. This type of strategy requires both buy-in from the road authority as well as the community using the roads. A public relations campaign is a useful tool to inform and gather support from local residents. This strategy has a relatively low cost.

Traffic calming refers to the installation of road features designed to decrease vehicle speeds without interfering with the flow of traffic. Some traffic calming methods, such as speed bumps (Photo 56), traffic circles, and raised medians, can only be implemented on low speed roads; whereas other methods, such as narrow lane widths, and rumble strip patches may be used on moderate to high speed roads. In some cases, speed bumps may interfere with snow removal; however installations can be used seasonally. This strategy has low to moderate costs dependent on the measure used.

Signage is a low-cost, widespread method of road-side messaging that is relatively easy to implement (Photo 57). The key objective for sign use is to instill awareness so motorists can avoid hitting wildlife along roads where the signs are placed. Effectiveness may be improved with a well thought-out strategy that avoids driver habituation and includes the following criteria (see Gunson and Schueler 2012; Kintsch et al. 2015):

- Seasonal placement of signs, or use of text indicating when target animals are likely crossing;
- Enhancement of signs with flags, flashing lights, or unique art work (Pojar et al. 1975, Hardy et al. 2006);
- Use of science and data to inform effective placement;

- Use of signs on moderate to high volume roads to deter theft;
- Strategic placement of signs and at the ends of exclusion fencing;
- Use of signs as temporary measures and markers in advance of more permanent mitigation measures (Ontario Ministry of Transportation 2012).

As with all of the other measures in this section, the effectiveness of signage can also be increased by combining it with other measures (e.g. reduced speeds, traffic calming). Benefits of signage for SAR amphibians and reptiles include driver awareness of wildlife on the road and heightened understanding of the importance of conservation efforts when used with a public awareness and education campaign (see example in Joyce and Mahoney 2001). In Ontario, signage has commonly been used on municipal and provincial park roads (Photo 58), and more recently on provincial roads (Ontario Ministry of Transportation 2012; Photo 59).

Public awareness and education campaigns are designed to inform drivers about wildlife and road issues and how they can help minimize or avoid wildlife road collisions. For amphibians and reptiles, public awareness campaigns typically target local communities near known high-risk road mortality locations, such as at Heart Lake Road in Brampton, Ontario. Local media attention generated awareness of the issue from local residents and subsequently a volunteer task force of 20-40 individuals was used to conduct on-road mortality surveys in 2011 and in 2013 (TRCA 2014).

While it is difficult to draw a direct correlation between heightened driver awareness and a decrease in road mortality, this strategy has the potential to improve effectiveness and public acceptance of other mitigation efforts, such as signage, reduced speed zones, or traffic calming measures. The cost of conducting a local-based public awareness campaign is comparable to that of the other strategies discussed; however, a regional, coordinated, long-term strategy (i.e. similar to the well-known Drinking and Driving Campaign) would entail greater funding and long-term commitment.

5.2 Influencing Wildlife Movement

Ramped curbs and escape gaps are used along roads (typically local, municipal roads) to replace vertical curbs that are too high for amphibians and reptiles to climb over. A good example is in Waterton Lakes National Park, where right-angle curbs were replaced with sloped curbs to allow Long-toed Salamanders to successfully escape the road (Photo 60). Additionally, escape gaps can be used where the structures meet the road (e.g., Banff National Park; Photo 61). Escape gaps would work well along high volume roads where continuous sections of jersey barriers divide opposing lanes of traffic and animals that enter the right-of-way cannot cross the road (e.g. Highway 401 and 417). This strategy has a relatively low cost.

Assisted migration can be used where a concentrated amphibian migration crosses a defined stretch of road. Temporary traps (typically drift fencing and buckets) may be used to prevent animals from crossing the road, which are then collected and moved across the road by volunteers. Alternatively, volunteers can survey the road during peak times and move any animals that are encountered. This strategy is labour-intensive and relies on having local volunteers to monitor traps during a migration event, and it requires safety precautions for the volunteers. However, if timed and coordinated effectively, facilitated migrations can be effective in reducing road mortality for amphibians (Photo 62).

Habitat creation can be used to reduce the need for individuals to access habitat close to the road or cross the road to access habitat on the other side. Since reptiles and amphibians often show high fidelity to specific habitats, many individuals will continue using historical habitat features and a population-level transition to the new habitat can take decades. Consequently, road-side barrier fencing is still necessary to prevent dispersing animals from accessing the road. The cost, feasibility and effectiveness of creating new habitat is variable and will be site and species specific (B.C. Ministry of Forests, Lands and Natural Resource Operations 2004).

New habitat creation may include wetlands as breeding sites for amphibians (e.g., Merrow 2007), artificial nesting sites for turtles; (Clarke and Gruenig 2002; Paterson et al. 2013); or gestation sites (Rouse 2005; Parent and Black 2006) and hibernacula (Willson 2005) for snakes. The B.C. Ministry of Forests, Lands and Natural Resource Operations BMP document (2004) describes the applicability of habitat restoration (or creation in this case) for amphibians and reptiles. General recommendations are as follows:

- A thorough understanding of the habitat use and movements of the target species is necessary.
- New habitat should be in close proximity and on the same side of the road as other habitat used by the target species.
- The created microhabitat should be suitable for the target populations.
- Other important habitats should not be manipulated to create new habitat.


Photo 55. Road Closure on King Road, Halton Region. © N. Finney


Photo 56. Speed bumps used to reduce speed on Cyprus Lake Road, Bruce Peninsula, Ontario. ©K. Gunson

Photo 57. Awareness sign on provincial park road in Point Pelee National Park. ©K. Gunson

Photo 58. Turtle signs used on municipal roads in Ontario. ©K. Gunson

Photo 59. Provincial Wildlife Habitat Awareness Sign on Highway 654. ©K. Gunson

Photo 60. Sloped curve in Waterton Lakes National Park, ©B. Johnstonh

Photo 61. Jersey barrier with gaps at the road surface ©K. Gunson

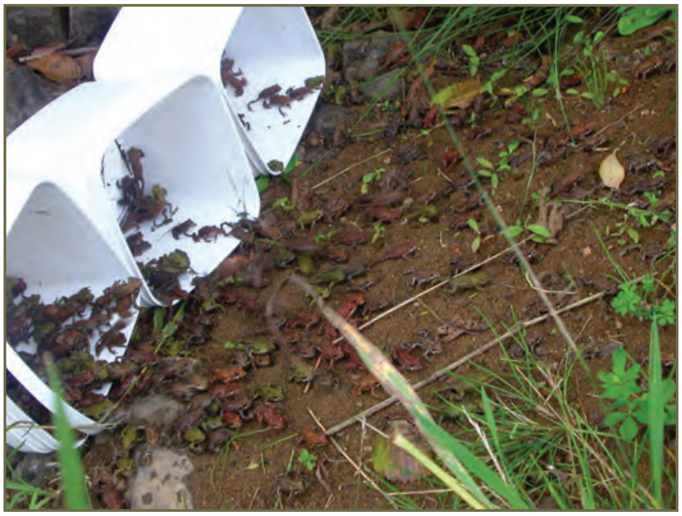

Photo 62. Assisted migration of toadlets in British Columbia. © E. Winde

6 TEMPORARY MITIGATION DURING ROAD CONSTRUCTION

This section provides general considerations for mitigation during construction when working in areas with SAR amphibians and reptiles. The following considerations address two components, timing construction activities to avoid construction-related impacts, and installing mitigation measures to minimize interactions with amphibians and reptiles and their habitat during construction.

Effective implementation of construction mitigation BMPs requires both oversight and consultation with experts. Regular consultation with local species experts is strongly recommended because active times for the target species will vary annually with changing climatic conditions and is site-specific especially in a landscape as large as Ontario.

6.1 Timing of Construction Activities

When road construction will occur within or near amphibian and reptile habitat, some impacts can be minimized by carefully scheduling the timing of the work to avoid habitats when they are occupied or during sensitive periods. Construction during the overwintering periods should avoid wetlands and other sites that are used for hibernation. This includes direct disturbance as well as indirect disturbance such as decreasing water levels in overwintering wetlands. Construction during the active season should avoid key habitat features or times when the species is most sensitive (see Appendix A). For example, avoiding work at breeding wetlands being used by Jefferson Salamander and Fowler's Toad in late March to June. Amphibian and reptile populations are active from March to October in southern Ontario and this time period lessens for more northern populations (Appendix A). Consultation with a local species expert and the district MNRF office may be required to assess annual variations of site-specific movements for the target species during construction activities.

6.2 Mitigation Measures for Construction Activities

On-site, temporary measures for all road projects that occur within, or adjacent to amphibian and reptile habitat help to avoid harming or killing individuals. BMPs for temporary measures include:

- Installation of exclusion fencing between the road construction zone and SAR habitat;
    - Use fencing that will last the duration of the road construction project (i.e., light-duty geotextile fence with a lifespan of up to one year)or, for longer projects, heavy-duty geotextile fence should be used (see section 5.2, OMNR 2013);
    - If permanent fencing is going to be installed as part of the mitigation plan (i.e. along roads), the permanent fence can be installed instead of temporary construction fence to avoid extra costs (Photo 63);
    - Fencing should be inspected and repaired daily to maintain effectiveness and avoid potential breaches; and
    - Fencing should be installed so that construction sediment does enter into wetlands or aquatic systems.
- When possible, alternative measures (e.g., rock barriers) should be integrated to create a sufficient barrier between construction sites and adjacent SAR habitat;
- Blast mats and other measures to control blast size and vibrations should be used within or adjacent (up to 250 m) to snake habitat (OMNR 2011);

- A qualified species expert should be present or available at all times to conduct searches, handle encounters, and translocate animals during construction;
- Searches should be conducted daily prior to and during construction activities;
- When SAR amphibians and reptiles are found on a construction site, proper handling, translocation and reporting protocols should be followed. Specific protocols for SAR encounters are available in the Ontario Species at Risk Handling Manual in addition to the Georgian Bay Biosphere Reserve BMP document (Clayton and Bywater 2012); and
- Project-specific reporting and handling protocols should be developed in coordination with the appropriate agency personnel. Observation records should include the observer's name, date and time, species, location (descriptive and georeferenced), photographs, and action taken.

Photo 63. Temporary fencing installed prior to installation of more permanent fencing along highway 69, note permanent fencing completed in Photo 48. © W. Kowbasniuk

7 MONITORING

Substantial research has been conducted to monitor the effectiveness of mitigation for large animals (e.g., Ford et al. 2010; Dodd et al. 2007); however, there exists a significant knowledge gap for amphibians and reptiles, and many mitigation projects have had no monitoring at all (Paulson 2010). This section provides recommendations for monitoring the effectiveness of road mitigation projects.

7.1 Study Design

Most studies that have evaluated the effectiveness of mitigation structures to-date are of low inferential strength due to poor study design, and this has resulted in results with high uncertainty (van der Grift et al. 2013). This uncertainty impedes implementation of mitigation measures and leads to inefficient use of limited financial resources.

Many monitoring plans only consider whether a specific species uses a structure at a specific location. However it is essential to monitor the viability of populations affected by a mitigated road (Figure 4). For example, if particular individuals, such as breeding females do not use a crossing structure to access breeding sites, this will lead to reduced breeding success and population declines, even though traffic mortality has been reduced and some individuals were observed using the tunnel.

Ideally, the population size (or density) of the target population should be measured at or near the road mitigation project to assess how the species responds (van der Grift et al. 2013). The population may increase, decrease or show no change in abundance after the road construction project (Rodenbeck et al. 2007). For example, Torres et al. (2011) performed visual census surveys for the Great Bustard

(*Otis tarda*), a globally threatened bird in Spain, and compared population trends in a Before-After-Control-Impact (BACI) design (see description below).

When it is not possible to measure a change in population size, the research questions should ask, "Is the current rate of road mortality sufficiently low, and/or is the rate of crossing sufficiently high to ensure a viable population?" If the answer to that question is no or possibly not, the next question is, "Which parameter of the road, traffic, or mitigation structure should be modified to improve viability to an acceptable level?" This question is more easily answered by assessing crossing and road mortality rates at different mitigation designs while controlling for habitat and road conditions.

Up to three years of monitoring data (from both before and after a road mitigation project) is likely necessary to measure changes in the ecological response (e.g. population size or road mortality rate) of the target species and reduce the influence of random, one-time events. The appropriate time-frame will depend on the ecological response and target species characteristics (e.g. longer-term monitoring for species that have longer generation times). This requires an understanding of the research goals among both the road planners and monitoring team early in the planning process to ensure the study design is adequately implemented in the road construction phase.

The optimal study design consists of data collected before and after the impact at sites where the impact has occurred and at control sites which have not been affected by the impact (Rodenbeck et al. 2007). This study design is referred to as a Before-After-Control-Impact (BACI) design and provides the highest level of inferential strength to measure the ability of the study to detect a change in the parameter of interest (e.g. population size, and rate of wildlife mortality on roads). A properly implemented BACI design allows the monitoring objectives to change from, "Are animals using crossing structures?" to "Has the mitigation prevented population decline?".

Other considerations for a study design are to select specific mitigation treatments at each monitoring site as well as carrying out consistent and repeatable sampling to ensure results are broadly applicable (van der Ree et al. 2015). Design elements are described below as well as in Figure 4:

- Treatments that can be manipulated allow for different structural features to be assessed (e.g. open-top vs. closed-top or varied fencing type and length) while controlling for other variables.
- Replication of treatments and controls among sites is important, as is monitoring each treatment in more than one location.
- Treatments that are randomly assigned will help to reduce bias and allow for a rigorous statistical analysis.
- Appropriate covariates need to be selected and controlled for. Examples of covariates include spatial and temporal variability in road design and traffic levels, mitigation structure design and the features of the surrounding landscape (van der Grift et al. 2013).
- Sampling and field protocols that are repeatable and consistent at monitoring locations before and after road mitigation help to ensure unbiased data collection.
- Inclusion of impact (mitigated) and control sites is essential to ensure that the apparent effects of mitigation (reduced mortality or increased permeability) are due to the mitigation and not a confounding variable such as weather, differences in habitat or road and terrain conditions.
- The variables being monitored (e.g. relative abundance) should be clearly identified prior to the commencement of the project.

Research Questions

Monitoring Goal
1. Maintain and restore population viability
   a. Measure trend in population size/density

Fencing
1. Reduce road mortality
   a. Ask is the reduced mortality sufficient to maintain or restore population viability?

Crossing Structures
1. Crossing use by population (e.g. male and females)
   a. Ask is use enough to maintain or restore population viability?

Planning

Long-term Monitoring
1. Multiple seasons
2. Multiple years (3 or more) prior to AND after mitigation measures have been installed or modified, e.g. Beofre, after and control impact (BACI studies).
   a. To reduce influence of random, one-time events

Expertise & Collaboration
1. SAR biologist
2. Road authority
3. Road developer
4. Monitoring team

Other
1. Obtain funds
2. Obtain permits
3. Start collaborating early!

Study Design

Treatments
1. Measure trend in population size/density
2. Vary crossing structure design
3. Combination of both

Site Selection
1. Obtain pool of potential treatment and control sites
2. Random assignment of treatment at impact sites
3. Replication of treatments and controls among sites
4. Include before, after, and control sites

Sampling
1. Repeatable
2. Consistent

Figure 4. **Study design recommendations for developing research questions, and a rigorous study design that will inform road mitigation effectiveness for amphibians and reptiles.**

7.2 Monitoring Techniques

This section outlines monitoring techniques that are used to evaluate crossing structure and fencing effectiveness for amphibians and reptiles. All techniques may be combined in a monitoring plan depending on budget, timelines, and the specific objectives.

7.2.1 Road Surveys

Road surveys are the most common method used to evaluate where amphibians and reptiles road mortality and interactions occur along roads (see Langen et al. 2007 for a description of methods). This information can be used to evaluate road impacts on wildlife, where animals are interacting with roads, and the effectiveness of crossing structures and fencing systems.

Data is collected by driving, cycling, or walking along a selected length of road looking for alive or dead individuals. The sampling method will vary depending on the objectives, road conditions, and the degree of detectability desired (Langen et al. 2007, Collinson et al. 2014). Driving surveys allow greater distances of road travelled over a sampling period, however the detectability of small vertebrates may be underestimated (Slater 2002; Langen et al. 2007).

General monitoring considerations for documenting amphibian and reptile SAR on roads include the following:

- Surveys should be conducted at least three years prior to the construction phase of a road improvement or rehabilitation project:
    - When a species is common, road surveys may generate a lot of data in 1 or 2 seasons (Ashley and Robinson 1996), however for SAR that are inherently rare, more time will be required to understand movements in relation to the project area.
- Surveys should take place during the active season or movement period for the target species (Appendix A).
- The frequency of surveys will depend on the goal of the study, the target species, traffic volume, rates of scavenging, carcass persistence, and when the species is moving (Slater 2002; Barthelmess and Brooks 2010; Santos et al. 2011). When the goal is to survey the majority of species on a road in an active season, the following recommendations should be considered for each taxon:
    - For species that move in well-defined time periods such as salamanders and toads that migrate to breeding ponds, surveys should be timed during peak movements (e.g., rainy, warm spring nights) because carcasses will be obliterated with rain and from traffic in a few hours even on low traffic roads.
    - Greater than 50% of snake carcasses will disappear in 24 hours so surveys should be conducted daily during peak movements in spring and fall (Antworth et al. 2006).
    - Dead turtles persist the longest on roads, so surveys two to three times a week during nesting season are recommended.
- Weather conditions, time of day and traffic volumes will all impact detectability of carcasses. For animals that move on rainy nights, such as the Jefferson Salamander, surveys must be conducted at night before rainfall and morning traffic obliterates carcass remains.
- Note that road surveys may not detect rare species where road mortality has already depleted the number of individuals adjacent to the road (Fahrig and Rytwinski 2009), or species that avoid crossing roads all together (Andrews and Gibbons 2005):
    - Other visual encounter survey techniques may be required to detect rare and elusive animals surrounding roads (Konze and McLaren 1997). Examples include cover boards for snakes (Patrick and Gibbs 2009), pit-fall traps for amphibians and toads (Gibbs and Shriver 2005), and hoop-net traps for turtles (Beaudry et al. 2009).
    - When information is lacking for rare species, data from common species (e.g. Painted Turtles) may supplement sample size.
- Surveys should be conducted with consistent and repeatable methods so the road can be surveyed the same way in a before and after mitigation design. Smith et al. (2015) discusses methods as well as how to avoid observer bias.
- Each specimen should be carefully examined and photographed to determine the species and, if possible, the sex and length of the animal should be recorded (e.g. plastron of a turtle, total length of snakes) (Photos 82 and 83). Depending on the project, it may also be important to collect a DNA sample or to mark live individuals.


Photo 64. Identifying amphibian specimen peeled off the road. ©K. Gunson

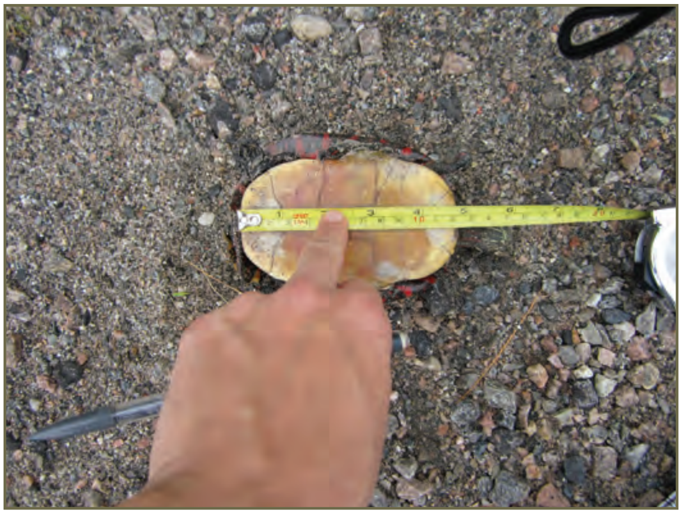
Photo 65. Measuring mid-plastron length for dead Painted Turtle found on the road. © K. Gunson

7.2.2 Crossing Structure and Fencing Effectiveness

This section focuses on monitoring techniques for measuring whether crossing structures and fence designs are effective at providing connectivity across roads. Previously the majority of studies that have monitored crossing structures have assessed use of tunnels by amphibians and reptiles (see review in Appendix C). Studies that assess fence-efficiency (proportion of animals encountering the fence that enter into the tunnel) and tunnel-efficiency (proportion of animals that enter tunnels and go through them) are needed to better inform mitigation designs (Jackson and Tyning 1989).

Smith et al. (2015) offer information for developing a monitoring plan to measure mitigation effectiveness for small vertebrates including reptiles and amphibians, and Clevenger and Huijser (2011) provide information on monitoring techniques based on mark-recapture methods. Further information regarding methods for surveying amphibians and/or reptiles can be found in Heyer et al. (1994), Konze et al. (1997) and McDiarmid et al. (2012). The Canadian Council on Animal Care (CCAC 2004) provides an excellent manual for handling and capturing amphibians and reptiles that can be integrated into the following monitoring techniques (http://www.ccac.ca/Documents/Standards/Guidelines/Add_PDFs/Wildlife_Amphibians_Reptiles.pdf)

Digital cameras are currently the most commonly used technique for measuring crossing structure use for animals in Ontario. Motion-activated cameras work well for large and medium-sized animals; however, they are not very effective at capturing pictures of ectothermic animals, such as amphibians and reptiles. This is because motion-triggered cameras only take a photograph when there is a temperature differential between the animal and the ambient temperature (Reconyx 2010). For example, Pagnucco (2012) found Reconyx infra-red motion triggered cameras only documented approximately 19% of salamanders in a 0.5 m by 0.5 m ACO tunnel. Since the motion-activated feature is not effective, the time lapse setting should be used instead to take pictures at regularly spaced intervals (e.g. every minute). Approximately 20,000 images are taken in a two week period with a one-minute interval and camera detection software can help to efficiently find wildlife in images (Dillon et al. 2011). Setting the camera to take photos over shorter intervals (e.g. every 10 seconds) will improve the quality of the data but would require the cameras to be checked more regularly. Cameras should be placed at both ends of the tunnel, securely fastened and locked to the undersurface of the tunnel top (photo 84). At larger tunnels, cameras can be mounted close to the ground to capture snakes and turtles.

Pitfall Traps: Pitfall traps consist of buckets, cans, or other containers that are buried flush with the ground and are set up along a fence that directs animals to the traps. Pitfall traps need to be large enough so that the target species cannot climb or jump out of the containers. In addition, once traps are set they need to be checked regularly (at least every day) to avoid drowning, desiccation or predation of individuals. They can be used at or near amphibian habitat to assess where animals are moving in relation to a road. For example, Gibbs et al. (2005) used metal cans

Photo 66. Camera securely fastened to top of culvert; note difficult to capture animals when water in culvert or tunnel. © K. Gunson

Photo 67. Using hand-held receiver to locate Blanding's turtles around highway 24 © K. Gunson

Photo 68. Blanding's turtle with radio transmitter on back of shell. © K. Gunson

Photo 69. Passive data logger receiver used to record turtle passage at culvert on highway 24. ©K. Gunson

50 cm deep and 7.5 cm in circumference to assess movements of salamanders across a road. Furthermore, pitfall traps have been used at entry and exit points of crossing structures to assess use of structures (Pagnucco et al. 2012). This also provides a useful technique to capture and mark individuals.

Mark-recapture: This technique involves capturing, marking and recapturing animals to determine if they cross the road. Several methods exist for marking amphibians and reptiles, including inserting Passive Integrated Transponders (PIT), notching scutes on turtles, marking salamanders with visible implant elastomer (e.g., MacNeil et al. 2011) and using image-recognition software. Some of these techniques are discussed in more detail in the CCAC (2004) manual. Mark-recapture methods for turtles are discussed in detail in Robertson et al. (2013) and for all reptiles in McDiarmid et al. (2012).

Radio-Telemetry and passive data loggers/ PIT tag readers: Radio-telemetry can be used to monitor animal movements using a hand-held receiver (photos 85 and 86) without the need to recapture the animals. Further, passive data loggers (photo 87) or PIT tag readers can be mounted near crossing structure entrances (James et al. 2011; Caverhill et al. 2011) to record the movement of marked individuals through them.

Table 4 provides a comparison of the advantages and disadvantages of these methodologies. A combination of several methods will provide the most robust data set and eliminate most of the disadvantages of any one method. For example, using both hand-held radio telemetry and passive receivers mounted in the crossing structures will provide high quality data on crossing events as well as the detailed movements of the individuals in relation to the crossing structures/road.

Table 4: **Advantages and disadvantages of the techniques used to monitor road crossing structures**

Technique	Advantages	Disadvantages
Mounted digital cameras	● Provides information on the time and date of the crossing event ● Provides direct evidence that the structures are used ● Should detect most individuals using the crossing structure if cameras are set to take photos regularly (e.g. every minute)	● Does not provide information on the individuals using the structure (e.g. sex) ● Effective cameras are expensive, and there is a risk of theft ● It can be very time-consuming to review photographs and maintain cameras (downloading pictures, adjustments, batteries, water levels, etc.) ● Cameras typically do not work under aquatic conditions

Technique	Advantages	Disadvantages
Pitfall traps	● Provides information on the individuals using the structure (e.g. sex) and the date of the crossing event ● Provides direct evidence that the crossing structures are used ● Should detect most individuals using the crossing structure ● Can use trapped animals for genetic sampling and mark-recapture	● Labour-intensive for set up and sampling as the traps should be checked a minimum of every day ● Risk of animals dying in traps ● Method is less suitable for reptiles
Mark-recapture	● Provides information on the individuals using the structure (e.g. sex) ● Allows for estimates of population abundance (with enough sampling)	● May not provide information on the time and date of crossings ● Does not provide direct evidence that animals used crossing structures (e.g. it is not possible to rule out crossing through holes in fence or at fence ends) ● Detection of individuals crossing the road is limited to the number of animals captured and subsequently recaptured
Radio-telemetry and passive data loggers	● Provides information on the individuals using the structure (e.g. sex) and the time and date of crossing ● Passive data loggers and PIT tag readers in the structure provide direct evidence that the structures are used ● Hand held radio-telemetry receiver can track movements in relation to the road (e.g. home range size, etc.) ● Will work under aquatic conditions	● Considerable field time, effort and cost can be required to capture, handle and monitor animals ● Detection of individuals crossing the road is limited to the number of animals that are captured and tagged or tracked ● Radio-telemetry with a hand-held receiver is unlikely to provide direct evidence that the structure is used, so it is ideal to combine this with passive readers mounted in the structure

7.2.3 Population Estimates

Monitoring that measures changes in population abundance, animal distribution, and genetic relatedness before and after a road mitigation project can answer questions related to how new road mitigation maintained or improved the long-term persistence of wildlife populations, especially when used in a BACI design. This section generally outlines inventory and survey techniques to measure whether a population is stable, increasing or decreasing as a result of the road mitigation measures and road construction project.

Mark-recapture studies may be used to estimate population size, but a large number of individuals need to be marked to produce statistically significant estimates.

Relative Abundance surveys are carried out using standardized methods, such as timed searches, grids or transects, that allow for comparisons over time or between sites. In addition to free searches, these surveys may consist of cover boards for snakes and salamanders or pit-fall traps for toads and frogs along. Abundance surveys (counts of animals per area and standardized by search effort) require a systematic study design with regular surveys by the same trained volunteers to reduce observer bias.

Call surveys may be used to collect relative abundance data for toads and frogs near roads, and do not require direct observation of the animals (Eigenbrod et al. 2008b). With respect to SAR amphibians and reptiles in Ontario this monitoring technique would only be applicable to the Fowler's Toad.

Genetic Sampling involves taking from blood or tissue samples from live or dead individuals to compare genetic relatedness and structuring (e.g. sex and age ratios) before and after a road mitigation project (e.g. James et al. 2011). For example, Clark et al. (2010) found roads have an effect on the genetic structure, connectivity and gene flow on Timber Rattlesnakes. In another study, Row et al. (2010) genetically analyzed blood samples from Eastern Foxsnake populations bisected by highways in Ontario, Ohio and Michigan. Notably, some populations bisected by Highway 401 were not genetically distinct, possibly because of underpasses that allowed snake passage.

7.3 Adaptive Management

Adaptive management consists of using the results from monitoring to inform decision making with regard to planning and designing subsequent phases of a project (Holling 1978). The Environmental Impact Assessment (EIA) process is meant to be a flexible, iterative and adaptive process that can adjust for uncertainty and preferences that emerge during the process (Lawrence 2003). With this in mind, and the typical long-term nature of road projects, there is an opportunity to integrate long-term and adaptive monitoring into the road planning processes.

Road construction and the implementation of mitigation strategies typically occurs in phases. The phased construction process allows for mitigation designs to be implemented in the initial section of highway so that lessons learned via monitoring can be integrated into subsequent phases of the road project. For example, the improvement of the Trans-Canada Highway in Banff National Park was conducted in 4 phases over 30 years, and long-term monitoring of crossing structures enabled lessons learned to be applied in each subsequent phase to improve crossing structure designs (Ford et al. 2010). Adaptive management of the project design based on monitoring results requires regular and close communication between the people conducting the monitoring and the transportation agency. Ongoing communication will permit timely changes to design plans that reflect the most current results from monitoring activities (Clevenger and Ford 2010).

8 REFERENCES

Allaback, M. L., and D. M. Laabs. 2002. Effectiveness of road tunnels for the Santa Cruz Long-toed Salamander. Transactions of the Western Section of the Wildlife Society 38:5–8.

Amphibian and Reptile Conservation. 2009. Common toads and roads: Guidance for planners and highways engineers (England). Booklet, published by Amphibian and Reptile Conservation.

Andrews, K. M., and J. W. Gibbons. 2005. How do highways influence snake movement? Behavioral responses to roads and vehicles. Copeia 2005:772–782.

Andrews, K. M., J. W. Gibbons, and D. M. Jochimsen. 2008. Ecological effects of roads on amphibians and reptiles: a literature review. Pages 121–143 in R. E. Mitchell, J. Brown, and B. Bartholomew, editors. Urban Herpetology, Society for the Study of Amphibians and Reptiles.

Antworth, R. L., D.A. Pike, and E.E. Stevens. 2005. Hit and Run: Effects of scavenging on estimates of roadkilled vertebrates. Southeastern Naturalist 4:647-656

Aresco, M. J. 2005. Mitigation measures to reduce highway mortality of turtles and other herpetofauna at a north Florida lake. Journal of Wildlife Management 69:549–560.

Arizona Game and Fish. 2010. Safe roads for people and wildlife: culverts and fencing to reduce wildlife-vehicle collisions and maintain permeability. Available from http://www.rtamobility.com/images/stories/pdfs/RTAWLL/2010/RTAWLL-2010-05-14-Presentation%20Safe%20Roads%20for%20%20People%20and%20Wildlife.pdf.

Ascensão, F., and A. Mira. 2007. Factors affecting culvert use by vertebrates along two stretches of road in southern Portugal. Ecological Research 22:57–66.

Ashley, E. P., and J. T. Robinson. 1996. Road mortality of amphibians, reptiles and other wildlife on the Long Point Causeway, Lake Erie, Ontario. Canadian Field Naturalist 110:403–412.

Ashley, E. P., A. Kosloski, and S. A. Petrie. 2007. Incidence of intentional vehicle-reptile collisions. Human Dimensions of Wildlife 12:137–143.

Bain, T.K. 2014.Evaluating the effect of moisture in wildlife crossing tunnels on the migration of the California tiger salamander, *Ambystoma californiense*. Master of Science thesis. Sonoma State University, Rohnert Park, California.

Barthelmess, E. L., and M. S. Brooks. 2010. The influence of body-size and diet on road-kill trends in mammals. Biodiversity and Conservation 19:1611–1629.

Baxter-Gilbert, J. H. 2014. The long road ahead: understanding road-related threats to reptiles and testing if current mitigation measures are effective at minimizing impacts. Master of Science thesis. Laurentian University.

British Columbia Ministry of Forests, Lands and Natural Resource Operations. 2004. Guidelines for Amphibians and Reptiles conservation during urban and rural land development in British Columbia. Victoria, British Columbia. 156 pp. http://www.env.gov.bc.ca/wld/BMP/bmpintro.html#second

Beasley, B. A. 2013. The SPLAT project: Mitigating amphibian road mortality in the Clayoquot Sound UNESCO Biosphere Reserve. FrogLog 21:20–22.

Beaudry, F., P. G. deMaynadier, and M. L. Hunter. 2008. Identifying road mortality threat at multiple spatial scales for semi-aquatic turtles. Biological Conservation 141:2550–2563.

Beaudry, F., P. G. deMaynadier, and M. L. Hunter. 2009. Seasonally dynamic habitat use by Spotted (*Clemmys guttata*) and Blanding's turtles (*Emydoidea blandingii*) in Maine. Journal of Herpetology 43:636–645.

Beaudry, F., P. G. deMaynadier, and M. L. Hunter. 2010. Nesting movements and the use of anthropogenic nesting sites by Spotted Turtles (*Clemmys guttata*) and Blanding's Turtles (*Emydoidea blandingii*). Herpetological Conservation and Biology 5:1–8.

Bellis, M., S. Jackson, C. Griffin, P. Warren, and A. Thompson. 2007. Utilizing a multi-technique, multi-taxa approach to monitoring wildlife passageways on the Bennington Bypass in Southern Vermont. Proceedings of the 2007 International Conference on Ecology and Transportation. Center for Transportation and the Environment, North Carolina State University, Raleigh, NC.

Biolinx Environmental Research. 2013. Western Toad monitoring study in Kentucky Alleyne Provincial Park, July - August 2013. Unpublished report to BC Parks.

Bissonette, J., C. A. Kassar, and L. J. Cook. 2008. Assessment of costs associated with deer–vehicle collisions: human death and injury, vehicle damage, and deer loss. Human-Wildlife Conflicts 2:122-130.

Bissonette, J. A., and W. Adair. 2008. Restoring habitat permeability to roaded landscapes with isometrically-scaled wildlife crossings. Biological Conservation 141: 482-488.

Bouchard, J., A. T. Ford, F. E. Eigenbrod, and L. Fahrig. 2009. Behavioral responses of Northern Leopard Frogs (*Rana pipiens*) to roads and traffic: Implications for population persistence. Ecology and Society 14. [online] URL: http://www.ecologyandsociety.org/vol14/iss2/art23/.

Brooks, R. J., G. P. Brown, and D. A. Galbraith. 1991. Effects of a sudden increase in natural mortality of adults on a population of the Common Snapping Turtle (*Chelydra serpentina*). Canadian Journal of Zoology 69:1314–1320.

Buchanan, I. D., and D. Basso. 2007. Under the boardwalk – case history – St. John's sideroad at the Mckenzie wetland, Aurora, Ontario, Canada. Pages 100–113 in C. L. Irwin, D. A. Nelson, and K. P. McDermott, editors. Proceedings of the 2007 International Conference on Ecology and Transportation. Center for Transportation and the Environment, North Carolina State University, Raleigh, NC. Available from http://escholarship.org/uc/item/6vr0n5bq (accessed February 25, 2014).

CCAC. 2004. CCAC species-specific recommendations on: AMPHIBIANS AND REPTILES. Canadian Council on Animal Care, Ottawa, Ontario. Available from http://www.ccac.ca/Documents/Standards/Guidelines/Add_PDFs/Wildlife_Amphibians_Reptiles.pdf.

Carr, L. W., and L. Fahrig, 2001. Effect of road traffic on two amphibian species of differing vagility. Conservation Biology 15: 1071–1078.

Carsignol. J. 2005 (translated to English 2007). Facilities and measures for small fauna: technical guide. Ministry of Transportation and Infrastructure, Technical Department for Transport, Road and Bridges Engineering and Road Safety. Bagneux Cedex, France.

Caverhill, B., B. Johnson, J. Phillips, E. Nadeau, M. Kula, and R. Holmes. 2011. Blanding's Turtle (*Emydoidea blandingii*) and Snapping Turtle (*Chelydra serpentina*) habitat use and movements in the Oakland Swamp wetland complex, Ontario, Canada, and their response to the Provincial Highway 24 exclusion fence and aquatic culvert ecopassage from 2010-2011. Report prepared by the Toronto Zoo, Adopt-A-Pond Programme, Toronto, ON.

Central Lake Ontario Conservation Authority March 2015. Watershed Wildlife and Corridors Protection and Enhancement Plan - Action Plan #5. Oshawa, ON.

Clark, R. W., W.S. Brown, R. Stechert, and K.R. Zamudio. 2010. Roads, interrupted dispersal, and genetic diversity in timber rattlesnakes. Conservation Biology 24:1059-1069.

Clarke, R. and A. Gruenig 2002. Summary Report: Painted Turtle (*Chrysemys picta belli*) nest site enhancement and monitoring Elizabeth Lake, Cranbrook, B.C. Unpublished report for Columbia Basin Fish and Wildlife Compensation Program Rocky Mountain Naturalists, Nelson, B.C.

Clayton, G. and D. Bywater. 2012. BMPs for Public Works Department working within the Georgian Bay Biosphere Reserve. Georgian Bay Biosphere Reserve. Parry Sound, Ontario. 16 pp. http://www.gbbr.ca/download/Species%20at%20Risk/BMPs%20Working%20in%20SAR%20Habitat.pdf

Clevenger, A. P. 2012. Mitigating continental-scale bottlenecks: How small-scale highway mitigation has large-scale impacts. Ecological Restoration 30:300–307.

Clevenger, A. P., and M. Huijser. 2011. Wildlife crossing structures handbook: Design and evaluation in North America. Report # FHWA-CFL/TD-11-003. Federal Highway Administration, Washington, D.C. 223 pp.

Clevenger, A. P., B. Churszcz, K. Gunson, and J. Wierzchowski. 2002. Roads and wildlife in the Canadian Rocky Mountain Parks – movement, mortality, and mitigation. Final Report to Parks Canada. Banff, AB.

Clevenger, A. P., M. McIvor, D. McIvor, B. Chruszcz, and K. Gunson. 2001. Tiger salamander, *Ambystoma tigrinum*, movements and mortality on the Trans-Canada Highway in southwestern Alberta. Canadian Field-Naturalist 115:199–204.

Collinson, W. J., D.M. Parker, R.T. Bernard, B.K. Reilly, and H.T. Davies-Mostert. 2014. Wildlife road traffic accidents: a standardized protocol for counting flattened fauna. Ecology and Evolution, 4:3060-3071.

Compton, B. W., and P. R. Sievert. 2002. An evaluation of turtle tunnels and curbs at Towermarc Office Park. Unpublished report. University of Massachusetts, Amherst, MA, USA.

Congdon, J. D., A. E. Dunham, and R. C. van Loben Sels. 1993. Delayed sexual maturity and demographics of Blanding's Turtles (*Emydoidea blandingii*): Implications for conservation and management of long-lived organisms. Conservation Biology 7:826–833.

COSEWIC. 2002a. COSEWIC assessment and update status report on the Spiny Softshell Turtle *Apalone spinifera* in Canada. Page vii + 17. Committee on the Status of Endangered Wildlife in Canada. Ottawa.

COSEWIC. 2002b. COSEWIC assessment and status report on the Milksnake *Lampropeltis triangulum* in Canada. Page vi + 29. Committee on the Status of Endangered Wildlife in Canada. Ottawa.

COSEWIC. 2004. COSEWIC assessment and update status report on the Spotted Turtle *Clemmys guttata* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa.

COSEWIC. 2005. COSEWIC assessment and update status report on the Blanding's Turtle *Emydoidea blandingii* in Canada. Page viii + 40. Committee on the Status of Endangered Wildlife in Canada. Ottawa.

COSEWIC. 2006. COSEWIC assessment and update status report on the Lake Erie watersnake *Nerodia sipedon insularum* Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa.

COSEWIC. 2007a. COSEWIC assessment and update status report on the Eastern Hog-nosed Snake *Heterodon platirhinos* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa.

COSEWIC. 2007b. COSEWIC assessment and update status report on the Wood Turtle *Glyptemys insculpta* in Canada. Page vii + 42. Committee on the Status of Endangered Wildlife in Canada. Ottawa.

COSEWIC. 2007c. COSEWIC assessment and update status report on the Gray Ratsnake *Elaphe spiloides* (Great Lakes/St. Lawrence population and Carolinian population) in Canada. Page vii + 33. Committee on the Status of Endangered Wildlife in Canada. Ottawa.

COSEWIC. 2007d. COSEWIC assessment and update status report on the Five-lined Skink *Eumeces fasciatus* (Carolinian population and Great Lakes/St. Lawrence population) in Canada. Page vii + 50. Committee on the Status of Endangered Wildlife in Canada. Ottawa.

COSEWIC. 2008a. COSEWIC assessment and status report on the Snapping Turtle *Chelydra serpentina* in Canada. Page vii + 47. Committee on the Status of Endangered Wildlife in Canada. Ottawa.

COSEWIC. 2008b. COSEWIC assessment and update status report on the Eastern Foxsnake *Elaphe gloydi*, Carolinian population and Great Lakes/St. Lawrence population, in Canada. Page vii + 45. Committee on the Status of Endangered Wildlife in Canada. Ottawa.

COSEWIC. 2010a. COSEWIC assessment and status report on the Jefferson Salamander *Ambystoma jeffersonianum* in Canada. Page xi + 38. Committee on the Status of Endangered Wildlife in Canadaa. Ottawa.

COSEWIC. 2010b. COSEWIC assessment and status report on the Fowler's Toad *Anaxyrus fowleri* in Canada. Page vii + 58. Committee on the Status of Endangered Wildlife in Canada. Ottawa.

COSEWIC. 2010c. COSEWIC assessment and status report on the Butler's Gartersnake *Thamnophis butleri* in Canada. Page xi + 51. Committee on the Status of Endangered Wildlife in Canada. Ottawa.

COSEWIC. 2010d. COSEWIC assessment and status report on the Queensnake *Regina septemvittata* in Canada. Page vii + 34. Committee on the Status of Endangered Wildlife in Canada. Ottawa.

COSEWIC. 2012a. COSEWIC assessment and status report on the Eastern Musk Turtle *Sternotherus odoratus* in Canada. Page xiii + 68. Committee on the Status of Endangered Wildlife in Canada. Ottawa.

COSEWIC. 2012b. COSEWIC assessment and status report on the Eastern Ribbonsnake *Thamnophis sauritus* Atlantic population, Great Lakes population in Canada. Page xii + 39. Committee on the Status of Endangered Wildlife in Canada. Ottawa.

COSEWIC. 2012c. COSEWIC assessment and status report on the Massasauga *Sistrurus catenatus* in Canada. Page xiii + 84. Committee on the Status of Endangered Wildlife in Canada. Ottawa.

COSEWIC. 2013. COSEWIC assessment and status report on the Northern Map Turtle *Graptemys geographica* in Canada. Page xi + 63. Committee on the Status of Endangered Wildlife in Canada. Ottawa.

Crowley, J. F. 2006. Are Ontario reptiles on the road to extinction? Anthropogenic disturbance and reptile distributions within Ontario. Master's thesis. University of Guelph, Guelph, Ontario.

deMaynadier, P. G., and M. L. Hunter Jr., 2000. Road effects on amphibian movements in a forested landscape. Natural Areas Journal 20: 56–65.

De Rivera, C. E., and L. L. Bliss-Ketchum. 2010. The effectiveness of vertebrate passage and prevention structures: a study of Boeckman Road in Wilsonville. Final report for Oregon Transportation Research and Education Consortium.

Dillon Consulting Limited. 2011. Terry Fox Drive extension project wildlife guide system monitoring report, Year 1 of 3. 10-3663. City of Ottawa, Ottawa, Ontario.

Dillon Consulting Limited. 2013. Terry Fox Drive extension project wildlife guide system monitoring report, Year 3 of 3; and, three year summary. 12-6019. City of Ottawa, Ottawa, Ontario.

Dodd, N. L., J. W. Gagnon, A.L. Manzo, and R. E. Schweinsburg. 2007. Video surveillance to assess highway underpass use by elk in Arizona. The Journal of Wildlife Management 71: 637-645.

Dodd, K. J., W. J. Barichivich, and L. L. Smith. 2004. Effectiveness of a barrier wall and culverts in reducing wildlife mortality on a heavily traveled highway in Florida. Biological Conservation 118:619–631.

Eads, B. 2013. Behavioral responses of two syntopic snakes (*genus Thamnophis*) to roads and culverts. Master of Science thesis. Purdue University, Fort Wayne, Indiana.

Eads, B., L. Hayter, and B. Kingsbury. 2012. Road responses and culverts as a tool for increasing habitat connectivity for the federally threatened Copper-bellied Watersnake (*Nerodia erythrogaster neglecta*) and other wetland snakes. Conference abstract, World Congress of Herpetology. Victoria, BC.

Eastern Foxsnake Recovery Team. 2010. Recovery strategy for the Eastern Foxsnake (*Pantherophis gloydi*) – Carolinian and Georgian Bay populations in Ontario. Page vi + 39. Ontario Recovery Strategy Series. Ontario Ministry of Natural Resources, Peterborough, Ontario.

Eberhardt, E., S. Mitchell, and L. Fahrig. 2013. Road kill hotspots do not effectively indicate mitigation locations when past road kill has depressed populations. The Journal of Wildlife Management 77:1353–1359.

EcoPlans. 2006. Environmental guide for wildlife in the Oak Ridges Moraine. Environmental Standards and Practices. Ontario Ministry of Transportation.

Eigenbrod, F., S. J. Hecnar, and L. Fahrig. 2008a. Accessible habitat: an improved measure of the effects of habitat loss and roads on wildlife populations. Landscape Ecology 23:159–168.

Eigenbrod, F., S. J. Hecnar, and L. Fahrig. 2008b. The relative effects of road traffic and forest cover on anuran populations. Biological conservation 141:35–46.

Ernst, C.H., and J.E. Lovich. 2009. Turtles of the United States and Canada. Second edition. Johns Hopkins University Press.

Faggyas, S., and M. Puky. 2012. Construction and preliminary monitoring results of the first ACO Wildlife Pro amphibian mitigation system on roads in Hungary. Állattani Közlemények 97: 85–93.

Fahrig, L., J. H. Pedlar, S. E. Pope, P. D. Taylor, and J. F. Wegner. 1995. Effect of road traffic on amphibian density. Biological Conservation 73:177–182.

Farmer, R. G., and R.J. Brooks. 2012. Integrated risk factors for vertebrate roadkill in southern Ontario. The Journal of Wildlife Management 76:1215-1224.

Fenech, A., B. Taylor, R. Hansell, and G. Whitelaw. 2001. Major road changes in southern Ontario 1935–1995: Implications for protected areas. Available from http://www.utoronto.ca/imap/papers/road_changes.htm (accessed April 10, 2014).

Findlay, C. S., and J. Houlahan. 1997. Anthropogenic correlates of species richness in southeastern Ontario wetlands. Conservation Biology 11:1000–1009.

Ford, A. T., A. P. Clevenger, and K. Rettie. 2010. The Banff Wildlife Crossings Project: an international public-private partnership. Pages 157–173 in J.P. Beckmann, A.P. Clevenger, M.P. Huijser, J.A. Hilty, editors. Safe passages—highways, wildlife and habitat connectivity. Island Press, Washington, DC. Island Press, Washington, DC.

Fortney, A. N., R. G. Poulin, J.A. Martino, D.L. Parker, and C.M. Somers. 2013. Proximity to hibernacula and road type influence potential road mortality of snakes in southwestern Saskatchewan. Canadian Field-Naturalist 126:194-203.

Garrah, E. 2012. Wildlife road mortality on the 1000 islands parkway in southeastern Ontario: peak times, hot spots, and mitigation using drainage culverts. Master of Environmental Studies thesis. Queen's University, Kingston, Ontario.

Gartner Lee, and EcoPlans. 2009. 407 East individual Environmental Assessment and preliminary design study: Natural environmental (terrestrial) impact assessment of the recommended design. Report to the Ministry of Transportation.

Gartshore, R. G., M. Purchase, R. I. Rook, and L. Scott. 2005. Bayview Avenue extension, Richmond Hill, Ontario, Canada habitat creation and wildlife crossings in a contentious environmental setting: a case study. Pages 55-76 in C.L. Irwin, P. Garrett, and K.P. McDermott, editors. Proceedings of the 2005 International Conference on Ecology and Transportation, Raleigh, NC.: Center for Transportation and the Environment, North Carolina State University.

Gates, J. E., and J. L. J. Sparks. 2012. An investigation into the use of road drainage structures by wildlife in Maryland, USA. Human-Wildlife Interactions 6:311–326.

Gibbs, J. P., and W. G. Shriver. 2002. Estimating the effects of road mortality on turtle populations. Conservation Biology 16:1647–1652.

Gibbs, J. P., and W. G. Shriver. 2005. Can road mortality limit populations of pool-breeding amphibians? Wetlands Ecology and Management 13:281–289.

Gillingwater, S. D. 2011. Recovery strategy for the Queensnake (*Regina septemvittata*) in Ontario. Page vi + 34. Ontario Recovery Strategy Series. Ontario Ministry of Natural Resources, Peterborough, Ontario.

Glenside Ecological Services. 2011. Community mobilization and habitat modelling. Pages 24 – 109. Species at Risk. Ontario Ministry of Natural Resources, Haliburton Highlands Land Trust.

Griffin, K. 2005. Use of low fencing with aluminum flashing as a barrier for turtles. Pages 366-368 in C.L. Irwin, P. Garrett, and K.P. McDermott, eds. Proceedings of the 2005 International Conference on Ecology and Transportation, Raleigh, NC: Center for Transportation and the Environment, North Carolina State University.

Gunson, K. E., G. Mountrakis, and L. J. Quackenbush. 2011. Spatial wildlife-vehicle collision models: A review of current work and its application to transportation mitigation projects. Journal of Environmental Management 92:1074–1082.

Gunson, K. E., and F. W. Schueler. 2012. Effective placement of road mitigation using lessons learned from turtle crossing signs in Ontario. Ecological Restoration 30:329–334.

Gunson, K.E., Ireland, D., Schueler, F.W. 2012. A tool to prioritize high-risk road mortality locations for wetland-forest herpetofauna in southern Ontario, Canada. NorthWestern Journal of Zoology 8:409-413.

Gunson, K. E., D. Lesbarrères, and D. C. Seburn. 2013. Monitoring turtle movements across highways 7 and 41: Final report. Unpublished report to Highway Infrastructure Innovation Funding Program. Ontario Ministry of Transportation.

Gunson, K.E., and F.Z. Teixeira. 2015. Road-wildlife mitigation planning can be improved by identifying the patterns and processes associated with wildlife-vehicle collisions. Pages 101-019 in R. van der Ree, D. Smith, C. Grilo, editors. Handbook of Road Ecology. Wiley-Blackwell Publications.

Hagood, S., and M. J. Bartels. 2008. Use of existing culverts by eastern box turtles (*Terrapene c. carolina*) to safely navigate roads. Pages 169–170 in J. C. Mitchell, R. E. J. Brown, and B. Bartholomew, editors. Urban Herpetology, Society for the Study of Amphibians and Reptiles.

Hardy, A., S. Lee, and A.F. Al-Kaisy. 2006. Effectiveness of animal advisory messages on dynamic message signs as a speed reduction tool: case study in Rural Montana. Transportation Research Record: Journal of the Transportation Research Board 1973:64-72.

Haxton, T. 2000. Road mortality of Snapping Turtles, *Chelydra serpentina*, in central Ontario during their nesting period. Canadian Field-Naturalist 114:106–110.

Helferty, N. J. 2002. Natural Heritage Planning for amphibians and their habitats with reference to populations on the south slope of the Oak Ridges Moraine. Page 71. Supplementary Report for Oak Ridges Moraine Richmond Hill, Ontario Municipal Board Hearing. Save the Rouge Valley System Inc. and the City of Toronto.

Hels, T., and E. Buchwald, 2001. The effect of road kills on amphibian populations. Biological Conservation 99: 331–340.

Heyer, W. R., M. A., Donnelly, R. W. McDiarmid, L. C. Hayek, and M. S. Foster (eds). 1994. Measuring and monitoring biological diversity. Standard methods for amphibians. Smithsonian Institution Press, Washington, D. C. 364 pp.

Holling, C. S. 1978. Adaptive environmental assessment and management. Adaptive environmental assessment and management. Available from http://www.cabdirect.org/abstracts/19800666996.html (accessed April 10, 2014).

Huijser, M. P., P. T. McGowen, J. Fuller, A. Hardy, and A. Kociolek. 2007. Wildlife-vehicle collision reduction study: report to congress. U.S. Department of Transportation, Federal Highway Administration, Washington, DC, USA. Available from http://trid.trb.org/view.aspx?id=884083 (accessed April 10, 2014).

IUCN. 2010. IUCN Red list of threatened species 2010. International Union for the Conservation of Nature (IUCN), Gland, Switzerland. [online] URL: http://www.iucn.org

Iuell, B. 2003. COST 341: Wildlife and Traffic: A European handbook for identifying conflicts and designing solutions. Utrecht, The Netherlands: KNNV Publishers.

Jackson, S. D., and T. F. Tyning. 1989. Effectiveness of drift fences and tunnels for moving spotted salamanders *Ambystoma maculatum* under roads. Pages 93–99 in T. E. S. Langton, editor. Amphibians and Roads, Proceedings of the toad tunnel conference. ACO Polymer Products, Shefford, England. Available from http://works.bepress.com/cgi/viewcontent.cgi?article=1017andcontext=scott_jackson (accessed April 10, 2014).

Jackson, S. D. 1996. Underpass systems for amphibians. In G. L. Evink, P. Garrett, D. Zeigler, and J. Berry, editors. Trends in Addressing Transportation Related Wildlife Mortality: Proceedings of the transportation related wildlife mortality seminar. State of Florida Department of Transportation, Environmental Management Office. Tallahassee, FL. FL-ER-58-96.

Jackson, S. D., and M. N. Marchand. 1998. Use of a prototype tunnel by Painted Turtles, *Chrysemys picta*. Unpublished report.

Jackson, S. D. 2003. Ecological considerations in the design of river and stream crossings. Page 10 in C. L. Irwin, P. Garrett, and K. P. McDermott, editors. 2003 Proceedings of the International Conference on Ecology and Transportation. Center for Transportation and the Environment, North Carolina State University, Raleigh, North Carolina. Available from http://works.bepress.com/scott_jackson/11/ (accessed April 10, 2014).

Jackson, S. D., D. J. Smith, and K. E. Gunson. 2015. Sharing the road: Mitigating road impacts on small vertebrates. Pages 177-208 in K. M. Andrews, P. Nanjappa, and S. P. D. Riley, editors. Roads and Ecological Infrastructure: Concepts and Applications for Small Animals. Johns Hopkins University Press, Baltimore, MD.

James, P.W., R.S. Wagner, K.A. Ernest, D. Beck, and J. Irwin. 2011. Monitoring fish and low-mobility vertebrates along a major mountain highway: a snapshot before construction of I-90 wildlife crossing structures. Pages 527-533 in P.J. Wagner, D. Nelson, and E. Murray, editors. Proceedings of the 2011 International Conference on Ecology and Transportation. Center for Transportation and the Environment, North Carolina State University, Raleigh, NC.

Jochimsen, D. M., C. R. Peterson, K. M. Andrews, and J. W. Gibbons. 2004. A literature review of the effects of roads on amphibians and reptiles and the measures used to minimize those effects. US Forest Service report. 79 pp.

Jacobson, S. L. 2007. An alternative to the openness "ratio" using underpass physical attributes and behavioral implications of deer vision and hearing capabilities. Page 605 in C.L. Irwin, D. Nelson, and K.P. McDermott, editors.Proceedings of the 2007 International Conference on Ecology and Transportation. Raleigh, NC.: Center for Transportation and the Environment, North Carolina State University.

Joyce, T. L., and S. P. Mahoney. 2001. Spatial and temporal distributions of moose-vehicle collisions in Newfoundland. Wildlife Society Bulletin 29:281–291.

Karraker, N. E., and J. P. Gibbs. 2011. Contrasting road effect signals in reproduction of long-versus short-lived amphibians. Hydrobiologia 664:213–218.

Kaye, D. R., K. M. Walsh, E. L. Rulison, and C. C. Ross. 2005. Spotted Turtle use of a culvert under relocated Route 44 in Carver, Massachusetts. Pages 426-432 in C.L. Irwin, P. Garrett, and K.P. McDermott, editors. Proceedings of the 2005 International Conference on Ecology and Transportation. Raleigh, NC.: Center for Transportation and the Environment, North Carolina State University.

Kintsch, J., and P. C. Cramer. 2011. Permeability of existing structures for terrestrial wildlife: A passage assessment system. WA-RD 777.1. Washington State Department of Transportation, Olympia, WA.

Kintsch, J., K. E. Gunson, and T. A. Langen. 2015. Engaging the public through public education and citizen science. Pages 94-110 in K. M. Andrews, P. Nanjappa, and S. P. D. Riley, editors. Roads and Ecological Infrastructure: Concepts and Applications for Small Animals. Johns Hopkins University Press, Baltimore, MD.

Konze, K. and McLaren, M. 1997. Wildlife monitoring programs and inventory techniques for Ontario. Ontario Ministry of Natural Resources. Northeast Science and Technology. Technical Manual TM-009. 139 pp.

Kraus, T., B. Hutchinson, S. Thompson, and K. Prior. 2010. Recovery strategy for the Gray Ratsnake (*Pantherophis spiloides*) – Carolinian and Frontenac Axis populations in Ontario. Page vi + 23. Ontario Recovery Strategy Series. Ontario Ministry of Natural Resources, Peterborough, Ontario.

Laidig, K. J., and D. M. Golden. 2004. Assessing Timber Rattlesnake movements near a residential development and locating new hibernacula in the New Jersey Pinelands. Unpublished report to the Pinelands Commission, New Lisbon, NJ. Available from http://199.20.64.195/pinelands/images/pdf%20files/final%20Sanctuary%20report.pdf (accessed April 10, 2014).

Lang, J. W. 2000. Blanding's turtles, roads and culverts at Weaver Dunes. File report on culvert utilization, The Nature Conservancy and Minnesota Department of Natural Resources, Contract# CFMS AO 9492.

Langen, T. A., A. Machniak, E. K. Crowe, C. Mangan, D. F. Marker, N. Liddle, and B. Roden. 2007. Methodologies for surveying herpetofauna mortality on rural highways. The Journal of Wildlife Management 71:1361–1368.

Langen, T. A. 2011. Design considerations and effectiveness of fencing for turtles: three case studies along northeastern New York State highways. Pages 521-532 in P.J. Wagner, D. Nelson, and E. Murray, editors. Proceedings of the 2011 International Conference on Ecology and Transportation. Center for Transportation and the Environment, North Carolina State University, Raleigh, NC.

Langton, T. 2014. Safe passage for all: A review of the adoption of surface tunnels and stop channels on roadways for wildlife/road impact mitigation worldwide. Report prepard for ACO Tunnel Safety Review July 2014.

Lawrence, D.P. 2003. Environmental Impact Assessment: Practical solutions to recurrent problems. John Wiley and Sons, Hoboken, New Jersey.

Lesbarrères, D., T. Lodé, and J. Merilä. 2004. What type of amphibian tunnel could reduce road kills? Oryx 38:220–223.

Lesbarrères, D., and L. Fahrig. 2012. Measures to reduce population fragmentation by roads: what has worked and how do we know? Trends in Ecology and Evolution 27:374–380.

Lininger, M., and M. Perlik. 2014. Effectiveness of the TRU-88 wildlife roadway crossing culverts and exclusion fencing. Unpublished report to the Ohio Department of Transportation.

MacKinnon, C. A., L. A. Moore, R. J. Brooks, G. Nelson, T. Nudds, M. Beveridge, and B. Dempster. 2005. Why did the reptile cross the road? Landscape factors associated with road mortality of snakes and turtles in the southeastern Georgian Bay area. Pages 18–25 Parks and Research Forum. Available from http://casiopa.mediamouse.ca/wp-content/uploads/2010/05/PRFO-2005-Proceedings-p153-166-MacKinnon-Moore-and-Brooks.pdf (accessed February 27, 2014).

MacNeil, J. E., G. Dharmarajan, and R.N. Williams. 2011. Salamarker: A code generator and standardized marking system for use with visible implant elastomers. Herpetological Conservation and Biology 6:260-265.

Marchand, M. N., and J. A. Litvaitis. 2004. Effects of habitat features and landscape composition on the population structure of a common aquatic turtle in a region undergoing rapid development. Conservation Biology 18:758–767.

Marsh, D., R. Page, T. Hanlon, R. Corritone, E. Little, D. Seifert, and P. Cabe, 2008. Effects of roads on patterns of genetic differentiation in red-backed salamanders, *Plethodon cinereus*. Conservation Genetics 9: 603–613.

McDiarmid, R.W., M.S. Foster, C. Guyer, J.W. Gibbons, and N. Chernoff (Eds.). 2012. Reptile Biodiversity: Standard Methods for Inventory and Monitoring. Berkeley: University of California Press.

Meese, R.G., F.M. Shilling, and J.F. Quinn. 2009. Wildlife crossings guidance manual. Report to the California Department of Transportation. Sacramento, CA. 111 pp.

Merrow, J. 2007. Effectiveness of amphibian mitigation measures along a new highway. Pages 370-376 n C.L. Irwin, D. Nelson, and K.P. McDermott, editors. Proceedings of the 2007 International Conference on Ecology and Transportation. Raleigh, NC.: Center for Transportation and the Environment, North Carolina State University.

Ontario Ministry of Natural Resources. 2011. Massasauga search protocol where site alteration will occur in gestation habitat for Hwy 69/400 ESA authorization requirements. Ontario Ministry of Natural Resources, Parry Sound Sudbury District. 5pp.

Ontario Ministry of Natural Resources. 2013. Reptile and Amphibian Exclusion Fencing: Best Practices, Version 1.0. Species at Risk Branch technical note. Prepared for the Ontario Ministry of Natural Resources, Peterborough, Ontario. 11 pp. Available from http://files.ontario.ca/environment-and-energy/species-at-risk/mnr_sar_tx_rptl_amp_fnc_en.pdf (accessed February 26, 2014).

Ontario Ministry of Transportation. 2012. Wildlife Habitat Awareness Signs. Policy Number 2012-03. Traffic Office, St. Catharines, Ontario.

Ontario Wood Turtle Recovery Team. 2010. Recovery strategy for the Wood Turtle (*Glyptemys insculpta*) in Ontario. Page vi + 25. Ontario Recovery Strategy Series. Ontario Ministry of Natural Resources, Peterborough, Ontario.

Ottburg, F. G. W. A., and E. A. van der Grift. 2013. Effectiveness of road mitigation for preserving a common toad population. Proceedings of the 2013 International Conference on Ecology and Transportation. Poster. Retrieved from http://www.icoet.net/ICOET_2013/proceedings.asp.

Pagnucco, K. S., C. A. Paszkowski, and G. J. Scrimgeour. 2011. Using cameras to monitor tunnel use by Long-toed Salamanders (*Ambystoma macrodactylum*): an informative, cost-efficient technique. Herpetological Conservation and Biology 6:277–286.

Pagnucco, K. S., C. A. Paszkowski, and G. J. Scrimgeour. 2012. Characterizing movement patterns and spatio-temporal use of under-road tunnels by long-toed salamanders in Waterton Lakes National Park, Canada. Copeia 2012:331–340.

Painter, M. L., and M. F. Ingraldi. 2007. Use of simulated highway underpass crossing structures by flat-tailed horned lizards (*Phrynosoma mcallii*). Final Report 594. Arizona Department of Transportation, Phoenix, AZ.

Parent, C and R. Black. 2006. Construction of artificial gestation sites for the Massasauga, Eastern Georgina Bay Population. Unpublished report submitted to the Ministry of Natural Resources.

Parren, S. G. 2013. A twenty-five year study of the Wood Turtle (*Glyptemys insculpta*) in Vermont: Movements, behavior, injuries, and death. Herpetological Conservation and Biology 8:176–190.

Paterson, J. E., B.D. Steinberg, and J.D. Litzgus. 2013. Not just any old pile of dirt: evaluating the use of artificial nesting mounds as conservation tools for freshwater turtles. Oryx 47:607-615.

Patrick, D.A., and Gibbs, J.P. 2009. Snake occurrences in grassland associated with road versus forest edges. Journal of Herpetology 43:716-720.

Patrick, D. A., C. M. Schalk, J. P. Gibbs, and H. W. Woltz. 2010. Effective culvert placement and design to facilitate passage of amphibians across roads. Journal of Herpetology 44:618–626.

Patrick, D. A., J. P. Gibbs, V. D. Popescu, and D. A. Nelson. 2012. Multi-scale habitat-resistance models for predicting road mortality "hotspots" for turtles and amphibians. Herpetological Conservation and Biology 7:407–426.

Paulson, D. J. 2010. Evaluating the effectiveness of road passage structures for freshwater turtles in Massachusetts. Master of Science thesis. University of Massachusetts, Amherst, Amherst, MA.

Pojar, T.M., D. F. Reed, and T.C. Reseigh. 1975. Effectiveness of a lighted, animated deer crossing sign. Journal of Wildlife Management 39:87-91.

Puky, M., J. Farkas, and M. T. Ronkay. 2007. Use of existing mitigation measures by amphibians, reptiles, and small to medium-size mammals in Hungary: crossing structures can function as multiple species-oriented measures. Pages 521-530 in C.L. Irwin, D. Nelson, and K.P. McDermott, editors. Proceedings of the 2007 International Conference on Ecology and Transportation, . Raleigh, NC.: Center for Transportation and the Environment, North Carolina State University.

Puky, M., B. Mester, and T. Mechura. 2013. How much does size matter? Tunnel size significantly influence amphibian crossings at Parassapuszta, Hungary according to mid-term monitoring used to delineate mitigation measure improvement plans. Proceedings of the 2013 International Conference on Ecology and Transportation. Available from http://www.icoet.net/ICOET_2013/proceedings-poster-sessions.asp.

Reconyx. 2010. HyperFireTM instruction manual. Holman, Wisconsin.

Reed, D. F., T. D. I. Beck, and T. N. Woodward. 1979. Regional deer-vehicle accident research. FHWA-RD-79-11. US Department of Transportation, Federal Highway Administration, Washington, DC.

Riley, J. L., J. H. Baxter-Gilbert, and J. D. Litzgus. 2013. A trifecta of insight: merging field biology, infrastructure planning and aboriginal community knowledge to design successful highway mitigation for at-risk reptiles. Proceedings of the 2013 International Conference on Ecology and Transportation. Available from http://www.icoet.net/ICOET_2013/proceedings.asp (accessed February 27, 2014).

Roberts, D. 2010. Mitigation of Red-sided Garter Snake mortality on provincial trunk Highway #17 at the Narcisse snake dens: A progress report. Unpublished report to Manitoba Conservation.

Robertson, C., N. Richards and M. Karch. 2013. Standard turtle handling and research practices and protocols. Prepared for the Ontario Turtle Conservation Group.

Robson, L. E., and G. Blouin-Demers. 2013. Eastern Hognose Snakes (*Heterodon platirhinos*) avoid crossing paved roads, but not unpaved roads. Copeia 2013:507–577.

Roedenbeck, I. A., L. Fahrig, C. S. Findlay, J.E. Houlahan, J. A. G. Jaeger, N. Klar, S. Kramer- Schadt and E. A. van der Grift. 2007. The Rauischholzhausen agenda for road ecology. Ecology and Society 12: 11. [online] URL: http://www.ecologyandsociety.org /vol12/iss1/art11/

Rogers, L., D. Stimson, K. Holden, D. Kay, D. Kaye, R. McAdow, B. Metcalfe, B. Windmiller, and N. Charney. 2009. Wildlife tunnels under a busy, suburban Boston roadway. Pages 102-115 in P.J. Wagner, D. Nelson, and E. Murray, editors. Proceedings of the 2009 International Conference on Ecology and Transportation. Raleigh, NC: Center for Transportation and the Environment, North Carolina State University.

Rosen, P. C., and C. H. Lowe. 1994. Highway mortality of snakes in the Sonoran Desert of southern Arizona. Biological Conservation 68:143–148.

Rouse, J. 2005. Monitoring the Eastern Massasauga and Eastern Hog-nosed Snake along the Highway 69 Extension. Ontario Ministry of Natural Resources, Parry Sound, ON.

Rouse, J. D., R. J. Willson, R. Black, and R. J. Brooks. 2011. Movement and spatial dispersion of *Sistrurus catenatus* and *Heterodon platirhinos*: implications for interactions with roads. Copeia 2011: 443–456.

Row, J. R., G. Blouin-Demers, and P. J. Weatherhead. 2007. Demographic effects of road mortality in Black Ratsnakes (*Elaphe obsoleta*). Biological Conservation 137:117–124.

Rytwinski, T., and L. Fahrig. 2012. Do species life history traits explain population responses to roads? A meta-analysis. Biological Conservation 147:87–98.

Santos, S. M., F. Carvalho, and A. Mira. 2011. How long do the dead survive on the road? Carcass persistence probability and implications for road-kill monitoring surveys. PloS one [electronic resource] 6:e25383–e25383.

Schmidt, B. R., and S. Zumbach. 2008. Amphibian road mortality and how to prevent it: A review. Pages 157–167 in J. C. Mitchell, R. E. Jung Brown, and B. Bartolomew, editors. Urban Herpetology. Society for the Study of Amphibians and Reptiles.

Seburn, D. C. 2007. Recovery strategy for species at risk turtles in Ontario. Draft Report for the Ontario Multi-species Turtles at Risk Recovery Team, Ontario, Canada.

Semlitsch, R. D. 2008. Differentiating migration and dispersal processes for pond-breeding amphibians. Journal of Wildlife Management 72:260-267.

Shine, R., M. Lemaster, M. Wall, T. Langkilde, and R. Mason. 2004. Why did the snake cross the road? Effects of roads on movement and location of mates by garter snakes (*Thamnophis sirtalis parietalis*). Ecology and Society 9:9.

Slater, F. M. 2002. An assessment of wildlife road casualties–the potential discrepancy between numbers counted and numbers killed. Web Ecology 3:33–42.

Smith, D. J. 2003. Monitoring wildlife use and determining standards for culvert design. Unpublished report to Florida Department of Transportation.

Smith, D. J., D. Marsh, K. E. Gunson, and S. Tonjes. 2015. Monitoring and adaptive management of road impacts and mitigation. Pages 240-261 in K. M. Andrews, P. Nanjappa, and S. P. D. Riley, editors. Roads and Ecological Infrastructure: Concepts and Applications for Small Animals. Johns Hopkins University Press, Baltimore, MD.

Smith, D. J., and R. F. Noss. 2011. A reconnaissance study of actual and potential wildlife crossing structures in Central Florida, final report. UCF-FDOT Contract No. BDB-10. Florida Department of Transportation.

Steen, D. A., and J. P. Gibbs. 2004. Effects of roads on the structure of freshwater turtle populations. Conservation Biology 18: 1143–1148.

Steen, D.A., J.P. Gibbs, K.A. Buhlmann, J.L. Carr, B.W. Compton, J.D. Congdon, J.S. Doody, J.C. Godwin, K.L. Holcomb, D.R. Jackson, F.J. Janzen, G. Johnson, M.T. Jones, J.T. Lamer, T. Langen, M.V. Plummer, J.W. Rowe, R.A. Saumure, J.K. Tucker, and D.S. Wilson. 2012. Terrestrial habitat requirements of nesting freshwater turtles. Biological Conservation 150:121–128.

Taylor, B. D., and R. L. Goldingay. 2003. Cutting the carnage: wildlife usage of road culverts in north-eastern New South Wales. Wildlife Research 30:529–537.

Taylor, P. D., L. Fahrig, K. Henein, and G. Merriam. 1993. Connectivity is a vital element of landscape structure. Oikos 68:571–573.

Torres, A., C. Palacín, J. Seoane, and J.C. Alonso. 2011. Assessing the effects of a highway on a threatened species using Before–During–After and Before–During–After-Control–Impact designs. Biological conservation 144, 2223–2232.

TRCA. 2013. Heart Lake Road Ecology Volunteer Monitoring Project, Phase II. Toronto and Region Conservation Authority (TRCA), Toronto, Ontario. Available from http://www.trca.on.ca/dotAsset/187823.pdf

van der Grift, E., F. Ottburg, and R. Snep. 2009. Monitoring wildlife overpass use by amphibians: Do artificially maintained humid conditions enhance crossing rates? Pages 341-347 in P.J. Wagner, D. Nelson, and E. Murray, editors. Proceedings of the 2009 International Conference on Ecology and Transportation. Raleigh, NC: Center for Transportation and the Environment, North Carolina State University.

van der Grift, E. A., S. Findlay, R. van der Ree, L. Fahrig, J. Houlahan, L. F. Madriñan, J.A.G. Jaeger, Nina Klar, and L. Olson. 2013. Evaluating the effectiveness of road mitigation measures. Biodiversity Conservation DOI 10.1007/s10531-012-0421-0.

van der Ree R., J.A.G. Jaeger, T. Rytwinski, and E. van der Grift. 2015. Good science and experimentation are needed in road ecology. Pages 71-81 in: R. van der Ree, C. Grilo, and D. Smith, editors. Handbook of Road Ecology. Wiley Publications.

van Gelder, J.J. 1973. A quantitative approach to the mortality resulting from traffic in a population of *Bufo bufo* L. Oecologia 13: 93-95.

Vos, C. C., and J. P. Chardon. 1998. Effects of habitat fragmentation and road density on the distribution pattern of the moor frog *Rana arvalis*. Journal of Applied Ecology 35:44–56.

Whitelock, C. 2014. 2013 Long Point causeway monitoring and adaptive management report. Unpublished report.

Willson, R. J., and G. M. Cunnington. 2014. DRAFT Recovery strategy for the Blue Racer (*Coluber constrictor foxii*) in Ontario. Page vi + 35. Ontario Recovery Strategy Series. Prepared for the Ontario Ministry of Natural Resources, Peterborough, Ontario.

Willson, R.J. 2005. Artificial hibernation site construction for Eastern Massasaugas in Georgian Bay. Report submitted to the Ontario Ministry of Natural Resources.

Wilson, J.S. and S. Topham. 2009. The negative effects of barrier fencing on the Desert Tortoise (*Gopherus agassizii*) and non-target species: is there room for improvement? Contemporary Herpetology 2009:1-4.

Wind, E. 2014. Amphibian road surveys and mitigation assessments at Wake Lake on Vancouver Island in 2012. Unpublished report to the BC Ministry of Transportation and Infrastructure.

Woltz, H. W., J. P. Gibbs, and P. K. Ducey. 2008. Road crossing structures for amphibians and reptiles: informing design through behavioral analysis. Biological Conservation 141:2745–2750.

Yannis, I. 2011. Effectiveness of road barriers and underpasses for reptiles: The case of Milos viper (*Macrovipera schweizeri*). Proceedings of the 2011 IENE conference.

Yorks, D. T., P. R. Sievert, and D. J. Paulson. 2011. Experimental tests of tunnel and barrier options for reducing road mortalities of freshwater turtles. Pages 1034 in P.J. Wagner, D. Nelson, and E. Murray, editors. Proceedings of the 2011 International Conference on Ecology and Transportation. Center for Transportation and the Environment, Raleigh, NC.

9 APPENDICES

Appendix A: SAR Amphibian and Reptile Habitat Use and Movements

General summary of seasonal habitat use, general movement distances within and between habitat and when this occurs for species at risk amphibians and reptiles in Ontario. Bold text indicates high risk of road mortality for the species during months indicated. Summary based on review of COSEWIC reports, Recovery Strategies, ESA Habitat Regulations, and ESA Habitat Descriptions. All of the COSEWIC reports that were used to inform this table are listed in the references section of the document. In some cases information was obtained from other sources and is indicated. More detailed summaries should be conducted for each target species on a project specific basis.

Species	Scientific name	Habitat		Home range	Movement	When movement occurs
		Spring and Summer	Winter			
Salamander						
Jefferson Salamander	*Ambystoma jeffersonianum*	Spring Breeding habitat: ephemeral ponds or other ponds without fish (Helferty 2002); Summer: Deciduous or mixed upland forest	Deep rock fissures and burrows below the frost line in upland forest habitat	Generally within 300 m of wetland	Adults may move up to 1 km, usually 300 m from breeding habitat; Juveniles up to 100 m	Explosive adult breeding migration from late March to late April; juvenile dispersal in July and August
Toad						
Fowler's Toad	*Anaxyrus fowleri*	Spring Breeding habitat: shallow ponds, sandy lakeshore bays and wetlands, ephemeral ponds, bedrock pools; Summer: Sand dunes, sand bars and beaches along Lake Erie shore	Burrows in moist sand along Lake Erie shore to just above water table and below frost line	Within a few hundred metres of of Lake Erie shoreline	Usually only move a few hundred metres during summer; seasonal migrations up to 1 km are typical	Adult breeding migration in May and June; juvenile dispersal in August and September
Turtles						
Blanding's Turtle	*Emydoidea blandingii*	Eutrophic, shallow lakes, ponds, slow-flowing rivers, streams, marshes, bog, open fens with basking sites and thick vegetation, upland woods; nest in loose soils (including road shoulders)	Permanent wetlands and other bodies of water, occasionally temporary ponds (Glenside Ecological Services 2011)	Up to 3 km^2	Typical adult movement to and from hibernation and nesting sites is 2 km, although longer migrations have been documented; hatchlings move 400m to water (M. Gartshore, F. Schueler pers. comm.)	Spring migration from hibernation sites to summer habitat (April – early May); Adult nesting migration from late May to early July; Inter-wetland movements in the summer; hatchling and adult overwintering movements in fall months

Species	Scientific name	Habitat		Home range	Movement	When movement occurs
		Spring and Summer	Winter			
Eastern Musk	*Sternotherus odoratus*	Shallow water with abundant floating and submerged vegetation; nest near water in direct sun	Similar to summer; buried in 30 cm of mud	Confined to single bodies of water	Overland movement limited; tend to nest at shorelines	Adult nesting migration from June to early July
Snapping Turtle	*Chelydra serpentina*	Slow-moving water with soft mud substrate and dense vegetation; nest on sand and gravel banks, roads (Patrick et al. 2012, M. Karch, F. Schueler pers. comm.)	Under floating vegetative mats, logs, overhanging banks in streams and lakes, or buried in mud	Up to 0.09 km^2	Adults move from 0.5km up to 5 km to and from hibernation site and in search of nesting sites	Spring migration from hibernation sites to summer habitat in April – early May; Adult nesting migration from late May to early July; hatchlings move to water in early fall
Spiny Softshell	*Apalone spinifera*	Rivers or lakes with shallow water and muddy or sandy substrate, deep pools, riffles, and inlets; nest in sunny areas with fine gravel or sandy substrate close to water	deep pools in rivers (>1 m in depth)	Confined to one body of water	Rarely leave water; nest close to water	Adult nesting from June to early July
Spotted Turtle	*Clemmys guttata*	Slow-moving or still shallow water wetlands with aquatic vegetation (fens, bogs, marshes and rocky pools); upland woods used for aestivation and movement; Mate in woodland pools connected to hibernacula; nest in sunny upland locations (Glenside Ecological Services 2011, Patrick et al. 2012)	Rock caverns in lakes, under hummocks and in burrows in sphagnum-rich wetlands, and in root cavities in swamps	Home range: 0.04 km^2	Adults can move on average 1120 m to and from hibernation site, in search of nesting site, and during inter- wetland movements; move on average 250 m from wetland to nest (Joyal et al. 2001).	Adult nesting migration from late May to June; inter-wetland movements in summer; spring and fall migration from and to hibernation sites

Species	Scientific name	Habitat		Home range	Movement	When movement occurs
		Spring and Summer	Winter			
Northern Map Turtle	*Graptemys geographica*	Well-oxygenated, shallow rivers, streams, creeks, and lakes with basking sites adjacent to deep water; nest in soft sand beaches or soil in full sun	Bottom of lakes or rivers in deep hollows	Home range: 1.2 – 13.5 km^2 (usually within waterways)	Travel inland in search of nesting sites 35-100 m from water	Adult nesting season in early June – late July; Migration to and from hibernation sites in April - early May and late August - October
Wood Turtle	*Glyptemys insculpta*	Clear-water streams with sand or gravel substrate, alder thickets, upland forested areas; nest on sand or gravel-sand beaches and farm fields, road shoulders (Glenside Ecological Services 2011)	Bottom of deep pools in streams	Home range up to 1.5 km^2	Female adults move to nesting sites; typical home range length of 2 km; extensive movement in upland habitats throughout active season, typically within 300 m of water (K. Barrett pers. comm.)	Adult nesting migration from late May to early July
Snakes						
Blue Racer	*Coluber constrictor foxii*	Edge habitat, open fields, woodlands with sunny vegetation piles or rocks; nests in decaying organic matter, logs and under rocks in full sun	Crevices in Pelee Island's limestone plain and in piles of rock and soil	Confined to Pelee Island	Adults travel up to 2.7 km from hibernacula to find mates, nesting locations; hatchlings cross roads from nests	Adult mating season in April and May; neonate dispersal in July and August; movement to hibernaculum in September and October
Butler's Garter-snake	*Thamnophis butleri*	Open prairies, grasslands, old fields and other open habitats; bask on roads; live birth under cover	Small mammal burrows, ant mounds, rocky dikes, possibly crayfish burrows (M. Gartshore pers. comm.)	Within specialized habitat confined by roads	Most adults only move a few hundred metres from hibernacula in active season, but some move > 1 km	Adult mating season in April and May; neonate dispersal in July and August; movement to hibernaculum in September and October

Species	Scientific name	Habitat		Home range	Movement	When movement occurs
		Spring and Summer	Winter			
Eastern Foxsnake, Georgian Bay population	*Pantherophis gloydi*	Open rock barrens, coastal meadow marshes, woodlands and forest clearings; nest in decaying vegetation piles, rock crevices	Granite or limestone fissures	3.5 km linear home range	Move extensively throughout active season to foraging, nesting and hibernation sites; Carolinian snakes move through vegetated corridors to find habitat	Adult mating season in April and May; neonate dispersal in July and August; movement to hibernaculum in September and October
Eastern Foxsnake, Carolinian population	*Pantherophis gloydi*	Wetlands complexes, unforested, early successional lands, hedgerows, riparian zones, woodlands; nest in decaying vegetation piles and fallen trees, road-side burrows, under concrete slabs	limestone bedrock fissures, mammalian burrows, tree root crevices, various man-made features	Up to 1.5 km linear home range, but varies with extent of habitat available		
Eastern Hog-nosed Snake	*Heterodon platirhinos*	Sandy areas or well-drained soil in open forests, forest edges or brushy habitats; sometimes wetlands close to conifer plantations; nest in south-facing open areas, under driftwood, or rock crevices in Shield (Glenside Ecological Services 2011)	Hibernate in upland burrows excavated by the snake, root cavities or abandoned mammal burrows (Glenside Ecological Services 2011)	Home range > 1 km^2	Very mobile throughout season; adults can move >4 km from hibernacula; max. adult movement 6.2 km	Adult mating season in spring and late summer; neonate dispersal and movement to hibernaculum in fall
Eastern Ribbon-snake	*Thamnophis sauritus*	Wetlands, shorelines, sloughs, and swamps. Sometimes give birth or seek cover in upland areas. Live-bearing.	Underground animal burrows and cracks and crevices ranging from well-drained to completely	Home range small, e.g. < 0.007 km^2 within their wetland	Typically found within 10 m of water; may move up to 200 m from water for birthing and hibernation	Adult mating season in spring, and birthing in July and August; neonate dispersal and movement to hibernacula in September and October

Species	Scientific name	Habitat		Home range	Movement	When movement occurs
		Spring and Summer	Winter			
Gray Ratsnake	*Pantherophis spiloides*	Forest edge and open forests; hide in hollow logs and trees, under rocks and in rock crevices; Gravid females prefer large trees; nest communally in standing snags, stumps, logs and compost piles (S. Thompson pers. comm.)	Moist hibernacula (rock fissures) below the frost line	On average 0.18 km^2	Adults move up to 4 km to and from hibernacula	Adult mating season late May to early June; neonate dispersal and movement to hibernacula in fall
Lake Erie Water-snake	*Nerodia sipedon insularum*	Limestone shorelines with ledges and cracks, cobblestone beaches, gravelly or sandy areas with debris. Will also use flooded quarries and drainage ditches in summer. Live-bearing.	Inland communal hibernacula are used: cavities and crevices in quarries, soil and rock piles, cracks in bedrock, tree root masses and animal dens	Generally found along shorelines	Generally restricted to the shoreline during the active season, but may travel several hundred metres inland to hibernacula	Adult mating season early May to early June; neonate dispersal and movement to hibernacula in fall
Massa-sauga, Great Lakes population	*Sistrurus catenatus*	Habitats with low canopy cover (rock barrens, forest clearings, alvars, beaver meadows, fens, bogs and shorelines); Live-bearing: gestation sites are in open habitat (e.g. rock barren), often with large table rocks and low vegetation	Forested areas on the Northern Bruce Peninsula; Wetlands on the Eastern Side of Georgian Bay; mammal burrows, old roots and rock crevices that extend below the frost line with access to the water table	Home range: 0.25 km^2	Can move >1 km to and from hibernacula; max. adult movement: 4 km; max. juvenile movement: 400 m	Mating season from July - August; Neonate dispersal in July - August; Movement to and from hibernacula in early May and September
Massa-sauga, Carolinian population	*Sistrurus catenatus*	Open shrubby areas and man-made piles of woody debris. Will also use grassy, prairie-like fields, wetlands and hedgerows in summer. Live-bearing.	Mammal burrows tree root cavities below the frost line with access to the water table			

Species	Scientific name	Habitat		Home range	Movement	When movement occurs
		Spring and Summer	Winter			
Milksnake	*Lampropeltis triangulum*	Forests, woodlands, fields, rocky outcrops, forest clearings and edges of wetlands	Mammal burrows, old foundations, old wells, gravel and dirt banks, hollow logs, rotting stumps	Home range up to 0.02 km^2	Adult movement: 400 m or more within the active season	Mating season in the spring; Neonate dispersal in July and August; Movement to hibernacula in September and October
Queen-snake	*Regina septemvittata*	Rocky streams, rivers and lake shorelines, wetlands, ponds, meadow marshes with full sun exposure	Underground and close to water	Linear home range (along waterways) 250m	Movement along waterways typically no more than 250m, but longer dispersal movements of > 1 km may occur; found within 15m of water during active season, but inland movements to hibernacula may be several hundred metres	Migrate to and from hibernacula in early April - mid-May and again in fall
Lizard						
Five-lined Skink	*Plestiodon fasciatus*	Great Lakes: open rocky areas in forests Carolinian: woody debris-strewn stable sand dunes, open forests, wetlands	same as spring, hibernate in rock crevices or buried in soil	Home range 270 – 578 m^2	Generally move short distances and adults move up to 210 m and juveniles up to 110 m	Breed in May or early June

Appendix B: Definitions

Connectivity - the degree to which the landscape facilitates or impedes movement among resource patches (Taylor et al. 1993)

Corrugated Steel Pipe (CSP) - round or elliptical culvert made with corrugated steel

Crossing Structure - general term for mitigation measures placed in roads to allow wildlife to cross safely

Culvert - general term for underpass structure type, traditionally used for conveyance of water under a road; in context of this document can be box or round
- **Arch Culvert** - portion of round culvert that allows natural bottom
- **Drainage Culvert** - a drain or pipe that allows water to flow under a road or railroad

Field-based information - Information measured within or near (few hundred metres) the road corridor used to inform impacts

Landscape scale - larger study area that may include an entire jurisdiction where information is available for an entire jurisdiction that is typically available in a GIS and informs broader level impacts of roads

Major road improvements - include road extensions, new alignments, and upgrades such as twinning from two to four lanes.

Population viability - the ability of a population to persist and avoid local extinction

Range length - maximum distance within animal's home range

Regional assessment - Integrate all multi-jurisdictional stakeholders and landscape information within the impact study area to develop a mitigation plan

Road-habitat interface - suitable habitat used by target species that is adjacent to the road

Road rehabilitation project - includes replacing bridges and pavements which are done under our capital program as opposed to our maintenance program

Skylight - structure on tunnel that permits ambient light to enter the structure

Target species – the species that the road mitigation measures are designed for; may include one, two or several species that are impacted by roads

Tunnel - type of crossing structure that is placed under the road surface for wildlife passage; in context of this document specifications are < 3 m width
- **Closed-bottom tunnels** - tunnel bottom is structural material
- **Open-bottom tunnels** - tunnel bottom is not structural material, provided by 3-sided concrete structure, arch pipe aluminum or corrugated steel
- **Open-grate tunnels** - provide ambient light through traditional metal grate structure that is placed on footings
- **Open-top tunnels** - provide ambient light through openings or slots at the top of the tunnel; openings must be at grade with road surface
- **Terrestrial tunnels** - dry tunnels installed for amphibians and reptiles undergoing overland movements

Underpass - general term for structural measures, e.g., culverts, bridge, viaducts, placed under roads to allow wildlife to cross safely

Appendix C: Crossing Structure Summary from Literature

Mole Salamander Crossing Structure and Fencing Review			
Species	**Comments**	**Crossing Structure**	**Crossing Structure Reference**
Projects with confirmed crossings			
Long-toed Salamander (*Ambystoma macrodactylum*)	No salamander >16 m from a tunnel was confirmed to cross. Tunnels ~200 m apart. Fences not angled to tunnels.	Six structures installed, two monitored. Two sizes of open-topped ACO Polymer tunnels: 0.47x0.32m (WxH); 0.23 x 0.21 (WxH). Did not indicate which size they monitored. Tunnels 11.1 m and 12.0 m long.	Allaback and Laabs 2002
California Tiger Salamander (*Ambystoma californiense*)	Salamanders readily used tunnels. Some individuals showed hesitancy to enter tunnels.	Three 0.25 m dia steel pipes, ~20 m long. Tunnels ~35 m apart.	Bain 2014
Northwestern Salamander (*Ambystoma gracile*), Rough-skinned Newt (*Taricha granulosa*), and Western Redback Salamander (*Plethodon vehiculum*)	Known Red-legged Frog (Rana aurora) migration route but also used by these spp. Juvenile newts and Redbacks could climb fence.	Concrete box culvert 1.8 x 0.9m (WxH). Half filled with soil and downed woody debris.	Beasley 2013
Spotted Salamander (*Ambystoma maculatum*)	At least 76% of salamanders that reached the tunnel entrances successfully crossed. Dark tunnel entrances may keep some salamanders from entering tunnels.	Two ACO open-topped tunnels, size not specified. Tunnels 7m long and ~60 m apart.	Jackson and Tyning 1989, Jackson 1996

Species	Comments	Crossing Structure	Crossing Structure Reference
Long-toed Salamander	More than 100 salamanders caught in tunnel exit traps in 2009, but only 23% of salamanders marked at the drift fence were caught exiting the tunnels.	Four open-topped ACO tunnels, 0.5 x 0.33m (WxH) and ~12 m long. Tunnels 80-110 m apart.	Pagnucco et al. 2011, 2012
Projects with no confirmed crossings			
Jefferson Salamander (*Ambystoma jeffersonianum*)	Not detected crossing through tunnels. Very few detected away from roads as well. Guidewalls not angled toward tunnel entrances.	5 tunnels installed. Four 1.2 m diameter CSP or concrete, and one 1.7m wide elliptical culvert. Tunnels 25-31 m long.	Gartshore et al. 2005
Spotted Salamander	Three years of monitoring failed to confirm usage by any amphibians. Migration routes not confirmed before construction.	2 bridges, 1 concrete box culvert 1.2 x 1.2m. Structure 17 m long and lined with soil.	Merrow 2007
Outdoor lab experiments			
Spotted Salamander	Found no major statistical differences in culvert crossing comparing the lengths, diameters and substrates tested. Thirty percent more salamanders crossed through the largest tunnel compared with the smallest.	Experimental culverts along migration route, not under road. Tested 0.3, 0.6, and 0.8 m diameter corrugated PVC pipes, 3, 6, or 9 m long. Also tested three kinds of substrate: bare plastic, sand/ gravel and concrete.	Patrick et al. 2010

Toad Crossing Structure and Fencing Review			
Species	**Comments**	**Crossing Structure**	**Crossing Structure Reference**
Projects with confirmed crossings			
Western Toad (*Anaxyrus boreas*)	Tunnel used by 1700-7000+ toadlets leaving breeding pond. Significant road kill at fence ends.	One semi-circular, closed-topped culvert with earthen floor. 1.8 x 0.5 m (WxH) x 3.7 m long.	Biolinx 2013
American Toad (*Anaxyrus americanus*)	Confirmed tunnel crossing by American Toads.	5 closed-topped tunnels, mainly 1.2 m diameter CSP or concrete, but one 1.7 m wide elliptical culvert; 25-31 m long.	Gartshore et al. 2005
Common Toad (*Bufo bufo*)	Marked all toads. 40% used tunnels, 27% got around fence, 33% did not cross.	2 ACO open-topped concrete tunnels, ~0.5 m wide on bottom, 0.33 m high. No soil on bottom.	Ottburg and van der Grift 2013
Western Toad	7 caught in exit traps.	4 ACO open-topped box culverts, 0.5 m wide and 0.33 m high and ~12 m long. Slots along the top. Tunnels 80-110 m apart.	Pagnucco et al. 2012
Common Toad (*Bufo bufo*)	Greater usage of larger rectangular culverts than smaller round culverts.	4 types. 0.4 and 0.6 m diameter concrete culverts; box culverts 1.6 and 1.7 m high (width not given, but appears variable in photos).	Puky et al. 2013
Western Toad	Dispersing toadlets from breeding pond crossed through culverts in the thousands.	2 CSP culverts, both 0.4 m in diameter.	Wind 2014
Outdoor lab experiments			
Frogs and Toads of France	Toads showed no difference in use of tunnels with or without soil.	0.5 m diameter concrete culvert. Compared bare concrete with layer of soil.	Lesbarrères et al 2004

Turtle Crossing Structure Research			
Species	**Comments**	**Crossing Structure**	**Crossing Structure Reference**
Projects with confirmed crossings			
Florida Cooter (*Pseudemys floridana floridana*), Slider (*Trachemys scripta*), and Florida Softshell (*Apalone ferox*)	Primarily Cooters and Sliders crossed through culvert.	Drainage culvert 3.5 m in diameter (46.6 m long).	Aresco 2005
Blanding's Turtle (*Emydoidea blandingii*), Snapping Turtle (*Chelydra serpentina*)	Individual Blanding's Turtles used culvert up to 13 times. Snapping Turtles also crossed using the culvert, no numbers provided. Virtually no roadkill (2 in 2 years).	1.8 m diameter corrugated steel culvert, 25 m long, pre-existing, with sediment and year round water.	Caverhill et al. 2011
Spotted Turtle (*Clemmys guttata*)	At least 7 turtles confirmed to cross through tunnel. Other turtles likely crossed as well.	1.8 x 1.8m concrete box tunnel, ~13m long; 0.1-0.15 m organic substrate in culvert.	Kaye et al. 2005
Blanding's Turtle	Blanding's Turtles showed no strong preference for culvert size. Turtles more apt to cross through culvert when light visible at end of culvert.	Tested 1.0 and 1.2 m diameter corrugated steel culverts and 1.1 m diameter arch culverts; length unspecified. Culverts tested in pairs along known in outdoor lab.	Lang 2000
Snapping Turtle	Crossed through culvert. No details on amount of usage. Fence end roadkill. Hatchling could get through 5x10cm mesh fence. Effectiveness of fence increased after first yr or two, as vegetation held bottom of fence better.	1.3 m diameter corrugated steel culvert.	Langen 2011

Species	Comments	Crossing Structure	Crossing Structure Reference
Wood Turtle (*Glyptemys insculpta*)	Long term study found turtles moved along a stream that passed through the culvert .	3 m diameter culvert, 26 m long.	Parren 2013
Wood Turtle	At least one Wood Turtle observed to cross through tunnel.	Open-top (grate) tunnel ~1.5 x 1.0 m (WxH) on dirt logging road.	Steinberg pers. comm.
Projects with unconfirmed crossings			
Painted Turtle (*Chrysemys picta*), Snapping Turtle	6 Painted Turtles, 1 Snapping Turtle photographed in culverts. Plus Snapper tracks in culverts observed but no photos. Crossing not confirmed.	3 crossing structures, each consisting of 2 culverts connected with fenced open area between. Size: 3.4 x 2.4 m box culvert, 24.1 m long, then 15.3 m fenced opening and then another culvert 24.1 m long.	Baxter-Gilbert 2014
Snapping Turtle and Painted Turtle	No turtles detected in dry culvert with trail camera.	1 dry culvert 1.2m diameter CSP; 2 wet culverts, one was 4m wide concrete box culvert, second unspecified.	Buchanan and Basso 2007
Blanding's Turtle, Painted Turtle	Turtles could climb over 0.2 m high curb. Tunnel used by at least 1 Painted Turtle.	Three 4.6 x 0.9m (WxH) and 17.1 m long, open-top, 3-sided box culverts.	Compton and Seivert 2002
Blanding's Turtle, Snapping Turtle, Painted Turtle	Blanding's Turtles commonly observed in dry and wet culverts. Snapping Turtles used wet culverts mainly, but one dry. Only 1 Painted found in a wet culvert.	4 dry and 6 wet culverts, multiple sizes, with skylights. Minimum size 1.8 x 0.9m (WxH) and ~50 m long.	Dillon 2011, 2013
Eastern Musk Turtle (*Sternotherus odoratus*), Florida Softshell	1 Musk Turtle and 3 Softshells detected in 0.9m culvert. No turtles detected in other tunnels.	3 sizes of tunnels: 0.9m diameter; 1.8x1.8 m box culvert, with 3 light boxes; 2.7 x 2.7m box culvert. All tunnels 44 m long.	Dodd et al. 2004

Species	Comments	Crossing Structure	Crossing Structure Reference
Turtles	Monitored culverts in area with little roadkill before mitigation. Turtle roadkill went from 1 to 0. No turtles photographed in culverts.	1 and 2 m diameter culverts (although described as square sometimes).	Garrah 2012
Painted Turtle	No sex difference in climbing ability. In trials ~4% of turtles climbed over 0.45m tall fence with no flashing, while no turtles climbed fence with flashing.	n/a	Griffin 2005
Eastern Box Turtle (*Terrapene carolina carolina*)	At least 3 turtles used pre-existing drainage culverts.	No details.	Hagood and Bartels 2008
Snapping Turtle, Painted Turtle	Snapping Turtle photographed in both 0.8 and 0.9m culverts. Painted Turtle photographed in 0.8 m culvert.	Two culverts: 0.8 and 0.9 m diameter CSP.	Gunson et al. 2013
Spotted Turtle	Review of other crossing structures. Reported Spotted Turtles using an arch culvert and a box culvert at two sites in Mass.	Arch culvert: 11 x 3.4m (WxH) and 12m long; Box culvert: 1.8 x 1.8 m and 16.8 m long.	Paulson 2010
Blanding's Turtle	No mitigation. Studied roadill hotspots and movement patterns. Suggested crossing structures be an average of 500 m apart and no more than 1.5 km apart.	n/a	Riley et al. 2013

Species	Comments	Crossing Structure	Crossing Structure Reference
Snapping Turtle	Detected by trail camera in at least one tunnel. No details on which tunnel.	4 sizes, from 1.5 x 0.9m (WxH) to 2.7 x 1.8m. ~5 cm soil spread in bottom of culverts.	Rogers et al. 2009
Snapping Turtle and other herps	Pooled use of all frogs, snakes, lizards and turtles. Most use of culverts 1.5m or more in width and 0.6-1.5m high.	Variety of existing culverts.	Smith 2003
Snapping Turtle, Painted Turtle, Map Turtle (*Graptemys geographica*)(?)	At least 7 Snapping and 1 Painted Turtle used culverts. Map Turtle may have been seen swimming in one culvert. All but one reptile detected in ACO tunnel.	1.8 m x 0.9 m concrete box culvert; 0.5 x 0.48 open-top ACO tunnel.	Whitelock 2014
Outdoor lab experiments			
Painted Turtle	Tunnel placed on path of females on nesting forays. All turtles that reached the tunnel crossed through. Mean crossing time 113 sec (range: 60-197 sec).	0.6 x 0.6m wooden tunnel, ~6 m long in field.	Jackson and Marchand 1998
Painted Turtles	>85% of turtles used all tunnels. Largest tunnel had highest success rate and fastest crossing times. Turtles more hesitant to enter tunnels below grade.	Outdoor lab with 3 types of culverts: 0.6 x 0.6m, 0.6 x 1.2m, 1.2 x 1.2 m all 12.2 m long. Plywood with soil bottom.	Paulson 2010
Snapping Turtle, Painted Turtle	Outdoor lab. No turtle climbed 0.6m fence. Turtles more apt to use tunnels at least 0.5m dia. All substrates used about equally. Longest tunnel had slightly less usage. Light did not affect usage.	Black PVC pipe culverts. Varied length (3-9.1 m), aperture size (0.3-0.8 m), substrate (bare, soil, gravel, concrete) and light permeability (0-4%).	Woltz et al 2008

Species	Comments	Crossing Structure	Crossing Structure Reference
Painted Turtle, Blanding's Turtle, Spotted Turtle	Outdoor lab. Increased light increased crossing success. In closed-topped tunnels, the percentage of turtles crossing increased with increased culvert size. Low crossing rate (54% or less) with 80' culverts.	3 tunnels sizes: 0.6 x 0.6m, 1.2 x 1.2m, 2.4 x 1.2m; two lengths: 40' and 80'. Varied light through ceiling (0, 75, 100%).	Yorks et al. 2011
Snake Crossing Structure Research			
Projects with confirmed crossings			
Eastern Massasauga (*Sistrurus catenatus*)	4 snakes detected under crossing structures (likely crossing) in 2013.	4 open-grate crossing structures. ~1 x 1m (WxH) under 2-lane gravel roads.	Colley pers. comm.
Eastern Garter Snake (*Thamnophis sirtalis sirtalis*), Ribbon Snake (*Thamnophis sauritus sauritus*)	Outdoor lab. At least 70% of Ribbons and 90% Garters crossed at all widths. All Garters crossed whether substrate was soil or water. In 1.3m culvert >90% of Ribbons crossed regardless of substrate. In 0.33 m culverts Ribbons had lower crossing success with soil (50%), compared with water (70%). In real culverts, Ribbons had low crossing success (<30%) in small culverts but high success (~80%) in large culverts.	Outdoor lab box culverts 0.66 m high and variable width (0.33-1.33m) and 5 m long. Also examined crossing of real culverts ~1 m and ~0.5 m in diameter and 10 m long. Some culverts dry (soil bottom) and some with liner with ~7 cm of water.	Eads 2013
Northern Watersnake (*Nerodia sipedon sipedon*)	>80% crossing success with both size culverts.	0.5 and 1.0 m culverts. No other detail.	Eads et al. 2012

Species	Comments	Crossing Structure	Crossing Structure Reference
Timber Rattlesnake (*Crotalus horridus*), Ratsnake (*Pantherophis spiloides*)	Two radio-tracked rattlesnakes used one culvert during the culvert's first year. Snakes spent 10-14 days near fence before crossing through culvert. Some snakes went around fence and others used gaps in fence. 1 possible Ratsnake (or Racer) was also detected in one culvert.	5 concrete closed-top box culverts 0.91 x 0.41 m (WxH) and 15 m long.	Laidig and Golden 2004
Eastern Garter Snake	Tunnels used commonly. Fence end roadkill, some snakes got over fence.	0.25-0.30 m diameter steel pipe.	Roberts 2010
Unidentified snakes	3 crossings by a snake detected in sand tracking.	Concrete box culvert 2.74 (W) x1.83 (H)m and 30.5 m long.	Rogers et al. 2009
Snakes	Used sand tracking to detect usage. 1 snake crossing over 8 days in spring, and 1 crossing over 8 days in summer.	9 concrete box culverts, 2.4 x 1.2m and 18 m long. Culvert bottoms scattered with small stones and a thin layer of silt.	Taylor and Goldingay 2003
Milos Viper (*Macrovipera schweizeri*)	No snakes found on roads in areas with barriers. Snakes crossed through underpasses. Mean of 77% of snakes that encountered an underpass crossed through.	6 underpasses, 4 types. No details.	Yannis 2011

Species	Comments	Crossing Structure	Crossing Structure Reference
Projects with unconfirmed crossings			
Various species	Snakes found in both sizes of round culvert.	looked at use of existing culverts: 0.6 m and 1.0 m diameter CSP, concrete box culverts (size not given).	Arizona Game and Fish 2010
Snakes and lizards pooled; no species named	In general, reptile use of culverts was negatively correlated with culvert length.	Existing drainage culverts, no specs provided.	Ascensão and Mira 2007
Northern Watersnake, Red-bellied Snakes (*Storeria occipitomaculata*)	3 Watersnakes photographed in culvert, 1 juvenile Red-bellied observed in culvert.	3 crossing structures, each consisting of 2 culverts connected with fenced open area between: 3.4 x 2.4 m box culvert, 24.1 m long, then 15.3 m fenced opening and then another culvert 24.1 m long.	Baxter-Gilbert 2014
Eastern Garter Snake	No confirmed crossing by any snake, and very few captures away from road.	2 bridges, 1 culvert 1.65m wide.	Bellis et al. 2007
Unspecified species of Garter Snake	20 detected under bridge via sand tracking. Culverts not well monitored.	Bridge 5-9'aboveground, 400' long; multiple size tunnels, as small as 0.5m diameter culverts.	de Rivera and Bliss-Ketchum 2010
Unidentified snakes (likely Garter and Northern Watersnake)	39-50 snakes per yr (3 yr) in wet and dry culverts. Largest percentage in dry culverts, but may have been easier to photograph in those culverts. Snakes photographed basking in light from skylights.	4 dry and 6 wet culverts, multiple sizes, with skylights. Smallest tunnel 1.8 x 0.9m (WxH).	Dillon 2011, 2013

Species	Comments	Crossing Structure	Crossing Structure Reference
Eastern Racer (*Coluber constrictor*), Eastern Ratsnake (*Pantherophis alleghaniensis*), Eastern Ribbonsnake, plus other non SAR spp	1 Racer, 1 Ratsnake and 4 Ribbonsnakes detected in 1.8 x1.8m tunnels but crossing not confirmed. Not detected in other size culverts.	3 sizes of tunnels: 0.9m diameter; 1.8 x 1.8 m box culvert, with 3 light boxes; 2.7 x 2.7m box culvert. All tunnels 44 m long.	Dodd et al. 2004
Snakes	Monitored culverts in an area with little road kill before mitigation. No change in roadkill. Snakes not photographed in culverts.	1 and 2 m diameter culverts (although described as square sometimes).	Garrah 2012
Northern Watersnake, Eastern Gartersnake, Black Ratsnake	Watersnake found in association with 6 culverts, Ratsnake with 3, and Gartersnake with 2 (sizes of culverts not given).	Monitored 265 culverts of various sizes.	Gates and Sparks 2011
Timber Rattlesnake	Used by some snakes.	~0.3m diameter culvert.	Jacobson pers. comm.
Snakes	To prevent snakes getting through fence attached a fine mesh (0.6x0.6 cm) to turtle fencing. 30 cm high mesh did not prevent all passage, but 60 cm high mesh was more successful. No monitoring of culvert for snakes.	1.3 m diameter corrugated steel culvert.	Langen 2011
Northern Watersnake, Eastern Gartersnake	Watersnake entered and turned around in 0.9 m culvert. Gartersnake observed in 0.9 m culvert.	Two culverts: 0.8 and 0.9m diameter CSP.	Lesbarrères Gunson et al. 2013

Species	Comments	Crossing Structure	Crossing Structure Reference
Massasauga	No proof of crossing, but no DOR snakes in 4 years of monitoring road.	6 open-topped structures, with rock substrate, ~1.0 x 1.5m (WxH) and ~6 m long.	Lewis pers. comm.
Wandering Garter Snake (*Thamnophis elegans vagrans*)	Photographed in tunnels 48 times.	4 ACO box culverts, 0.5 m wide and 0.33 m high and ~12 m long. Slots along the top. Tunnels 80-110 m apart.	Pagnucco et al 2011, 2012
Grass Snake (*Natrix natrix*)	Detected in culverts. Believed to be hunting frogs in wet culvert.	Three 1m dia concrete culverts, 34 m long. Opening in middle of culvert to allow in light and water.	Puky et al. 2007
Grass Snake	Shed skins found in tunnels.	Eight 0.6-0.9 m diameter culverts, 8-9 m long. Five culverts had light shafts.	Puky et al. 2007
Massasauga, Eastern Hog-nosed Snake, Milksnake (*Lampropeltis elapsoides*), Northern Ribbonsnake (*Thamnophis sauritus septentrionalis*)	Milksnake and Northern Ribbonsnake confirmed in tunnels. Possible Hog-nosed, but photo blurry.	Concrete box culvert 1.8 x 1.2 m (WxH).	Rouse 2005
Eastern Garter Snake and other herps	Pooled use of all frogs, snakes, lizards and turtles. Most use of culverts 1.5m or more in width and 0.6-1.5m high.	Variety of existing culverts.	Smith 2003
Eastern Garter, unidentified snakes	At least 2 Garter and 2 unidentified snakes used culverts. All but one reptile detected in ACO tunnel. May have been more use but trail cameras set to shoot every 15 min.	1.8 m x 0.9 m concrete box culvert; 0.5 x 0.48 open-top ACO tunnel.	Whitelock 2014

Species	Comments	Crossing Structure	Crossing Structure Reference
Outdoor lab experiments			
Small (<20g) and medium-sized (75-250g) snakes	No snake able to climb over any fence. Medium-sized snakes could escape through ½" mesh. Small snakes could escape through ½ and ¼" mesh. Some snakes got caught in ½" mesh and had to be cut free.	n/a Tested fencing types.	Smith and Noss 2011
Lizard Crossing Structure and Fencing Review			
Projects with confirmed crossings			
Various lizards (no skinks)	Lizards found in all 3 types of culverts. More spp in smallest size culvert. Highest crossing rate (0.4) in box culverts.	looked at use of existing culverts: 0.6m and 1.0m dia CSP, concrete box culverts (size not given).	Arizona Game and Fish 2010
Flat-tailed Horned Lizards (*Phrynosoma mcallii*)	Experimental tests of simulated culverts. 12 of 54 lizards crossed. All size tunnels used, but the 1.0m CSP without skylights was used by more lizards. Dark culverts were used more frequently than culverts with skylights.	tested 3 sizes of tunnel: 0.6 m and 1.0 m CSP, and 2.6 x 1.3m (WxH) plywood box culverts. Two of each culvert size, one with skylights and one without. All tunnels were ~13 m long and had 2.5-7.5 cm of sand in the bottom of the tunnels.	Painter and Ingraldi 2007
Lace Monitor (*Varanus varius*) and other unidentified lizards	Australian study. 11 crossings by lizards during limited monitoring.	9 concrete box culverts, 2.4 x 1.2m and 18 m long. Culvert bottoms scattered with small stones and a thin layer of silt.	Taylor and Goldingay 2003

Species	Comments	Crossing Structure	Crossing Structure Reference
Projects with unconfirmed crossings			
Snakes and lizards pooled; no species named	In general, reptile use of culverts was negatively correlated with culvert length.	Existing drainage culverts, no specs provided.	Ascensão and Mira 2007
Five-lined Skink (*Plestiodon fasciatus*)	Skinks observed around the entrance of 5 culverts (sizes not given). Apparently used culvert entrances for basking and foraging but did not appear to cross through culverts.	Monitored 265 culverts of various sizes.	Gates and Sparks 2011
Northern Fence Lizard (*Sceloporus undulatus hyacinthinus*)	Detected in culverts 12 times during two month period.	5 concrete closed-topped box culverts 0.91 x 0.41m (WxH) and 15 m long.	Laidig and Golden 2004
Sand Lizard (*Lacerta agilis*)	Lizards lived on overpasses, using them for hiding places, basking sites and foraging habitat.	Wildlife overpass. Details not provided. Shrubs planted at side of overpass.	Puky et al. 2007
Five-lined Skink and other herps (pooled all amphibians and reptiles)	In general, amphibians and reptiles made most use of culverts 1.5m or more in width and 0.6-1.5m high.	Variety of existing culverts.	Smith 2003
Outdoor lab experiments			
Five-lined Skink	Skinks able to crawl through ¼ mesh fence. The aluminum flashing was the only fence that stopped all skinks from escaping.	n/a Tested fencing types.	Smith and Noss 2011

Appendix D: Links and Other Resources

Applicable Legislation and MNRF policies

General Regulation under the Endangered Species Act, 2007: Ontario Regulation 242/08
https://www.e-laws.gov.on.ca/html/regs/english/elaws_regs_080242_e.htm

Permits under the Endangered Species Act
http://www.ontario.ca/environment-and-energy/endangered-species-permits-and-authorizations

Overall Benefit Permit
http://www.ontario.ca/environment-and-energy/endangered-species-act-overall-benefit-permits

Step-by-step guide to applying for an overall benefit permit
http://www.ontario.ca/environment-and-energy/endangered-species-act-overall-benefit-permits (click link on right side of above page: "How to apply")

Streamlined approvals under the Endangered Species Act
(also known as Registering online for Natural Resources activities)
https://www.ontario.ca/environment-and-energy/natural-resources-registration-guide

Development and infrastructure projects and endangered or threatened species
http://www.ontario.ca/environment-and-energy/development-and-infrastructure-projects-and-endangered-or-threatened-species

Ontario Species at Risk Information

Ontario Species at Risk website
http://www.ontario.ca/environment-and-energy/species-risk

Species at Risk Reference Toolbox
http://www.ontario.ca/environment-and-energy/species-risk-guides-and-resources

Best Practices and Guidance

Reptile and Amphibian Exclusion Fencing: Best Practices
http://files.ontario.ca/environment-and-energy/species-at-risk/mnr_sar_tx_rptl_amp_fnc_en.pdf

Passage Assessment System for Evaluating the Permeability of Existing Structures
http://www.wsdot.wa.gov/research/reports/fullreports/777.1.pdf

Design Examples

Amphibian Tunnel Project in Waterton Lakes National Park, Vancouver
http://naturevancouver.ca/sites/naturevancouver.ca/VNHS%20files/Amphibian%20Tunnel%20Project.pdf

Appendix E: Sample Tunnel Costs Table (2014)

Tunnel type	Model Number	Provider	Size of culvert	Length (m) (estimate)	Cost	Installation costs (very approximate)	Cost/m (culvert only)
Terrestrial concrete box culvert	Reinforced non-standard concrete box culvert	M-CON Pipe and products Inc.	1.8m x 0.9m	16.3	$25,000	$15,000	$1,533
Terrestrial open-top culvert	ACO AT500	ACO Systems Ltd.	0.50m x 0.48m	16.2	$13,000	$11,000	$802
Hydraulic Concrete Box culvert	Reinforced non-standard concrete box culvert	M-CON Pipe and products Inc.	3.0 m x 2.1m	18.3	$65,000	$45,000	$3,551
Concrete Box culvert	Includes all materials	MTO	1.8m x 1.8m	48	$225,000		$4,687
Concrete Box culvert	Considered a structure, so includes only the cost of culvert	MTO	3.3m x 2.8m	48	$375,000	$325,000	$7,812
Concrete Box culvert		MTO	1.0m x 1.0m	48	$150,000		$3,125

Cost/m (installed)	Comments (installation limitations)	Additional information:	Source
$2,453		Additional fixed costs associated with each mobilization, special environmental precautions and insurances -Soil conditions play a crucial part in costs; -Generally, add 20% per project over $150,000, add 30% for smaller projects- Add $250,000 per site for special shoring-.	Rick Levick, Longpoint Improvement Committee
$1,481			
$6,010	Cost about 30% more than typical installation reflected in table due to digging to connect channels to marsh on one side and the bay on the other.		
		Actually for 2 culverts (= 1 eco-passage) for 4-lane hwy 69: each culvert is 24m long (spanning 2 lanes of highway, plus shoulders), and they're separated by a 15.3m gap (the median)	Andrew Healy, MTO
$14,583	True cost is much greater than structure alone due to blasting, footings etc., costs could be up to 700 K with installation		
$3,125	This is a guess and can range from 100 - 200 K		

Tunnel type	Model Number	Provider	Size of culvert	Length (m) (estimate)	Cost	Installation costs (very approximate)	Cost/m (culvert only)
Corrugated steel Pipe culverts		Atlantic Industries Ltd.	1.2 m round	16.5	$2,392	+	$145.00
Corrugated Metal Arch c/w metal footings		Atlantic Industries Ltd.	0.6 m rise x 1.22 m span	16.5	$16,360	+	$991.56
Corrugated steel Pipe culverts		Atlantic Industries Ltd.	3 m round	16.5	$9,240	+	$560.00
Corrugated Metal Arch c/w metal footings		Atlantic Industries Ltd.	2.99 m span x 1.45 m rise	16.5	$24,024	+	$1,456

Cost/m (installed)	Comments (installation limitations)	Additional information:	Source
+	Minimal assembly required.	Various coatings available. Price based on a coating common on low volume roads. Pipe material is subjective to enviornmental conditions. Reference Ontario Gravity Pipe Study for more specific detail.	Kevin Williams, Atlantic Industries Ltd.
+	Available preassembled or assembled in place. Can be assembled by person (no hoisting equipment) for a rough estimated cost of $50/m.	Open-bottom which can be constructed to maintain a more natural environment. Pricing based on low to moderate covers (0.6 m to 2 m cover). Greater covers are permitted but price will vary.	Kevin Williams, Atlantic Industries Ltd.
+	Minimal assembly required.	Various coatings available. Price based on a coating common on low volume roads. Pipe material is subjective to environmental conditions. Reference Ontario Gravity Pipe Study for more specific detail.	Kevin Williams, Atlantic Industries Ltd.
+	Available preassembled or assembled in place. Can be assembled by person (no hoisting equipment) for a rough estimated cost of $50/m.	Open-bottom which can be constructed to maintain a more natural environment. Pricing based on low to moderate covers (0.6 m to 2 m cover). Greater covers are permitted but price will vary.	Kevin Williams, Atlantic Industries Ltd.

Tunnel type	Model Number	Provider	Size of culvert	Length (m) (estimate)	Cost	Installation costs (very approximate)	Cost/m (culvert only)
Corrugated Metal Arch c/w concrete footings and headwall	Includes headwall costs. Shorter lengths conduits required with headwalls.	Atlantic Industries Ltd.	2.99 m span x 1.45 m rise	10	$29,617	+	$2,961

Cost/m (installed)	Comments (installation limitations)	Additional information:	Source
+	Available preassembled or assembled in place. Hoisting equipment required for headwalls and footings.	Open-bottom which can be constructed to maintain a more natural environment. Price/m value is inflated by inclusion of headwalls but headwalls permit shorter length conduits. Pricing based on low to moderate covers (0.6 m to 2.5 m cover). Greater covers are permitted but price will vary. Headwalls are intended for more aesthetically pleasing requirements.	Kevin Williams, Atlantic Industries Ltd.

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RESEARCH ARTICLE

Genetic source–sink dynamics among naturally structured and anthropogenically fragmented puma populations

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Abstract

Fragmentation of wildlife populations is increasing on a global scale and understanding current population genetic structure, genetic diversity, and genetic connectivity is key to informing wildlife management and conservation. We genotyped 992 pumas (*Puma concolor*) at 42 previously developed microsatellite loci and identified 10 genetic populations throughout the states of California and Nevada, USA. Although some genetic populations had large effective population sizes, others were small and inbred. Genetic diversity was extremely variable (heterozygosity, uHe = 0.33–0.53), with some populations nearly as low as an endangered subspecies, the Florida Panther (*P. c. coryi*, uHe = 0.24). Specifically, pumas in the Sierra Nevada were genetically diverse and formed the largest genetic source population in the region. In contrast, coastal and southern populations surrounded by urbanization had low genetic diversity, fragmented gene flow, and tended to be genetic sinks. The strong population genetic structuring of pumas across California (F_{ST} = 0.05–0.39) is vastly different than other genetic studies in less-urbanized states, including our analysis in Nevada, where pumas had few barriers to gene flow and weak population differentiation. Our results have far-reaching conservation and management implications for pumas and indicate large-scale fragmentation in one of North America's most biodiverse and rapidly-urbanizing regions.

Keywords Mountain lion · Cougar · *Puma concolor* · Population genetics · Genetic structure

Introduction

Fragmentation of wildlife habitat and resultant impacts to populations are increasing worldwide and urbanization is one of the primary contributors (Crooks et al. 2017; Fahrig 2003; Haddad et al. 2015; Newbold et al. 2016). Unlike

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natural barriers that have impacts over a geological timescale (Albert et al. 2016), urbanization can have more immediate effects on gene flow among populations (Balkenhol and Waits 2009; Karlson et al. 2014). Gene flow is critically important to individual fitness and to the evolutionary potential of populations because successful migrants can diversify gene combinations (i.e., increase heterozygosity) and introduce new genetic material (i.e., increase allelic richness) (Caballero and García-Dorado 2013; Chapman et al. 2009; Frankham 2015). Without receiving gene flow, small populations are especially subject to inbreeding, genetic drift, and increased extinction risk (Carlson et al. 2014; Wootton and Pfister 2015).

Population fragmentation is increasingly evident for species located in the urbanized western United States (Buchalski et al. 2016; Delaney et al. 2010; Fisher and Shaffer 1996; Tuma et al. 2016), including the puma (*Puma concolor*) (Beier 1995; Gray et al. 2016), which is becoming a model for studying genetics of isolated populations (Ernest et al. 2014; Gustafson et al. 2017; Johnson et al. 2010; Riley et al. 2014). Despite the long-distance dispersal ability of pumas (Hawley et al. 2016; Newby et al. 2013; Pierce et al. 1999; Thompson and Jenks 2005), gene flow among adjacent puma populations has been nearly negated by freeways in densely populated Southern California (Ernest et al. 2014; Gustafson et al. 2017; Riley et al. 2014). Consequently, some California puma populations have become functionally isolated and have experienced rapid population divergence and inbreeding (Ernest et al. 2014; Gustafson et al. 2017; Riley et al. 2014; Vickers et al. 2015) with concerns for extinction (Benson et al. 2016). Given that *P. concolor* and other wide-ranging species serve as umbrella species (Carroll et al. 2001; Maehr et al. 2002; Thorne et al. 2006)—the conservation of which indirectly provides protection for many other species (Roberge and Angelstam 2004)—the low genetic diversity of puma populations in human-fragmented habitats suggests that a large-scale ecological problem may be occurring in some of the most biologically-diverse regions of North America (Calsbeek et al. 2003; Dobson et al. 1997).

During the late Pleistocene, pumas were extirpated from North America and repopulated by migrants from South America (Culver et al. 2000). As a result, pumas in North America compose a single phylogenetic group (based on mtDNA) and exhibit founder effects (i.e., reduced population genetic diversity based on mtDNA and microsatellites) compared to pumas in South America and Central America (Culver et al. 2000). Therefore, it is critical to understand effects of fragmentation on populations from this North American lineage. A previous genetic analysis along the west coast of the United States indicated that pumas in California did not exist as a single population and suggested urbanization may have led to genetically-depauperate, fragmented populations (Ernest et al. 2003). In addition, a population genetic analysis in Nevada indicated there were asymmetric migration rates between the two states, and that pumas from Nevada were a genetic source for genetic-sink populations in California (Andreasen et al. 2012). However, these previous reports relied on a limited number of genetic loci (≤ 13 microsatellites) and investigators did not sample across the two states. In this study, we attempted to address these limitations and provide a more comprehensive view of puma genetic diversity and gene flow within and among California and Nevada.

Our aim was to identify the number and spatial structure of puma populations across California and Nevada and the extent of gene flow among the populations. In doing so, we were able to identify genetic source and sink populations as well as isolated populations with limited gene flow. We expected pumas would exhibit genetic structure associated with both natural geographic features and anthropogenic development. Given the complex structure of ecoregions and large human population in California (> 39 million people; 92.5/km^2; US Census Bureau 2016), we hypothesized pumas in California would exhibit more population divergence and less interpopulation gene flow relative to pumas in Nevada, which have access to more contiguous ecoregions with fewer humans (< 3 million people; 10.3/km^2; US Census Bureau 2016). To address these hypotheses, we genotyped 992 pumas at 42 microsatellite loci across California and Nevada. We then identified regional populations using population assignment models and evaluated functional connectedness of puma populations by modeling population divergence and computing bi-directional migration rate estimates.

Materials and methods

Sampling and extractions

We obtained tissue or blood samples from 992 pumas captured alive, found dead, or legally killed by authorized agencies for livestock depredation, public safety, or sport hunting (Nevada only) during 1992–2016 (Fig. 1). Approximately 49% of individuals sampled were legally killed, 31% were from captures, 11% were hit by vehicles, and the rest were found dead of other causes. We isolated genomic DNA using QIAGEN DNeasy Blood & Tissue kits (QIAGEN Inc., Valencia, CA, USA).

Genotyping

We genotyped each individual puma at 42 previously developed microsatellite loci, plus a single sex-linked locus (Ernest et al. 2003, 2014; Riley et al. 2014) and ran polymerase chain reactions on ABI 2720 thermocyclers (Life Technologies, Carlsbad, CA, USA) using QIAGEN

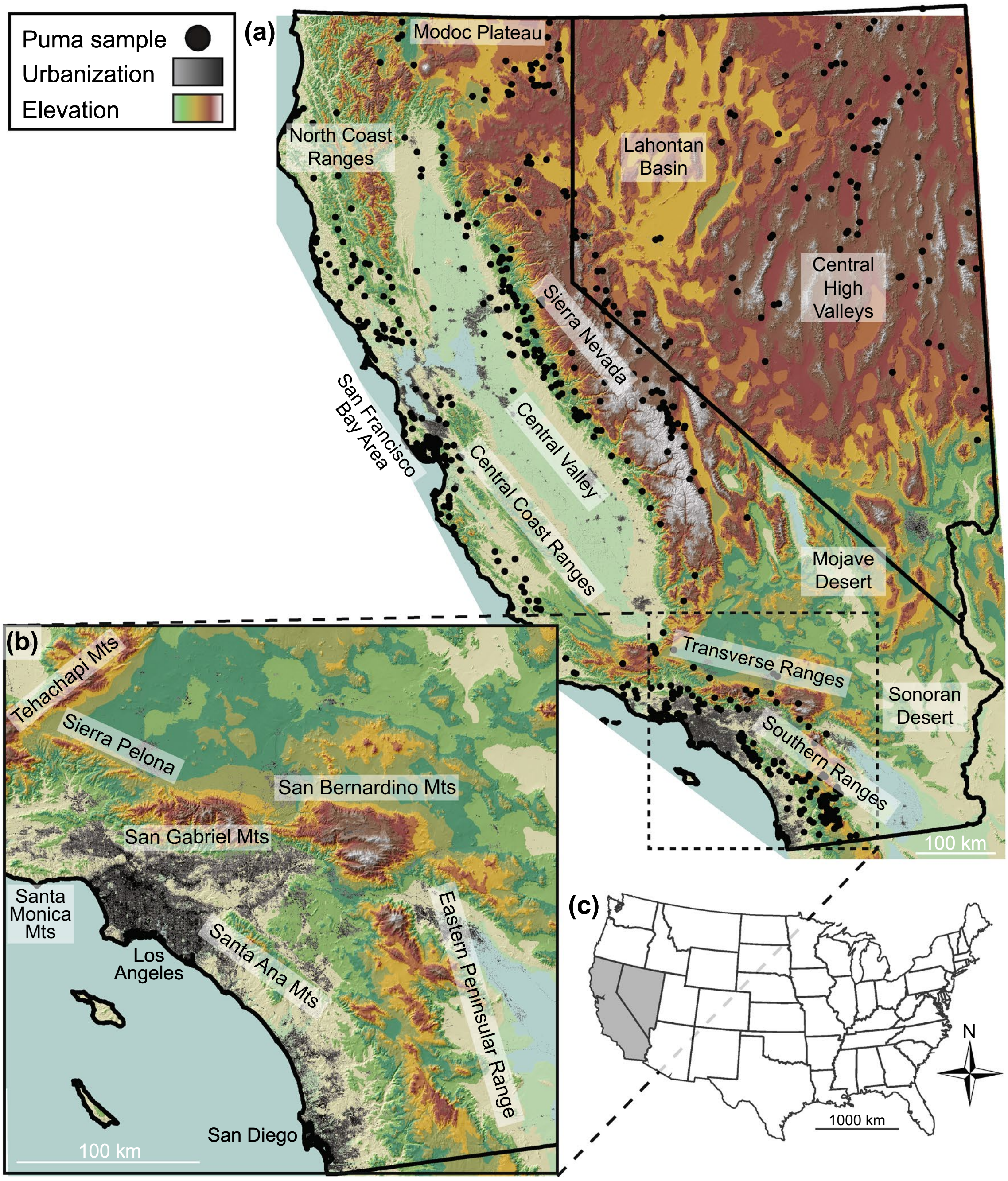

Fig. 1 Map of our study system, including **a** sampling locations of 992 pumas and ecoregions, **b** specific mountain ranges within the Transverse and Southern Ranges, and **c** an inset map of the United States of America showing the locations of California and Nevada. Elevation data source: USGS national elevation dataset (http://nationalmap.gov). Dark circles indicate locations where pumas were sampled, the gray to black scale indicates low to high urbanization, and the blue to white scale indicates 0 m elevation (sea level) to 4,421 m elevation

Multiplex PCR kits with Q solution (Table S1) following the protocols of Gustafson et al. (2017). We included negative and positive controls in each PCR run and visualized fragments with STRand version 2.3.69 (Toonen and Hughes 2001). For each locus, we confirmed heterozygous genotypes at least twice and homozygous genotypes at least three times.

Population genetic structure

The spatial arrangement of sample locations can confound population genetic analyses (Meirmans 2012; Schwartz and McKelvey 2009). Thus, we used spatially-explicit hierarchical Bayesian clustering programs TESS 2.3 (Durand et al. 2009a) and GENELAND 4.0 (Guillot et al. 2005b). We tested for consistency among programs because TESS has been shown to identify finer-scale hierarchical puma population genetic structure compared to GENELAND (Gustafson et al. 2017). In general, TESS outperforms GENELAND in the presence of isolation-by-distance (Safner et al. 2011) whereas GENELAND outperforms TESS at detecting genetic barriers to dispersal (Blair et al. 2012; Safner et al. 2011).

In TESS, the number of populations (K) must be specified and tested over a range of possible values. Model selection must be used to determine the K with the best fit to the data. We followed developer instructions for determining K and population assignments. First, we ran 10 non-admixture models for each K from 2 to 20. For model comparisons, TESS computes a deviance information criterion (DIC). We ran 10 spatially-conditional auto-regressive admixture models for each K to the DIC plateau of non-admixture models (Figs. S1, S2). All models included pairwise great circle geographic distances for weighting the Voronoi neighborhood, 100,000 iterations, and a 25,000 iteration burn-in period. We retained 20% of the models exhibiting the lowest DIC scores and used CLUMPP 1.1.2 to perform model-averaging (Jakobsson and Rosenberg 2007).

In GENELAND, K is optimized by the model. We followed developer recommendations for determining K and individual population assignments (Guillot et al. 2005a). First, we identified a distribution of K from initial models, and then we ran correlated allele frequency models allowing K to vary within its distribution from the initial models (Fig. S1). Finally, we ran 5 spatial, correlated allele frequency models with K fixed at the mode and selected the model with the highest negative log-likelihood value for further inference. Each run included an uncertainty on GPS coordinates of 0.1 decimal degrees (~ 11 km), 1,000,000 iterations, a thinning interval of 10,000, and a 25% burn-in period prior to extracting model output. We assigned individuals to populations based on their highest assignment probability. To visualize the probability of population membership across the study area, we used package POPSutilities 1.0 in R 3.3.0, which interpolates admixture coefficients using geospatial kriging (Jay et al. 2012).

Temporal variation in sampling can bias spatial population genetic analyses; however, spatially-explicit Bayesian clustering models should account for most temporal variation (Durand et al. 2009b; François and Durand 2010). Populations did not group based on sampling date in TESS or GENELAND. Additionally, isolation-by-distance was significant across our study area ($R^2 = 0.15$, $P < 0.001$). Although TESS and GENELAND showed nearly identical results, we used TESS admixture models for analyses and inferences because TESS outperforms GENELAND in the presence of isolation-by-distance.

Genetic diversity

We tested for linkage disequilibrium, deviations from Hardy–Weinberg proportions, and null alleles in GENEPOP 4.5.1 (Rousset 2008). For each identified population, we calculated standard measures of genetic diversity and used 1000 permutations to test for significant genetic isolation-by-distance in GenAlEx 6.502 (Peakall and Smouse 2006, 2012). To measure the number of alleles, we calculated allelic richness using rarefaction methods which correct for sample size in FSTAT 2.9.3.2 (Goudet 1995). To assess inbreeding, we calculated internal relatedness using package Rhh 1.0.2 in Program R 3.3.0 (Alho et al. 2010). We calculated effective population size (N_e) for each population using NeEstimator 2.01 using the linkage disequilibrium method assuming random mating (Do et al. 2014). Because the inclusion of low-frequency alleles can upwardly bias estimates of N_e (Waples and Do 2010), we ran two separate models including alleles with frequencies $\geq 5\%$ or $\geq 1\%$. To test for evidence of recent reductions in N_e (i.e., genetic bottlenecks), we used program BOTTLENECK 1.2.02 to determine if a population exhibited a significant number of loci with heterozygote excess (Piry et al. 1999). For each population identified by assignment models, we performed bottleneck analyses using two-phase (70:30 step-wise:infinite-alleles) microsatellite mutation models for 100,000 iterations.

We used biotools 3.1 (da Silva et al. 2017) in R to obtain spatial unbiased genetic diversity estimates [uHe: unbiased expected heterozygosity; (Nei 1978)] based on the interpolation of individual estimates (Manel et al. 2007). We minimized spatial extrapolation by using a radius of 500 m and reduced bias by setting the neighborhood size (i.e., minimum number of individuals used to calculate uHe) to 2. The mean size of each neighborhood was 14.6 and 42.5% of the neighborhoods contained at least 10 individuals.

Population differentiation and genetic source–sink dynamics

We used three complementary approaches to assess functional population connectivity, including a discriminant analysis of principal components (DAPC), pairwise estimates of population divergence (F_{ST}), and pairwise estimates of bi-directional migration rates (*m*). The DAPC uses linear combinations of alleles to maximize between-population genetic variation and provides a graphical representation of functional connectivity among genetic clusters (Jombart et al. 2010).

We implemented the DAPC in program R using package adegenet 2.0.1 (Jombart 2008). The identified number of genetic clusters in adegenet agreed with TESS and GENELAND (Fig. S3). Because the algorithm for individual assignments in adegenet is not as powerful as Bayesian population assignment algorithms (Jombart et al. 2010), we defined populations in the DAPC using results from the Bayesian population assignments. Because we were not assigning individual membership probabilities in the DAPC, we retained all information (i.e., 344 PCA axes and all 9 discriminant functions) in the analysis. Our results from retaining all information did not differ from results when only retaining an estimated optimal number of PCA axes using the α-score method. Pairwise population divergence estimates (F_{ST}) were calculated in GenAlEx using 999 permutation tests for significance. To conform to the expectations of genetic isolation-by-distance, rather than an island model, we also calculated Rousset's $F_{ST}/(1-F_{ST})$ (Rousset 1997).

We used program BayesAss 3.0 to estimate migration rates (*m*) among populations identified by population assignment models (Wilson and Rannala 2003). We used 10 randomly-seeded runs each with 5,000,000 iterations, a burnin of 1,000,000, and thinning interval of 1000. Posterior mean parameter estimates were nearly identical among runs, and all trace files indicated convergence of model parameters (Meirmans 2014). We tested the hypothesis of Andreasen et al. (2012) that Nevada pumas were a genetic source for California pumas by summing emigration rates and subtracting the sum of immigration rates for each population (Andreasen et al. 2012). Positive numbers indicate the population was a genetic source whereas negative numbers indicate a sink. We used package circlize 0.3.7 in program R to visualize bi-directional migration rates estimated in BayesAss (Gu et al. 2014).

Results

Population genetic structure and diversity

Our analyses revealed that pumas in California exhibited strong population genetic structure and some California populations had extremely low levels of genetic diversity. We identified nine genetic clusters in California and one genetic cluster in Nevada (Figs. 2, S1, S2, S4). We classified these 10 genetic clusters as genetic populations, including the Nevada (NV), Eastern Sierra Nevada (ESN), Western Sierra Nevada (WSN), North Coast (NC), Northern section of the Central Coast (CC-N), Central section of the Central Coast (CC-C), Southern section of the Central Coast (CC-S), San Gabriel/San Bernardino (SGSB), Santa Ana (SA), and Eastern Peninsular Range (EP) populations (Fig. 2).

The genetic diversity of California puma populations exhibited a large amount of variation with some populations having estimates similar to other large populations and some exhibiting estimates nearly as low as the endangered Florida Panther. The NV, ESN, and WSN populations had the highest estimates of genetic diversity compared to other populations (Table 1). Regionally, the Modoc Plateau and Sierra Nevada contained individuals that had consistently high genetic diversity (Fig. 3). Although the NV population had high genetic diversity, the individual-based analysis indicated spatially-heterogenous genetic diversity across Nevada with low levels occurring near the Lahontan Basin (Fig. 3). The CC-C population had relatively intermediate levels of genetic diversity (Table 1). The SA population had the lowest genetic diversity observed across all estimates, followed by the SGSB, NC, CC-S, and CC-N populations. SA also had the highest measure of internal relatedness. WSN had the largest effective population size (N_e), followed by NV, NC, and CC-C (Table 2). All other populations had an N_e of < 50 (often given as a desirable minimum from a conservation genetics point of view; Frankham 1995; Mace et al. 2008), and CC-S and SGSB had extremely low effective population sizes (≤ 5). All populations except NV and NC exhibited evidence of a prior genetic bottleneck (Table 2).

Population differentiation and genetic source–sink dynamics

Our discriminant analysis of principal components (DAPC) revealed that puma populations in California had low connectivity compared to pumas in Nevada which were composed of a single genetic population that exhibited high connectivity with several California populations. The first axis (x-axis; 33.3% of total variation) of the DAPC broadly corresponded to a latitudinal population separation with north to the left and south to the right (Fig. 4a). The second axis (y-axis; 24.4%) separated populations longitudinally and primarily separated central coast populations from southern populations (Fig. 4a). The NV, ESN, WSN, and NC populations grouped together, as did the CC-N, CC-C, and CC-S populations. The SA and EP populations grouped slightly but were separated from all other populations (Fig. 4a). Lastly, the SGSB was intermediate relative to all other populations, but was most closely-related to the WSN population (Fig. 4a).

Bi-directional migration rate models indicated there were 5 genetic source populations (i.e., ESN, WSN, CC-N, CC-C, EP) and 5 genetic sink populations (i.e., NV, NC, CC-S, SGSB, SA), however, there was only weak evidence indicating CC-N and NC were source and sink populations, respectively. Bi-directional migration

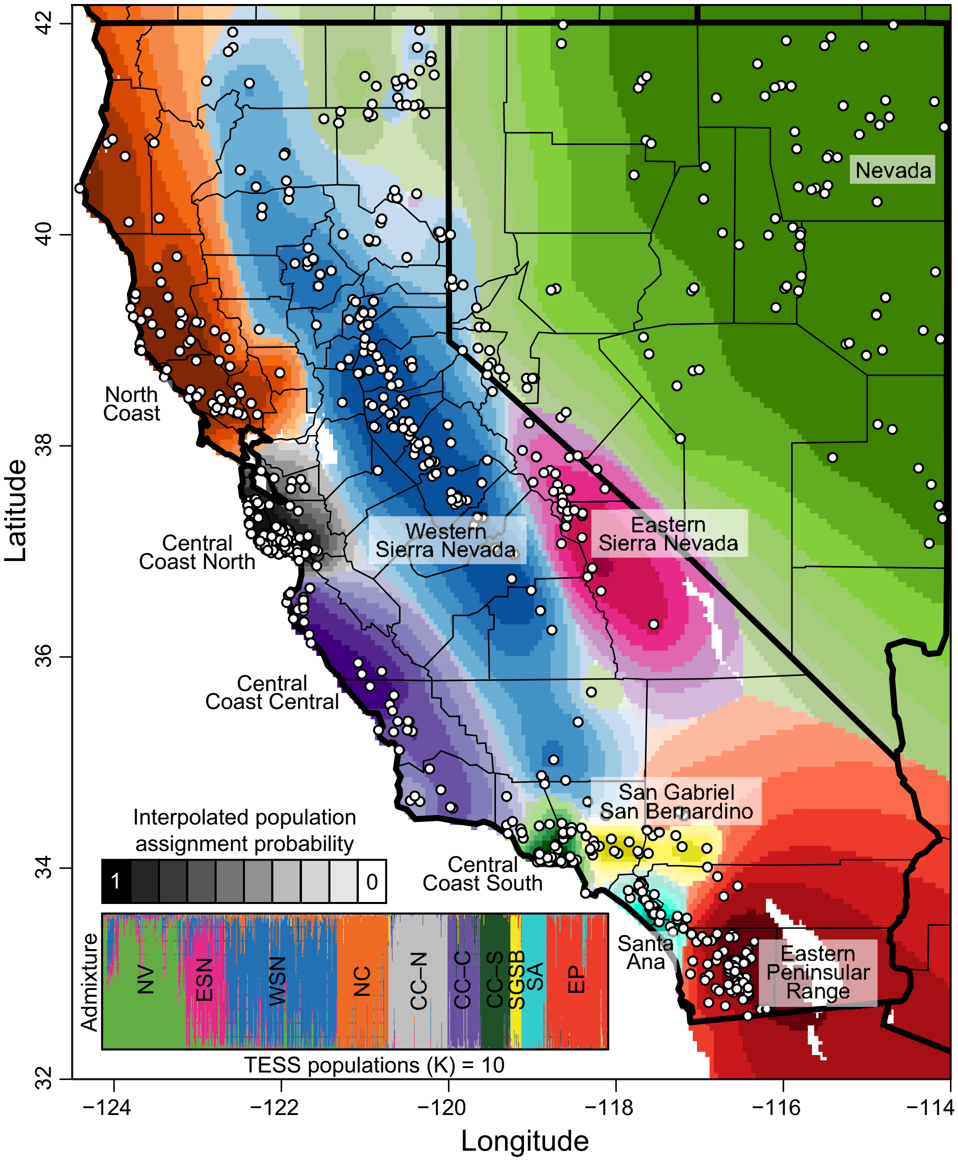

Fig. 2 Population genetic structure of pumas across California and Nevada. Individual admixture proportions from TESS (inset barplot) were spatially-interpolated. Each color represents a genetic population. The decay in color intensity on the map represents lower probabilities of population assignment and indicates areas with admixture between populations. State and county borders are displayed for reference. *NV* Nevada, *ESN* Eastern Sierra Nevada, *WSN* Western Sierra Nevada, *NC* North Coast, *CC-N* Northern section of the Central Coast, *CC-C* Central section of the Central Coast, *CC-S* Southern section of the Central Coast, *SGSB* San Gabriel/San Bernardino, *SA* Santa Ana, *EP* Eastern Peninsular Range

rate estimates showed connectivity patterns similar to the DAPC (Fig. 4). Although there was gene flow among the NV, ESN, and WSN populations based on bi-directional migration rates, the NC population primarily exchanged migrants with the ESN and WSN populations (Fig. 4b). The populations in the Sierra Nevada (ESN, WSN) were the greatest genetic source populations but exhibited limited gene flow with the populations along the central coast of California (CC-N, CC-C, CC-S), and neither NV nor NC exhibited appreciable gene flow with central coast populations (Fig. 4b; Table S2). The SA population exhibited gene flow only with the EP population, and the EP population had low connectivity with the SGSB population (Fig. 4b). The puma population in the Transverse Ranges (SGSB) was the largest genetic sink but exchanged some genetic material with the WSN, CC-C, and EP populations (Fig. 4b). Populations in the Southern Ranges (SA, EP) were largely disconnected from all other populations (Fig. 4b).

Table 1 Allelic and genetic diversity of puma populations, including sample-size corrected allelic richness, the number of private alleles, the percent of polymorphic loci, observed heterozygosity, unbiased expected heterozygosity, and average internal relatedness (a measure of inbreeding)

Population	N	Allelic richness	Private alleles	Polymorphic Loci (%)	Observed heterozygosity	Expected heterozygosity	Internal relatedness
NV	166	3.47 (0.09)	9	100	0.50 (0.03)	0.52 (0.03)	0.15 (0.01)
ESN	79	3.46 (0.13)	5	100	0.52 (0.03)	0.53 (0.03)	0.11 (0.01)
WSN	217	3.63 (0.08)	5	100	0.51 (0.03)	0.52 (0.03)	0.09 (0.01)
NC	101	3.06 (0.10)	5	97.6	0.40 (0.03)	0.41 (0.03)	0.28 (0.01)
CC-N	116	2.62 (0.08)	1	97.6	0.41 (0.03)	0.42 (0.03)	0.27 (0.01)
CC-C	63	3.00 (0.12)	1	95.2	0.45 (0.03)	0.46 (0.03)	0.19 (0.02)
CC-S	60	2.63 (0.13)	1	92.9	0.41 (0.04)	0.41 (0.03)	0.27 (0.02)
SGSB	22	2.75 (0.17)	0	95.2	0.40 (0.03)	0.42 (0.03)	0.29 (0.03)
SA	48	2.27 (0.12)	0	85.7	0.34 (0.03)	0.33 (0.03)	0.39 (0.02)
EP	120	3.07 (0.11)	3	100	0.44 (0.03)	0.44 (0.03)	0.21 (0.01)

NV Nevada, *ESN* Eastern Sierra Nevada, *WSN* Western Sierra Nevada, *NC* North Coast, *CC-N* Northern section of the Central Coast, *CC-C* Central section of the Central Coast, *CC-S* Southern section of the Central Coast, *SGSB* San Gabriel/San Bernardino, *SA* Santa Ana, *EP* Eastern Peninsular Range. Standard errors are presented in parentheses

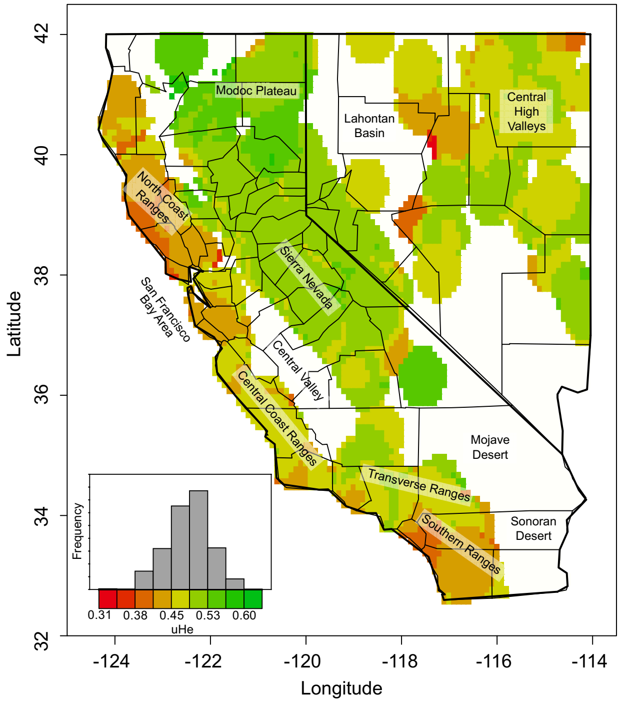

Fig. 3 Gene diversity (uHe: unbiased expected heterozygosity) heat map of pumas in California and Nevada. Neighborhood size was not significantly related to uHe ($R^2 = 0.005$, $P < 0.001$)

Discussion

We identified 10 genetically-distinct puma populations within California and Nevada that varied considerably in genetic diversity (uHe range 0.33–0.53) and effective population size (N_e range 5–157). Some of our previous analyses identified family-level genetic structure which was not observed here (Ernest et al. 2014; Gustafson et al. 2017; Riley et al. 2014), indicating these genetic populations are not the result of sampling related individuals. The large number of populations (N = 9) and the strong genetic differences among neighboring puma populations in California differed from other studies at similar spatial scales (Anderson et al. 2004; Holbrook et al. 2012; Loxterman 2011; McRae et al. 2005), including Nevada (Andreasen et al. 2012). Most state-wide studies have been conducted in less-developed locations with more continuous habitat and showed that geographic distance and natural landscape components were the most common factors associated with the broad-scale genetic structure of puma populations (Anderson et al. 2004; Holbrook et al. 2012; Loxterman 2011; McRae et al. 2005; Wright 1943). In contrast, mountain ranges in California are variable in size and arrangement and there are vast areas of inter-mountain anthropogenic development throughout the state. Previous local studies in California have identified individual roadways and associated human development as major barriers to puma movements (Ernest et al. 2014; Gustafson et al. 2017; Riley et al. 2014; Vickers et al. 2015), and our study confirms, on a broad geographic scale, strong population structure among adjacent puma populations. The considerable variation in genetic diversity and effective population size among California and Nevada populations is likely attributable to the variation in the amount of suitable habitat and their degree of isolation. The Western Sierra Nevada population had the largest effective size and was closely related (i.e., lowest F_{ST} values) to every population except for the Northern Central Coast population and populations south of Los Angeles (Santa Ana, Eastern Peninsular Range), suggesting puma populations form a

Table 2 Summary of effective population size and bottleneck analyses for each population

Population	Sample size	Effective population size (N_e) N_e with AFs ≥ 0.05	Bottleneck N_e with AFs ≥ 0.01	P-value
NV	166	92.2 (84.2–101.4)	107.2 (98.5–117.1)	0.123
ESN	79	22.6 (20.8–24.5)	26.5 (24.7–28.5)	**< 0.001**
WSN	217	157.5 (141.2–176.8)	180.6 (164.1–199.7)	**0.038**
NC	101	82.5 (71.3–96.8)	66 (59.3–73.9)	0.256
CC-N	116	16.6 (15.1–18.2)	15.5 (14.2–16.8)	**0.001**
CC-C	63	56.6 (47.4–69.0)	63 (53.3–75.8)	**0.018**
CC-S	60	2.7 (2.5–2.9)	3.6 (3.4–3.9)	**0.008**
SGSB	22	5 (3.3–6.4)	7.5 (6.2–9.1)	**0.046**
SA	48	15.6 (13–18.7)	21.7 (18–26.4)	**0.007**
EP	120	31.6 (29.1–34.4)	37.4 (34.5–40.5)	**0.021**

AF allele frequencies, *NV* Nevada, *ESN* Eastern Sierra Nevada, *WSN* Western Sierra Nevada, *NC* North Coast, *CC-N* Northern section of the Central Coast, *CC-C* Central section of the Central Coast, *CC-S* Southern section of the Central Coast, *SGSB* San Gabriel/San Bernardino, *SA* Santa Ana, *EP* Eastern Peninsular Range. Parametric 95% confidence intervals are presented in parentheses. Bottleneck P-values from standardized differences tests are presented

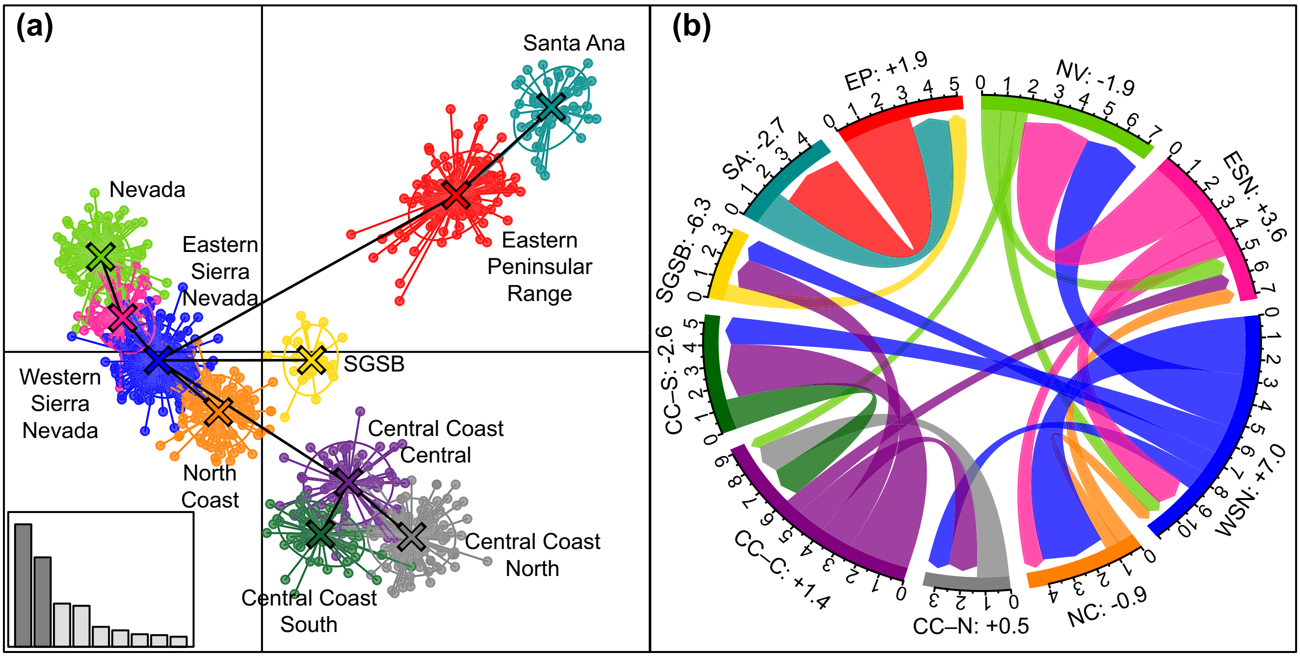

Fig. 4 Functional connectedness of puma populations, based on **a** a discriminant analysis of principal components and **b** bi-directional migration rate estimates (multiplied by 100 for visualization). Each dot represents an individual (**a**). Each color **a, b** represents a population. Black lines **a** indicate the most closely-related population based on genetic dissimilarities. The inset barplot **a** shows which axes are being displayed (i.e., discriminant functions 1 and 2) and the relative proportion of variation explained by each of the 9 discriminant functions. Two-thirds of the individuals in each population are contained within the corresponding ellipsoid. For a biologically meaningful interpretation, only estimates of interpopulation migration rates with 95% confidence intervals that do not cross 0 are presented (b; Table S2). Net genetic source–sink migration rates are presented next to population names with positive values indicating a net genetic source and negative values indicating a net genetic sink (e.g., WSN exported 9% of migrants and received 2%, so its net rate is + 7.0). *NV* Nevada, *ESN* Eastern Sierra Nevada, *WSN* Western Sierra Nevada, *NC* North Coast, *CC-N* Northern section of the Central Coast, *CC-C* Central section of the Central Coast, *CC-S* Southern section of the Central Coast, *SGSB* San Gabriel/San Bernardino, *SA* Santa Ana, *EP* Eastern Peninsular Range

"horseshoe" network around the Central Valley with San Francisco Bay acting as a major barrier along the coast (Hooper 1944). The large National Parks and National Forests (e.g., Sequoia–Kings Canyon and Yosemite National Parks) in the Sierra Nevada provide contiguous habitat for pumas with minimal anthropogenic infrastructure (Ernest et al. 2000).

Our results are consistent with a previous report (Andreasen et al. 2012) indicating pumas from Nevada form a single genetic cluster and are distinct from pumas in the Sierra Nevada of California, but our results contrast with their suggestion that pumas from Nevada are a genetic source for pumas in California. There are several differences between the studies that could explain the inconsistencies. Andreasen et al. (2012) used considerably fewer genetic markers than the present study (9 microsatellites vs. 42). Because the number of loci used in bi-directional migration rate models has the largest effect on the accuracy of the estimates (Faubet and Gaggiotti 2008; Wilson and Rannala 2003), we expect the differences are driven by the different number of loci. Although we sampled fewer pumas from Nevada and more pumas from California, sample size differences generally only affect the variance and not the accuracy of the bi-directional migration rate estimates (Faubet and Gaggiotti 2008; Wilson and Rannala 2003). Further, sample size alone likely does not explain the contrasting results and the multiple lines of evidence supporting the Sierra Nevada populations as a genetic source for the surrounding populations, including Nevada.

Both our population-level and individual-based analyses clearly indicated that the Western Sierra Nevada population had the highest genetic diversity, which is likely being maintained by the large effective population size and not via migrants from the Nevada population, which had lower genetic diversity estimates. Further, instead of testing migration rates among the two populations ($K=2$) which had the highest model support in their study, Andreasen et al. (2012) tested among five genetic clusters ($K=5$) which had average within-cluster migration estimates of only 54% (and a large SD of 8.4%) compared to our within-population migration estimates of 94% (±1.9%). Thus, their examination of genetic source–sink dynamics was based on significantly less distinct genetic units ($F_{ST}=0.05$–0.09 compared to our study where Rousset's $F_{ST}=0.05$–0.39), which is computationally problematic with a small number of loci (Faubet and Gaggiotti 2008; Wilson and Rannala 2003). Additionally, puma hunting is legal in Nevada but not California, and puma densities that have been reduced regionally from hunter harvest are known to be compensated by higher immigration rates from neighboring populations (Cooley et al. 2009; Robinson et al. 2008), which is biologically consistent with our observations.

The North Coast and inland populations (Nevada, Eastern Sierra Nevada, Western Sierra Nevada) appear to be large (i.e., high N_e), genetically diverse, and well-connected, and may form an evolutionary significant unit (ESU: a group of populations that have accumulated adaptive differences from other populations in part from reproductive isolation; Palsbøll et al. 2007). However, genome-wide data and gene–environment correlation studies will be needed to evaluate whether these population are exhibiting adaptations to specific habitats or ecoregions. Within this group of populations, we detected evidence for bottlenecks in the Eastern Sierra Nevada population and Western Sierra Nevada population. The bottleneck in the Eastern Sierra Nevada population is not surprising given that the puma abundance in this region may have been reduced by 50% after a severe decline in mule deer (Pierce and Bleich 2014; Pierce et al. 2000; Villepique et al. 2011). Besides the North Coast and Nevada populations, all of the other populations also exhibited evidence of genetic bottlenecks; however, we do not know if this was caused by urbanization, a decrease in prey abundance, or some other factor, because the demographic and genetic histories of these populations are not well-documented.

The Central population of the Central Coast exhibited intermediate levels of genetic diversity, and maintaining gene flow from this population to the genetically-depauperate Northern and Southern Central Coast populations is critically important for their long-term viability (Benson et al. 2016; Gray et al. 2016; Riley et al. 2014). A previous report examined the southern area of the central coast region specifically and observed extremely low genetic diversity in the Santa Monica Mountains, south of Highway 101 in the Los Angeles Area (Riley et al. 2014). At a statewide level, we found pumas in the Santa Monica Mountains to be part of a larger genetic population including pumas in the Simi Hills and Santa Susana Mountains; however, our larger sample from the Southern Central Coast population revealed only slightly higher estimates of genetic diversity than pumas sampled from the Santa Monica Mountains alone (Riley et al. 2014). Road-isolated pumas in the Santa Monica Mountains only receive rare migrants from the Simi Hills and Santa Susana Mountains and are at a high risk of extirpation from isolation and subsequent demographic and genetic stochasticity (Benson et al. 2016). These results emphasize the need to conserve within-population connectivity, specifically from the Coast Ranges and the Sierra Nevada through the Santa Susana Mountains and Simi Hills to the Santa Monica Mountains.

Despite being very close geographically, the puma populations around Los Angeles (Southern Central Coast, San Gabriel/San Bernardino, Santa Ana) are highly diverged. For example, the Santa Ana and Southern Central Coast population are among the closest populations geographically

(~ 100 km apart) but are among the most genetically distant populations we observed (Rousset's $F_{ST} = 0.32$). Additionally, the Southern Range populations (Santa Ana, Eastern Peninsular Range) are largely disconnected from all other populations in this study, including those just to the north of the Los Angeles Basin. These observations are consistent with the hypothesis of reduced connectivity from habitat fragmentation by human development (i.e., the Los Angeles metropolitan area), including major roads (i.e., I-10, I-15, I-210, etc.) (Ernest et al. 2003). The San Gabriel/San Bernardino population was most genetically similar to the Western Sierra Nevada, Central region of the Central Coast, and Eastern Peninsular Range populations, indicating it is an area of intersection between multiple populations. We suggest the small mountain ranges in this area (i.e., Tehachapi, Sierra Pelona, San Gabriel, and San Bernardino Mountains) are necessary for contiguous statewide genetic connectivity and that pumas occupying those ranges, and the wildlands habitat in those ranges, should be considered conservation priorities (Beier et al. 2009; Ernest et al. 2003; Wildlands 2008).

The Santa Ana population exhibited the lowest measures of genetic diversity and the highest measures of inbreeding among all populations, with levels nearing those of Florida panthers (most recent estimates of He = 0.24), which nearly went extinct from genetic factors prior to artificial genetic rescue (Johnson et al. 2010). It is important to note, however, that out of the 42 microsatellite loci used in this study, only 4 were shared with the 23 microsatellite loci used in the Florida panther study. A set of shared markers would be most appropriate for direct interpopulation comparisons (e.g., Culver et al. 2000). A single immigrant from the Eastern Peninsular Range recently enhanced the genetic diversity of Santa Ana pumas and is likely responsible for the higher effective population size than previously observed (Ernest et al. 2014). Nevertheless, genetic diversity of Santa Ana pumas will decline without additional immigration (Gustafson et al. 2017). The Eastern Peninsular Range population had the highest genetic diversity and effective size among the populations in the Los Angeles—San Diego area (Southern Central Coast, San Gabriel/San Bernardino, Santa Ana, Eastern Peninsular Range). Restoring connectivity with the Eastern Peninsular Range and reducing further impacts from development on gene flow among the adjacent populations, including pumas from Arizona and Mexico (Gustafson et al. 2017), are critically important to avoiding extirpation of genetically-depauperate populations (Benson et al. 2016).

By identifying puma populations and measuring gene flow among them, our analyses can help guide and inform puma conservation and management. Whenever possible, government agencies and other stakeholders should consider population connectivity and prevent further fragmentation by human development both within and among populations. In contrast to other studies in 7 western states that generally indicated weak puma genetic structure (Anderson et al. 2004; Holbrook et al. 2012; Loxterman 2011; McRae et al. 2005), our study showed strong genetic structure. Although puma habitat in California is aggregated and separated by valleys, it is unlikely these valleys would have been such strong barriers to gene flow pre-development given that pumas have been documented to move across the entire Central Valley post-development (Ernest et al. 2003; McClanahan et al. 2017). Further, similar geographic features, such as the Wyoming Basin, have not been reported to structure puma populations (Anderson et al. 2004). Instead, we hypothesize that human-associated infrastructure within the valleys are artificially isolating pumas beyond what they would naturally experience among ecoregions.

Population-level conservation strategies are needed to reintegrate fragmented, at-risk populations into a connected multi-state, multi-landscape population network (Zeller et al. 2017). Gene flow via maintenance of existing occupied habitat combined with improved and additional networks of wildlife corridors (Bennett 2017; Gloyne and Clevenger 2001; Johnson et al. 2010; Sawaya et al. 2013) will ultimately be necessary to promote the long-term persistence of isolated populations (Benson et al. 2016; Ernest et al. 2014; Gustafson et al. 2017; Riley et al. 2014). Without such measures, it is likely too late to expect a natural increase in genetic connectivity or selection for increased dispersal (Burdett et al. 2010; Cheptou et al. 2017), and assisted gene flow may be needed in perpetuity for several populations to remain viable (Benson et al. 2011, 2016; Ernest et al. 2014; Gustafson et al. 2017; Johnson et al. 2010; Vickers et al. 2015).

In some of these populations, individual migrants are of immediate conservation importance, and human-induced mortality should be avoided to the extent possible. The effects of fragmentation on multiple populations of this umbrella species are likely indicative of a larger ecological problem in one of the most biologically diverse regions of North America (Calsbeek et al. 2003; Dobson et al. 1997; Thorne et al. 2006). We strongly encourage land owners and managers to proactively consider broad-scale wildlife connectivity in future development proposals. However, in the absence of maintaining habitat of a spatial scale grand enough to ensure the persistence of prey and predator populations, the issue of connectivity will become a moot point.

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Data availability Through agreements with non-profit organizations, private landowners, and Native American Tribes, exact GPS locations of puma samples are not to be publicly shared. Thus, puma GPS locations are referenced to the nearest town or city. Sampling locations and microsatellite genotypes are available on Dryad: https://doi.org/10.5061/dryad.j76c4k4.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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References

Albert JS, Schoolmaster DR, Tagliacollo V, Duke-Sylvester SM (2016) Barrier displacement on a neutral landscape: toward a theory of continental biogeography. Syst Biol 66:167–182. https://doi.org/10.1093/sysbio/syw080

Alho JS, Valimaki K, Merila J (2010) Rhh: an R extension for estimating multilocus heterozygosity and heterozygosity-heterozygosity correlation. Mol Ecol Resour 10:720–722. https://doi.org/10.1111/j.1755-0998.2010.02830.x

Anderson CR, Lindzey FG, McDonald DB (2004) Genetic structure of cougar populations across the Wyoming Basin: Metapopulation or megapopulation. J Mamm 85:1207–1214. https://doi.org/10.1644/BEL-111.1

Andreasen AM, Stewart KM, Longland WS, Beckmann JP, Forister ML (2012) Identification of source–sink dynamics in mountain lions of the Great Basin. Mol Ecol 21:5689–5701. https://doi.org/10.1111/j.1365-294X.2012.05740.x

Balkenhol N, Waits LP (2009) Molecular road ecology: exploring the potential of genetics for investigating transportation impacts on wildlife. Mol Ecol 18:4151–4164. https://doi.org/10.1111/j.1365-294X.2009.04322.x

Beier P (1995) Dispersal of juvenile cougars in fragmented habitat. J Wildl Manag 59:228–237. https://doi.org/10.2307/3808935

Beier P, Majka DR, Newell SL (2009) Uncertainty analysis of least-cost modeling for designing wildlife linkages. Ecol Appl 19:2067–2077. https://doi.org/10.1890/08-1898.1

Bennett VJ (2017) Effects of road density and pattern on the conservation of species and biodiversity. Curr Landsc Ecol Rep 2:1–11. https://doi.org/10.1007/s40823-017-0020-6

Benson JF et al (2011) Intentional genetic introgression influences survival of adults and subadults in a small, inbred felid population. J Anim Ecol 80:958–967. https://doi.org/10.1111/j.1365-2656.2011.01809.x

Benson JF, Mahoney PJ, Sikich JA, Serieys LE, Pollinger JP, Ernest HB, Riley SP (2016) Interactions between demography, genetics, and landscape connectivity increase extinction probability for a small population of large carnivores in a major metropolitan area. Proc R Soc B 283:20160957. https://doi.org/10.1098/rspb.2016.0957

Blair C et al (2012) A simulation-based evaluation of methods for inferring linear barriers to gene flow. Mole Ecol Resour 12:822–833. https://doi.org/10.1111/j.1755-0998.2012.03151.x

Buchalski MR, Sacks BN, Gille DA, Penedo MCT, Ernest HB, Morrison SA, Boyce WM (2016) Phylogeographic and population genetic structure of bighorn sheep (*Ovis canadensis*) in North American deserts. J Mammal 97:823–838. https://doi.org/10.1093/jmammal/gyw011

Burdett CL et al (2010) Interfacing models of wildlife habitat and human development to predict the future distribution of puma habitat. Ecosphere 1:1–21. https://doi.org/10.1890/ES10-00005.1

Caballero A, García-Dorado A (2013) Allelic diversity and its implications for the rate of adaptation. Genetics 195:1373–1384. https://doi.org/10.1534/genetics.113.158410

Calsbeek R, Thompson JN, Richardson JE (2003) Patterns of molecular evolution and diversification in a biodiversity hotspot: The California Floristic Province. Mol Ecol 12:1021–1029. https://doi.org/10.1046/j.1365-294X.2003.01794.x

Carlson SM, Cunningham CJ, Westley PA (2014) Evolutionary rescue in a changing world. TREE 29:521–530. https://doi.org/10.1016/j.tree.2014.06.005

Carroll C, Noss RF, Paquet PC (2001) Carnivores as focal species for conservation planning in the Rocky Mountain region. Ecol Appl 11:961–980. https://doi.org/10.2307/3061005

Chapman J, Nakagawa S, Coltman D, Slate J, Sheldon B (2009) A quantitative review of heterozygosity–fitness correlations in animal populations. Mol Ecol 18:2746–2765. https://doi.org/10.1111/j.1365-294X.2009.04247.x

Cheptou P-O, Hargreaves AL, Bonte D, Jacquemyn H (2017) Adaptation to fragmentation: evolutionary dynamics driven by human influences. Philos Trans R Soc B 372:20160037. https://doi.org/10.1098/rstb.2016.0037

Cooley HS, Wielgus RB, Koehler GM, Robinson HS, Maletzke BT (2009) Does hunting regulate cougar populations? A test of the compensatory mortality hypothesis. Ecology 90:2913–2921. https://doi.org/10.1890/08-1805.1

Crooks KR, Burdett CL, Theobald DM, King SRB, Di Marco M, Rondinini C, Boitani L (2017) Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals. PNAS 114:7635–7640. https://doi.org/10.1073/pnas.1705769114

Culver M, Johnson WE, Pecon-Slattery J, O'Brien SJ (2000) Genomic ancestry of the American puma (*Puma concolor*). J Hered 91:186–197

da Silva A, Malafaia G, Menezes I (2017) Biotools: an R function to predict spatial gene diversity via an individual-based approach. Gene Mol Res 16:gmr16029655. https://doi.org/10.4238/gmr16029655

Delaney KS, Riley SP, Fisher RN (2010) A rapid, strong, and convergent genetic response to urban habitat fragmentation in four divergent and widespread vertebrates. PLoS ONE 5:e12767. https://doi.org/10.1371/journal.pone.0012767

Do C, Waples RS, Peel D, Macbeth GM, Tillett BJ, Ovenden JR (2014) NeEstimator v2: Re-implementation of software for the estimation of contemporary effective population size (Ne) from genetic data. Mol Ecol Resour 14:209–214. https://doi.org/10.1111/1755-0998.12157

Dobson AP, Rodriguez JP, Roberts WM, Wilcove DS (1997) Geographic distribution of endangered species in the United States. Science 275:550–553

Durand E, Chen C, François O (2009a) TESS version 2.3 Reference Manual. http://membres-timc.imag.fr/Olivier.Francois/manual.pdf. Accessed 9 May 2018

Durand E, Jay F, Gaggiotti OE, François O (2009b) Spatial inference of admixture proportions and secondary contact zones. Mol Biol Evol 26:1963–1973. https://doi.org/10.1093/molbev/msp106

Ernest HB, Penedo MCT, May BP, Syvanen M, Boyce WM (2000) Molecular tracking of mountain lions in the Yosemite Valley region in California: Genetic analysis using microsatellites and faecal DNA. Mol Ecol 9:433–441. https://doi.org/10.1046/j.1365-294x.2000.00890.x

Ernest HB, Boyce WM, Bleich VC, May B, Stiver SJ, Torres SG (2003) Genetic structure of mountain lion (*Puma concolor*) populations in California. Conserv Genet 4:353–366. https://doi.org/10.1023/A:1024069014911

Ernest HB, Vickers TW, Morrison SA, Buchalski MR, Boyce WM (2014) Fractured genetic connectivity threatens a southern California puma (*Puma concolor*) population. PLoS One 9:e107985. https://doi.org/10.1371/journal.pone.0107985

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34:487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Faubet P, Gaggiotti OE (2008) A new Bayesian method to identify the environmental factors that influence recent migration. Genetics 178:1491–1504. https://doi.org/10.1534/genetics.107.082560

Fisher RN, Shaffer HB (1996) The decline of amphibians in California's Great Central Valley. Conserv Biol 10:1387–1397. https://doi.org/10.1046/j.1523-1739.1996.10051387.x

François O, Durand E (2010) Spatially explicit Bayesian clustering models in population genetics. Mol Ecol Resour 10:773–784. https://doi.org/10.1111/j.1755-0998.2010.02868.x

Frankham R (1995) Efective population size/adult population size ratios in wildlife: a review. Genet Res 66:95–107

Frankham R (2015) Genetic rescue of small inbred populations: meta-analysis reveals large and consistent benefits of gene flow. Mol Ecol 24:2610–2618. https://doi.org/10.1111/mec.13139

Gloyne CC, Clevenger AP (2001) Cougar *Puma concolor* use of wildlife crossing structures on the Trans-Canada highway in Banff National Park, Alberta. Wildl Biol 7:117–124

Goudet J (1995) FSTAT (version 1.2): a computer program to calculate F-statistics. J Hered 86:485–486. https://doi.org/10.1093/oxfordjournals.jhered.a111627

Gray M, Wilmers CC, Reed SE, Merenlender AM (2016) Landscape feature-based permeability models relate to puma occurrence. Landsc Urban Plan 147:50–58. https://doi.org/10.1016/j.landurbplan.2015.11.009

Gu Z, Gu L, Eils R, Schlesner M, Brors B (2014) *circlize* implements and enhances circular visualization in R. Bioinformatics 30:btu393. https://doi.org/10.1093/bioinformatics/btu393

Guillot G, Estoup A, Mortier F, Cosson JF (2005a) A spatial statistical model for landscape genetics. Genetics 170:1261–1280. https://doi.org/10.1534/genetics.104.033803

Guillot G, Mortier F, Estoup A (2005b) GENELAND: a computer package for landscape genetics. Mol Ecol Notes 5:712–715. https://doi.org/10.1111/j.1471-8286.2005.01031.x

Gustafson KD, Vickers TW, Boyce WM, Ernest HB (2017) A single migrant enhances the genetic diversity of an inbred puma population. R Soc Open Sci 4:170115. https://doi.org/10.1098/rsos.170115

Haddad NM et al (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci Adv 1:e1500052. https://doi.org/10.1126/sciadv.1500052

Hawley JE et al (2016) Long-distance dispersal of a subadult male cougar from South Dakota to Connecticut documented with DNA evidence. J Mamm 97:1435–1440. https://doi.org/10.1093/jmammal/gyw088

Holbrook JD, DeYoung RW, Janecka JE, Tewes ME, Honeycutt RL, Young JH (2012) Genetic diversity, population structure, and movements of mountain lions (*Puma concolor*) in Texas. J Mamm 93:989–1000. https://doi.org/10.1644/11-Mamm-a-326.2

Hooper ET (1944) San Francisco Bay as a factor influencing speciation in rodents. Miscellaneous Publications, Museum of Zoology, University of Michigan 59:9–89

Jakobsson M, Rosenberg NA (2007) CLUMPP: a cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. Bioinformatics 23:1801–1806. https://doi.org/10.1093/bioinformatics/btm233

Jay F et al (2012) Forecasting changes in population genetic structure of alpine plants in response to global warming. Mol Ecol 21:2354–2368. https://doi.org/10.1111/j.1365-294X.2012.05541.x

Johnson WE et al (2010) Genetic restoration of the Florida panther. Science 329:1641–1645. https://doi.org/10.1126/science.1192891

Jombart T (2008) *adegenet*: a R package for the multivariate analysis of genetic markers. Bioinformatics 24:1403–1405. https://doi.org/10.1093/bioinformatics/btn129

Jombart T, Devillard S, Balloux F (2010) Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. BMC Genet 11:94. https://doi.org/10.1186/1471-2156-11-94

Karlson M, Mörtberg U, Balfors B (2014) Road ecology in environmental impact assessment. Environ Impact Assess Rev 48:10–19. https://doi.org/10.1016/j.eiar.2014.04.002

Loxterman JL (2011) Fine scale population genetic structure of pumas in the Intermountain West. Conserv Genet 12:1049–1059. https://doi.org/10.1007/s10592-011-0208-y

Mace GM et al (2008) Quantification of extinction risk: IUCN's system for classifying threatened species. Conserv Biol 22:1424–1442. https://doi.org/10.1111/j.1523-1739.2008.01044.x

Maehr DS, Land ED, Shindle DB, Bass OL, Hoctor TS (2002) Florida panther dispersal and conservation. Biol Conserv 106:187–197. https://doi.org/10.1016/S0006-3207(01)00245-2

Manel S et al (2007) A new individual-based spatial approach for identifying genetic discontinuities in natural populations. Mol Ecol 16:2031–2043. https://doi.org/10.1111/j.1365-294X.2007.03293.x

McClanahan KA, Duplisea BN, Dellinger JA, Kenyon MW (2017) Documentation of mountain lion occurrence and reproduction in the Sacramento Valley of California. Calif Fish Game 103:7–14

McRae B, Beier P, Dewald L, Huynh L, Keim P (2005) Habitat barriers limit gene flow and illuminate historical events in a wide-ranging carnivore, the American puma. Mol Ecol 14:1965–1977. https://doi.org/10.1111/j.1365-294x.2005.02571.x

Meirmans PG (2012) The trouble with isolation by distance. Mol Ecol 21:2839–2846. https://doi.org/10.1111/j.1365-294X.2012.05578.x

Meirmans PG (2014) Nonconvergence in Bayesian estimation of migration rates. Mol Ecol Resour 14:726–733. https://doi.org/10.1111/1755-0998.12216

Nei M (1978) Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89:583–590

Newbold T et al (2016) Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. Science 353:288–291. https://doi.org/10.1126/science.aaf2201

Newby JR et al (2013) Human-caused mortality influences spatial population dynamics: Pumas in landscapes with varying mortality risks. Biol Conserv 159:230–239. https://doi.org/10.1016/j.biocon.2012.10.018

Palsbøll PJ, Berube M, Allendorf FW (2007) Identification of management units using population genetic data. TREE 22:11–16. https://doi.org/10.1016/j.tree.2006.09.003

Peakall R, Smouse PE (2006) GENALEX 6: Genetic analysis in Excel. Population genetic software for teaching and research. Mol Ecol Notes 6:288–295. https://doi.org/10.1111/j.1471-8286.2005.01155.x

Peakall R, Smouse PE (2012) GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research—an update. Bioinformatics 28:2537–2539. https://doi.org/10.1093/bioinformatics/bts460

Pierce BM, Bleich VC (2014) Enumerating mountain lions: a comparison of two indices. Calif Fish Game 100:527–537

Pierce BM, Bleich VC, Wehausen JD, Bowyer RT (1999) Migratory patterns of mountain lions: Implications for social regulation and conservation. J Mamm 80:986–992. https://doi.org/10.2307/1383269

Pierce BM, Bleich VC, Bowyer RT (2000) Social organization of mountain lions: does a land-tenure system regulate population size? Ecology 81:1533–1543

Piry S, Luikart G, Cornuet J-M (1999) BOTTLENECK: a program for detecting recent effective population size reductions from allele data frequencies. J Hered 90:502–50.3

Riley SP, Serieys LE, Pollinger JP, Sikich JA, Dalbeck L, Wayne RK, Ernest HB (2014) Individual behaviors dominate the dynamics of an urban mountain lion population isolated by roads. Curr Biol 24:1989–1994. https://doi.org/10.1016/j.cub.2014.07.029

Roberge JM, Angelstam P (2004) Usefulness of the umbrella species concept as a conservation tool. Conserv Biol 18:76–85. https://doi.org/10.1111/j.1523-1739.2004.00450.x

Robinson HS, Wielgus RB, Cooley HS, Cooley SW (2008) Sink populations in carnivore management: cougar demography and immigration in a hunted population. Ecol Appl 18:1028–1037. https://doi.org/10.1890/07-0352.1

Rousset F (1997) Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. Genetics 145:1219–1228

Rousset F (2008) GENEPOP'007: a complete re-implementation of the GENEPOP software for Windows and Linux. Mol Ecol Resour 8:103–106. https://doi.org/10.1111/j.1471-8286.2007.01931.x

Safner T, Miller MP, McRae BH, Fortin M-J, Manel S (2011) Comparison of Bayesian clustering and edge detection methods for inferring boundaries in landscape genetics. Int J Mol Sci 12:865–889. https://doi.org/10.3390/ijms12020865

Sawaya MA, Clevenger AP, Kalinowski ST (2013) Demographic connectivity for Ursid populations at wildlife crossing structures in Banff National Park. Conserv Biol 27:721–730. https://doi.org/10.1111/cobi.12075

Schwartz MK, McKelvey KS (2009) Why sampling scheme matters: the effect of sampling scheme on landscape genetic results. Conserv Genet 10:441–452. https://doi.org/10.1007/s10592-008-9622-1

Thompson DJ, Jenks JA (2005) Long-distance dispersal by a subadult male cougar from the Black Hills, South Dakota. J Wildl Manag 69:818–820. https://doi.org/10.2193/0022-541X(2005)069%5B0818:LDBASM%5D2.0.CO;2

Thorne JH, Cameron D, Quinn JF (2006) A conservation design for the central coast of California and the evaluation of mountain lion as an umbrella species. Nat Area J 26:137–148. https://doi.org/10.3375/0885-8608(2006)26%5B137:Acdftc%5D2.0.Co;2

Toonen RJ, Hughes S (2001) Increased throughput for fragment analysis on an ABI Prism® 377 automated sequencer using a membrane comb and STRand software. Biotechniques 31:1320–1325

Tuma MW, Millington C, Schumaker N, Burnett P (2016) Modeling Agassiz's desert tortoise population response to anthropogenic stressors. J Wildl Manag 80:414–429. https://doi.org/10.1002/jwmg.1044

US Census Bureau (2016) United States Census. http://www.census.gov. Accessed 9 May 2018

Vickers TW et al (2015) Survival and mortality of pumas (*Puma concolor*) in a fragmented, urbanizing landscape. PLoS ONE 10:e0131490. https://doi.org/10.1371/journal.pone.0131490

Villepique JT, Pierce BM, Bleich VC, Bowyer RT (2011) Diet of cougars (*Puma Concolor*) following a decline in a population of mule deer (*Odocoileus Hemionus*): lack of evidence for switching prey. Southwest Nat 56:187–192. https://doi.org/10.1894/F07-TAL.1

Waples RS, Do C (2010) Linkage disequilibrium estimates of contemporary Ne using highly variable genetic markers: a largely untapped resource for applied conservation and evolution. Evol Appl 3:244–262. https://doi.org/10.1111/j.1752-4571.2009.00104.x

Wildlands, South Coast (2008) South Coast Missing Linkages: a wildland network for the South Coast Ecoregion. Produced in cooperation with partners in the South Coast Missing Linkages Initiative. http://www.scwildlands.org. Accessed 9 May 2018

Wilson GA, Rannala B (2003) Bayesian inference of recent migration rates using multilocus genotypes. Genetics 163:1177–1191

Wootton JT, Pfister CA (2015) Processes affecting extinction risk in the laboratory and in nature. PNAS 112:E5903. https://doi.org/10.1073/pnas.1516561112

Wright S (1943) Isolation by distance. Genetics 28:114–138

Zeller KA, Vickers TW, Ernest HB, Boyce WM (2017) Multi-level, multi-scale resource selection functions and resistance surfaces for conservation planning: Pumas as a case study. PLoS ONE 12:e0179570. https://doi.org/10.1371/journal.pone.0179570

CALIFORNIA WILDFIRES

As California burns, volunteer firefighters become harder to find

Melody Gutierrez and **Megan Cassidy** | Aug. 11, 2018 | Updated: Aug. 12, 2018 7:19 a.m.

Volunteer firefighter Dick Brown works with the Calaveras Consolidated Fire Protection District in Calaveras County.

Photo: Paul Chinn / The Chronicle

Dick Brown isn't sure how much longer he will be a volunteer firefighter. At 66 years old, he doesn't douse flames much anymore, instead driving the water tender to blazes in rural Calaveras County.

But he’s worried about who will replace him. And who will replace thousands of volunteer firefighters in local departments across the state in the coming years as the number of residents willing to do the job dwindles and fires burn at record-breaking pace.

Hard numbers charting the decline of the volunteer firefighting force in California are hard to come by. But in rural county after rural county — including those hit hard by this summer’s wildfires — local officials are sounding the alarm.

They say current volunteers are aging out of the job, and that with extensive training requirements having been put in place in recent years, fewer recruits are stepping up. That puts residents at risk in counties where there isn’t enough money in the budget for a large, full-time force.

“Typically, volunteer fire departments exist because there isn’t money for a paid one,” said Brown, who is the California director for the National Volunteer Fire Council, an industry group representing nonpaid firefighters.

One-third of the 28,000 firefighters in California are volunteers, most of them in rural areas. Across the country, where 70 percent of firefighters are volunteers, departments say they are struggling to recruit new people for a dangerous job. The number of volunteer firefighters in the United States fell by 10 percent over the past three decades, even as the number of emergency calls tripled, according to the National Fire Protection Association, an industry trade group whose figures are often cited by the federal government.

"It's becoming more difficult to recruit and retain volunteers because it's a huge demand on your time," Brown said. "People are busier. They commute longer, work more. Their kids are in sports.

"But, if not for volunteers, who will do it?" Brown said.

Volunteer firefighter Mike Beyer battles a Carr Fire flareup in July.
Photo: Paul Kitagaki Jr. / Sacramento Bee

That's the question fire officials are asking as deadly fires rage from one end of California to the other, with 17 states and Australia sending crews to help.

There were 17 major wildfires burning in California at the end of last week, including the Mendocino Complex, which at more than 300,000 acres is the largest wildfire in state history. Five firefighters have died battling the blazes, making it the most lethal year for firefighters in the state since 2008.

"The new normal is we are busier than we've ever been," said Cliff Allen, president of Cal Fire Local 2881, the union that represents paid firefighters with the state Department of Forestry and Fire Protection. "Demand is higher and staffing levels aren't meeting those needs."

Allen advocates for paid union firefighting jobs. But he said that in rural parts of the state, volunteers fill a critical need.

"It's a necessary evil, so to speak," he said.

Every minute counts after a fire breaks out — a quick response can be the difference between a small brushfire and a blaze that burns for weeks. That means a rural community with a depleted volunteer firefighting force is at greater risk, said Fire Chief Kim Zagaris of the state Office of Emergency Services.

“We have hired more paid people, but we have less people in rural areas stepping up,” Zagaris said.

In Tuolumne County, impacted by the Ferguson Fire that has been raging for nearly a month, county officials and grand juries have been warning for years about the dwindling number of volunteer firefighters. The county contracts with Cal Fire for some services, but its local departments are primarily staffed with volunteers.

The fire warden for Tuolumne County told a grand jury last year that 250 to 300 volunteers are needed for stations to be adequately staffed. There were just 36 volunteer firefighters before an aggressive marketing campaign brought the total to 70 last year.

Under state law, volunteer firefighters have to undergo the same certification training as paid firefighters. Depending on their responsibilities, volunteers may have a long list of qualifications to satisfy.

“We just don’t have the number of people interested in doing it,” said Tuolumne County Supervisor John Gray. “I’m 70. When I was a young man, you could show up and help put out a fire. Now you have to be trained and certified. In a rural county like Tuolumne, the majority of our population is over 50, and you can’t find people who can do the physical tasks.”

Departments around the state offer various incentives to join, such as a nominal stipend to help defray out-of-pocket costs. Some provide a retirement account depending on how long a person volunteers. In some cases, a retiree can receive $1,200 a month for life if they volunteered for 20 years.

The National Fire Protection Association says that nationwide, there were 1.2 million firefighters in 2015. Of those, 815,000 were volunteers, down from 897,750 in 1984.

There has been an uptick since 2011, when the ranks of volunteers bottomed out at 756,000. But the number isn’t keeping up with the increased demand, said Curt Floyd of the fire protection association.

“This is a trend that is a concern,” Floyd said. “Some communities have had to hire (paid firefighters). There is a cost involved, and some communities can’t bear that weight.”

Nearly every fire department in Lake County, center of the Mendocino Complex fire, and Shasta County, which has been devastated by the Carr Fire, is feeling the strain.

The Lake County Fire Protection District in Clearlake considers its volunteer roster filled when it has 55 volunteers. Lately the total has been around 20. The Lakeport Fire Department also has 20 volunteers, about 15 short of the ideal.

The Shasta County Fire Department is authorized to deploy 385 volunteers. Last month, when the Carr Fire burned into Redding, destroying more than 1,000 homes, the department had 149 volunteers. Among the homes burned were those of several volunteer firefighters, who continued to work, said Julia Haven, a staff services analyst for Cal Fire/Shasta County Fire.

Lakeport Fire Chief Doug Hutchison said his department's force has dwindled as training standards became more rigorous and the economy improved.

"People just don't have the time to volunteer like they used to," he said. "We're actually pretty fortunate — we've had 10 new volunteers in the last year."

He added, "We did some outreach at high schools, to seniors, to get people interested in this as a career. Volunteering is a first step to it."

Mandi Huff, office clerk for South Lake County Fire Protection in Middletown, said the agency has about 30 volunteers on the books, but only about 16 show up consistently.

Huff said volunteer staffing plummeted after the 2015 Valley Fire. The blaze charred more than 76,000 acres, killed four people and destroyed more than 1,200 homes.

People who were volunteer firefighters "had to focus on themselves" and moved away to start over, Huff said. "We've been trying to rebuild the number ever since."

Some local officials brought their concerns to Sacramento this year, to push for a bill that would have offered volunteer firefighters a tax credit of up to $1,500 a year for expenses they incur.

The measure, AB2727, would have cost the state up to $30 million a year in lost revenue, according to the bill's analysis. It stalled in the Assembly Appropriations Committee.

“This isn’t a partisan issue — this is a save-my-house issue,” said Shasta County Supervisor Les Baugh, who testified before a legislative committee. “We have a need for this everywhere.”

The bill’s author, Assemblyman Heath Flora, R-Ripon (San Joaquin County), said he will introduce another incentive bill in January in hopes of drawing more interest in volunteer firefighting. Flora, who became a volunteer firefighter in Modesto in 2000, said he’s watched as some agencies struggled to recruit new people.

“That’s a public safety issue,” he said. “People call 911 and they expect someone to show up and help them in their time of need.”

It was a 911 call that originally sparked Brown’s interest in volunteering in western Calaveras County. He said he called for help 29 years ago when his 10-year-old daughter was kicked in the face by her horse at their Valley Springs home.

Two dozen firefighters showed up to help. Each one was a volunteer. He still feels he owes the fire department that helped treat his daughter’s broken nose and concussion.

“When I get to the point where I feel I paid my debt, I will retire,” Brown said.

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CALIFORNIA WILDFIRES

California blazes tax budgets, firefighters: ‘Fatigue is starting to set in’

Melody Gutierrez

July 31, 2018 | Updated: July 31, 2018 6:41 p.m.

Firefighters at the Mendocino Complex fire. California has been using inmate firefighters to fight a series of large and complex fires all over the state. A new program partially fixes a big problem with the practice -- the inmate firefighters haven't been allowed to work in fire departments after their release from prison.

Photo: AFP Contributor#AFP

SACRAMENTO — California’s firefighters are stretched as thin as they have ever been, state officials said Tuesday, with no indication that the wave of fires scorching the Golden State will ease in the coming months.

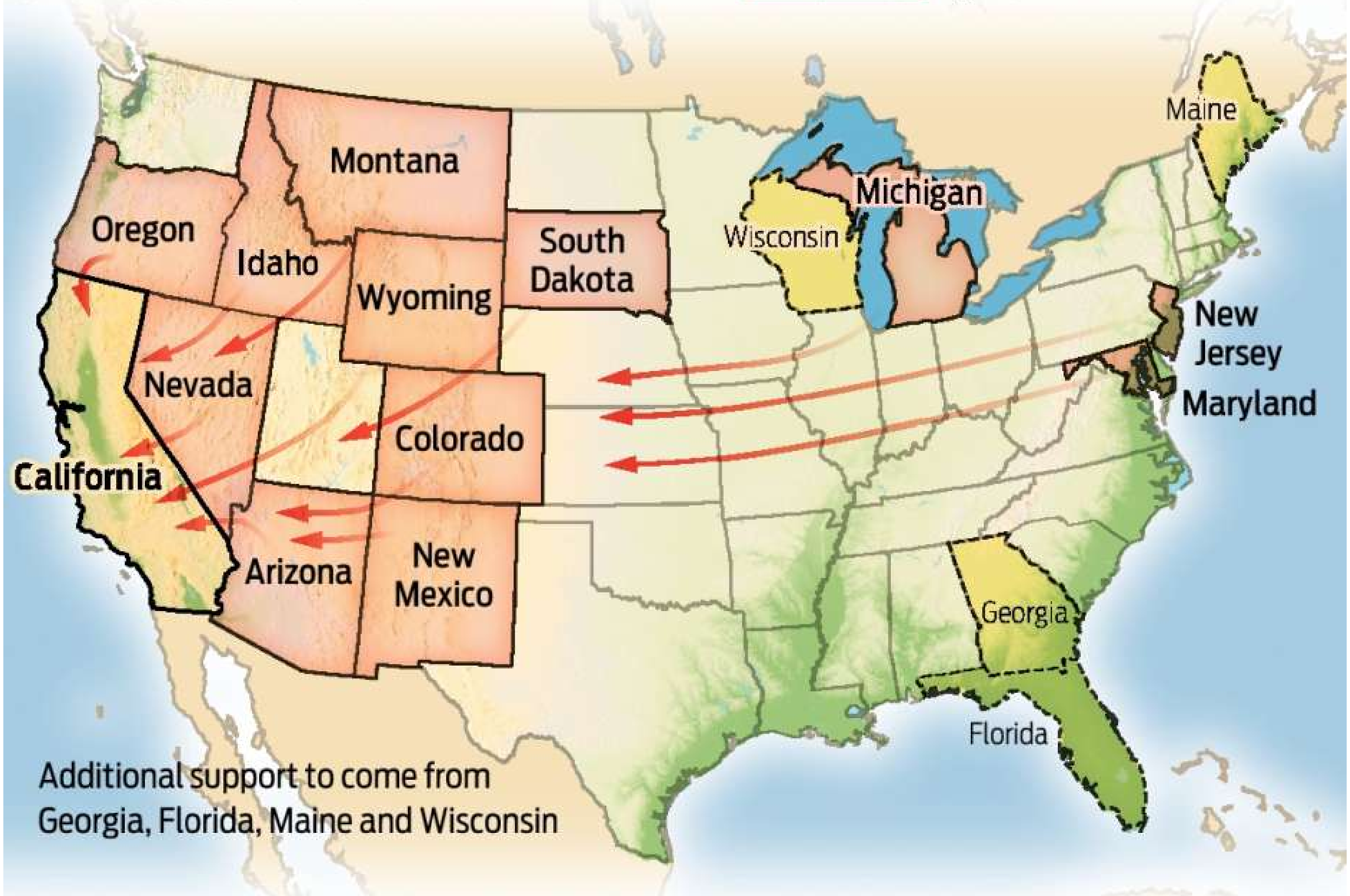
It used to be that the fire season picked up at the end of August and ran through October. That changed with the state’s five-year drought, and this year’s outbreak in July has officials worried about firefighter fatigue.

It was an unprecedented month for fires, both in the number of acres burned and the cost of fielding crews to douse the flames.

The state spent $125 million in July fighting wildfires. That was more than one-fourth of what was budgeted for the entire fiscal year, which began July 1 and won’t end until June 30, 2019.

Who's sending firefighters

Where firefighters battling California wildfires come from



Additional support to come from Georgia, Florida, Maine and Wisconsin

Source: Cal Fire

John Blanchard / The Chronicle

Ashes from the Sky
Now Playing
San Francisco Chronicle

‘They May Be Too Big,’ California Sen. Thinks PG&E May Need To Be Split Up
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Carr Fire: Latest news from Shasta County

Video: San Francisco Chronicle

It was also a tragic month for firefighters. Four died while battling blazes, two on the Ferguson Fire near Yosemite National Park and two on the Carr Fire as it threatened Redding.

“Unfortunately, no one is going home,” said Mark Ghilarducci, director of the Governor’s Office of Emergency Services. “There is no rest. ... We are literally moving firefighters and personnel from one fire to another, and will continue to do so until the threat is mitigated.”

Cliff Allen, president of Cal Fire Local 2881, the union that represents employees with the state Department of Forestry and Fire Protection, said the workload is taking a toll.

“Fatigue is starting to set in,” Allen said.

Nearly 300,000 acres of state and local lands have burned in California since January, 70,000 acres more than at this time last year and close to triple the five-year average for the date. Cal Fire has had to tap agencies in 12 other states to help build the force of 10,500 firefighters who are on the lines fighting the largest fires.

State officials even persuaded Australia and New Zealand to send firefighters. And Ghilarducci said his office is considering asking the Pentagon to deploy ground troops from the Marines or Army who can help clear brush to stop fires from spreading.

“We have fire literally from one end of the state to the other, and we have weather conditions that are making this an even more dynamic situation,” Ghilarducci said. “We have to get resources to the right place at the right time. It’s like a chess board.”

Ghilarducci said that in recent days, state officials redirected fire crews from the Ferguson Fire near Yosemite to the Carr Fire as it threatened Redding and to the Mendocino Complex Fire when it took aim at communities in Lake County.

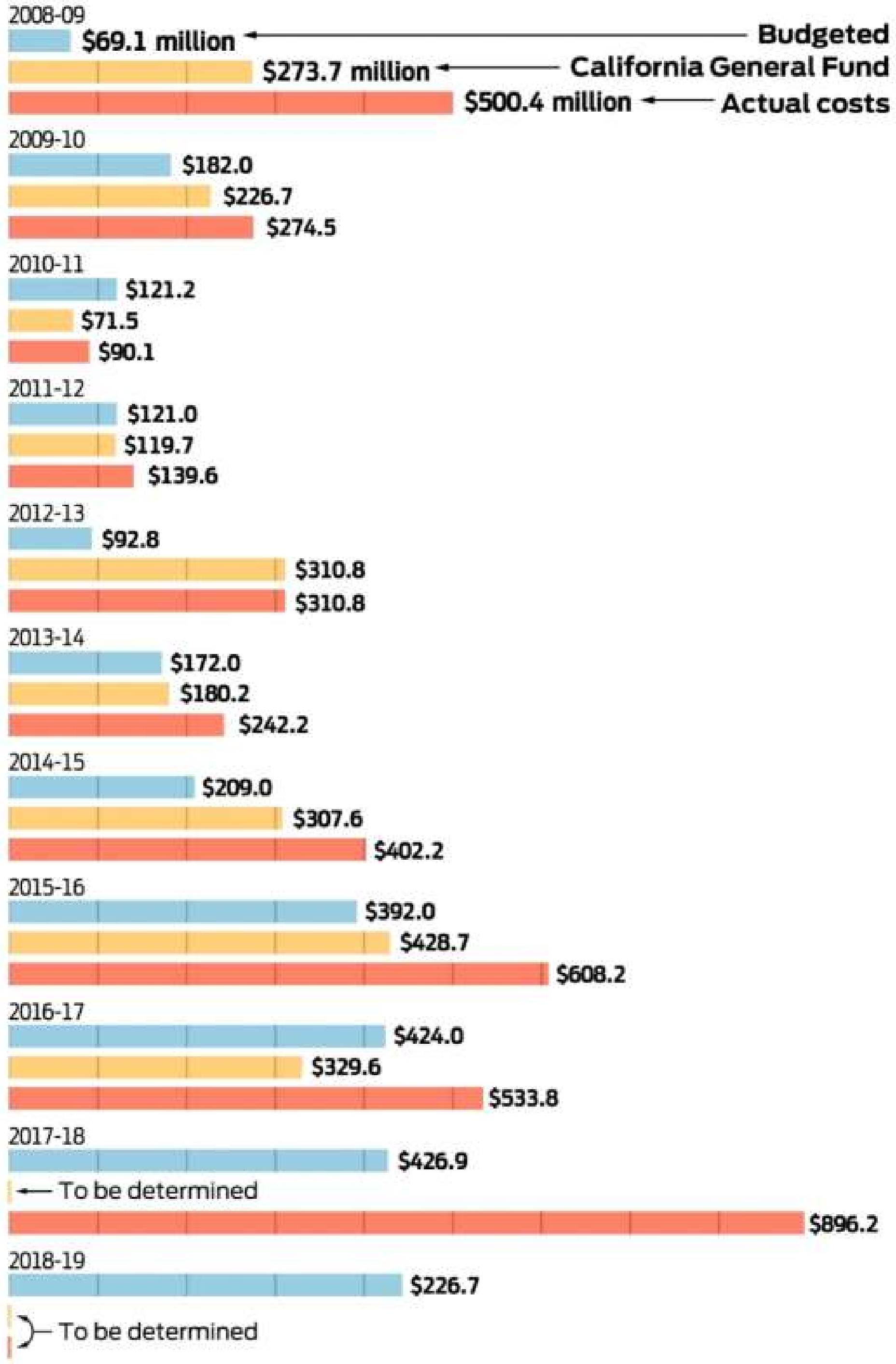
When those fires are contained, Ghilarducci said, it’s unlikely firefighters will get a break. The way the summer is going, they’ll probably have another fire to put out.

“It’s really all hands on deck,” he said.

California firefighting costs

Amounts budgeted for Cal Fire wildfire fighting, total state costs in those years and total overall costs, including local and federal reimbursements.

Emergency fund in millions of dollars



Source: State Department of Finance

John Blanchard / The Chronicle

And that comes at a cost.

The state is likely to need to dip into reserves for the eighth time in the past decade to cover the cost of putting out wildfires. That’s despite an ever-increasing budget for fighting fires.

Last year, the state budgeted $427 million. The outburst of fires in the North Bay and elsewhere in October, and then in Southern California in December, left the state, local governments and the federal government having to come up with another $470 million to cover costs.

California has budgeted $443 million for this fiscal year that began July 1, and has spent $125 million so far. That’s more than the state spent during the entire 2010-11 fiscal year.

“This is why the governor has been so insistent over the years of having a healthy budget reserve because, as this year may very well show, Mother Nature doesn’t always coordinate with the state budget,” said H.D. Palmer, spokesman for the state Department of Finance. “The second thing it speaks to is that it underscores what the governor has talked about in terms of the kind of effect that climate change has had on conditions in California and how they set the state up for these kinds of catastrophic wildfires.”

Edward Struzik, author of the book “Firestorm: How Wildfire Will Shape Our Future,” said rising firefighting costs are going to put pressure on budgets across the U.S. in coming years. The only way to prevent that is to keep people from moving into wildland areas and investing in technology that predicts where fires are likely to happen, he said.

“There is no indication we will get cooler and wetter in the West,” Struzik said. “Every study I’ve seen shows California and most of the American West will get hotter and drier. We have more people working and living in these forest areas, and that is increasing the likelihood of fires. I don’t see any other future other than one with more fires.”

And, he added, a future of “really stressed-out fire crews.”

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APPLIED ECOLOGY

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Habitat fragmentation and its lasting impact on Earth's ecosystems

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We conducted an analysis of global forest cover to reveal that 70% of remaining forest is within 1 km of the forest's edge, subject to the degrading effects of fragmentation. A synthesis of fragmentation experiments spanning multiple biomes and scales, five continents, and 35 years demonstrates that habitat fragmentation reduces biodiversity by 13 to 75% and impairs key ecosystem functions by decreasing biomass and altering nutrient cycles. Effects are greatest in the smallest and most isolated fragments, and they magnify with the passage of time. These findings indicate an urgent need for conservation and restoration measures to improve landscape connectivity, which will reduce extinction rates and help maintain ecosystem services.

INTRODUCTION

Destruction and degradation of natural ecosystems are the primary causes of declines in global biodiversity (*1*, *2*). Habitat destruction typically leads to fragmentation, the division of habitat into smaller and more isolated fragments separated by a matrix of human-transformed land cover. The loss of area, increase in isolation, and greater exposure to human land uses along fragment edges initiate long-term changes to the structure and function of the remaining fragments (*3*).

Ecologists agree that habitat destruction is detrimental to the maintenance of biodiversity, but they disagree—often strongly—on the extent to which fragmentation itself is to blame (*4*, *5*). Early hypotheses based on the biogeography of oceanic islands (*6*) provided a theoretical framework to understand fragmentation's effect on extinction in terrestrial landscapes composed of "islands" of natural habitat scattered across a "sea" of human-transformed habitat. Central to the controversy has been a lingering uncertainty about the role of decreased fragment size and increased isolation relative to the widespread and pervasive effects of habitat loss in explaining declines in biodiversity and the degradation of ecosystems (*7*). Observational studies of the effects of fragmentation have often magnified the controversy because inference from nonmanipulative studies is limited to correlation and because they have individually often considered only single aspects of fragmentation (for example, edge, isolation, and area) (*8*). However, together with these correlative observations, experimental studies reveal that fragmentation has multiple simultaneous effects that are interwoven in complex ways and that operate over potentially long time scales (*9*).

Here, we draw on findings of the world's largest and longest-running fragmentation experiments that span 35 years and disparate biomes on five continents. Their rigorous designs and long-term implementation overcome many limitations of observational studies. In particular, by manipulating and isolating individual aspects of fragmentation while controlling for others, and by doing so on entire ecosystems, they provide a powerful way to disentangle cause and effect in fragmented landscapes. Here, we present experimental evidence of unexpected long-term ecological changes caused by habitat fragmentation.

Highlighting one ecosystem type as an example, we first present a global analysis of the fragmentation of forest ecosystems, quantifying for the first time the global hotspots of intensive historical fragmentation. We then synthesize results from the set of long-term experiments conducted in a wide variety of ecosystems to demonstrate consistent impacts of fragmentation, how those impacts change over time, and how they align with predictions from theory and observation. Finally, we identify key knowledge gaps for the next generation of fragmentation experiments.

GLOBAL ANALYSIS OF THE EXTREME MAGNITUDE AND EXTENT OF FRAGMENTATION

New satellite data sets reveal at high resolution how human activities are transforming global ecosystems. Foremost among these observations are those of forest cover because of the high contrast between forest

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and anthropogenic land cover types. Deforestation, which was already widespread in temperate regions in the mid-18th to 20th centuries and increased in the tropics over the past half century, has resulted in the loss of more than a third of all forest cover worldwide (*10*, *11*). Beyond the direct impacts of forest loss and expanding anthropogenic land cover (for example, agricultural fields and urban areas), remnant forests are likely to suffer from being smaller, more isolated, and with a greater area located near the edge of the forest (*12*).

We analyzed the world's first high-resolution map of global tree cover (*13*) to measure the magnitude of forest fragmentation. This analysis revealed that nearly 20% of the world's remaining forest is within 100 m of an edge (Fig. 1, A and B)—in close proximity to agricultural, urban, or other modified environments where impacts on forest ecosystems are most severe (*14*). More than 70% of the world's forests are within 1 km of a forest edge. Thus, most forests are well within the range where human activities, altered microclimate, and nonforest species may influence and degrade forest ecosystems (*15*). The largest contiguous expanses of remaining forests are in the humid tropical regions of the Amazon and Congo River Basins (Fig. 1A). Large areas of more disjunct forest also remain in southeastern Asia, New Guinea, and the boreal biomes.

Historical data enable the study of the process of forest fragmentation over time. We reconstructed the historical forest extent and timing of fragmentation in two forested regions of Brazil that provide a stark contrast in land-use dynamics. The Brazilian Amazon is a rapidly changing frontier (*10*), yet most of its forests remain contiguous and far from an edge despite recent increases in fragmentation (Fig. 1, C and D). In contrast, the Brazilian Atlantic Forest is a largely deforested landscape, cleared for agriculture and logged for timber over the last three centuries (*11*). This remaining forest is dominated by small fragments, with most fragments smaller than 1000 ha and within 1000 m of a forest edge (Fig. 1, E and F) (*16*). In the Brazilian Amazon, the proportion of forest farther than 1 km from the forest edge has decreased from 90% (historical) to 75% (today), and in the Brazilian Atlantic, from 90% to less than 9%.

These two forested regions of Brazil define extremes of the fragmentation process and are representative of the extent of fragmentation in forested landscapes worldwide (Fig. 1), as well as many other biomes including temperate grasslands, savannas, and even aquatic systems (*17*). For example, although a spatial analysis similar to that of forest is not currently possible in grasslands, 37% of the world's grassland eco-regions are classified as "highly fragmented" (*18*, *19*).

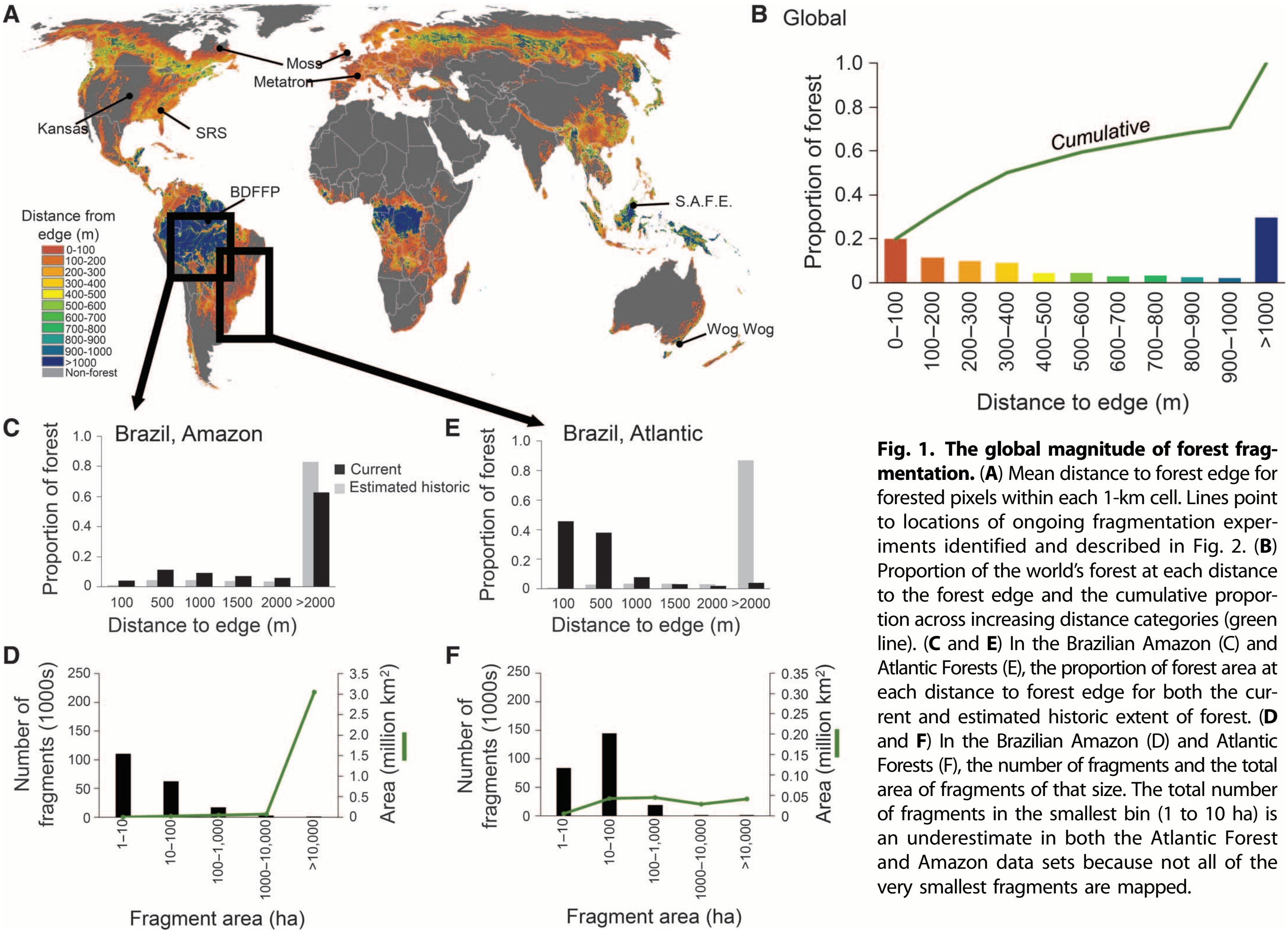


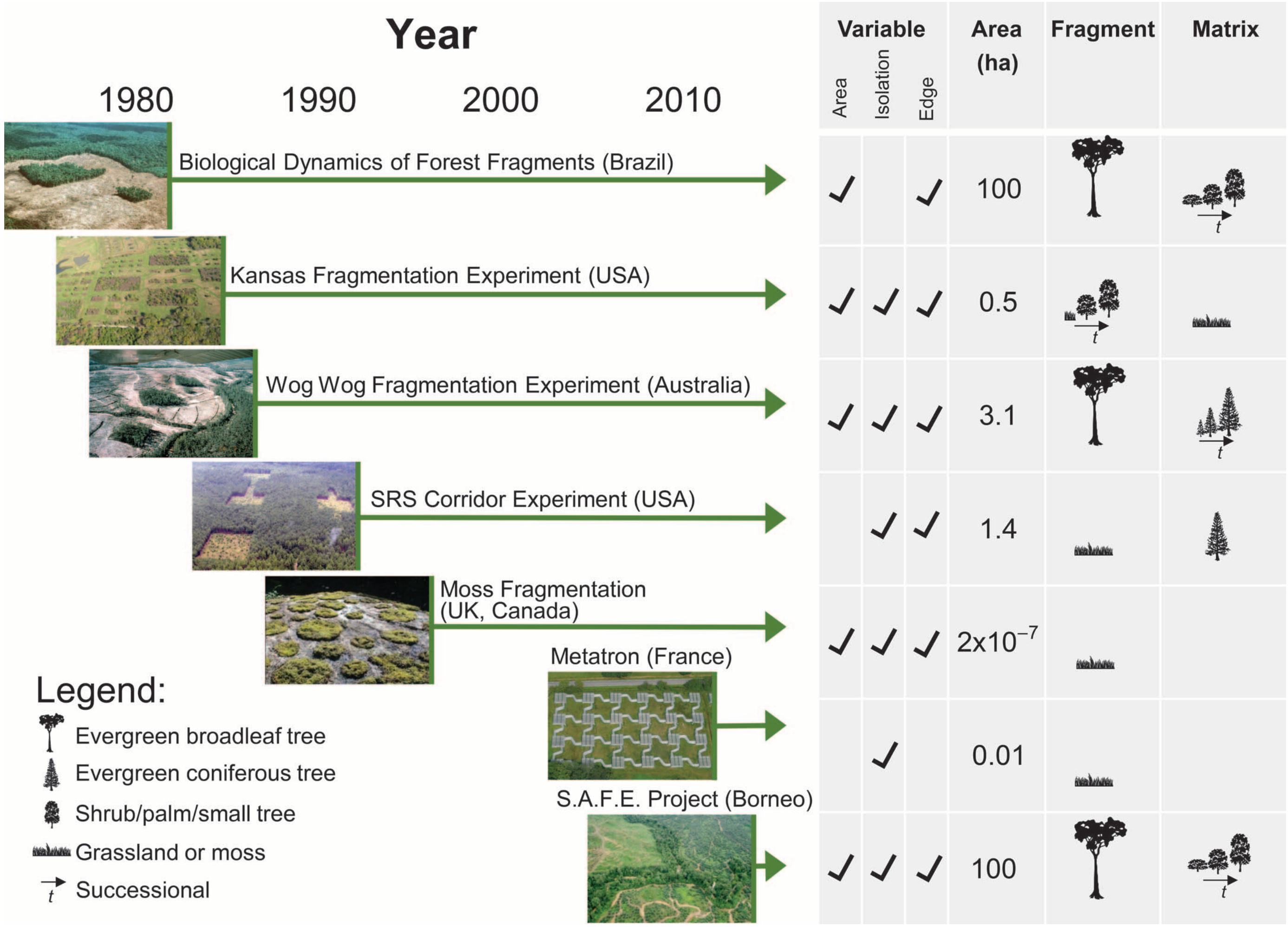
Fig. 1. The global magnitude of forest fragmentation. (**A**) Mean distance to forest edge for forested pixels within each 1-km cell. Lines point to locations of ongoing fragmentation experiments identified and described in Fig. 2. (**B**) Proportion of the world's forest at each distance to the forest edge and the cumulative proportion across increasing distance categories (green line). (**C** and **E**) In the Brazilian Amazon (C) and Atlantic Forests (E), the proportion of forest area at each distance to forest edge for both the current and estimated historic extent of forest. (**D** and **F**) In the Brazilian Amazon (D) and Atlantic Forests (F), the number of fragments and the total area of fragments of that size. The total number of fragments in the smallest bin (1 to 10 ha) is an underestimate in both the Atlantic Forest and Amazon data sets because not all of the very smallest fragments are mapped.

Robust knowledge of how habitat fragmentation affects biodiversity and ecosystem processes is needed if we are to comprehend adequately the implications of this global environmental change.

THE VALUE OF LONG-TERM FRAGMENTATION EXPERIMENTS

Long-term experiments are a powerful tool for understanding the ecological consequences of fragmentation (*20*). Whereas observational studies of fragmented landscapes have yielded important insights (*9*, *21*), they typically lack rigorous controls, replication, randomization, or baseline data. Observational studies have limited ability to isolate the effects of fragmentation from concomitant habitat loss and degradation per se (*4*, *7*, *22*). Remnant fragments are embedded in different types and qualities of surrounding habitat, complicating interpretation because the surrounding habitat also influences biodiversity and ecosystem productivity (*23*).

The long-term fragmentation experiments we analyze here comprise the entire set of ongoing terrestrial long-term experiments. They occur in several biomes (Fig. 2 and Supplementary Materials) and were designed to manipulate specific components of fragmentation—habitat size, isolation, and connectivity—while controlling for confounding factors such as the amount of habitat lost across a landscape (Fig. 2). The largest fragments across these experiments match the size of fragments commonly created by anthropogenic activities (Figs. 1 and 2). Distances to the edge of experimental fragments range to 500 m, encompassing edge distances found in more than half of forests worldwide (Fig. 1B). In each experiment, different fragmentation treatments with replication were established, starting from continuous, nonfragmented landscapes and controlling for background environmental variation either by experimental design (blocking) or by measurement of covariates for use in subsequent analyses. Tests were conducted within fragments that varied experimentally in area or edge, within fragments that were experimentally isolated or connected, or within experimental fragments compared to the same area within continuous habitat. All treatments were replicated. Experiments were created by destroying or creating precise amounts of habitat across replicate landscapes, allowing tests of fragmentation effects independent of habitat loss. The robust



Variable			Area (ha)	Fragment	Matrix
Area	Isolation	Edge			
✓		✓	100	🌳	🌳 → t
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✓	✓	✓	2×10^{-7}	🌾	
	✓		0.01	🌾	
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Fig. 2. The world's ongoing fragmentation experiments. All experiments have been running continuously since the time indicated by the start of the associated arrow (with the exception of the moss fragmentation experiment, which represents a series of studies over nearly two decades). The variables under study in each experiment are checked. The area is that of the experiment's largest fragments. Icons under "Fragment" and "Matrix" indicate the dominant community and its relative height, with multiple trees representing succession.

and comparable experimental designs allow for powerful tests of the mechanisms underpinning the ecological impacts of fragmentation, and the long-term nature of ensuing studies has revealed consistent emergent effects.

These experiments mimic anthropogenic fragmentation; they are whole-ecosystem manipulations in which all species and processes experienced the same treatment (*24*). Emergent responses thus reflect the multiple direct and indirect effects of interacting species and processes. Further, because experimentally fragmented ecosystems are open to fluxes of individuals and resources, fragmentation effects can manifest across multiple levels of ecological organization (Fig. 3). Long-term experiments have the power to detect lagged and/or chronic impacts.

The first fragmentation experiments, now more than three decades old, were created to test effects of fragment area on both species persistence and patterns of immigration, reflecting concern in conservation biology about the role of fragmentation in reducing population sizes below viable levels (*25*) (Fig. 2). Subsequent experiments, created two decades ago, shifted focus to modifying habitat isolation, reflecting recognition of the potential to mitigate negative effects of fragmentation by recreating habitat—specifically with corridors—to increase connectivity among fragments (*26*) (Fig. 2). The newest experiments test emerging questions about potentially deleterious synergies between fragmentation and global changes in climate and land use (Fig. 2).

We synthesized results available 31 January 2014 for all studies within these experiments that were conducted in all treatments and replicates, and tested fragmentation effects on dispersal, abundance, extinction, species richness, community composition, and ecosystem functioning. We first calculated effect sizes of fragmentation as log response ratios (Fig. 3). Data from 76 different studies across the five longest-running experiments were drawn from published and unpublished sources (table S1). We synthesized results according to three fragmentation treatments: reduced fragment area [the focus of Biological Dynamics of Forest Fragments Project (BDFFP), Wog Wog, and Kansas; see Fig. 2 for identifiers of experiments], increased fragment isolation [Savannah River Site (SRS) and Moss], and increased proportion of edge (all experiments). Fragmented treatments were compared directly to non- or less-fragmented habitats that were either larger or connected via structural corridors (table S1).

Strong, consistent, and accumulating effects of habitat fragmentation

Our synthesis revealed strong and consistent responses of organisms and ecosystem processes to fragmentation arising from decreased fragment area, increased isolation, and the creation of habitat edges (Fig. 3).

Community and ecosystem responses emerge from observed responses at the level of populations. Reduced area decreased animal

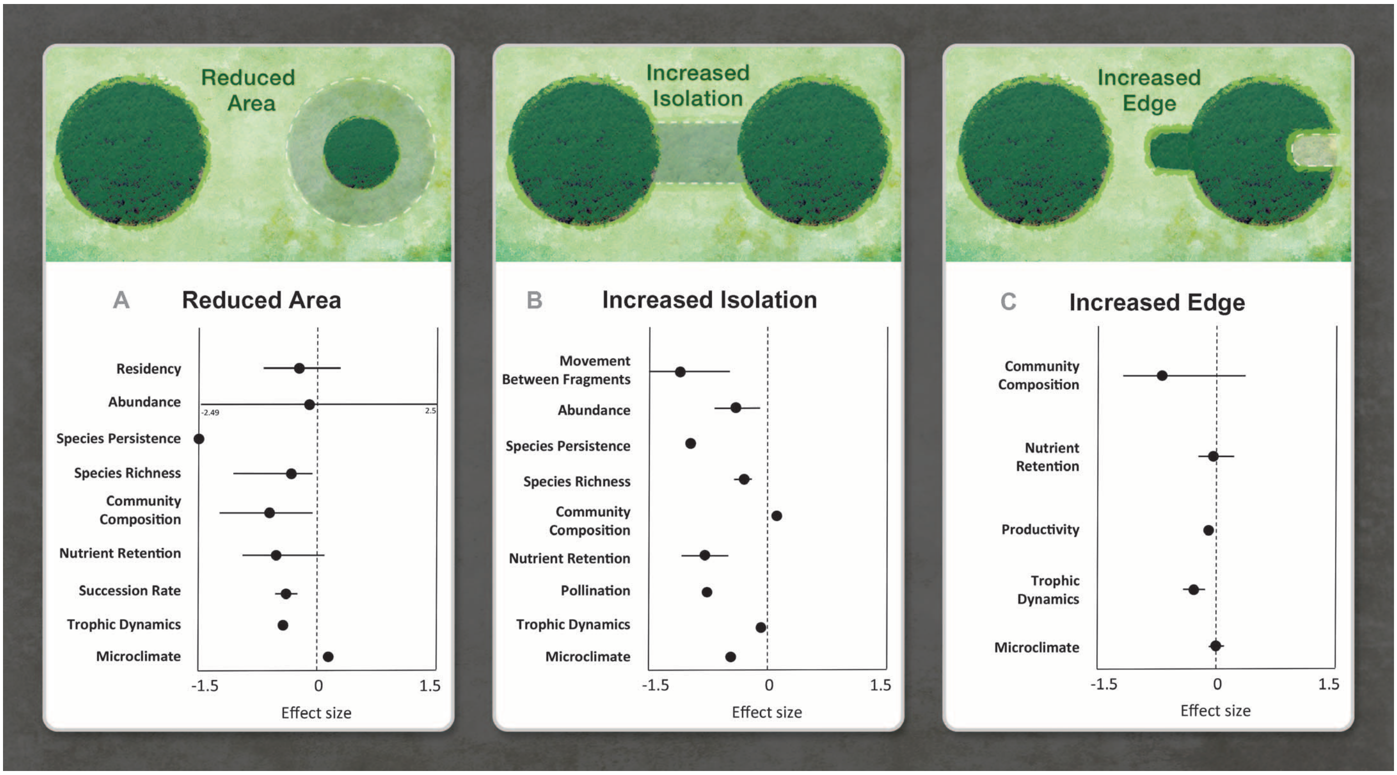

Fig. 3. Fragmentation effects propagate through the whole ecosystem. (**A** to **C**) For each fragmentation treatment [reduced area in BDFFP, Wog Wog, Kansas (A); increased isolation in SRS and Moss (B); and increased edge in all experiments (C)], we summarize major findings for ecological processes at all levels of ecological organization. Each dot represents the mean effect size [computed as log response ratio: ln(mean in more fragmented treatment/mean in non- or less-fragmented treatment)] for an ecological process. Effect sizes are statistical, such that negative or positive values could represent degrading function. Horizontal bars are the range when a dot is represented by more than one study. Details, including individual effect sizes for each study, are reported in table S1.

residency within fragments, and increased isolation reduced movement among fragments, thus reducing fragment recolonization after local extinction (Fig. 3, A and B). Reduced fragment area and increased fragment isolation generally reduced abundance of birds, mammals, insects, and plants (Fig. 3, A and B). This overall pattern emerged despite complex patterns of increases or declines in abundance of individual species (Fig. 3A) with various proximate causes such as release from competition or predation, shifts in disturbance regimes, or alteration of abiotic factors (*14*, *27–29*). Reduced area, increased isolation, and increased proportion of edge habitat reduced seed predation and herbivory, whereas increased proportion of edge caused higher fledgling predation that had the effect of reducing bird fecundity (represented together as trophic dynamics in Fig. 3, A to C). Perhaps because of reduced movement and abundance, the ability of species to persist was lower in smaller and more isolated fragments (Fig. 3, A and B).

As predicted by theory (*6*, *30*, *31*), fragmentation strongly reduced species richness of plants and animals across experiments (Fig. 3, A and B), often changing the composition of entire communities (Fig. 3, A to C). In tropical forests, reduced fragment size and increased proportion of edge habitat caused shifts in the physical environment that led to the loss of large and old trees in favor of pioneer trees (Fig. 3, A and C), with subsequent impacts on the community composition of insects (*32*). In grasslands, fragment size also affected succession rate, such that increased light penetration and altered seed pools in smaller fragments impeded the rate of ecological succession relative to that of larger fragments (*33*) (Fig. 3A).

Consistently, all aspects of fragmentation—reduced fragment area, increased isolation, and increased edge—had degrading effects on a disparate set of core ecosystem functions. Degraded functions included reduced carbon and nitrogen retention (Fig. 3, A to C), productivity (Fig. 3C), and pollination (Fig. 3B).

In summary, across experiments spanning numerous studies and ecosystems, fragmentation consistently degraded ecosystems, reducing species persistence, species richness, nutrient retention, trophic dynamics, and, in more isolated fragments, movement.

Long-term consequences of fragmentation

To synthesize all time series of species richness and ecosystem functioning gathered across experiments, we measured effects of fragmentation over the course of each study. The effect of fragmentation was calculated over time as the proportional change in fragmented relative to non- or less-fragmented treatments (Fig. 4).

In most cases, the large and consistent effects of fragmentation revealed by the experiments were predicted from theory. However, we were struck by the persistence of degradation to biodiversity and ecosystem processes and by the increase in many of the effects over time (Fig. 4). For example, extreme rainfall events at Wog Wog appeared to delay the decline in plant species richness for 5 years after fragmentation. In the Kansas Experiment, a lag of 12 years occurred before fragmentation effects on plant succession were detected. Our results thus reveal long-term and progressive effects of fragmentation and provide support for three processes proposed by recent studies in spatial ecology: extinction debt, immigration lag, and ecosystem function debt (Fig. 4).

First, we found strong evidence for temporal lags in extinction [that is, "extinction debt" (*30*)] in fragments. Species richness of plants, arthropods, and birds sampled in the experiments conducted in mature forest fragments and replicated moss landscapes showed decreases of

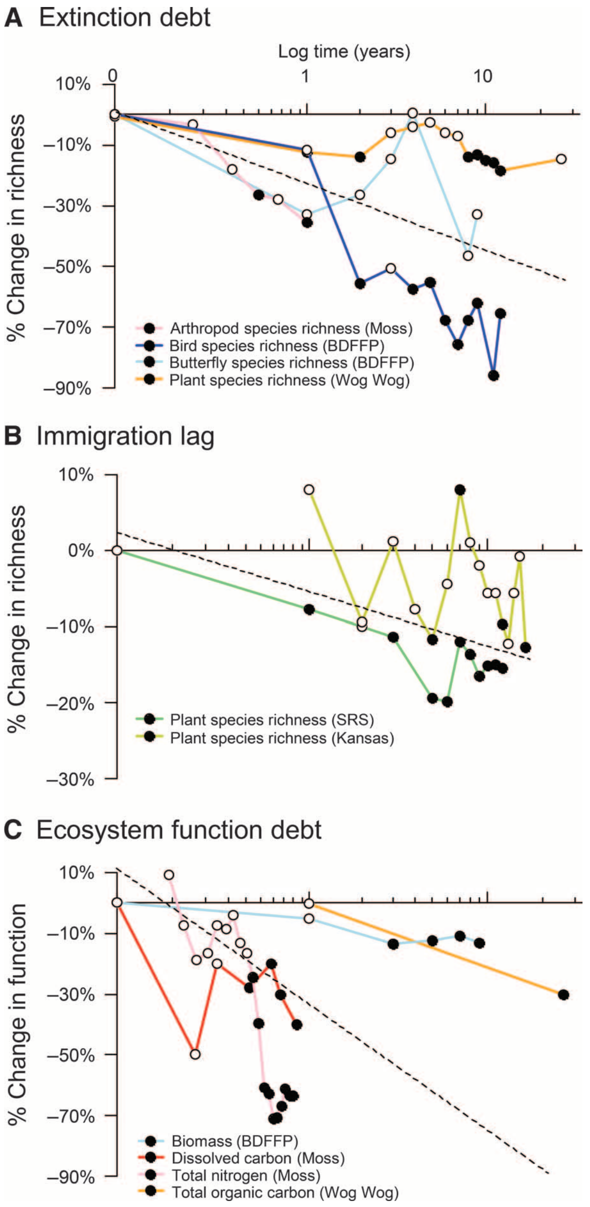

Fig. 4. Delayed effects of fragmentation on ecosystem degradation. (**A**) The extinction debt represents a delayed loss of species due to fragmentation. (**B**) The immigration lag represents differences in species richness caused by smaller fragment area or increased isolation during fragment succession. (**C**) The ecosystem function debt represents delayed changes in ecosystem function due to reduced fragment size or increased isolation. Percent loss is calculated as proportional change in fragmented treatments [for example, (no. of species in fragment − no. of species in control)/(no. of species in control) × 100]. Fragments and controls were either the same area before and after fragmentation, fragments compared to unfragmented controls, or small compared to large fragments. Filled symbols indicate times when fragmentation effects became significant, as determined by the original studies (see table S2). Mean slopes (dashed lines) were estimated using linear mixed (random slopes) models. Mean slope estimates (mean and SE) were as follows: (A) −0.22935 (0.07529); (B) −0.06519 (0.03495); (C) −0.38568 (0.16010).

20 to 75% after fragmentation (Fig. 4A). Some declines were evident almost immediately after fragmentation, whereas others increased in magnitude over the experiment's duration. Across experiments, average loss was >20% after 1 year, >50% after 10 years, and is still increasing in the longest time series measured (more than two decades). The rate of change appears to be slower in larger fragments [in BDFFP, 50% decline in bird species after 5 years in 1-ha fragments, but after 12 years in 100-ha fragments; in Moss, 40% decline in arthropod species richness of small fragments and 26% reduction in large fragments after 1 year (*34*, *35*)]. As predicted by theory (*36*), the extinction debt appears to take longer to pay in larger fragments.

Second, we observed that reduced richness was coincident with an "immigration lag" (*37*), whereby small or isolated fragments are slower to accumulate species during community assembly (*33*, *38*) (Fig. 4B). Immigration lags were observed in experiments conducted in successional systems that were initiated by creating new habitat fragments, rather than by fragmenting existing habitats. After more than a decade, immigration lags resulted in 5% fewer species after 1 year, and 15% fewer species after 10 years in small or isolated fragments compared to large or connected fragments (Fig. 4B).

Third, we observed an ecosystem function debt caused by fragmentation (*39*) in forest and moss fragments (Fig. 4C). An ecosystem function debt is manifest both as delayed changes in nutrient cycling and as changes to plant and consumer biomass. Loss of function amounted to 30% after 1 year, rising to 80% after a decade in small and isolated fragments when compared to larger and more connected fragments (Fig. 4C). Functional debts can result from biodiversity loss, as when loss of nutrients and reduction in decomposition are caused by simplification of food webs. Alternatively, the impact is exhibited through pathways whereby fragmentation changes biotic (for example, tree density in successional systems) or abiotic conditions (for example, light regimes or humidity) in ways that alter and potentially impair ecosystem function [for example, biomass collapse in fragments; Figs. 3 and 4; altered nitrogen and carbon soil dynamics (*40*)].

A new understanding of the effects of fragmentation

By testing existing theory, experiments play a pivotal role in advancing ideas and developing new theory. We draw on experimental evidence to highlight two ways that the understanding of fragmentation has been enriched by the interplay between long-term experiments and development of theory.

First, island biogeography (*6*) was among the earliest theories to predict extinction and immigration rates and patterns of species richness in isolated biotas, which were later used to predict the effects of fragmentation on these variables. Experiments in continental settings tested the theory and gave rise to fresh perspectives. For example, islands are surrounded by sea, a thoroughly inimical matrix for island-dwelling species. Habitat islands, or fragments, are surrounded by a matrix that may not be so unsuitable for some species. In terms of all of the ecological variables studied in our long-term experiments, our results support the conclusion that ecological dynamics in human-modified fragments are a stark contrast to the dynamics in intact habitats that remain. Observational studies that have devoted more detailed consideration to the countryside within which fragments are embedded explain the diversity of ecological responses in remaining fragments (*41*). At the same time as experiments supported the core predictions of classical theories about effects of fragment size and isolation (Figs. 3 and 4), they spurred and tested new theories such as metacommunity theory (*42*) to account for variation in connectivity and habitat quality within and between fragments (*33*, *43*–*45*), spatial dynamics (*14*, *46*), and spatially varying interspecific interactions (*47*).

Second, experiments have demonstrated that the effects of fragmentation are mediated by variation in traits across species. More realistic predictions of community responses to fragmentation emerged after explicit consideration of species traits such as rarity and trophic levels (*48*, *49*), dispersal mode (*50*–*52*), reproductive mode and life span (*29*, *53*), diet (*54*), and movement behavior (*55*, *56*). Increasingly, the simple theoretical prediction that fragmentation reduces species richness is being modified to account for species identity through models that focus on how species vary in their traits (*4*, *21*, *36*, *48*, *57*, *58*). Consideration of traits may help to interpret variation around the overarching pattern that fragmentation consistently reduces species richness across many species and biomes (Figs. 3 and 4).

A NEW GENERATION OF FRAGMENTATION EXPERIMENTS

New foci are emerging for studying ecosystem fragmentation, including (i) synergies between fragmentation and global changes, (ii) eco-evolutionary responses of species to fragmentation, and (iii) ecological responses to fragmentation in production landscapes—that is, ecosystems whose services are under extreme appropriation by humans (*59*).

First, conclusions from experiments thus far are likely to have been conservative because impacts from other environmental changes have been mostly excluded. Most forms of global change known to reduce population sizes and biodiversity will be exacerbated by fragmentation (*58*, *60*), including climate change (*61*), invasive species (*62*, *63*), hunting (*64*), pollution [including light, noise, and chemicals (*65*)], and altered disturbance regimes (*66*).

More complex experiments with unparalleled control and capacity to simultaneously manipulate fragmentation and other global changes are now under way (*53*). The Metatron, created in 2011 in southern France (*67*), enables ecologists to assess effects of variation in temperature and other abiotic factors in addition to habitat isolation. The SAFE Project is being created in the rainforest of Borneo (*68*) and will embed a fragmentation experiment within a production agricultural plantation in which poaching will occur. Other synergies should be investigated experimentally, including the interaction between fragmentation and hunting, fire, infectious disease outbreaks, or nitrogen deposition. Within these experiments, fragmentation and loss of habitat can then be varied independently.

Second, current experiments have stopped short of examining how fragmentation drives evolution through genetic bottlenecks, ecological traps, changing patterns of selection, inbreeding, drift, and gene flow (*69*–*72*). Extensive fragmentation has occurred over many years, and in some regions over millennia (*11*). Changes caused by fragmentation undoubtedly lead to altered patterns of selection and trait evolution. Evolutionary responses to fragmentation have already been suggested (*73*, *74*), and it is likely that such changes will, in turn, feed back to influence population persistence and ecosystem resilience in fragmented landscapes. Linking long-term experiments with the tools of landscape genetics (*75*) may provide powerful insights into the evolutionary dynamics of species inhabiting fragmented landscapes.

Third, new experiments should address the management of natural habitats in production landscapes by monitoring vegetation, networks of interacting species, and ecosystem services at ecologically relevant spatial and temporal scales (*76–78*). Some ecosystem services have global consequences, for example, local carbon sequestration affects global atmospheric CO_2. However, in many cases the benefits obtained by people depend on their proximity to habitat fragments (*79*). For example, crop pollination and biological pest control from natural areas adjacent to farms are made available by the very process of habitat fragmentation, bringing people and agriculture closer to those services. Yet, further fragmentation reduces access to many services and ultimately may push landscapes past tipping points, beyond which essential ecosystem services are not merely diminished but lost completely (*80*). This complex relationship creates a double-edged sword, for which locally optimal levels and arrangements of habitat must be sought. New fragmentation experiments should consider how multiple fragments in a landscape interact, creating an ecological network in which the collective benefit of ecosystem services may be greater than the sum of services provided by individual fragments (*81*, *82*). Experimental inferences may then be tested beyond their spatiotemporal domains and, if successful, extrapolated across scales. Such research will be aided by satellite monitoring of ecosystems and human land use across the globe. The most powerful research programs will integrate experiments, observational studies, air- and space-borne imaging, and modeling.

CONCLUSIONS

Fragmentation experiments—some of the largest and longest-running experiments in ecology—provide clear evidence of strong and typically degrading impacts of habitat fragmentation on biodiversity and ecological processes. The findings of these experiments extend to a large fraction of the terrestrial surface of the Earth. Much of the Earth's remaining forest fragments are less than 10 ha in area, and half of the world's forest is within 500 m of the forest edge—areas and distances matched to existing long-term experiments (Figs. 1 and 2) from which consistent effects of fragmentation have emerged (Figs. 3 and 4).

Reduced fragment area, increased isolation, and increased edge initiate changes that percolate through ecosystems (Fig. 3). Fragmentation has the capacity to generate persistent, deleterious, and often unpredicted outcomes, including surprising surges in abundance of some species and the pattern that long temporal scales are required to discern many strong system responses. In light of these conclusions and ongoing debates, we suggest that fragmentation's consistency, pervasiveness, and long-term degrading effect on biodiversity and ecosystem function have not been fully appreciated (*9*).

Without gains in yield and efficiency of agricultural systems (*83*), the expansion of human populations will inevitably continue to reduce and fragment natural areas. The area of Earth's land surface devoted to cropland already occupies 1.53 billion hectares (*83*) and may expand 18% by the middle of this century (*84*), and the area committed to urban centers is predicted to triple to 0.18 billion hectares by 2030 (*85*). The capacity of the surviving forests and other natural habitats to sustain biodiversity and ecosystem services will hinge upon the total amount and quality of habitat left in fragments, their degree of connectivity, and how they are affected by other human-induced perturbations such as climate change and invasive species. Long-term experiments will be even more needed to appreciate, explain, and predict long-term effects. New efforts should work in concert, coordinating a network of experiments across ecosystems and spatial extents.

The effects of current fragmentation will continue to emerge for decades. Extinction debts are likely to come due, although the counteracting immigration debts may never fully be paid. Indeed, the experiments here reveal ongoing losses of biodiversity and ecosystem functioning two decades or longer after fragmentation occurred. Understanding the relationship between transient and long-term dynamics is a substantial challenge that ecologists must tackle, and fragmentation experiments will be central for relating observation to theory.

Experimental results to date show that the effects of fragmentation are strong and markedly consistent across a diverse array of terrestrial systems on five continents. Increasingly, these effects will march in concert with other global changes. New experiments should be coupled with emerging technologies, landscape genetics, and detailed imagery of our planet, and should be coordinated with current ecological theory to understand more deeply the coupled dynamics of ecological and social systems. These insights will be increasingly critical for those responsible for managing and prioritizing areas for preservation and ecological restoration in fragmented landscapes.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/1/2/e1500052/DC1
Materials and Methods
Fig. S1. Map of the BDFFP experiment and location within Brazil.
Fig. S2. Map of the Kansas fragmentation experiment.
Fig. S3. Map of the Wog Wog experiment and location within Australia.
Fig. S4. Map of the SRS experiment showing locations of the eight blocks in the second SRS Corridor Experiment within the SRS, South Carolina, USA.
Fig. S5. Design of the Moss experiment.
Fig. S6. Design of the Metatron experiment with 48 enclosed fragments and adjoining enclosed corridors.
Fig. S7. Map of the SAFE experiment and location within Borneo [after Ewers *et al.* (*68*)].
Table S1. Metadata for Fig. 3 in the main text.
Table S2. Metadata for Fig. 4 in the main text.

REFERENCES AND NOTES

1. H. M. Pereira, P. W. Leadley, V. Proenca, R. Alkemade, J. P. W. Scharlemann, J. F. Fernandez-Manjarres, M. B. Araujo, P. Balvanera, R. Biggs, W. W. L. Cheung, L. Chini, H. D. Cooper, E. L. Gilman, S. Guenette, G. C. Hurtt, H. P. Huntington, G. M. Mace, T. Oberdorff, C. Revenga, P. Rodrigues, R. J. Scholes, U. R. Sumaila, M. Walpole, Scenarios for global biodiversity in the 21st century. *Science* **330**, 1496–1501 (2010).
2. M. R. W. Rands, W. M. Adams, L. Bennun, S. H. M. Butchart, A. Clements, D. Coomes, A. Entwistle, I. Hodge, V. Kapos, J. P. W. Scharlemann, W. J. Sutherland, B. Vira, Biodiversity conservation: Challenges beyond 2010. *Science* **329**, 1298–1303 (2010).
3. D. B. Lindenmayer, J. Fischer, *Habitat Fragmentation and Landscape Change: An Ecological and Conservation Synthesis* (Island Press, Washington, DC, 2006).
4. R. K. Didham, V. Kapos, R. M. Ewers, Rethinking the conceptual foundations of habitat fragmentation research. *Oikos* **121**, 161–170 (2012).
5. L. Fahrig, Rethinking patch size and isolation effects: The habitat amount hypothesis. *J. Biogeogr.* **40**, 1649–1663 (2013).
6. R. H. MacArthur, E. O. Wilson, *The Theory of Island Biogeography* (Princeton University Press, Princeton, NJ, 1967).
7. L. Fahrig, Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* **34**, 487–515 (2003).
8. S. K. Collinge, *The Ecology of Fragmented Landscapes* (The Johns Hopkins University Press, Baltimore, MD, 2009).
9. I. Ibanez, D. S. W. Katz, D. Peltier, S. M. Wolf, B. T. C. Barrie, Assessing the integrated effects of landscape fragmentation on plants and plant communities: The challenge of multiprocess–multiresponse dynamics. *J. Ecol.* **102**, 882–895 (2014).
10. M. C. Hansen, P. V. Potapov, R. Moore, M. Hancher, S. A. Turubanova, A. Tyukavina, D. Thau, S. V. Stehman, S. J. Goetz, T. R. Loveland, A. Kommareddy, A. Egorov, L. Chini, C. O. Justice, J. R. G. Townshend, High-resolution global maps of 21st-century forest cover change. *Science* **342**, 850–853 (2013).

11. M. Williams, *Deforesting the Earth*: *From Prehistory to Global Crisis* (University of Chicago Press, Chicago, 2003).
12. D. Skole, C. Tucker, Tropical deforestation and habitat fragmentation in the Amazon: Satellite data from 1978 to 1988. *Science* **260**, 1905–1910 (1993).
13. J. O. Sexton, X. P. Song, M. Feng, P. Noojipady, A. Anand, C. Q. Huang, D. H. Kim, K. M. Collins, S. Channan, C. DiMiceli, J. R. Townshend, Global, 30-m resolution continuous fields of tree cover: Landsat-based rescaling of MODIS vegetation continuous fields with lidar-based estimates of error. *Int. J. Digital Earth* **6**, 427–448 (2013).
14. W. F. Laurance, T. E. Lovejoy, H. L. Vasconcelos, E. M. Bruna, R. K. Didham, P. C. Stouffer, C. Gascon, R. O. Bierregaard, S. G. Laurance, E. Sampaio, Ecosystem decay of Amazonian forest fragments: A 22-year investigation. *Conserv*. *Biol*. **16**, 605–618 (2002).
15. E. N. Broadbent, G. P. Asner, M. Keller, D. E. Knapp, P. J. C. Oliveira, J. N. Silva, Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. *Biol. Conserv*. **141**, 1745–1757 (2008).
16. M. C. Ribeiro, J. P. Metzger, A. C. Martensen, F. J. Ponzoni, M. M. Hirota, The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biol. Conserv*. **142**, 1141–1153 (2009).
17. T. P. Hughes, D. R. Bellwood, C. Folke, R. S. Steneck, J. Wilson, New paradigms for supporting the resilience of marine ecosystems. *Trends Ecol*. *Evol*. **20**, 380–386 (2005).
18. T. Ricketts, E. Dinerstein, D. Olson, C. Loucks, W. Eichbaum, K. Kavanagh, P. Hedao, P. Hurley, K. Carney, R. Abell, S. Walters, *A Conservation Assessment of the Terrestrial Ecoregions of North America* (Island Press, Washington, DC, 1999).
19. R. P. White, S. Murray, M. Rohweder, *Grassland Ecosystems* (World Resources Institute, Washington, DC, 2000).
20. K. McGarigal, S. A. Cushman, Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecol. Appl*. **12**, 335–345 (2002).
21. H. M. Martinson, W. F. Fagan, Trophic disruption: A meta-analysis of how habitat fragmentation affects resource consumption in terrestrial arthropod systems. *Ecol. Lett*. **17**, 1178–1189 (2014).
22. J. I. Watling, M. A. Donnelly, Fragments as islands: A synthesis of faunal responses to habitat patchiness. *Conserv*. *Biol*. **20**, 1016–1025 (2006).
23. K. M. Flinn, M. Vellend, P. L. Marks, Environmental causes and consequences of forest clearance and agricultural abandonment in central New York, USA. *J. Biogeogr*. **32**, 439–452 (2005).
24. D. A. Saunders, R. J. Hobbs, C. R. Margules, Biological consequences of ecosystem fragmentation: A review. *Conserv*. *Biol*. **5**, 18–32 (1991).
25. M. E. Soulé, *Viable Populations for Conservation* (Cambridge University Press, Cambridge, UK, 1987).
26. E. O. Wilson, E. O. Willis, in *Ecology and Evolution of Communities*, M. L. Cody, J. M. Diamond, Eds. (The Belknap Press, Cambridge, MA, 1975), pp. 522–534.
27. H. L. Vasconcelos, E. M. Bruna, Arthropod responses to the experimental isolation of Amazonian forest fragments. *Zoologia* **29**, 515–530 (2012).
28. N. M. Haddad, L. A. Brudvig, E. I. Damschen, D. M. Evans, B. L. Johnson, D. J. Levey, J. L. Orrock, J. Resasco, L. L. Sullivan, J. J. Tewksbury, S. A. Wagner, A. J. Weldon, Potential negative ecological effects of corridors. *Conserv*. *Biol*. **28**, 1178–1187 (2014).
29. C. D. Collins, R. D. Holt, B. L. Foster, Patch size effects on plant species decline in an experimentally fragmented landscape. *Ecology* **90**, 2577–2588 (2009).
30. D. Tilman, R. M. May, C. L. Lehman, M. A. Nowak, Habitat destruction and the extinction debt. *Nature* **371**, 65–66 (1994).
31. I. Hanski, A. Moilanen, M. Gyllenberg, Minimum viable metapopulation size. *Am. Nat*. **147**, 527–541 (1996).
32. W. F. Laurance, P. Delamonica, S. G. Laurance, H. L. Vasconcelos, T. E. Lovejoy, Conservation: Rainforest fragmentation kills big trees. *Nature* **404**, 836 (2000).
33. W. M. Cook, J. Yao, B. L. Foster, R. D. Holt, L. B. Patrick, Secondary succession in an experimentally fragmented landscape: Community patterns across space and time. *Ecology* **86**, 1267–1279 (2005).
34. A. Gonzalez, Community relaxation in fragmented landscapes: The relation between species richness, area and age. *Ecol. Lett*. **3**, 441–448 (2000).
35. G. Ferraz, G. J. Russell, P. C. Stouffer, R. O. Bierregaard, S. L. Pimm, T. E. Lovejoy, Rates of species loss from Amazonian forest fragments. *Proc. Natl. Acad. Sci. U.S.A*. **100**, 14069–14073 (2003).
36. J. L. Orrock, J. I. Watling, Local community size mediates ecological drift and competition in metacommunities. *Proc. Biol. Sci*. **277**, 2185–2191 (2010).
37. S. T. Jackson, D. F. Sax, Balancing biodiversity in a changing environment: Extinction debt, immigration credit and species turnover. *Trends Ecol*. *Evol*. **25**, 153–160 (2010).
38. J. Clobert, J. F. Le Galliard, J. Cote, S. Meylan, M. Massot, Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol. Lett*. **12**, 197–209 (2009).
39. P. Staddon, Z. Lindo, P. D. Crittenden, F. Gilbert, A. Gonzalez, Connectivity, non-random extinction and ecosystem function in experimental metacommunities. *Ecol. Lett*. **13**, 543–552 (2010).
40. S. A. Billings, E. A. Gaydess, Soil nitrogen and carbon dynamics in a fragmented landscape experiencing forest succession. *Landsc*. *Ecol*. **23**, 581–593 (2008).
41. C. D. Mendenhall, D. S. Karp, C. F. J. Meyer, E. A. Hadly, G. C. Daily, Predicting biodiversity change and averting collapse in agricultural landscapes. *Nature* **509**, 213–217 (2014).
42. A. Gonzalez, J. H. Lawton, F. S. Gilbert, T. M. Blackburn, I. Evans-Freke, Metapopulation dynamics, abundance, and distribution in a microecosystem. *Science* **281**, 2045–2047 (1998).
43. H. M. Alexander, B. L. Foster, F. Ballantyne, C. D. Collins, J. Antonovics, R. D. Holt, Metapopulations and metacommunities: Combining spatial and temporal perspectives in plant ecology. *J. Ecol*. **100**, 88–103 (2012).
44. C. R. Margules, The Wog Wog habitat fragmentation experiment. *Environ*. *Conserv*. **19**, 316–325 (1992).
45. E. I. Damschen, L. A. Brudvig, Landscape connectivity strengthens local–regional richness relationships in successional plant communities. *Ecology* **93**, 704–710 (2012).
46. W. M. Cook, K. T. Lane, B. L. Foster, R. D. Holt, Island theory, matrix effects and species richness patterns in habitat fragments. *Ecol. Lett*. **5**, 619–623 (2002).
47. K. F. Davies, B. A. Melbourne, C. R. Margules, Effects of within- and between-patch processes on community dynamics in a fragmentation experiment. *Ecology* **82**, 1830–1846 (2001).
48. K. F. Davies, C. R. Margules, K. F. Lawrence, Which traits of species predict population declines in experimental forest fragments? *Ecology* **81**, 1450–1461 (2000).
49. K. F. Davies, C. R. Margules, J. F. Lawrence, A synergistic effect puts rare, specialized species at greater risk of extinction. *Ecology* **85**, 265–271 (2004).
50. J. Yao, R. D. Holt, P. M. Rich, W. S. Marshall, Woody plant colonization in an experimentally fragmented landscape. *Ecography* **22**, 715–728 (1999).
51. E. I. Damschen, L. A. Brudvig, N. M. Haddad, D. J. Levey, J. L. Orrock, J. J. Tewksbury, The movement ecology and dynamics of plant communities in fragmented landscapes. *Proc*. *Natl*. *Acad*. *Sci*. *U.S.A*. **105**, 19078–19083 (2008).
52. L. L. Sullivan, B. L. Johnson, L. A. Brudvig, N. M. Haddad, Can dispersal mode predict corridor effects on plant parasites? *Ecology* **92**, 1559–1564 (2011).
53. Z. Lindo, J. Whiteley, A. Gonzalez, Traits explain community disassembly and trophic contraction following experimental environmental change. *Glob*. *Chang*. *Biol*. **18**, 2448–2457 (2012).
54. S. A. Boyle, A. T. Smith, Can landscape and species characteristics predict primate presence in forest fragments in the Brazilian Amazon? *Biol*. *Conserv*. **143**, 1134–1143 (2010).
55. J. E. Diffendorfer, M. S. Gaines, R. D. Holt, Habitat fragmentation and movements of three small mammals (Sigmodon, Microtus, and Peromyscus). *Ecology* **76**, 827–839 (1995).
56. K. S. Van Houtan, S. L. Pimm, J. M. Halley, R. O. Bierregaard Jr., T. E. Lovejoy, Dispersal of Amazonian birds in continuous and fragmented forest. *Ecol*. *Lett*. **10**, 219–229 (2007).
57. I. Hanski, Extinction debt at different spatial scales. *Anim*. *Conserv*. **16**, 12–13 (2013).
58. R. Dirzo, H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, B. Collen, Defaunation in the Anthropocene. *Science* **345**, 401–406 (2014).
59. C. Kueffer, C. N. Kaiser-Bunbury, Reconciling conflicting perspectives for biodiversity conservation in the Anthropocene. *Front*. *Ecol*. *Environ*. **12**, 131–137 (2014).
60. W. F. Laurance, D. C. Useche, Environmental synergisms and extinctions of tropical species. *Conserv*. *Biol*. **23**, 1427–1437 (2009).
61. M. Krosby, J. Tewksbury, N. M. Haddad, J. Hoekstra, Ecological connectivity for a changing climate. *Conserv*. *Biol*. **24**, 1686–1689 (2010).
62. R. K. Didham, J. M. Tylianakis, N. J. Gemmell, T. A. Rand, R. M. Ewers, Interactive effects of habitat modification and species invasion on native species decline. *Trends Ecol*. *Evol*. **22**, 489–496 (2007).
63. L. Gibson, A. J. Lynam, C. J. A. Bradshaw, F. L. He, D. P. Bickford, D. S. Woodruff, S. Bumrungsri, W. F. Laurance, Near-complete extinction of native small mammal fauna 25 years after forest fragmentation. *Science* **341**, 1508–1510 (2013).
64. C. A. Peres, Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. *Conserv*. *Biol*. **15**, 1490–1505 (2001).
65. K. J. Gaston, T. W. Davies, J. Bennie, J. Hopkins, Review: Reducing the ecological consequences of night-time light pollution: Options and developments. *J*. *Appl*. *Ecol*. **49**, 1256–1266 (2012).
66. M. A. Cochrane, W. F. Laurance, Fire as a large-scale edge effect in Amazonian forests. *J*. *Trop*. *Ecol*. **18**, 311–325 (2002).
67. D. Legrand, O. Guillaume, M. Baguette, J. Cote, A. Trochet, O. Calvez, S. Zajitschek, F. Zajitschek, J. Lecomte, Q. Benard, J. F. Le Galliard, J. Clobert, The Metatron: An experimental system to study dispersal and metaecosystems for terrestrial organisms. *Nat*. *Methods* **9**, 828–833 (2012).
68. R. M. Ewers, R. K. Didham, L. Fahrig, G. Ferraz, A. Hector, R. D. Holt, V. Kapos, G. Reynolds, W. Sinun, J. L. Snaddon, E. C. Turner, A large-scale forest fragmentation experiment: The Stability of Altered Forest Ecosystems Project. *Philos*. *Trans*. *R*. *Soc*. *Lond*. *B Biol*. *Sci*. **366**, 3292–3302 (2011).
69. A. R. Templeton, K. Shaw, E. Routman, S. K. Davis, The genetic consequences of habitat fragmentation. *Ann*. *Mo*. *Bot*. *Gard*. **77**, 13–27 (1990).
70. A. Young, T. Boyle, T. Brown, The population genetic consequences of habitat fragmentation for plants. *Trends Ecol*. *Evol*. **11**, 413–418 (1996).

71. M. S. Gaines, J. E. Diffendorfer, R. H. Tamarin, T. S. Whittam, The effects of habitat fragmentation on the genetic structure of small mammal populations. *J. Hered.* **88**, 294–304 (1997).
72. J. L. Orrock, Conservation corridors affect the fixation of novel alleles. *Conserv. Genet.* **6**, 623–630 (2005).
73. T. Merck, H. Van Dyck, B. Karlsson, O. Leimar, The evolution of movements and behaviour at boundaries in different landscapes: A common arena experiment with butterflies. *Proc. Biol. Sci.* **270**, 1815–1821 (2003).
74. S. P. Ripperger, M. Tschapka, E. K. V. Kalko, B. Rodriguez-Herrera, F. Mayer, Life in a mosaic landscape: Anthropogenic habitat fragmentation affects genetic population structure in a frugivorous bat species. *Conserv. Genet.* **14**, 925–934 (2013).
75. S. Manel, R. Holderegger, Ten years of landscape genetics. *Trends Ecol. Evol.* **28**, 614–621 (2013).
76. M. Keller, D. S. Schimel, W. W. Hargrove, F. M. Hoffman, A continental strategy for the National Ecological Observatory Network. *Front. Ecol. Environ.* **6**, 282–284 (2008).
77. H. Tallis, H. Mooney, S. Andelman, P. Balvanera, W. Cramer, D. Karp, S. Polasky, B. Reyers, T. Ricketts, S. Running, K. Thonicke, B. Tietjen, A. Walz, A global system for monitoring ecosystem service change. *Bioscience* **62**, 977–986 (2012).
78. J. O. Sexton, R. D. Ramsey, D. L. Bartos, Habitone analysis of quaking aspen in the Utah Book Cliffs: Effects of site water demand and conifer cover. *Ecol. Model.* **198**, 301–311 (2006).
79. A. K. Fremier, F. A. J. DeClerck, N. A. Bosque-Perez, N. E. Carmona, R. Hill, T. Joyal, L. Keesecker, P. Z. Klos, A. Martinez-Salinas, R. Niemeyer, A. Sanfiorenzo, K. Welsh, J. D. Wulfhorst, Understanding spatiotemporal lags in ecosystem services to improve incentives. *Bioscience* **63**, 472–482 (2013).
80. T. H. Keitt, Habitat conversion, extinction thresholds, and pollination services in agroecosystems. *Ecol. Appl.* **19**, 1561–1573 (2009).
81. P. Opdam, E. Steingrover, S. van Rooij, Ecological networks: A spatial concept for multi-actor planning of sustainable landscapes. *Landsc. Urban Plan.* **75**, 322–332 (2006).
82. M. Cabeza, A. Moilanen, Design of reserve networks and the persistence of biodiversity. *Trends Ecol. Evol.* **16**, 242–248 (2001).
83. J. A. Foley, N. Ramankutty, K. A. Brauman, E. S. Cassidy, J. S. Gerber, M. Johnston, N. D. Mueller, C. O'Connell, D. K. Ray, P. C. West, C. Balzer, E. M. Bennett, S. R. Carpenter, J. Hill, C. Monfreda, S. Polasky, J. Rockstrom, J. Sheehan, S. Siebert, D. Tilman, D. P. M. Zaks, Solutions for a cultivated planet. *Nature* **478**, 337–342 (2011).
84. D. Tilman, Global environmental impacts of agricultural expansion: The need for sustainable and efficient practices. *Proc. Natl. Acad. Sci. U.S.A.* **96**, 5995–6000 (1999).
85. K. C. Seto, B. Guneralp, L. R. Hutyra, Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 16083–16088 (2012).

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Review

Biodiversity management in the face of climate change: A review of 22 years of recommendations

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ABSTRACT

Climate change creates new challenges for biodiversity conservation. Species ranges and ecological dynamics are already responding to recent climate shifts, and current reserves will not continue to support all species they were designed to protect. These problems are exacerbated by other global changes. Scholarly articles recommending measures to adapt conservation to climate change have proliferated over the last 22 years. We systematically reviewed this literature to explore what potential solutions it has identified and what consensus and direction it provides to cope with climate change. Several consistent recommendations emerge for action at diverse spatial scales, requiring leadership by diverse actors. Broadly, adaptation requires improved regional institutional coordination, expanded spatial and temporal perspective, incorporation of climate change scenarios into all planning and action, and greater effort to address multiple threats and global change drivers simultaneously in ways that are responsive to and inclusive of human communities. However, in the case of many recommendations the how, by whom, and under what conditions they can be implemented is not specified. We synthesize recommendations with respect to three likely conservation pathways: regional planning; site-scale management; and modification of existing conservation plans. We identify major gaps, including the need for (1) more specific, operational examples of adaptation principles that are consistent with unavoidable uncertainty about the future; (2) a practical adaptation planning process to guide selection and integration of recommendations into existing policies and programs; and (3) greater integration of social science into an endeavor that, although dominated by ecology, increasingly recommends extension beyond reserves and into human-occupied landscapes.

Contents

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1. Introduction

Climate change poses major new challenges to biodiversity conservation. As atmospheric CO_2 increases over the next century, it is expected to become the first or second greatest driver of global biodiversity loss (Sala et al., 2000; Thomas et al., 2004). Global average temperatures have increased 0.2 °C per decade since the 1970s, and global average precipitation increased 2% in the last 100 years (IPCC, 2007a). Moreover, climate changes are spatially heterogeneous. Some locations, such as the Arctic, experience much larger changes than global means, while others are exposed to secondary effects like sea level rise (IPCC, 2007a). Climate change may have already resulted in several recent species extinctions (McLaughlin et al., 2002; Pounds et al., 2006). Many species ranges have moved poleward and upward in elevation in the last century (Parmesan and Yohe, 2003; Root et al., 2003) and will almost certainly continue to do so. Local communities are disaggregrating and shifting toward more warm-adapted species (Parmesan, 2005). Phenological changes in populations, such as earlier breeding or peak in biomass, are decoupling species interactions (Walther et al., 2002).

These changes raise concerns about the effectiveness of existing biodiversity protection strategies (Halpin, 1997; Hannah et al., 2002; Peters and Darling, 1985; Scott et al., 2002). Biodiversity conservation relies predominately on fixed systems of protected areas, and the mandated goals of many conservation agencies and institutions are to protect particular species assemblages and ecosystems within these systems (Lemieux and Scott, 2005; Scott et al., 2002). With the magnitude of climate change expected in the current century, many vegetation types and individual species are expected to lose representation in protected areas (Araujo et al., 2004; Burns et al., 2003; Lemieux and Scott, 2005; Scott et al., 2002). Reserves at high latitudes and high elevations, on low-elevation islands and the coast, and those with abrupt landuse boundaries are particularly vulnerable (Sala et al., 2000; Shafer, 1999). Landscapes outside of protected areas are hostile to the survival of many species due to human infrastructure and associated stressors, such as invasive species, hunting, cars, and environmental toxins. Such fragmentation directly limits species migration and gene flow. Projected rates of climate change are also faster than they were in the past – so rapid that in situ genetic adaptation of most populations to new climate conditions is not likely (Jump and Penuelas, 2005), nor is migration likely to be fast enough for many species (Davis and Shaw, 2001). Moreover, even if major global action reduced emissions significantly within the next years or capped them at year 2000 levels, the thermal inertia of the oceans will continue to drive climate change for decades and will require adaptive responses (Meehl et al., 2005; Wigley, 2005). A recent update of atmospheric CO_2 growth rate, which has more than doubled since the 1990s as global economic activity increases and becomes more carbon-intensive, makes clear that significant global emissions reductions are a distant goal at best (Canadell et al., 2007).

How should we modify our biodiversity protection strategies to deal with climate change? Here we focus on adaptation strategies. Adaptation is broadly defined as adjustment in human or natural systems, including structures, processes, and practices (IPCC, 2007b). Scientists have written about adaptation with increasing frequency over the last two decades, but developments in this area have progressed slowly. For years, emissions mitigation has largely been the only game in town, with little governmental or private support for climate change adaptation. For instance, the United States National Park Service (NPS) in collaboration with the Environmental Protection Agency (EPA) has created a 'Climate Friendly Park' program. It aims to reduce greenhouse gas emissions, but it does not include measures or incentives to park managers to build and test adaptation strategies to preserve biodiversity under climate change. In many ways, adaptation science has begun to develop only very recently in response to recent widespread acceptance by governments and private citizens of the certainty of climate change.

In this paper we review the growing, published literature specifically addressed at biodiversity management and adaptation in the face of climate change. We consider biodiversity to include all types of organisms at all scales, from genes to ecosystems. The genesis for our review was the 2006 annual meeting of the California Invasive Plant Council, where climate change was identified by both researchers and practitioners as a key issue for action. Discussions throughout the meeting, however, made clear that practitioners felt at a loss for practical steps to take. Managers working at local preserves were particularly uncertain about what, if anything, they could do to prepare for climate change. We use this review in order to highlight what actions and actors scientists have so far identified to address climate change, and to explore how recommendations inform an adaptation planning process at various management scales. Scott and Lemieux (2005) reviewed a similar literature but focused on park management. Here we explore adaptation planning across scales and in both protected and unprotected areas.

2. Methods

We used Web of Science, including Science Citation Index Expanded, Social Science Citation Index, and Arts and Humanities Citation databases from 1975 to March 2007, to search for published journal articles on climate change and biodiversity management. We used the search terms "climate change", "global warming", "climatic change", "climate-change" and "changing climate" in all possible combinations with the search string "management OR biodiversity OR adaptation OR conservation OR restoration OR planning OR reserve design OR strategy OR land-use OR landuse OR landscape OR protected area OR park". Articles that discussed strategies for both biodiversity and related ecosystem services were included, but we excluded articles that only addressed ecosystem services such as management strategies for carbon stocks, human infrastructure, and food security. We also did not attempt to review studies that explore climate impacts on ecosystem components and processes without making explicit recommendations for biodiversity management. This literature is large and has been reviewed elsewhere (Kappelle et al., 1999; McCarty, 2001; Walther et al., 2002). From these searches, we identified and read 281 prospective articles, and from these culled those that provided explicit recommendations for management in the face of climate change. An additional four articles published after March 2007 were included, which were found through personal communication.

To analyze recommendations, we created a database in which we recorded every recommendation for action or information in the exact language used in the paper and answered a series of questions designed to synthesize recommendations and identify biases in the literature to date. We asked:

(1) *In what formal and informal contexts does action need to occur?* To answer this question, we categorized recommendations into broad spheres of activity: (1) policy reform, (2) science and technology effort and advances, (3) changes in conservation sector activity including restoration, or (4) changes in individual and community behavior, such as by farmers, ranchers, and other private landowners.

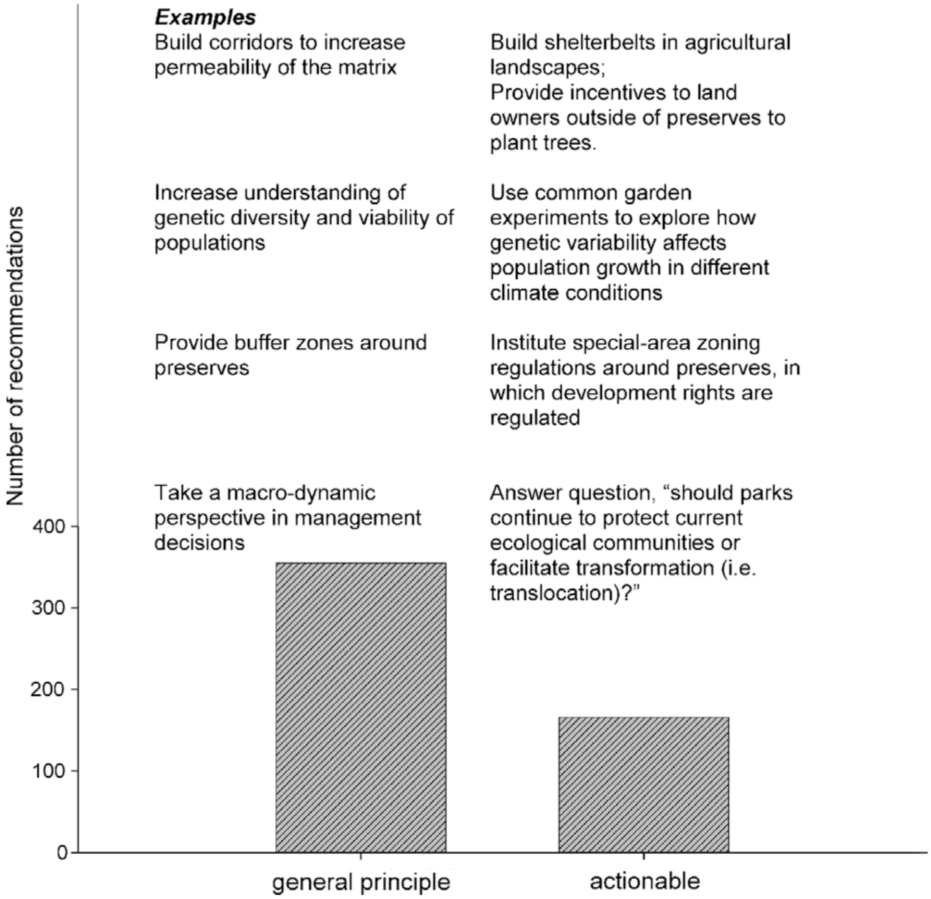

Fig. 1 – Examples and distribution of recommendations classified as "general principle" and "actionable". Most recommendations offer general principles for climate change adaptation but lack specificity needed for implementation.

(2) *What is the basis for the recommendation?* We recorded what information an author used to formulate their recommendation. Categories included empirical experimental data, simulation, literature review, case studies, interviews, or workshops. We also included the term 'ecological reasoning' to encompass studies based predominately on theory and opinion.
(3) *Is the recommendation a general principle or actionable?* A recommendation was considered a "general principle" if it provided a guiding concept, such as "build flexibility", but was generic open-ended and without example of who should act or what one should do (see Fig. 1). "Actionable" was given to those recommendations that identified a very clear who and what and often gave examples, such as, "[in restoration] use a broader range of species than prescribed solely on local basis to build system resilience (Harris et al., 2006)".
(4) *Is the recommendation for biodiversity or for biodiversity and related ecosystem services?*
(5) *Is there a geographic context for the recommendation?*
(6) *Does the article focus on a biome or ecosystem-type?*
(7) *Where in the landscape would the recommendation apply?* We categorized recommendations as applying to reserve (any public or private land-holding dedicated to biodiversity protection and maintenance, synonymous with protected area), or human-use lands (the matrix), or non-specific, meaning the recommendation could be enacted in either reserve or matrix land.
(8) *Does the recommendation describe an information need or a necessary action?* All recommendations for research were categorized as information needs, while the 'action' category included recommendations such as building corridors, reforming policy or buying more land.

To minimize variation in how articles were classified as a function of when they were read (i.e. the 1st paper entered compared to the 100th), records in the database were periodically shuffled by different criteria (i.e. year published or geographic context) and then re-classified. In addition, both authors coded a sub-sample of recommendations. After compiling the database, similar records were grouped into 'recommendation' categories. We tabulated the most common recommendations and ranked them by frequency cited overall.

3. Results and discussion

We recorded 524 recommendations from 113 papers, published in 57 different source journals and three books. Recommendations ranged from calls for specific types of modeling (e.g. inexact-fuzzy multiobjective programming (Huang et al., 1998) to broad shifts in governance structures (Tompkins and Adger, 2004) (Table 1). The number of papers published on this topic has increased dramatically in recent years (Fig. 2). Thirty-three percent of recommendations addressed biodiversity protection in conjunction with related ecosystem services, including forest products, fisheries and hunting, agriculture and grazing, and human health. Recommendations call for research, leadership and reform by a range of actors in several sectors; Emphasis in this set of literature is on science and nature conservation rather than on social or political adaptation measures (Fig. 3), with an emphasis somewhat more focused on reserve land over the matrix (Fig. 4a). Action is weighted more than information needs (Fig. 4b). When information needs were identified, they were overwhelmingly calls for more ecological rather than social scientific data (Fig. 4c). Recommendations are biased toward North America and Europe (Fig. 5a) and forests ecosystems (Fig. 5b).

Recommendations address various stages in an adaptation process, from research needs to methods for impact assessments to large-scale changes in policies by governmental, academic or non-governmental institutions (Table 1). About 70% of recommendations were classified as general principles under our classification scheme rather than specific, actionable strategies or tactics (Fig. 1). For example, seven authors suggest flexibility in management approaches, but only Millar et al. (2007) suggest flexibility and follow with a definition of what that means: willingness to change course, risk-taking including doing nothing, and capacity to reassess conditions frequently. Climate change adaptation work, at least in this literature, is still largely at the "idea" stage – it is based predominately on ecological reasoning rather than specific research, case studies, or empirical data (Fig. 5c), and it is largely nonspecific in the geographic areas or biome types that it targets (Fig. 5a and b). Many articles based on concrete modeling work or empirical studies of species responses to climate change tended either to not elaborate their results to management directives, or to present recommendations in vague terms such as, "restoration should be considered". Alternatively, very specific recommendations were proposed and not generalized for use outside of the target system. There appears to be a need for a happy medium between highly specific recommendations useful only in target areas and highly generalized recommendations that fail to inspire application (Halpin, 1997). This happy medium is likely to emerge rapidly as climate change adaptation science grows.

In the literature reviewed here, few recommendations suggested a process a manager could use to develop an adaptation plan and evaluate its usefulness (but see Hannah et al., 2002). More information on adaptation frameworks are developed in reports by Parks Canada (Welch, 2005), the NCEAS Conservation and Climate Change Working Group 2 (personal communication), and England's Department for Food Environment and Rural Affairs (http://www.defra.gov.uk/wildlife-countryside/resprog/findings/ebs-climate-change.pdf), which were not reviewed here. In practice, planners and managers could apply recommendations in at least three ways. At the broadest scale, long-term planning and policy formulation should tackle adaptation for whole landscapes and regions, with tools like reserve selection, ecosystem management, and landuse zoning schemes. Second, managers of individual reserves might want to know what they can do at their sites, individually or in concert with other sites. Third, rather than initially pursuing an idealized regional, landscape, or site-scale plan, the first practical step for many managers, conservation stakeholders and policymakers is to evaluate and adapt existing conservation plans. In the following

Table 1 – List of recommendations for climate change adaptation strategies for biodiversity management assembled from 112 scholarly articles. 524 records were condensed into 113 recommendation categories and are ranked by frequency of times cited in different articles.

Rank	Recommendation	No. articles	References
1	Increase connectivity (design corridors, remove barriers for dispersal, locate reserves close to each other, reforestation	24	Beatley (1991), Chambers et al. (2005), Collingham and Huntley (2000), Da Fonseca et al. (2005), de Dios et al. (2007), Dixon et al. (1999), Eeley et al. (1999), Franklin et al. (1992), Guo (2000), Halpin (1997), Hulme (2005), Lovejoy (2005), Millar et al. (2007), Morecroft et al. (2002), Noss (2001), Opdam and Wascher (2004), Rogers and McCarty (2000), Schwartz et al. (2001), Scott et al. (2002), Shafer (1999), Welch (2005), Wilby and Perry (2006) and Williams (2000)
2	Integrate climate change into planning exercises (reserve, pest outbreaks, harvest schedules, grazing limits, incentive programs	19	Araujo et al. (2004), Chambers et al. (2005), Christensen et al. (2004), Dale and Rauscher (1994), Donald and Evans (2006), Dyer (1994), Erasmus et al. (2002), Hulme (2005), LeHouerou (1999), McCarty (2001), Millar and Brubaker (2006), Peters and Darling (1985), Rounsevell et al. (2006), Scott and Lemieux (2005), Scott et al. (2002), Soto (2001), Staple and Wall (1999), Suffling and Scott (2002) and Welch (2005)
3	Mitigate other threats, i.e. invasive species, fragmentation, pollution	17	Bush (1999), Chambers et al. (2005), Chornesky et al. (2005), Da Fonseca et al. (2005), de Dios et al. (2007), Dixon et al. (1999), Halpin (1997), Hulme (2005), McCarty (2001), Noss (2001), Opdam and Wascher (2004), Peters and Darling (1985), Rogers and McCarty (2000), Shafer (1999), Soto (2001), Welch (2005) and Williams (2000)
4	Study response of species to climate change physiological, behavioral, demographic	15	Alongi (2002), Chambers et al. (2005), Crozier and Zabel (2006), Dyer (1994), Erasmus et al. (2002), Fukami and Wardle (2005), Gillson and Willis (2004), Honnay et al. (2002), Hulme (2005), Kappelle et al. (1999), McCarty (2001), Mulholland et al. (1997), Noss (2001), Peters and Darling (1985) and Swetnam et al. (1999)
	Practice intensive management to secure populations	15	Bartlein et al. (1997), Buckland et al. (2001), Chambers et al. (2005), Chornesky et al. (2005), Crozier and Zabel (2006), Dixon et al. (1999), Dyer (1994), Franklin et al. (1992), Hulme (2005), Morecroft et al. (2002), Peters and Darling (1985), Soto (2001), Thomas et al. (1999), Williams (2000) and Williams et al. (2005)
	Translocate species	15	Bartlein et al. (1997), Beatley (1991), Chambers et al. (2005), de Dios et al. (2007), Halpin (1997), Harris et al. (2006), Honnay et al. (2002), Hulme (2005), Millar et al. (2007), Morecroft et al. (2002), Pearson and Dawson (2005), Peters and Darling (1985), Rogers and McCarty (2000), Schwartz et al. (2001), Shafer (1999) and Williams et al. (2005)
5	Increase number of reserves	13	Burton et al. (1992), Dixon et al. (1999), Hannah et al. (2007), Hughes et al. 2003, LeHouerou (1999), Lovejoy (2005), Peters and Darling (1985), Pyke and Fischer (2005), Scott and Lemieux (2005) (2007), van Rensburg et al. (2004), Wilby and Perry (2006) and Williams et al. (2005)
6	Address scale problems match modeling, management, and experimental spatial scales for improved predictive capacity	12	Chornesky et al. (2005), Da Fonseca et al. (2005), Dale and Rauscher (1994), Ferrier and Guisan (2006), Guisan and Thuiller (2005), Huang (1997), Hughes et al. (2003), Kueppers et al. (2004), Kueppers et al. (2005), Mulholland et al. (1997), Noss (2001), Root and Schneider (1995) and Root and Schneider (2006)
	Improve inter-agency, regional coordination	12	Bartlein et al. (1997), Cumming and Spiesman (2006), Da Fonseca et al. (2005), Grumbine (1991), Hannah et al. (2002), Lemieux and Scott (2005), Rounsevell et al. (2006), Scott and Lemieux (2005), Soto (2001), Suffling and Scott (2002), Tompkins and Adger (2004) and Welch (2005)
7	Increase and maintain basic monitoring programs	11	Chambers et al. (2005), Cohen (1999), Huang (1997), Rogers and McCarty (2000), Root and Schneider (1995), Schwartz et al. (2001), Shafer (1999), Staple and Wall (1999), Suffling and Scott (2002), Wilby and Perry (2006) and Williams (2000)
	Practice adaptive management	11	Allison et al. (1998), Chambers et al. (2005), Hulme (2005), Lasch et al. (2002), Maciver and Wheaton (2005), Millar et al. (2007), Scott and Lemieux (2005), Staple and Wall (1999), Suffling and Scott (2002), Tompkins and Adger (2004) and Welch (2005)
	Protect large areas, increase reserve size	11	Beatley (1991), Bellwood and Hughes (2001), Burton et al. (1992), Bush (1999), Halpin (1997), Hulme (2005), Morecroft et al. (2002), Peters and Darling (1985), Shafer (1999), Soto (2001) and Watson (2005)

Table 1 – continued

Rank	Recommendation	No. articles	References
8	Create and manage buffer zones around reserves	10	Bush (1999), de Dios et al. (2007), Halpin (1997), Hannah et al. (2002), Hartig et al. (1997), Hughes et al. (2003), Millar et al. (2007), Noss (2001), Shafer (1999) and van Rensburg et al. (2004)
9	Create ecological reserve networks large reserves, connected by small reserves, stepping stones	8	Allison et al. (1998), Collingham and Huntley (2000), de Dios et al. (2007), Gaston et al. (2006), Opdam et al. (2006), Opdam and Wascher (2004), Shafer (1999) and Welch (2005)
	Develop improved modeling and analysis capacity i.e. more effective software, integration with GIS, integrate greater complexity	8	Chornesky et al. (2005), Ferrier and Guisan (2006), Guisan and Thuiller (2005), Guo (2000), Huang et al. 1998, Mulholland et al. (1997), Peters and Darling (1985) and Rounsevell et al. (2006)
	Do integrated study of multiple global change drivers	8	Dale and Rauscher (1994), Desanker and Justice (2001), Donald and Evans (2006), Halpin (1997), Hannah et al. (2002), McCarty (2001), Watson (2005) and Williams (2000)
	Improve techniques for and do more restoration wetlands, rivers, matrix	8	Da Fonseca et al. (2005), de Dios et al. (2007), Dyer (1994), Hartig et al. (1997), Lovejoy (2005), Millar et al. (2007), Mulholland et al. (1997) and Shafer (1999)
	Increase interdisciplinary collaboration	8	Gillson and Willis (2004), Guisan and Thuiller (2005), Hannah et al. (2002), Hulme (2005), Kappelle et al. (1999), Root and Schneider 1995, Soto (2001) and Williams (2000)
	Promote conservation policies that engage local users and promote healthy human communities	8	Chapin et al. (2006), Desanker and Justice (2001), Eeley et al. (1999), Lovejoy (2005), Opdam and Wascher (2004), Ramakrishnan (1998), Tompkins and Adger (2004) and McClanahan et al. (2008)
	Protect full range of bioclimatic variation	8	Bush (1999), Eeley et al. (1999), McCarty (2001), Noss (2001), Pyke et al. (2005), Pyke and Fischer (2005), Shafer (1999) and Thomas et al. (1999)
	Soften landuse practices in the matrix	8	Beatley (1991), Burton et al. (1992), Da Fonseca et al. (2005), Franklin et al. (1992), Hannah et al. (2002), Noss (2001), Williams (2000) and Woodwell (1991)
10	Adopt long-term and regional perspective in planning, modeling, and management	7	Eeley et al. (1999), Ferrier and Guisan (2006), Franklin et al. (1992), Guo (2000), Lovejoy (2005), Millar and Brubaker (2006), Opdam and Wascher (2004), Peters and Darling (1985), Peterson et al. (1997), Scott et al. (2002) and Welch (2005)
	Re-asses conservation goals (i.e. move away from concepts of natural, embrace processes over patterns	7	Franklin et al. (1992), Hulme (2005), Millar et al. (2007), Scott and Lemieux (2005) (2007), Scott et al. (2002) and Suffling and Scott (2002)
	Study species dispersal across landuse boundaries, gene flow, migration rates, historic flux	7	Guo (2000), Halpin (1997), Hughes et al. (2003), Kappelle et al. (1999), Lovejoy (2005), Opdam and Wascher (2004) and Rice and Emery (2003)
	Study species distributions current and historic	7	Da Fonseca et al. (2005), Eeley et al. (1999), Erasmus et al. (2002), Guo (2000), Hannah et al. (2002), Kappelle et al. (1999) and Millar and Brubaker (2006)
11	Broaden genetic and species diversity in restoration and forestry	6	Burton et al. (1992), de Dios et al. (2007), Harris et al. (2006), Maciver and Wheaton (2005), McCarty (2001), Millar et al. (2007), Rice and Emery (2003) and Staple and Wall (1999)
	Develop adaptation strategies now; early adaptation is encouraged	6	Huang et al. (1998), Hulme (2005), Lemieux and Scott (2005), Scott and Lemieux (2005) (2007) and Welch (2005)
	Do not implement CO_2 emission mitigation projects that negatively impact biodiversity	6	Chambers et al. (2005), Klooster and Masera (2000), Koziell and Swingland (2002), Kueppers et al. (2004) and Streck and Scholz (2006), Welch (2005)
	Manage for flexibility, use of portfolio of approaches, maintain options	6	Eeley et al. (1999), Hulme (2005), Kappelle et al. (1999), Lovejoy (2005), Millar et al. (2007) and Welch (2005)
	Validate model results with empirical data	6	Dale and Rauscher (1994), Guisan and Thuiller (2005), Hulme (2005), Malcom et al. (2006), Opdam and Wascher (2004) and Watson (2005)
12	Do regional impact assessments	5	Cohen (1999), Desanker and Justice (2001), Lasch et al. (2002), Lindner et al. (1997) and Suffling and Scott (2002)
	Identify indicator species	5	Chambers et al. (2005), Hulme (2005), Noss (2001), Underwood and Fisher (2006) and Welch (2005)
	Initiate long-term studies of species responses to climate	5	Mulholland et al. (1997), Noss (2001), Opdam and Wascher (2004), Peters and Darling (1985) and Root and Schneider (2006)
	Model species ranges in the future	5	Allison et al. (1998), Da Fonseca et al. (2005), Hannah et al. (2002), Kerr and Packer (1998) and Kriticos et al. (2003)
	Protect refugia current and predicted future	5	Bush (1999), Chambers et al. (2005), Eeley et al. (1999), Noss (2001) and Scott et al. (2002)
	Study adaptive genetic variation	5	Harris et al. (2006), Hughes et al. (2003), Jump and Penuelas (2005), Kappelle et al. (1999) and Rice and Emery (2003)

(*continued on next page*)

Table 1 – continued

Rank	Recommendation	No. articles	References
13	Leadership by those with power senior management, government agencies	4	Scott and Lemieux (2005) (2007), Tompkins and Adger (2004) and Welch (2005)
	Limit CO_2 emissions	4	Hannah et al. (2007), Hannah et al. (2005), Mayer and Rietkerk (2004) and Rogers and McCarty (2000)
	Predict effects of directional climate change on ecosystems, communities, populations	4	Allison et al. (1998), de Dios et al. (2007), Kappelle et al. (1999) and Root and Schneider (2006)
	Preserve genetic diversity in populations	4	Chambers et al. (2005), de Dios et al. (2007) and Lovejoy (2005), Noss (2001)
	Represent each species in more than one reserve	4	Halpin (1997), Millar et al. (2007), Peters and Darling (1985) and Shafer (1999)
14	Create culturally appropriate adaptation/ management options	3	Dixon et al. (1999), Huang (1997), Tompkins and Adger (2004)
	Create education programs for public about landuse practices and effects on and with climate	3	Bush (1999) and Welch (2005), Williams (2000)
	Develop best management practices for climate change scenarios	3	Mulholland et al. (1997), Rogers and McCarty (2000) and de Dios et al. (2007)
	Institute flexible zoning around reserves	3	Halpin (1997), Peters and Darling (1985) and Soto (2001)
	Increase investment in climate related research	3	Lemieux and Scott (2005), Lovejoy (2005) and Peters and Darling (1985)
	Increase communication of knowledge about climate change impacts to policymakers and stakeholders	3	Erasmus et al. (2002), Opdam and Wascher (2004) and Welch (2005)
	Initiate dialogue among stakeholders	3	McKenzie et al. (2004), Rogers and McCarty (2000) and Scott et al. (2002)
	Institute government reform (i.e. adaptive governance)	3	Chapin et al. (2006), Tompkins and Adger (2004) and Williams (2000)
	Locate reserves in areas of high heterogeneity, endemism	3	Halpin (1997), Opdam and Wascher (2004) and Peters and Darling (1985)
	Maintain natural disturbance dynamics of ecosystems	3	Halpin (1997), Noss (2001) and Shafer (1999)
	Practice proactive management of habitat to mitigate warming	3	Halpin (1997), Mulholland et al. (1997) and Wilby and Perry (2006)
	Secure boundaries of existing preserves	3	Hannah et al. (2007), van Rensburg et al. (2004) and Welch (2005)
	Start strategic zoning of landuse to minimize climate related impacts	3	Bush (1999), Solecki and Rosenzweig (2004) and Tompkins and Adger (2004)
	Study and monitor ecotones and gradients	3	Halpin (1997), Lovejoy (2005) and Stohlgren et al. (2000)
	Study effectiveness of corridors	3	Graham 1988, Halpin (1997) and Williams et al. (2005)
	Use predictive models to make decisions on where to situate new reserves	3	Bush (1999), Hannah et al. (2007) and Pearson and Dawson (2005)
15	Anticipate surprises and threshold effects i.e. major extinctions or invasions	2	Bartlein et al. (1997) and Millar et al. (2007)
	Design biological preserves for complex changes in time, not just directional change	2	Bartlein et al. (1997) and Graham (1988)
	Locate reserves at northern boundary of species' ranges	2	Peters and Darling (1985) and Shafer (1999)
	Manage the matrix	2	Eeley et al. (1999) and Lovejoy (2005)
	Practice proactive research on climate change	2	Harris et al. (2006) and Williams (2000)
	Protect many small reserves rather than single large	2	Opdam and Wascher (2004) and Pearson and Dawson (2005)
	Provide education opportunities and summaries of primary literature for management staff to learn and network about climate change	2	Grumbine (1991) and Welch (2005)
	Study and protect metapopulations	2	Crozier and Zabel (2006) and Opdam and Wascher (2004)
	Study processes of change at multiple spatial and temporal scales	2	Dale and Rauscher (1994) and Watson (2005)
	Use GIS to study species distributions and landscape patterns	2	Brown (2006) and Da Fonseca et al. (2005)

Table 1 – continued

Rank	Recommendation	No. articles	References
16	Action plans must be time-bound and measurable	1	Welch (2005)
	Adjust park boundaries to capture anticipated movement of critical habitats	1	Welch (2005)
	Create institutional flexibility	1	Millar et al. (2007)
	Create linear reserves oriented longitudinally	1	Pearson and Dawson (2005)
	Establish cross-national collaboration	1	Desanker and Justice (2001)
	Establish neo-native forests plant species where they were in the past, but are not found currently	1	Millar et al. (2007)
	Experiment with refugia	1	Millar et al. (2007)
	Focus protection on sensitive biomes	1	Scott et al. (2002)
	Focus on annual plants rather than perennials near climate boundaries	1	Buckland et al. (2001)
	Increase wetland protection	1	Hartig et al. (1997)
	Institutional capacity enhancement to address climate change	1	Lemieux and Scott (2005)
	Institute reform to improve support for interdisciplinary, multi-institutional research	1	Root and Schneider (1995)
	Locate reserves so major vegetation transitions are in core	1	Halpin (1997)
	Locate reserves at core of ranges	1	Araujo et al. (2004)
	Manage for landscape asynchrony	1	Millar et al. (2007)
	Manage human-wildlife conflict as change occurs	1	Wilby and Perry (2006)
	Manage populations to reduce temporal fluctuations in population sizes	1	Rice and Emery (2003)
	Develop guidelines for climate sensitive restoration and infrastructure development	1	Welch (2005)
	Need to increase social acceptance of shared resilience goals	1	Tompkins and Adger (2004)
	Promote personal action plans among employees to reduce emissions	1	Welch (2005)
	Protect endangered species ex situ	1	Noss (2001)
	Protect functional groups and keystone species	1	Noss (2001)
	Protect mountains	1	Peterson et al. (1997)
	Protect primary forests	1	Noss (2001)
	Protect urban green space	1	Wilby and Perry (2006)
	Quantify environmental susceptibility versus adaptive capacity to inform conservation planning	1	McClanahan et al. (2008)
	Schedule dam releases to protect stream temperatures	1	Rogers and McCarty (2000)
	Study changes in populations at rear of range rather than only range fronts	1	Willis and Birks (2006)
	Study response of undisturbed areas to climate change	1	Mulholland et al. (1997)
	Study social agency and human decision making	1	Desanker and Justice (2001)
	Study time-series data on species dynamics	1	Erasmus et al. (2002)
	Substitute space for time to study the responses of species to climate change	1	Millar and Brubaker (2006)
	Train more taxonomists	1	Huber and Langor (2004)
	Use caution in predictive modeling because the responses of some species are not well predicted	1	Willis and Birks (2006)
	Use simple decision rules for reserve planning	1	Meir et al. (2004)
	Use social networks for education about climate change	1	Huang (1997)
	Use triage in short-term to prioritize action	1	Millar et al. (2007)

sections, we discuss how recommendations in the literature to date inform these three scales of application.

4. Regional policy and planning

Species historically respond to changing climate with distributional shifts, and many species are expected to lose current habitat representation in the future. In light of this, many recommendations call for greater integration of species protection plans, natural resource management, research and development agendas across wider geographic areas, on longer time-scales, and involving more diverse actors than in current practice. (1) Long-term, regional perspective and (2) improved coordination among scientists, land managers, politicians and conservation organizations at regional scales are among the most frequently cited recommendations to protect biodiversity in the face of climate change (Rank 10 and 6 respectively, see references in Table 1 and for all ranks mentioned hereafter). Increased interdisciplinary collaboration (Rank 9) as well as regional-scale impact assessments are also frequently identified (Rank 12). Recommendations for adaptation to regional policy and planning focus on two comple-

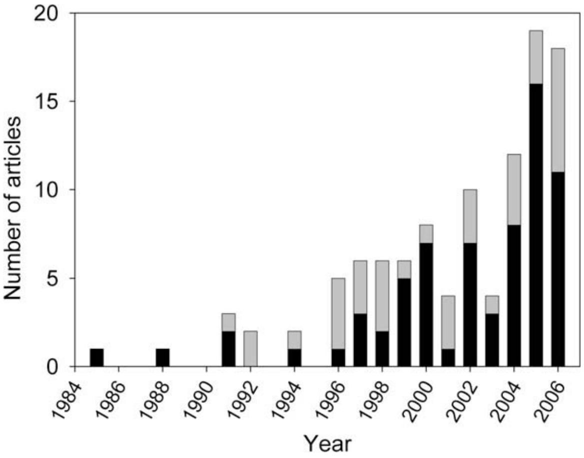

Fig. 2 – Frequency distribution by publication year of papers included in this review, including articles addressing biodiversity only (black) or biodiversity in conjunction with ecosystem services (grey). Records from 2007 were only partially covered in this review and not included.

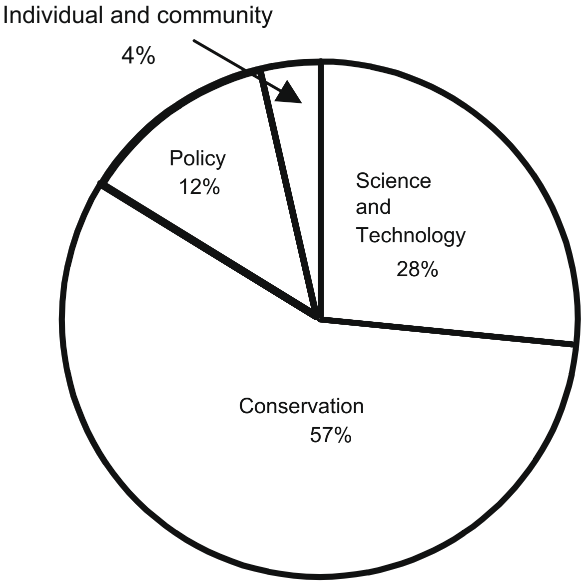

Fig. 3 – Distribution of recommendations calling for climate change adaptation among different activity sectors: conservation (e.g. reserve purchases, management, restoration and regional coordination), science and technology (e.g. research and modeling), policy (e.g. land-zoning, governance structure and institutional capacity), and individuals and communities (e.g. private landowner practices and grassroots action). Recommendations were counted in all applicable sectors.

mentary strategies: reserve planning and improving landscape connectivity. We discuss these issues further in the following two sections.

4.1. *Reserve planning*

Basing reserve acquisition priorities on predictions of future biome, community or individual species distributions under different climate scenarios is one method for climate change adaptation. The guiding principle is that reserves should be accumulated in areas predicted to be hotspots for biodiversity in the future or to provide habitat for species of high conservation value, warranting increased effort to model species distributions in the future (Rank 12). There are, however, several limitations to the accuracy and precision of simulation and analytical models of future species, biome or community distributions, leading some authors to recommend improved modeling capacity as the first step (Rank 9).

Model prediction error results from variation in model types, emissions, landuse and socio-economic scenarios. There are little-understood, but important, interactions between climate change and other global change drivers that could influence where species and habitats occur in the future (Rank 9). Insufficient data on species distributions (Rank 10) the effects of species interactions on distribution (Ferrier and Guisan, 2006; Kappelle et al., 1999), dispersal (Rank 10) and species, community or ecosystem responses to climate change (Rank 4) are also widely expressed concerns and lead authors to advocate for increased research in these areas before models are accepted. For example, bioclimatic envelope modeling uses current species distributions to predict future distributions as a function of climate. For many species such models can be productive, but in cases where species distributions are limited by factors other than climate, this extrapolation will prove misleading. Willis and Birks (2006) discuss the accuracy of bioclimatic models. Species-envelope model runs were conducted for backward predictions of species distributions and compared to paleo-ecological records. Many species distributions were predicted well, but some were largely inaccurate.

Problems of scaling also raise uncertainty (Rank 6), including scaling-down global climate models (GCMs) to fit management scales, or scaling-up empirical observations typically made at small spatial scales to predict larger scale processes (Root and Schneider, 1995). The scales of global climate models (GCM) and management activities simply do not match. Most reserves are smaller than a single grid cell in a GCM. Climate can vary sharply within this scale, and this variation often drives local patterns of species distribution and abundance – particularly in mountainous or coastal areas. Regional climate models, which are only available for small areas of the globe, are a more appropriate choice for management and planning (Dale and Rauscher, 1994; Guisan and Thuiller, 2005; Kueppers et al., 2005; Mulholland et al., 1997), though they remain limited by key uncertainties, assumptions and costs (Root and Schneider, 1995).

Not surprisingly, these inherent limitations of bioclimatic envelope models generate debate about whether and how to apply them to reserve selection. Some strongly advocate including climate change in reserve selection models and locating new reserves with expected changes in climate (Araujo et al., 2004; Bush, 1996; Dyer, 1994; Pearson and Dawson, 2005). Araujo et al. (2004) compare the ability of six existing reserve selection methods to secure European plant species in the context of climate change. They found species loss from protected reserves on the order of 6–11% of taxa for all models, and they conclude that new reserve-selection models specific to climate change are needed. Hannah et al. (2007)

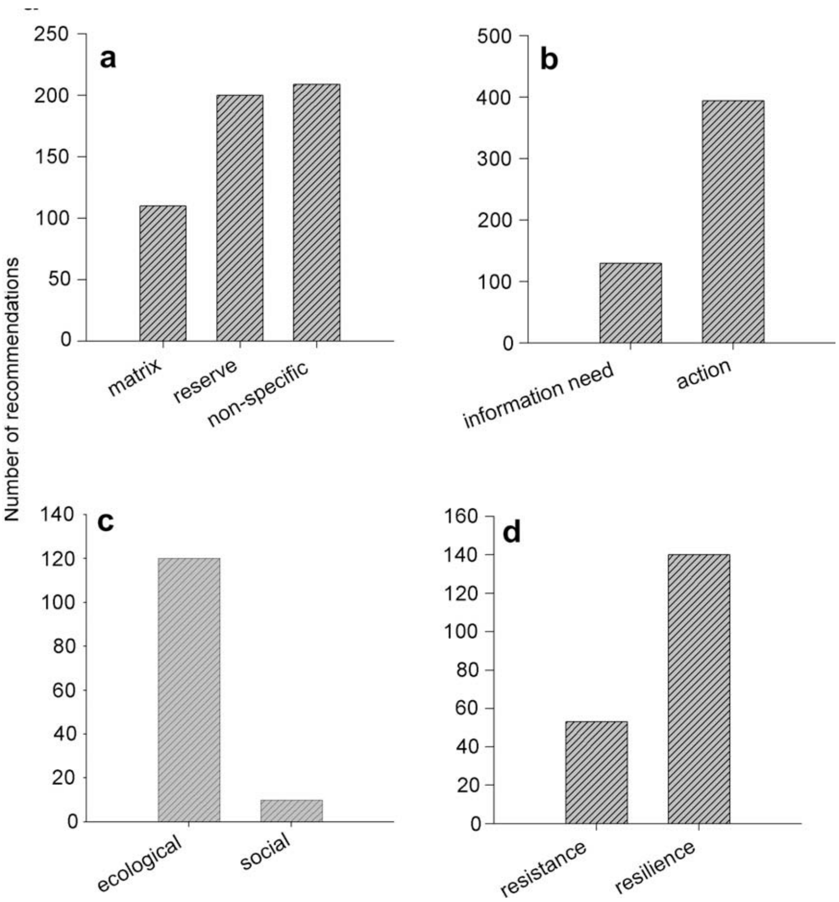

Fig. 4 – Distribution of recommendations among broad categories referring to (a) type of land targeted, (b) information need or action, (c) type of information need, and (d) management goal. Y-axis ranges vary across graphs because not all recommendations fit into every set of categories.

make a compelling case for not waiting to incorporate climate change forecasts into reserve selection models despite uncertainty. They use bioclimatic envelope models to explore the need for additional protected areas to achieve representation for thousands of species in three regions (Mexico, South Africa Cape, and Europe) in current and future climate and find that less land is needed in the long-term if planning models are designed to solve for both current and future conditions simultaneously.

Others argue, however, that given tremendous uncertainty, the priority should be to acquire new reserves in locations that minimize the spatial distances among new and existing reserves so that species can migrate (Allison et al., 1998; Collingham and Huntley, 2000; Halpin, 1997; Opdam and Wascher, 2004; Shafer, 1999). Williams et al. (2005) used a simulation model to estimate that 50% more protected land area in particular locations was needed to create reserve corridors to protect *Proteaceae* in the South African Cape region through 2050. Citing a number of sources of potential error in model results, however, they recommend that as much reserve area as possible be set aside. Such strategies do not require extensive modeling capacity and resources and instead focuse on rapid acquisition of land as it becomes available to create porous landscapes. Other authors reason that to facilitate migration and adaptation potential, reserves should be located with reference to focal species or community distributions, such as in their cores (Araujo et al., 2004; Halpin, 1997) or at their northern boundaries (Peters and Darling, 1985; Shafer, 1999). There seems to be little consensus or data to inform this debate. More research is needed about where in a species' range individuals are most likely to survive, migrate or adapt to rapid environmental change (Willis and Birks, 2006).

Debate also arises around the relative advantages of few large versus several small reserves in the context of climate change. The tension is whether large reserves will be large enough to allow species to track changing climate and remain inside reserve boundaries, and whether small preserves along latitudinal, elevational or other climate gradients will be close enough together for species to move between them. Eleven sources recommend protecting large areas (Beatley 1991; Bellwood and Hughes 2001; Burton et al. 1992; Bush 1996; Halpin 1997; Hulme 2005; Morecroft et al. 2002; Peters and Darling 1985; Shafer 1999; Soto 2001; Watson 2005), while two advocate focusing on many small areas (Opdam and Wascher, 2004; Pearson and Dawson, 2005). Eight suggest a compromise strategy of creating ecological networks of small and large reserves embedded within intermediate land uses (Allison et al., 1998; Collingham and Huntley, 2000; de Dios et al., 2007; Gaston et al., 2006; Opdam et al., 2006; Opdam and Wascher, 2004; Shafer, 1999; Welch, 2005).

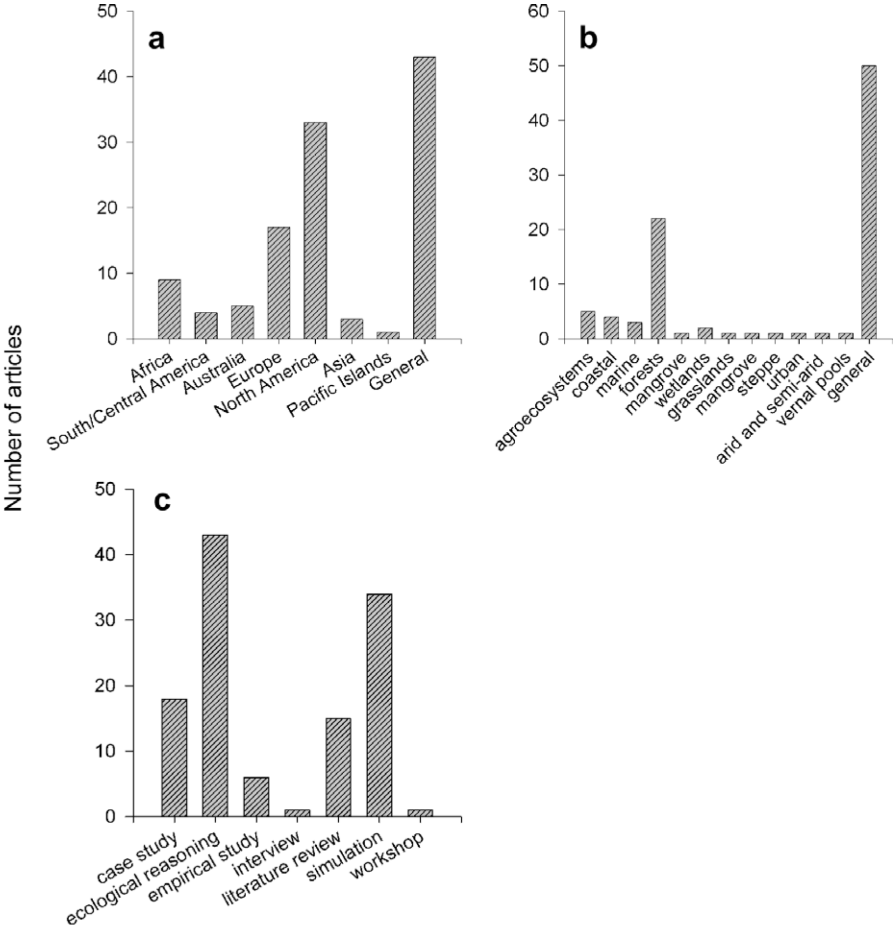

Fig. 5 – The (a) geographic focus, (b) biome focus, and (c) evidence basis for recommendations addressing climate change adaptation strategies for biodiversity management.

What all of the recommendations for reserve selection share is an urge to protect more land rapidly (Rank 5). This push will certainly help buffer biodiversity against climate change as well as other threats. However, climate change is likely to exacerbate existing tensions and tradeoffs between protecting areas and meeting basic human needs. Creating more new reserves might be feasible in some settings but must be guided by targeted, well-informed strategies likely to maximize effectiveness in the face of climate change. In most areas, action in lands outside of reserves must also be a part of climate change strategies for biodiversity conservation (Franklin et al., 1992; Lovejoy, 2005).

4.2. *Landscape connectivity*

To improve landscape connectivity, so that species can move, is the most frequent recommendation for climate change adaptation in the literature reviewed here (Rank 1). Authors recommend some form of corridor creation via the designation of new parks (de Dios et al., 2007; Halpin, 1997; Scott et al., 2002) oriented longitudinally (Eeley et al., 1999; Noss, 2001; Shafer, 1999), or through actions in non-reserve land, such as protecting riparian habitat and railway lines in cities (Wilby and Perry, 2006), or by planting trees and shrubs to create shelterbelts and hedgerows in farmlands (Donald and Evans, 2006; Guo, 2000; Schwartz et al., 2001). There was little guidance in this literature set for corridor implementation beyond common-sense reasoning, however. Illustrative examples of current corridor projects or elaboration of specific ecological or political tactics for corridor creation might help jump-start this process. For example, case studies of the Dutch Ecological Network and other similar national models to plan and link protected areas may be particularly informative at this stage of adaptation planning (Gaston et al., 2006). Further, despite widespread favor for ecological networks, assessment of their effectiveness remains in its infancy. Similarly, the field of corridor ecology, while recognized as integral to conservation practice in fragmented landscapes for years, is still young (see Hilty et al., 2006). Some authors warn of a significant need for more empirical data to support the effectiveness of corridors, optimize their spatial arrangement, and minimize risks of increased transmission of disease or invasive species before the conservation community embraces corridors uniformly as the tool to combat biodiversity loss in the face of global climate change (Graham, 1988; Halpin, 1997; Scott and Lemieux, 2005; Williams et al., 2005).

A second popular recommendation for improving landscape connectivity is to change how we manage the matrix

(Da Fonseca et al., 2005; Eeley et al., 1999; Lovejoy, 2005). Many authors advocate creating buffer zones around reserves (Rank 8) or flexible landuse zoning at reserve boundaries to allow for land swaps in the future as species distributions shift (Rank 14). Others recommend urban planning and zoning to avoid climate-related risks (Rank 14). In general, enlisting people and human communities to 'soften' landuse through sustainable or less damaging practices (e.g. low intensity forestry or alternatives to building sea walls) (Rank 9) and to restore habitat (Rank 9) will facilitate species movement and persistence in the future.

Despite wide acknowledgement, these connectivity strategies were among the most poorly developed recommendations, limited mainly to very general actions (e.g. "build flexibility", "manage the matrix", "modify landuse practices") without identification of kinds of actors that might need to be involved (e.g. reserve managers, policymakers, individuals) or information gaps. Landuse reform likely needs to bring together local governments, urban planners, community groups and conservation organizations and to involve high degrees of coordination across multiple jurisdictions to provide landscape cohesion (Press et al., 1995). Substantial work to flesh out this process, as well as to guide information acquisition, is needed before new forms of management across landuse types can be implemented.

Even with good landscape connectivity, some species will not be able to migrate. For these species – such as dispersal-limited species, those restricted to rare or confined habitat types, or those with life history traits like low reproductive rates – translocations from within their current range to locations suitable in the future are widely advocated (Rank 4). Translocations are a contentious issue because of the challenges associated with moving populations successfully and predicting suitable future habitats, as well as the potential for unintended consequences from introducing new species into existing communities (Lemieux and Scott, 2005; McLachlan et al., 2007). Empirical evidence suggests that animal translocations tend to be unsuccessful and costly (Fischer and Lindenmayer, 2000). Despite these real problems, we did not find discussion of the feasibility of such programs. Climate change adaptation strategies would likely necessitate moving at least some species outside of their current range, an action that has rarely been pursued thus far. To fully evaluate the feasibility of translocations would require stronger understanding of best available methods, potential risks, and policies for regional coordination to avoid situations in which different conservation objectives are put in conflict (McLachlan et al., 2007).

5. Site-scale action

Many land managers feel that there is little they can do about climate change beyond what they are already doing, such as trying to maintain basic ecosystem functioning and mitigate other threats like invasive species and pollution. To a certain extent, recommendations we reviewed validate this perspective. A number of "business as usual" recommendations rank high in their frequency in the literature, e.g. mitigating current threats, such as invasive species and habitat loss (Rank 2), increasing or continuing basic monitoring programs (Rank 7) or managing populations for natural disturbance dynamics (Halpin, 1997; Noss, 2001; Shafer, 1999). Franklin et al. (1992) describe how in forest ecosystems mature trees slow the effects of climate change because they tolerate a wide range of temperatures, while seedling establishment is far more sensitive. Under climate change, removal of long-lived trees will therefore act to intensify and speed-up the rate at which forest ecosystems change compared to intact forests. Restoration and greening efforts function as proactive management to mitigate local-scale warming (Halpin, 1997; Mulholland et al., 1997; Wilby and Perry, 2006). Mulholland et al. (1997) point out that restoration of riparian vegetation, needed to secure wildlife populations and ecosystem services now, will also function to decrease stream temperatures in the future. Wilby and Perry (2006) highlight how green building and landscaping techniques, such as planting green roofs, neighborhood trees, and water structures, will help to counter increasing problems of urban heat-island effects.

Other authors point out that business as usual is probably not enough in many cases. Peters and Darling (1985) suggest that managers consider rescue measures such as adding irrigation or drainage systems to secure sensitive populations. Buckland et al. (2001) anticipate that soil fertility in some grasslands may require manipulation to impede species invasions under warmer conditions. Advice to incorporate a broader range of species and genotypes in restoration and forestry than prescribed based on local provenance was common (Rank 11). This type of strategy would depart significantly from the preference for local genotypes prevailing in restoration and forestry practice to date (Millar and Brubaker, 2006; Millar et al., 2007; Scott and Lemieux, 2007) and warrants increased experimentation to better understand potential costs and benefits (Harris et al., 2006; Rice and Emery, 2003).

5.1. *Resilience versus resistance*

A first step for managers will be to wrestle with the question of whether and when they will attempt to resist biotic change, such as by adding irrigation if precipitation declines, rather than try to build resilience to change, such as by facilitating population adaptive capacity through introduction of a wider range of genotypes. In theory resistant strategies attempt to bolster a system's defenses to rapid environmental change, while resilience strategies attempt to bolster a system's ability to absorb rapid environmental change. More recommendations advocate resilience than resistance strategies (Fig. 4d). However, intensive management actions to protect historical species in their current distributions are widely advocated (Rank 4). The latter align best with a fixed-reserve approach focusing on local species precedence, an approach that will be increasingly costly and challenging to maintain as directional global changes accelerate.

For some species and systems, options other than intervention might not exist. Resistance approaches designed to maintain the status quo are nevertheless risky – they may leave systems vulnerable to total collapse if interventions are not maintained or compromise other system components (Harris et al., 2006; Walker et al., 2002). For example, the removal of invasive species has sometimes resulted in unpredicted and negative impacts to ecosystem structure and function (Zavaleta et al., 2001). Managing for resilience (sensu Holling, 1973) on the other hand explicitly focuses on increasing the flexibility and ability of systems to adapt and self-organize in response to change. To build resilience to climate change into systems, however, may require radical shifts in perspective for many conservation stakeholders and re-evaluation of conservation goals (Rank 10). Land managers might need to view a broader range of ecosystem states as desirable, such as novel or dynamic local assemblages that maintain functioning and trophic complexity but not necessarily species identity (Hulme, 2005), or to re-evaluate operational definitions and guidelines, such as what constitutes an invasive species or when a species can be added to a risk list (Scott and Lemieux, 2005; Scott et al., 2002).

Examples of broad perspective shift are found in the restoration literature. Millar and Brubaker (2006) emphasize the use of paleo-ecological perspectives to guide restoration goals and interventions. They ask that managers and restoration practitioners "make friends with physical and climatic change," arguing for instance that which species are deemed 'natural' or 'invasive' depends on the spatial and temporal resolution of data used to inform perspective. For example, Monterey pines (*Pinus radiata*) are considered native to a small region of California in which they were found at the time of European colonization. The species has since naturalized widely in California from landscaping plantings and is targeted for removal as an unwanted exotic in these regions. Paleo-ecological records of *P. radiata* reveal strong climate-driven dynamics in range, with widespread distribution during favorable periods and retreat during unfavorable periods. Millar and Brubaker (2006) suggest that naturalized populations be restored rather than removed in locations where *P. radiata* thrived when the climate was similar to the present or predicted future. Pearsall (2005) describes an experimental landscape-scale project in North Carolina, USA designed to test a range of restoration options for combating peat-land loss as a result of rising sea level. Options include oyster bed formation, dune formation, native plant establishment, as well as nonnative plant establishment. The experiment is scheduled to run for 25 years with regular evaluation intervals. Bradley and Wilcove (in press) imagine a "transformative restoration" in which the plant species used to repopulate restoration sites are determined by future climate conditions rather than historical presence. For example, based on results of bioclimatic envelope models, areas in the Great Basin ecoregion of the Western US may be restored best with plants introduced from the Mojave Desert, a more arid, neighboring biome. These projects share a broad, long-term and pragmatic perspective on acceptable restoration outcomes, one that may be necessary to tackle climate change.

A key strategy for building the adaptive capacity of systems is to enhance diversity at various scales. Diverse populations tend to be more adaptable, placing a premium on protecting and managing for high genetic diversity (Rank 13). Capturing the full range of bioclimatic variability within preserves and across landscapes and designing high species, structural, and landscape diversity into constructed and managed systems are also recommended (Rank 9). Pockets of outlier vegetation, areas of high endemism, ecotones, and refugia that protected species during climate shifts in the past are anticipated to be important sources for species re-colonization and radiation in the future, as well as provide retreats for migrating or translocated species (Rank 12). Willis and Birks (2006) discuss methods that combine genetic and paleo-ecological evidence to identify sites with distinctive patterns of genetic diversity that resulted from past geological events and refugial isolation.

Resistance and resilience strategies are not mutually exclusive. Very special communities or organisms that are of high conservation value may warrant highly invasive, intense and costly management regimes to maintain them. Regimes for intensive management are likely to be implemented through existing threatened species management frameworks, such as recovery plans. For more widespread populations, communities and ecosystems, which often provide important ecosystem services, a focus on resilience might be most appropriate. At the site-scale, managers need to address a host of practical issues such as the cost and cost-effectiveness of adaptation options, their compatibility with existing regulatory and institutional constraints, and their likely effectiveness in the absence of coordination with adjoining private lands.

6. Adapting existing conservation plans

The existing literature does provide an array of actions for managers to build on and consider incorporating into existing conservation plans. A practical first step to climate change adaptation planning is to evaluate the likely outcomes for biodiversity of continuing current management and conservation directions. Most conservation policies and management plans do not yet explicitly consider climate change (Chambers et al., 2005; Groves et al., 2002; Hannah et al., 2002; Scott and Lemieux, 2007). A consistent theme in the literature is at the very least to immediately appraise current conservation and management practice in the context of climate change (Rank 2) with the goal of developing and adopting specific climate change adaptation policies in the near future (Rank 11). The literature here contained some suggestions for how to do this. A few articles emphasized the use of models to guide evaluation and adaptation of existing practices. For example, Christensen et al. (2004) used a simulation model to investigate a coupled system of plants and grazers in the Inner Mongolia Steppe under different climate scenarios. They determined that grasslands were likely to undergo a state-transition to shrublands if existing grazer densities are maintained, and they advocate reducing grazers in this area as well as in other semi-arid managed grassland systems. Hulme (2005) provided a general overview of how mathematical models can integrate long-term demographic and climate data to set climate change-appropriate harvest or stocking schedules or to forecast pest outbreaks.

Some authors highlight existing efforts that are well-suited to tackle climate change and warrant increased funding and research. Donald and Evans (2006) argue that agri-environment incentives and easement programs in the US and the EU, which are growing due to shifts in farm policies, warrant increased funding priority because of their potential to improve habitat availability and landscape connectivity across managed ecosystems. They discuss how these policies could be modified to tackle climate change directly. Site-specific climate conditions and biotic responses could be mapped on to landscapes and used to prioritize locations for farm diversification. Similar gains could be made by targeting other private landowner biodiversity enrichment programs, like the USDA Forest Legacy Program (http://www.fs.fed.us/spf/coop/programs/loa/flp.shtml) or the National Wildlife Federation's Urban Backyard Wildlife Program (http://www.nwf.org/gardenforwildlife/).

6.1. *Holistic strategies*

Issues that currently challenge conservation practice may need to be addressed before the added stress of climate change complicates them further. Communities of local users are often in conflict with conservation objectives (Chan et al., 2007; Suffling and Scott, 2002). Identifying opportunities for reduced conflict and increased synergy between conservation and local communities will become more important as climate changes. A number of authors warn that conservation policies must create positive economic outcomes for local peoples to buffer them against potentially dramatic shifts in livelihoods that will accompany climate shifts (Rank 9). Adaptation requires community buy-in and participation (Chapin et al., 2006). To this end, conservation policies that foster learning and participation (Ramakrishnan, 1998) and provide options that are culturally and economically appropriate, such as those that honor traditional management systems and do not rely on expensive technologies, are more likely to be embraced and implemented (Rank 14). McClanahan et al. (2008) argue that climate-informed conservation planning necessitates site-specific understanding of environmental susceptibility and societal capacity to cope and adapt. They illustrate this process for five western Indian Ocean countries with respect to coral reef conservation. Locations with high environmental susceptibility and low adaptive capacity will be most difficult to secure effectively in the future, while those with low environmental susceptibility and high adaptive capacity will be easiest. Locations with low environmental susceptibility and low adaptive capacity are good candidates for biodiversity investment, but to be effective these locations also require investments in human infrastructure, livelihood diversification and social capital.

Climate change is acting in concert with multiple other drivers of biodiversity loss including habitat degradation, soil loss, nitrogen enrichment, and acidification. Strong policies must simultaneously address more than one issue (Watson, 2005) or risk exacerbating environmental problems in the process of trying to combat them. Emission reduction programs are a significant push for many governments, organizations and individuals. They warrant an important place in any climate change combat strategy (Rank 13). A number of authors in this review urge, however, that emissions reduction programs and the Clean Development Mechanisms (CDMs) in the Kyoto Protocol be implemented in ways that simultaneously address carbon sequestration, biodiversity conservation and human livelihoods, rather than carbon sequestration in isolation (Rank 11).

Finally, climate change provides a much-needed impetus to evaluate how conservation policies respond to change in general. Climate change is only one of several global environmental trends to which biodiversity and its conservation must respond. Uncertainty in the climate change arena and about the future in general should not limit action to strengthen existing conservation strategies, with a focus on enhancing the ability of ecosystems to absorb and recover from rapid and unpredictable change.

7. A complete strategy

Climate change challenges conservation practice with the need to respond to both rapid directional change and tremendous uncertainty. Climate change adaptation therefore requires implementation of a range of measures, from short- to long-term and from precautionary and robust to more risky or deterministic, but specifically anticipatory (Fig. 6). To cer-

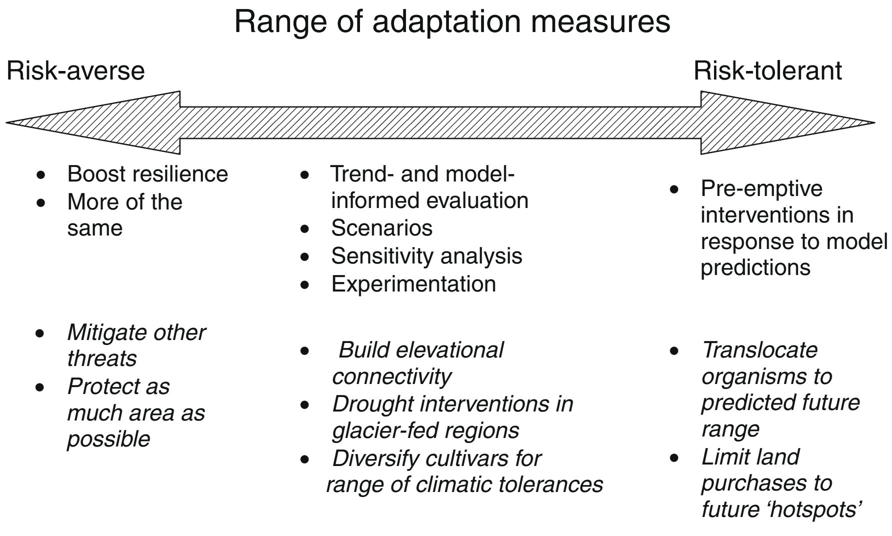

Fig. 6 – Adaptation measures classified along a risk continuum. Under each risk category are examples of general approaches followed by examples of specific adaptation measures. A complete strategy should span a risk continuum.

tain degree, risk tolerance of individual actors will guide strategy selection. Millar et al. (2007) discuss how managers must proactively decide whether to adopt deterministic or indeterministic approaches.

Each type of approach has benefits and drawbacks. Precautionary measures such as restoration, increased monitoring of species distribution, and increased investment in reserve protection do not necessarily require highly certain and precise climate change predictions, but such precautionary steps will help managers respond to current biodiversity threats as well as threats that emerge in the future. Precautionary measures alone, however, will not expand our ability to absorb and respond to rapid directional changes in climate, nor do they capitalize on available predictive information and efforts. In worst-case climate scenarios, over-reliance on bet-hedging measures may spread resources too thin or prove insufficient to help biodiversity weather the rapid changes underway. On the other hand, forecast-interventions bear significant risks if they are too deterministic, not robust to alternative futures or have negative unanticipated consequences (Suffling and Scott, 2002). They could also deliver great rewards and should be weighed with sensitivity analyses and scenarios, tested in pilot programs, and implemented initially at small scales (McLachlan et al., 2007). Scenario building – done in ways that are amenable to local data limitations and useable by policymakers and managers – is particularly apt for exploring the range of magnitudes and direction of possible futures and trends without commitment to specific forecasts (Brown, 2006; Millar et al., 2007).

While the range of recommendations in the literature is great, four consistent, broad themes emerge in this review for conservation stakeholders to apply to climate change planning and adaptation: (1) the need for regional institutional coordination for reserve planning and management and to improve landscape connectivity; (2) the need to broaden spatial and temporal perspective in management activities and practice, and to employ actions that build system resilience; (3) the need to incorporate climate change into all conservation planning and actions, which will require increased research and capacity to forecast future conditions and species responses and to deal effectively with unavoidable uncertainty; and (4) the need to address multiple threats and global change drivers simultaneously and in ways that are responsive to and inclusive of diverse human communities and cultures. Action along each of these fronts will involve difficult tradeoffs, barriers to implementation, and collaboration across diverse actors.

Action will also require an adaptation planning process or series of processes appropriate for various scales and applications. Most of the literature to date fails to distinguish adap-

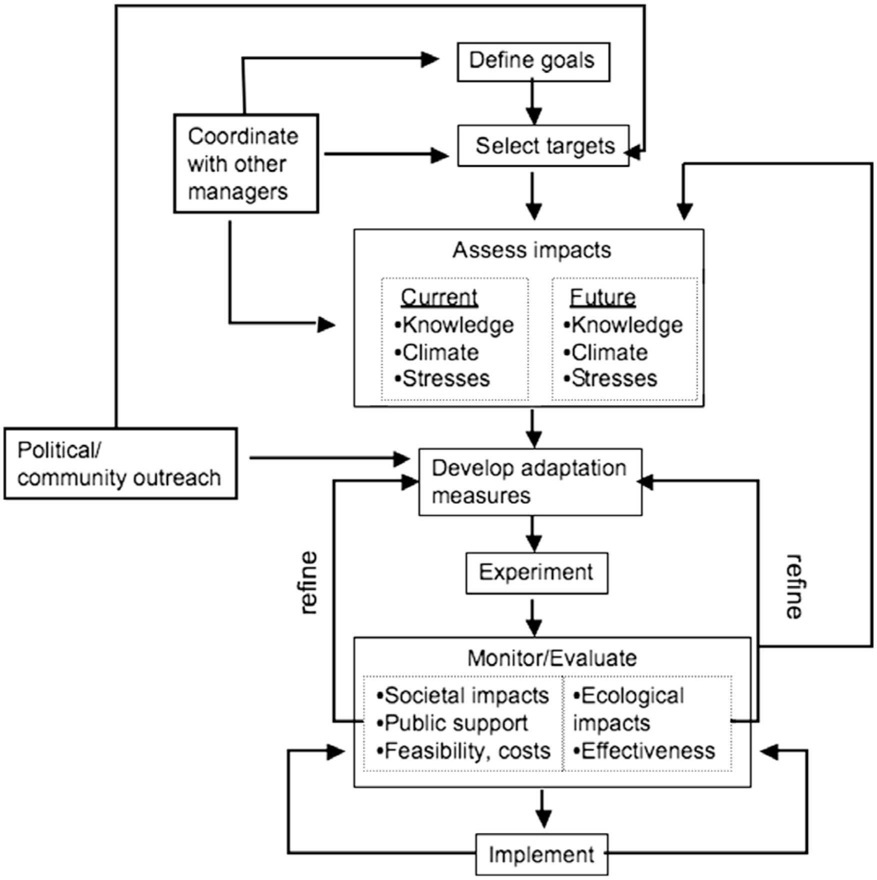

Fig. 7 – Adaptation planning involves at least a few key steps, each complex and requiring collaboration among actors such as land managers, the public, scientists, funders and lawmakers. Recommendations reviewed here address aspects of these steps, but without specifying where they fit in relation to one another.

tation from climate change impact assessment, or adaptation planning from implementation. These are distinct steps in an as-yet largely undefined process that the recommendations we survey could inform. We propose a series of general steps that should be modified, elaborated, and tailored to specific needs (Fig. 7). Key to any adaptation planning process will be to follow the principles of adaptive management (Rank 7), in which later steps inform earlier steps in an iterative and on going process.

8. Conclusions

Widespread calls exist for immediate action to adapt conservation practice to ongoing climate change in order to ensure the persistence of many species and related ecosystem services. However, the majority of recommendations in the published journal literature lack sufficient specificity to direct this action. Over the last 22 years, general recommendations have been reiterated frequently without the elaboration necessary to operationalize them. Greater effort to increase the availability and applicability of climate change adaptation options for conservation—through concrete strategies and case studies illustrating how and where to link research agendas, conservation programs and institutions—is badly needed.

Recommendations to date also largely neglect social science and are overwhelmingly focused on ecological data (Fig. 4c). This bias is alarming given the obvious importance of human behavior and preferences in determining conservation outcomes (Watson, 2005) and the increasingly important role of multi-use public and private lands in conservation practice. A holistic landscape approach to conservation, driven by a vision of humans and other species co-mingling across reserves and developed lands, has gradually gained prominence over the last 20 years. In their seminal paper, Peters and Darling (1985) provided a number of recommendations that continue to be widely advocated (Table 1), but they did not address the roles of conservation and restoration in human-dominated landscapes. These ideas emerge strongly in more recent literature highlighting a need to integrate ecology with other disciplines and approaches that explicitly address the roles of institutions, policy, politics and people in successful conservation strategies.

Finally, few resources or capacity exist to guide an adaptation planning process at any scale (Hannah et al., 2002; Scott and Lemieux, 2007; Welch, 2005). Such a process would place the sea of adaptation ideas and recommendations in framework and provide practitioners with tools, roles and a structure to evaluate what ideas might be useful and feasible for particular situations. Large-scale adaptation efforts that incorporate many of the recommendations found in this review are currently underway, including governmental efforts such as by Parks Canada or DEFRA in England, and by international non-governmental organizations such as The Nature Conservancy and the Wildlife Conservation Society. Well-documented case studies that focus not only on the outcome but also on the development process of adaptation plans are a promising avenue. These efforts can best enhance and encourage more widespread climate change adaptation, particularly at smaller scales, by capturing what they learn and disseminating it widely.

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REFERENCES

Allison, G.W., Lubchenco, J., Carr, M.H., 1998. Marine reserves are necessary but not sufficient for marine conservation. Ecological Applications 8, S79–S92.

Alongi, D.M., 2002. Present state and future of the world's mangrove forests. Environmental Conservation 29, 331–349.

Araujo, M.B., Cabeza, M., Thuiller, W., Hannah, L., Williams, P.H., 2004. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. Global Change Biology 10, 1618–1626.

Bartlein, P.J., Whitlock, C., Shafter, S.L., 1997. Future climate in the Yellowstone National Park region and its potential impact on vegetation. Conservation Biology 11, 782–792.

Beatley, T., 1991. Protecting biodiversity in coastal environments – introduction and overview. Coastal Management 19, 1–19.

Bellwood, D.R., Hughes, T.P., 2001. Regional-scale assembly rules and biodiversity of coral reefs. Science 292, 1532–1534.

Bradley, B.A., Wilcove, D.A., in press. When invasive plants disappear: transformative restoration possibilities in the western United States resulting from climate change. Restoration Ecology.

Brown, I., 2006. Modelling future landscape change on coastal floodplains using a rule-based GIS. Environmental Modelling & Software 21, 1479–1490.

Buckland, S.M., Thompson, K., Hodgson, J.G., Grime, J.P., 2001. Grassland invasions: effects of manipulations of climate and management. Journal of Applied Ecology 38, 301–309.

Burns, C.E., Johnston, K.M., Schmitz, O.J., 2003. Global climate change and mammalian species diversity in US national parks. Proceedings of the National Academy of Sciences of the United States of America 100, 11474–11477.

Burton, P.J., Balisky, A.C., Coward, L.P., Cumming, S.G., Kneeshaw, D.D., 1992. The value of managing for biodiversity. Forestry Chronicle 68, 225–237.

Bush, M.B., 1996. Amazonian conservation in a changing world. Biological Conservation 76, 219–228.

Canadell, J.G., Le Quéré, C., Raupach, M.R., Field, C.B., Buitenhuis, E.T., Ciais, P., Conway, T.J., Gillett, N.P., Houghton, R.A., Marland, G., 2007. Contributions to accelerating atmospheric CO_2 growth from economic activity, carbon intensity, and efficiency of natural sinks. Proceedings of the National Academy of Sciences of the United States of America 104, 18866–18870.

Chambers, L.E., Hughes, L., Weston, M.A., 2005. Climate change and its impact on Australia's avifauna. Emu 105, 1–20.

Chan, K., Pringle, R.M., Ranganathan, J., Boggs, C., Chan, Y.L., Ehrlich, P.R., Haff, P.K., Heller, N.E., Al-Khafaji, K., Macmynowski, D.P., 2007. When agendas collide: human welfare and biological conservation. Conservation Biology 21, 59–68.

Chapin, F.S., Lovecraft, A.L., Zavaleta, E.S., Nelson, J., Robards, M.D., Kofinas, G.P., Trainor, S.F., Peterson, G.D., Huntington, H.P., Naylor, R.L., 2006. Policy strategies to address sustainability of Alaskan boreal forests in response to a directionally changing climate. Proceedings of the National Academy of Sciences of the United States of America 103, 16637–16643.

Chornesky, E.A., Bartuska, A.M., Aplet, G.H., Britton, K.O., Cummings-Carlson, J., Davis, F.W., Eskow, J., Gordon, D.R., Gottschalk, K.W., Haack, R.A., Hansen, A.J., Mack, R.N., Rahel, F.J., Shannon, M.A., Wainger, L.A., Wigley, T.B., 2005. Science priorities for reducing the threat of invasive species to sustainable forestry. Bioscience 55, 335–348.

Christensen, L., Coughenour, M.B., Ellis, J.E., Chen, Z.Z., 2004. Vulnerability of the Asian typical steppe to grazing and climate change. Climatic Change 63, 351–368.

Cohen, S.J., 1996. Integrated regional assessment of global climatic change: lessons from the Mackenzie basin impact study (MBIS). Global and Planetary Change 11, 179–185.

Collingham, Y.C., Huntley, B., 2000. Impacts of habitat fragmentation and patch size upon migration rates. Ecological Applications 10, 131–144.

Crozier, L., Zabel, R.W., 2006. Climate impacts at multiple scales: evidence for differential population responses in juvenile Chinook salmon. Journal of Animal Ecology 75, 1100–1109.

Cumming, G.S., Spiesman, B.J., 2006. Regional problems need integrated solutions: pest management and conservation biology in agroecosystems. Biological Conservation 131, 533–543.

Da Fonseca, G.A.B., Sechrest, W., Oglethorpe, J., 2005. Managing the matrix. In: Lovejoy, T.E., Hannah, L. (Eds.), Climate Change and Biodiversity. Yale University Press, New Haven, pp. 346–358.

Dale, V.H., Rauscher, H.M., 1994. Assessing impacts of climate-change on forests – the state of biological modeling. Climatic Change 28, 65–90.

Davis, M.B., Shaw, R.G., 2001. Range shifts and adaptive responses to quaternary climate change. Science 292, 673–679.

de Dios, V.R., Fischer, C., Colinas, C., 2007. Climate change effects on Mediterranean forests and preventive measures. New Forests 33, 29–40.

Desanker, P.V., Justice, C.O., 2001. Africa and global climate change: critical issues and suggestions for further research and integrated assessment modeling. Climate Research 17, 93–103.

Dixon, R.K., Perry, J.A., Vanderklein, E.L., Hiol, F.H., 1996. Vulnerability of forest resources to global climate change: case study of Cameroon and Ghana. Climate Research 6, 127–133.

Donald, P.F., Evans, A.D., 2006. Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. Journal of Applied Ecology 43, 209–218.

Dyer, J.M., 1994. Implications of habitat fragmentation on climate change-induced forest migration. Professional Geographer 46, 449–459.

Eeley, H.A.C., Lawes, M.J., Piper, S.E., 1999. The influence of climate change on the distribution of indigenous forest in KwaZulu-Natal, South Africa. Journal of Biogeography 26, 595–617.

Erasmus, B.F.N., Van Jaarsveld, A.S., Chown, S.L., Kshatriya, M., Wessels, K.J., 2002. Vulnerability of South African animal taxa to climate change. Global Change Biology 8, 679–693.

Ferrier, S., Guisan, A., 2006. Spatial modelling of biodiversity at the community level. Journal of Applied Ecology 43, 393–404.

Fischer, J., Lindenmayer, D., 2000. An assessment of the published results of animal relocations. Biological Conservation 96, 1–11.

Franklin, J.F., Swanson, F.J., Harmon, M.E., Perry, D.A., Spies, T.A., Dale, V.H., McKee, A., Ferrell, W.K., Means, J.E., Gregory, S.V., Lattin, J.D., Schowalter, T.D., Larsen, D., 1992. Effects of global climatic change on forests in northwestern North America. In: Peters, R.L., Lovejoy, T.E. (Eds.), Global Warming and Biodiversity. Yale University Press, New Haven, pp. 244–254.

Fukami, T., Wardle, D.A., 2005. Long-term ecological dynamics: reciprocal insights from natural and anthropogenic gradients. Proceedings of the Royal Society B – Biological Sciences 272, 2105–2115.

Gaston, K.J., Charman, K., Jackson, S.F., Armsworth, P.R., Bonn, A., Briers, R.A., Callaghan, C.S.Q., Catchpole, R., Hopkins, J., Kunin, W.E., Latham, J., Opdam, P., Stoneman, R., Stroud, D.A., Tratt, R., 2006. The ecological effectiveness of protected areas: the United Kingdom. Biological Conservation 132, 76–87.

Gillson, L., Willis, K.J., 2004. 'As earth's testimonies tell': wilderness conservation in a changing world. Ecology Letters 7, 990–998.

Graham, R.W., 1988. The role of climatic-change in the design of biological reserves – the paleoecological perspective for conservation biology. Conservation Biology 2, 391–394.

Groves, C.R., Jensen, D.B., Valutis, L.L., Redford, K.H., Shaffer, M.L., Scott, J.M., Baumgartner, J.V., Higgins, J.V., Beck, M.W., Anderson, M.G., 2002. Planning for biodiversity conservation: putting conservation science into practice. Bioscience 52, 499–512.

Grumbine, R.E., 1991. Cooperation or conflict – interagency relationships and the future of biodiversity for United-States parks and forests. Environmental Management 15, 27–37.

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8, 993–1009.

Guo, Q.F., 2000. Climate change and biodiversity conservation in Great Plains agroecosystems. Global Environmental Change-Human and Policy Dimensions 10, 289–298.

Halpin, P.N., 1997. Global climate change and natural-area protection: management responses and research directions. Ecological Applications 7, 828–843.

Hannah, L., Midgley, G.F., Millar, D., 2002. Climate change-integrated conservation strategies. Global Ecology and Biogeography 11, 485–495.

Hannah, L., Midgley, G., Hughes, G., Bomhard, B., 2005. The view from the cape. Extinction risk, protected areas, and climate change. Bioscience 55, 231–242.

Hannah, L., Midgley, G., Andelman, S., Araujo, M., Hughes, G., Martinez-Meyer, E., Pearson, R., Williams, P., 2007. Protected area needs in a changing climate. Frontiers in Ecology and the Environment 5, 131–138.

Harris, J.A., Hobbs, R.J., Higgs, E., Aronson, J., 2006. Ecological restoration and global climate change. Restoration Ecology 14, 170–176.

Hartig, E.K., Grozev, O., Rosenzweig, C., 1997. Climate change, agriculture and wetlands in eastern Europe: vulnerability, adaptation and policy. Climatic Change 36, 107–121.

Hilty, J., Lidicker, W., Merenlender, A., Dobson, A.P., 2006. Corridor Ecology: The Science and Practice of Linking Landscapes for Biodiversity Conservation. Island Press, San Diego.

Holling, C.S., 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4, 1–23.

Honnay, O., Verheyen, K., Butaye, J., Jacquemyn, H., Bossuyt, B., Hermy, M., 2002. Possible effects of habitat fragmentation and climate change on the range of forest plant species. Ecology Letters 5, 525–530.

Huang, J.C.K., 1997. Climate change and integrated coastal management: a challenge for small island nations. Ocean & Coastal Management 37, 95–107.

Huang, G.H., Cohen, S.J., Yin, Y.Y., Bass, B., 1998. Land resources adaptation planning under changing climate – a study for the Mackenzie Basin. Resources Conservation and Recycling 24, 95–119.

Huber, J.T., Langor, D.W., 2004. Systematics: its role in supporting sustainable forest management. Forestry Chronicle 80, 451–457.

Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J.B.C., Kleypas, J., Lough, J.M., Marshall, P., Nystrom, M., Palumbi, S.R., Pandolfi, Rosen, B., Roughgarden, J., 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301, 929–933.

Hulme, P.E., 2005. Adapting to climate change: is there scope for ecological management in the face of a global threat? Journal of Applied Ecology 42, 784–794.

IPCC, 2007a. Climate Change 2007 – The Physical Science Basis. Cambridge University Press, Cambridge.

IPCC, 2007b. Climate Change 2007 – Impacts, Adaptation and Vulnerability. Cambridge University Press, Cambridge.

Jump, A.S., Penuelas, J., 2005. Running to stand still: adaptation and the response of plants to rapid climate change. Ecology Letters 8, 1010–1020.

Kappelle, M., Van Vuuren, M.M.I., Baas, P., 1999. Effects of climate change on biodiversity: a review and identification of key research issues. Biodiversity and Conservation 8, 1383–1397.

Kerr, J., Packer, L., 1998. The impact of climate change on mammal diversity in Canada. Environmental Monitoring and Assessment 49, 263–270.

Klooster, D., Masera, O., 2000. Community forest management in Mexico: carbon mitigation and biodiversity conservation through rural development. Global Environmental Change-Human and Policy Dimensions 10, 259–272.

Koziell, I., Swingland, I.R., 2002. Collateral biodiversity benefits associated with 'free-market' approaches to sustainable land use and forestry activities. Philosophical Transactions of the Royal Society of London Series A-Mathematical Physical and Engineering Sciences 360, 1807–1816.

Kriticos, D.J., Sutherst, R.W., Brown, J.R., Adkins, S.W., Maywald, G.F., 2003. Climate change and the potential distribution of an invasive alien plant: *Acacia nilotica* ssp *indica* in Australia. Journal of Applied Ecology 40, 111–124.

Kueppers, L.M., Baer, P., Harte, J., Haya, B., Koteen, L.E., Smith, M.E., 2004. A decision matrix approach to evaluating the impacts of land-use activities undertaken to mitigate climate change – an editorial essay. Climatic Change 63, 247–257.

Kueppers, L.M., Snyder, M.A., Sloan, L.C., Zavaleta, E.S., Fulfrost, B., 2005. Modeled regional climate change and California enaemic oak ranges. Proceedings of the National Academy of Sciences of the United States of America 102, 16281–16286.

Lasch, P., Lindner, M., Erhard, M., Suckow, F., Wenzel, A., 2002. Regional impact assessment on forest structure and functions under climate change – the Brandenburg case study. Forest Ecology and Management 162, 73–86.

LeHouerou, H.N., 1996. Climate change, drought and desertification. Journal of Arid Environments 34, 133–185.

Lemieux, C.J., Scott, D.J., 2005. Climate change, biodiversity conservation and protected area planning in Canada. Canadian Geographer–Geographe Canadien 49, 384–399.

Lindner, M., Bugmann, H., Lasch, P., Flechsig, M., Cramer, W., 1997. Regional impacts of climatic change on forests in the state of Brandenburg, Germany. Agricultural and Forest Meteorology 84, 123–135.

Lovejoy, T.E., 2005. Conservation with a changing climate. In: Lovejoy, T.E., Hannah, L. (Eds.), Climate Change and Biodiversity. Yale University Press, New Haven, pp. 325–328.

Maciver, D.C., Wheaton, E., 2005. Tomorrow's forests: adapting to a changing climate. Climatic Change 70, 273–282.

Malcom, J.R., Liu, C., Neilson, R.P., Hansen, L., Hannah, L., 2006. Global warming and extinctions of endemic species from biodiversity hotspots. Conservation Biology 20, 538–548.

Mayer, A.L., Rietkerk, M., 2004. The dynamic regime concept for ecosystem management and restoration. Bioscience 54, 1013–1020.

McCarty, J.P., 2001. Ecological consequences of recent climate change. Conservation Biology 15, 320–331.

McClanahan, T.R., Cinner, J.E., Maina, J., Graham, N.A.J., Daw, T.M., Stead, S.M., Wamukota, A., Brown, K., Ateweberhan, M., Venus, Polunin, N.V.C., 2008. Conservation action in a changing climate. Conservation Letters 1, 53–59.

McKenzie, D., Gedalof, Z., Peterson, D.L., Mote, P., 2004. Climatic change, wildfire, and conservation. Conservation Biology 18, 890–902.

McLachlan, J., Hellmann, J., Schwartz, M., 2007. A framework for debate of assisted migration in an era of climate change. Conservation Biology 21, 297–302.

McLaughlin, J.F., Hellmann, J.J., Boggs, C.L., Ehrlich, P.R., 2002. Climate change hastens population extinctions. Proceedings of the National Academy of Sciences of the United States of America 99, 6070–6074.

Meehl, G.A., Washington, W.M., Collins, W.D., Arblaster, J.M., Hu, A., Buja, L.E., Strand, W.G., Teng, H., 2005. How much more global warming and sea level rise? Science 307, 1769–1772.

Meir, E., Andelman, S., Possingham, H.P., 2004. Does conservation planning matter in a dynamic and uncertain world? Ecology Letters 7, 615–622.

Millar, C.I., Brubaker, L.B., 2006. Climate change and paleoecology: new contexts for restoration ecology. In: Falk, D.A., Palmer, M.A., Zedler, J.B. (Eds.), Foundations of Restoration Ecology. Island Press, Washington, DC, pp. 315–340.

Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecological Applications 17, 2145–2151.

Morecroft, M.D., Bealey, C.E., Howells, E., Rennie, S., Woiwod, I.P., 2002. Effects of drought on contrasting insect and plant species in the UK in the mid-1990s. Global Ecology and Biogeography 11, 7–22.

Mulholland, P.J., Best, G.R., Coutant, C.C., Hornberger, G.M., Meyer, J.L., Robinson, P.J., Stenberg, J.R., Turner, R.E., VeraHerrera, F., Wetzel, R.G., 1997. Effects of climate change on freshwater ecosystems of the south-eastern United States and the Gulf coast of Mexico. Hydrological Processes 11, 949–970.

Noss, R.F., 2001. Beyond Kyoto: forest management in a time of rapid climate change. Conservation Biology 15, 578–590.

Opdam, P., Wascher, D., 2004. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. Biological Conservation 117, 285–297.

Opdam, P., Steingrover, E., van Rooij, S., 2006. Ecological networks: a spatial concept for multi-actor planning of sustainable landscapes. Landscape and Urban Planning 75, 322–332.

Parmesan, C., 2005. Biotic response: range and abundance changes. In: Lovejoy, T.E., Hannah, L. (Eds.), Climate Change and Biodiversity. Yale University Press, New Haven, pp. 41–55.

Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42.

Pearsall, S.H., 2005. Managing for future change on the Albemarle sound. In: Lovejoy, T.E., Hannah, L. (Eds.), Climate change and Biodiversity. Yale University Press, New Haven, pp. 359–362.

Pearson, R.G., Dawson, T.P., 2005. Long-distance plant dispersal and habitat fragmentation: identifying conservation targets for spatial landscape planning under climate change. Biological Conservation 123, 389–401.

Peters, R.L., Darling, J.D.S., 1985. The greenhouse-effect and nature reserves. Bioscience 35, 707–717.

Peterson, D.L., Schreiner, E.G., Buckingham, N.M., 1997. Gradients, vegetation and climate: spatial and temporal dynamics in the Olympic mountains, USA. Global Ecology and Biogeography Letters 6, 7–17.

Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P.L., Foster, P.N., La Marca, E., Masters, K.L., Merino-Viteri, A., Puschendorf, R., Ron, S.R., Sanchez-Azofeifa, G.A., Still, C.J., Young, B.E., 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. Nature 439, 161–167.

Press, D., Doak, D.F., Steinberg, P., 1995. The role of local government in the conservation of rare species. Conservation Biology 10, 1538–1548.

Pyke, C.R., Fischer, D.T., 2005. Selection of bioclimatically representative biological reserve systems under climate change. Biological Conservation 121, 429–441.

Pyke, C.R., Andelman, S.J., Midgley, G., 2005. Identifying priority areas for bioclimatic representation under climate change: a case study for *Proteaceae* in the Cape Floristic Region, South Africa. Biological Conservation 125, 1–9.

Ramakrishnan, P.S., 1998. Sustainable development, climate change and tropical rain forest landscape. Climatic Change 39, 583–600.

Rice, K.J., Emery, N.C., 2003. Managing microevolution: restoration in the face of global change. Frontiers in Ecology and the Environment 1, 469–478.

Rogers, C.E., McCarty, J.P., 2000. Climate change and ecosystems of the Mid-Atlantic Region. Climate Research 14, 235–244.

Root, T.L., Schneider, S.H., 1995. Ecology and climate: research strategies and implications. Science 269, 334–341.

Root, T.L., Schneider, S.H., 2006. Conservation and climate change: the challenges ahead. Conservation Biology 20, 706–708.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., Pounds, J.A., 2003. Fingerprints of global warming on wild animals and plants. Nature 421, 57–60.

Rounsevell, M.D.A., Berry, P.M., Harrison, P.A., 2006. Future environmental change impacts on rural land use and biodiversity: a synthesis of the ACCELERATES project. Environmental Science & Policy 9, 93–100.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Biodiversity – global biodiversity scenarios for the year 2100. Science 287, 1770–1774.

Schwartz, M.W., Iverson, L.R., Prasad, A.M., 2001. Predicting the potential future distribution of four tree species in ohio using current habitat availability and climatic forcing. Ecosystems 4, 568–581.

Scott, D., Lemieux, C., 2005. Climate change and protected area policy and planning in Canada. Forestry Chronicle 81, 696–703.

Scott, D., Lemieux, C., 2007. Climate change and protected areas policy, planning and management in Canada's boreal forest. Forestry Chronicle 83, 347–357.

Scott, D., Malcom, J., Lemieux, C.J., 2002. Climate change and biome representation in Canada's National Park system: implications for system planning and park mandates. Global Ecology and Biogeography 11, 475–484.

Shafer, C.L., 1999. National park and reserve planning to protect biological diversity: some basic elements. Landscape and Urban Planning 44, 123–153.

Solecki, W.D., Rosenzweig, C., 2004. Biodiversity, Biosphere Reserves, and the Big Apple – A Study of the New York Metropolitan Region. Urban Biosphere and Society, Partnership of Cities. pp. 105–124.

Soto, C.G., 2001. The potential impacts of global climate change on marine protected areas. Reviews in Fish Biology and Fisheries 11, 181–195.

Staple, T., Wall, G., 1996. Climate change and recreation in Nahanni National Park Reserve. Canadian Geographer–Geographe Canadien 40, 109–120.

Stohlgren, T.J., Owen, A.J., Lee, M., 2000. Monitoring shifts in plant diversity in response to climate change: a method for landscapes. Biodiversity and Conservation 9, 65–86.

Streck, C., Scholz, S.M., 2006. The role of forests in global climate change: whence we come and where we go. International Affairs 82, 861–879.

Suffling, R., Scott, D., 2002. Assessment of climate change effects on Canada's national park system. Environmental Monitoring and Assessment 74, 117–139.

Swetnam, T.W., Allen, C.D., Betancourt, J.L., 1999. Applied historical ecology: using the past to manage for the future. Ecological Applications 9, 1189–1206.

Thomas, J.A., Rose, R.J., Clarke, R.T., Thomas, C.D., Webb, N.R., 1999. Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range. Functional Ecology 13, 55–64.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqueira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L., Williams, S.E., 2004. Extinction risk from climate change. Nature 427, 145–148.

Tompkins, E.L., Adger, W.N., 2004. Does adaptive management of natural resources enhance resilience to climate change. Ecology and Society 9 (<http://www.ecologyandsociety.org/vol9/iss2/art10/>).

Underwood, E.C., Fisher, B.L., 2006. The role of ants in conservation monitoring: if, when, and how. Biological Conservation 132, 166–182.

van Rensburg, B.J., Erasmus, B.F.N., van Jaarsveld, A.S., Gaston, K.J., Chown, S.L., 2004. Conservation during times of change: correlations between birds, climate and people in South Africa. South African Journal of Science 100, 266–272.

Walker, B., Carpenter, S., Anderies, J., Abel, N., Cumming, G., Janssen, M., Lebel, L., Norberg, J., Peterson, G.D., Pritchard, R., 2002. Resilience management in social–ecological systems: a working hypothesis for a participatory approach. Conservation Ecology 6 (<http://www.consecol.org/vol6/iss1/art14>).

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. Nature 416, 389–395.

Watson, R.T., 2005. Turning science into policy: challenges and experiences from the science-policy interface. Philosophical Transactions of the Royal Society B – Biological Sciences 360, 471–477.

Welch, D., 2005. What should protected area managers do in the face of climate change. The George Wright Forum 22, 75–93.

Wigley, T.M., 2005. The climate change commitment. Science 307, 1766–1769.

Wilby, R.L., Perry, G.L.W., 2006. Climate change, biodiversity and the urban environment: a critical review based on London, UK. Progress in Physical Geography 30, 73–98.

Williams, J.E., 2000. The biodiversity crisis and adaptation to climate change: a case study from Australia's forests. Environmental Monitoring and Assessment 61, 65–74.

Williams, P., Hannah, L., Andelman, S., Midgley, G., Araujo, M., Hughes, G., Manne, L., Martinez-Meyer, E., Pearson, R., 2005. Planning for climate change: identifying minimum-dispersal corridors for the Cape Proteaceae. Conservation Biology 19, 1063–1074.

Willis, K.J., Birks, H.J.B., 2006. What is natural? The need for a long-term perspective in biodiversity conservation. Science 314, 1261–1265.

Woodwell, G.M., 1991. Forests in a warming world – a time for new policies. Climatic Change 19, 245–251.

Zavaleta, E.S., Hobbs, R., Mooney, H.A., 2001. Viewing invasive species removal in a whole-ecosystem context. Trends in Ecology and Evolution 16, 454–459.

Guidelines for conserving connectivity through ecological networks and corridors

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Craig Groves, Series Editor

Best Practice Protected Area Guidelines Series No. 30

IUCN WCPA's BEST PRACTICE PROTECTED AREA GUIDELINES SERIES

IUCN-WCPA's Best Practice Protected Area Guidelines are the world's authoritative resource for protected area managers. Involving collaboration among specialist practitioners dedicated to supporting better implementation of ideas in the field, the Guidelines distil learning and advice drawn from across IUCN. Applied in the field, they build institutional and individual capacity to manage protected area systems effectively, equitably and sustainably, and to cope with the myriad of challenges faced in practice. The Guidelines also assist national governments, protected area agencies, non-governmental organisations, communities and private sector partners in meeting their commitments and goals, and especially the Convention on Biological Diversity's Programme of Work on Protected Areas.

A full set of guidelines is available at: www.iucn.org/pa_guidelines
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IUCN PROTECTED AREA DEFINITION, MANAGEMENT CATEGORIES AND GOVERNANCE TYPES

IUCN defines a protected area as:
A clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values.

The definition is expanded by six management categories (one with a sub-division), summarized below.
Ia Strict nature reserve: Strictly protected for biodiversity and also possibly geological/ geomorphological features, where human visitation, use and impacts are controlled and limited to ensure protection of the conservation values.
Ib Wilderness area: Usually large unmodified or slightly modified areas, retaining their natural character and influence, without permanent or significant human habitation, protected and managed to preserve their natural condition.
II National park: Large natural or near-natural areas protecting large-scale ecological processes with characteristic species and ecosystems, which also have environmentally and culturally compatible spiritual, scientific, educational, recreational and visitor opportunities.
III Natural monument or feature: Areas set aside to protect a specific natural monument, which can be a landform, sea mount, marine cavern, geological feature such as a cave, or a living feature such as an ancient grove.
IV Habitat/species management area: Areas to protect particular species or habitats, where management reflects this priority. Many will need regular, active interventions to meet the needs of particular species or habitats, but this is not a requirement of the category.
V Protected landscape or seascape: Where the interaction of people and nature over time has produced a distinct character with significant ecological, biological, cultural and scenic value: and where safeguarding the integrity of this interaction is vital to protecting and sustaining the area and its associated nature conservation and other values.
VI Protected areas with sustainable use of natural resources: Areas which conserve ecosystems, together with associated cultural values and traditional natural resource management systems. Generally large, mainly in a natural condition, with a proportion under sustainable natural resource management and where low-level non-industrial natural resource use compatible with nature conservation is seen as one of the main aims.

The category should be based around the primary management objective(s), which should apply to at least three-quarters of the protected area – the 75 per cent rule.

The management categories are applied with a typology of governance types – a description of who holds authority and responsibility for the protected area. IUCN defines four governance types.
Type A. Governance by government: Federal or national ministry/agency in charge; sub-national ministry or agency in charge (e.g. at regional, provincial, municipal level); government-delegated management (e.g. to NGO).
Type B. Shared governance: Trans-boundary governance (formal and informal arrangements between two or more countries); collaborative governance (through various ways in which diverse actors and institutions work together); joint governance (pluralist board or other multi-party governing body).
Type C. Private governance: Conserved areas established and run by individual landowners; non-profit organisations (e.g. NGOs, universities) and for-profit organisations (e.g. corporate landowners).
Type D. Governance by Indigenous peoples and local communities: Indigenous peoples' conserved areas and territories - established and run by Indigenous peoples; community conserved areas – established and run by local communities.

For more information on the IUCN definition, categories and governance types see Dudley (2008). *Guidelines for applyingprotected area management categories*, which can be downloaded at: www.iucn.org/pa_categories

For more on governance types, see Borrini-Feyerabend, et al., (2013). *Governance of Protected Areas: From understanding to action*, which can be downloaded at https://portals.iucn.org/library/node/29138

Guidelines for conserving connectivity through ecological networks and corridors

IUCN

International Union for Conservation of Nature (IUCN)

IUCN is a membership Union uniquely composed of both government and civil society organisations. It provides public, private and non-governmental organisations with the knowledge and tools that enable human progress, economic development and nature conservation to take place together.

Created in 1948, IUCN is now the world's largest and most diverse environmental network, harnessing the knowledge, resources and reach of more than 1,400 Member organisations and some 15,000 experts. It is a leading provider of conservation data, assessments and analysis. Its broad membership enables IUCN to fill the role of incubator and trusted repository of best practices, tools and international standards.

IUCN provides a neutral space in which diverse stakeholders including governments, NGOs, scientists, businesses, local communities, indigenous peoples organisations and others can work together to forge and implement solutions to environmental challenges and achieve sustainable development.

Working with many partners and supporters, IUCN implements a large and diverse portfolio of conservation projects worldwide. Combining the latest science with the traditional knowledge of local communities, these projects work to reverse habitat loss, restore ecosystems and improve people's well-being.

www.iucn.org
https://twitter.com/IUCN/

WCPA
WORLD COMMISSION
ON PROTECTED AREAS

IUCN World Commission on Protected Areas (WCPA)

IUCN's World Commission on Protected Areas (WCPA) is the world's premier network of protected area expertise. It is administered by IUCN Programme on Protected Areas and has more than 2,500 members, spanning 140 countries. WCPA is one of IUCN's six voluntary Commissions and its mission is to promote the establishment and effective management of a worldwide representative network of terrestrial and marine protected areas, as an integral contribution to the IUCN mission. WCPA works by helping governments and others plan protected areas and integrate them into all sectors, providing strategic advice to policy makers and practitioners to help strengthen capacity and investment in protected areas, and convening the diverse constituency of protected area stakeholders to address challenging issues. For more than 60 years, IUCN and WCPA have been at the forefront of global action on protected areas.

www.iucn.org/wcpa

Convention on
Biological Diversity

Convention on Biological Diversity (CBD)

Opened for signature at the Earth Summit in Rio de Janeiro in 1992, and entered into force in December 1993, the Convention on Biological Diversity is an international treaty for the conservation of biodiversity, the sustainable use of the components of biodiversity and the equitable sharing of the benefits derived from the use of genetic resources. With 196 Parties so far, the Convention has near universal participation among countries.

www.cbd.int

WCPA Connectivity Conservation Specialist Group (CCSG)

CCSG was established in 2016 under the IUCN World Commission on Protected Areas (WCPA) to support information sharing, active participation, global awareness, and action to maintain, enhance, and restore ecological connectivity conservation around the world. Its objective is to advance the science, policy, and practice at international, national, and subnational levels to meet the growing demand for solutions that advance the identification, recognition, and implementation of consistent connectivity conservation measures.

www.iucn.org/wcpa-connectivity
www.conservationcorridor.org/ccsg

Yellowstone to Yukon Conservation Initiative (Y2Y)

Y2Y connects and protects habitat in North America spanning the Yellowstone to Yukon ecosystems so people and nature can thrive. It highlights and focuses on local issues that have implications for the region as a whole, and works to set the context for regional conservation work by providing the vision for a healthy Yellowstone to Yukon. Working across an area covering over 3,200 square kilometres, Y2Y engages partners across jurisdictions to knit together an interconnected system of wild lands and waters that harmonizes the needs of people and nature.

www.y2y.net

Center for Large Landscape Conservation (CLLC)

CLLC develops solutions, implements projects and contributes to global efforts that connect and protect crucial habitat across terrestrial, marine and freshwater ecosystems. It provides expertise through four key focus areas: science and research, mentorship and networking, community resilience and policy. By bringing knowledge and experience to bear on connectivity conservation issues worldwide, the Center works with communities, governments and other stakeholders to stop fragmentation and safeguard the legacy of protected and conserved areas by making them part of larger ecological networks for conservation.

www.largelandscapes.org

Guidelines for conserving connectivity through ecological networks and corridors

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Back cover photo: Connectivity is important for all species, but especially so for large-ranging carnivores such as the leopard (*Panthera pardus*). © Alison Woodley

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Foreword

Life on Earth thrives when ecosystems are healthy and ecologically connected. With the vast majority of the world experiencing increasing human impacts, natural ecosystems have been diminished and fragmented into smaller and smaller pieces. The destruction and fragmentation of natural ecosystems are a key cause of the global biodiversity crisis.

The need to both maintain and restore ecological connectivity is critical to the conservation of biological diversity, which provides irreplaceable functions and services, such as the provision of freshwater, food, climate regulation and pollination, just to name a few.

Ensuring that protected and other conserved areas are well-connected across landscapes and seascapes, as part of ecological networks, will both maintain biodiversity and provide an opportunity for species to adapt to climate change as local conditions change. Given the importance of healthy ecosystems to our own health and well-being, we need to urgently address and reverse the current trends of biodiversity loss and fragmentation.

The need for ecological connectivity is essential for the survival of wild species. Internationally, the Convention on the Conservation of Migratory Species of Wild Animals (CMS), a multilateral environment agreement under the United Nations, provides a global platform for States to take necessary collaborative actions to address the conservation and sustainable use of migratory animals and their habitats. At the national level, many countries have passed legislation to foster ecological connectivity, and this number is growing. The thirteenth meeting of the CMS Conference of the Parties (February 2020) affirmed that a commitment to maintaining and restoring ecological connectivity is one of the top priorities for CMS, and invited Parties to make use of these IUCN guidelines.

The World Business Council on Sustainable Development has come out with a call to action stating: “Creating landscapes with healthy, functioning ecosystems is not only key to making progress toward the environmental targets embedded in the Sustainable Development Goals, but also to addressing multiple social and economic targets that depend partly or wholly on the benefits that ecosystems provide to people.”

One of the key roles of the International Union for Conservation of Nature is to develop global guidance toward its vision of “a just world that values and conserves nature.” These guidelines, developed by the Connectivity Conservation Specialist Group of IUCN’s World Commission on Protected Areas, build on this tradition. They bring together the science of connectivity, and a range of case studies from terrestrial, freshwater and marine ecosystems, to provide practical solutions for meeting connectivity challenges. Moreover, they stress the need to connect protected areas and other effective area-based conservation measures into large-scale ecological networks, and are extremely timely, as we embark on a new decade in which better protecting our planet’s biodiversity must be a priority.

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Executive summary

Ecological connectivity is the unimpeded movement of species and the flow of natural processes that sustain life on Earth. This definition has been endorsed by the Convention on Migratory Species (CMS, 2020) and underlines the urgency of protecting connectivity and its various elements, including dispersal, seasonal migration, fluvial processes and the connectivity that is inherently present in large wild areas. Fragmentation caused by human activities continues to disrupt habitats, threatening biodiversity and impeding climate change adaptation. A large body of science and theory has been developing to address this problem in the context of protected areas.

The purpose of these Guidelines for Conserving Connectivity through Ecological Networks and Corridors is to consolidate this wealth of knowledge and best-available practices to support efforts to combat fragmentation. These Guidelines provide tools and examples (1) for applying ecological connectivity between protected areas and other effective area-based conservation measures, and (2) for developing ecological networks for conservation. In doing so, these Guidelines advance best practices for protecting ecological networks that maintain, enhance and restore connectivity across both intact and human-dominated systems. As demand grows for innovative solutions at international, national and subnational levels, these Guidelines recommend formal recognition of ecological corridors to develop conservation networks and thus ensure effective conservation of biological diversity.

Key messages

- Science overwhelmingly shows that interconnected protected areas and other areas for biological diversity conservation are much more effective than disconnected areas in human-dominated systems, especially in the face of climate change.
- Although it is well understood that ecological connectivity is critical to the conservation of biodiversity, approaches to identify, retain and enhance ecological connectivity have been scattered and inconsistent. At the same time, countries on every continent, along with regional and local governments, have advanced various forms of corridor legislation and policy to enhance connectivity.
- It is imperative that the world moves toward a coherent global approach for ecological connectivity conservation, and begins to measure and monitor the effectiveness of efforts to protect connectivity and thereby achieve functional ecological networks. To promote these goals, these Guidelines define ecological corridors as ways to identify, maintain, enhance and restore connectivity; summarise a large body of related science; and recommend means to formalise ecological corridors and networks.

Acronyms

ABNJ	Areas Beyond National Jurisdictions
CBD	Convention on Biological Diversity
CCSG	Connectivity Conservation Specialist Group of WCPA
CMS	Convention on Migratory Species of Wild Animals
COP	Conference of the Parties
EEZ	Exclusive Economic Zone
EU	European Union
IUCN	International Union for Conservation of Nature
OECM	Other Effective Area-based Conservation Measure
SSC	IUCN Species Survival Commission
UN	United Nations
UNEP	United Nations Environment Programme
WCPA	IUCN World Commission on Protected Areas

Migratory species such as the humpback whale (*Megaptera novaeangliae*) demonstrate the need for connectivity conservation. © Adobe Stock

Introduction: The need for connectivity

1

The annual wildebeest (*Connochaetes* spp.) migration between Tanzania and Kenya is one of the world's great wildlife movement spectacles. © Gary Tabor

The 21st century is a time of crisis in the human relationship with the rest of nature. The climate is changing in dangerous ways, and up to one million species are currently at risk of extinction (IPBES, 2019).

Our planet is not in a uniform condition. For example, about 17% of land has been heavily transformed by cities and agriculture; 56% is characterised by less intense modifications such as mixed rural, urban and suburban development where half or less has been transformed; and about 26% is large wild areas that are largely intact (Locke et al., 2019). Different conservation strategies are needed for these three conditions, but all share the need for ecological connectivity within and across them.

'Ecological connectivity' is the unimpeded movement of species and the flow of natural processes that sustain life on Earth (CMS, 2020). This is not an overstatement. Without connectivity, ecosystems cannot function properly, and without well-functioning ecosystems, biodiversity and other fundamentals of life are at risk. The disruption or absence of ecological connectivity occurs because of human-induced 'fragmentation', the breaking up of a habitat, ecosystem or land-use type into smaller and smaller parcels.

The fundamental problem is that much of the world has been degraded and fragmented already by human activity (Venter et al., 2016). Over 75% of terrestrial ecosystems (excluding Antarctica) have been directly modified by anthropogenic activities (Ellis et al., 2010), and 70% of the world's remaining wilderness is now restricted to just five countries (Watson et al., 2018). The human footprint also extends into the oceans, with 87% of marine biomes impacted by overfishing, nutrient run-off and climate change (Jones et al., 2018).

The goal of conservation must be to retain intact ecosystems, as they provide the best chance to conserve biodiversity in a fast-changing world (Scheffers et al., 2016). Protected areas therefore are the foundation of nature conservation, even in fragmented areas of land, sea or freshwater. However, while protected areas and other effective area-based conservation measures (OECMs) are essential, they are no longer considered sufficient in many places (IUCN WCPA, 2019). It is now understood that active measures must also be taken to maintain, enhance or restore ecological connectivity among and between protected areas and OECMs (Tabor, 2019). Science has clearly demonstrated that in order to achieve long-term biodiversity outcomes, retaining ecological connectivity is essential in a time of climate change (Foden & Young, 2016; Gross et al., 2016). This new understanding is driving a fundamental shift in conservation practice in which actions and goals must vary according to land, freshwater and seascape context. With increasing human alteration of Earth, especially by rapid climate change, it is necessary to think and act at the larger spatial scales at which many species and processes actually operate.

Just one third of the world's rivers remain free-flowing. Dams are the primary barrier to freshwater connectivity. Here, a dam is under construction on the emblematic river Bâsca Mare, Romania, found in the heart of the Carpathian ecoregion of Europe. © Leeway Collective / Balkan River Defence, Courtesy Calin Dejeu

Wildlife crossing signage in Kananaskis Country in Alberta, Canada © Aerin Jacob/Yellowstone to Yukon Conservation Initiative

These Guidelines have been drafted to help clarify and standardise a shift in conservation practice from a narrow focus on individual protected areas to considering them as essential parts of large landscape conservation networks. This is done through creating 'ecological networks for conservation' that are specifically designed, implemented and managed to ensure that ecological connectivity is maintained and enhanced where it is present, or restored where it has been lost (see Bennett, 2003; Bennett & Mulongoy, 2006). Unless systems of protected areas and OECMs retain all essential ecosystem processes, they are not sufficient. A key component of this is ecological connectivity across land, freshwater and marine regions and among and between sites.

Chapter 2 of these Guidelines gives a brief, accessible explanation of the scientific basis for ecological connectivity. With ecological modelling playing an increasing role in connectivity conservation, this chapter also gives an overview of some of the most important methods to identify and model connectivity.

Because conservation at broader scales relies on a common understanding of the concepts involved, Chapter 3 sorts out the terminology that is emerging (both within IUCN and in the wider literature) to describe the ongoing shift in practice. The focus is on two key terms: 'ecological networks for conservation' and 'ecological corridors'. A clear grasp of these terms, and their relationship to established concepts, is essential to creating a common language that promotes better cooperation, sharing of experiences and, ultimately, more effective conservation.

With this foundation in place, Chapter 4 focuses on the concept of 'ecological networks for conservation', explaining what they are and why they are more effective in delivering conservation outcomes than a disconnected collection of individual protected areas.

To address the need for common guidelines regarding connected protected areas, Chapter 5 proposes 'ecological corridors' as a formal conservation designation, thereby recognising them as indispensable parts of ecological networks for conservation of biological diversity. This chapter offers detailed guidelines for establishing, planning, managing, monitoring and evaluating ecological corridors.

Chapter 6 reviews the applications and benefits of ecological corridors in terrestrial, freshwater, marine and mixed environments, as well as emerging considerations of connectivity in Earth's airspaces. Because climate change is affecting all of these environments, a short discussion of climate considerations for ecological corridor management is provided.

Chapter 7 discusses how the scientific understanding of connectivity conservation is increasingly being reflected in global conservation law and policy.

After a brief conclusion (Chapter 8, including a Glossary and References), an Annex provides numerous examples from around the world of efforts to create ecological corridors as part of ecological networks for conservation.

Box 1
Definition of key terms

Connectivity

- **Ecological connectivity:** The unimpeded movement of species and the flow of natural processes that sustain life on Earth (CMS, 2020). There are various sub-definitions of ecological connectivity that are useful in the context of these Guidelines:
    - **Ecological connectivity for species (scientific-detailed definition):** The movement of populations, individuals, genes, gametes and propagules between populations, communities and ecosystems, as well as that of non-living material from one location to another.
    - **Functional connectivity for species:** A description of how well genes, gametes, propagules or individuals move through land, freshwater and seascape (Rudnick et al., 2012; Weeks, 2017; see Chapter 2, section on 'Modelling Ecological Corridors').
    - **Structural connectivity for species:** A measure of habitat permeability based on the physical features and arrangements of habitat patches, disturbances and other land, freshwater or seascape elements presumed to be important for organisms to move through their environment. Structural connectivity is used in efforts to restore or estimate functional connectivity where measures of it are lacking (Hilty et al., 2019; see Chapter 2, section on 'Modelling Ecological Corridors').
- **Ecological corridor:** A clearly defined geographical space that is governed and managed over the long term to maintain or restore effective ecological connectivity. The following terms are often used similarly: 'linkages', 'safe passages', 'ecological connectivity areas', 'ecological connectivity zones', and 'permeability areas'.
- **Ecological network (for conservation):** A system of core habitats (protected areas, OECMs and other intact natural areas), connected by ecological corridors, which is established, restored as needed and maintained to conserve biological diversity in systems that have been fragmented. (See Chapter 3, Table 2, for related terms.)
- **OECM (Other Effective Area-Based Conservation Measure):** A geographically defined area, other than a protected area, which is governed and managed in ways that achieve positive and sustained long-term outcomes for the *in situ* conservation of biodiversity with associated ecosystem functions and services and, where applicable, cultural, spiritual, socio-economic and other locally relevant values are also conserved (IUCN WCPA, 2019).
- **Protected area:** A clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values (Dudley, 2008; Stolton et al., 2013).]

More than half of the world's wild tigers (*Panthera tigris*) are found in India, and they depend on defined corridors within highly fragmented landscapes to survive. Here, a young tiger traverses Tadoba National Park, Central India. © Grégoire Dubois

The scientific basis for connectivity

2

Movement ecology is critical for many species. Invertebrates range widely to complete their life cycles. Painted lady butterflies (*Vanessa cardui*) migrate thousands of kilometers each year. © Adobe Stock

Habitat loss and fragmentation are a leading cause of biodiversity loss worldwide, and climate change is exacerbating this problem. Species loss, decreasing population sizes and significant range contractions are caused by human activities that have negative impacts on biodiversity as well as ecosystem functions and services. These changes are happening more rapidly than in previous extinctions (Ceballos et al., 2017).

Historically, establishing individual protected areas, such as national parks, has been the primary focus of *in situ* conservation. The area of land and sea included in protected areas has increased steadily (Figure 1). In addition, protected areas are now supplemented by a range of OECMs – territories currently delivering effective conservation under a range of governance and management regimes even though conservation may not be a primary management objective (IUCN WCPA, 2019). Nevertheless, on a global scale, biodiversity loss continues to accelerate.

The scientific foundations of connectivity conservation

Protected areas do not always adequately conserve biodiversity, either because they are not well placed or else need stronger management (Venter et al., 2017; Jones et al., 2018). Increasingly, many terrestrial protected areas within human-dominated systems are isolated from one another (Wittemyer et al., 2008). Isolation increases the risk of species extinctions within these areas (Newmark, 1987, 1995, 2008; Brashares et al., 2001; Parks & Harcourt, 2002; Prugh et al., 2008). The relationship between isolation and extinction is founded on island biogeography and metapopulation theory (MacArthur & Wilson, 1963, 1967; McCullough, 1996; Hanski, 1999). The theory of island biogeography states that, on an island, the rates of new species arrival and species extinctions depend on the size and shape of the island and its distance from the mainland. This concept has been transferred from islands to mainland ecosystems, where isolated protected areas are like islands in an ocean of human-dominated systems. In reality, human-dominated systems act as a filter, wherein individuals of some species can pass through freely while others cannot. Metapopulation theory states that many spatially distinct subpopulations can be reconnected by movement of individuals, leading to genetic exchange and the possibility of re-establishing formerly extirpated subpopulations. Together, these theories support the conclusion that larger and more well-connected areas are likely to maintain higher biodiversity over time. They support the need for ecological networks in large-scale land, freshwater and seascape conservation.

It is clear that sufficiently large, well-placed and well-managed protected areas and OECMs can provide connectivity among different habitat patches or resources within their boundaries.

Linear infrastructure development continues to rise unabated in large, previously intact landscapes and in high-biodiversity regions of the world. Deforestation and landscape fragmentation, Cameroon © Grégoire Dubois

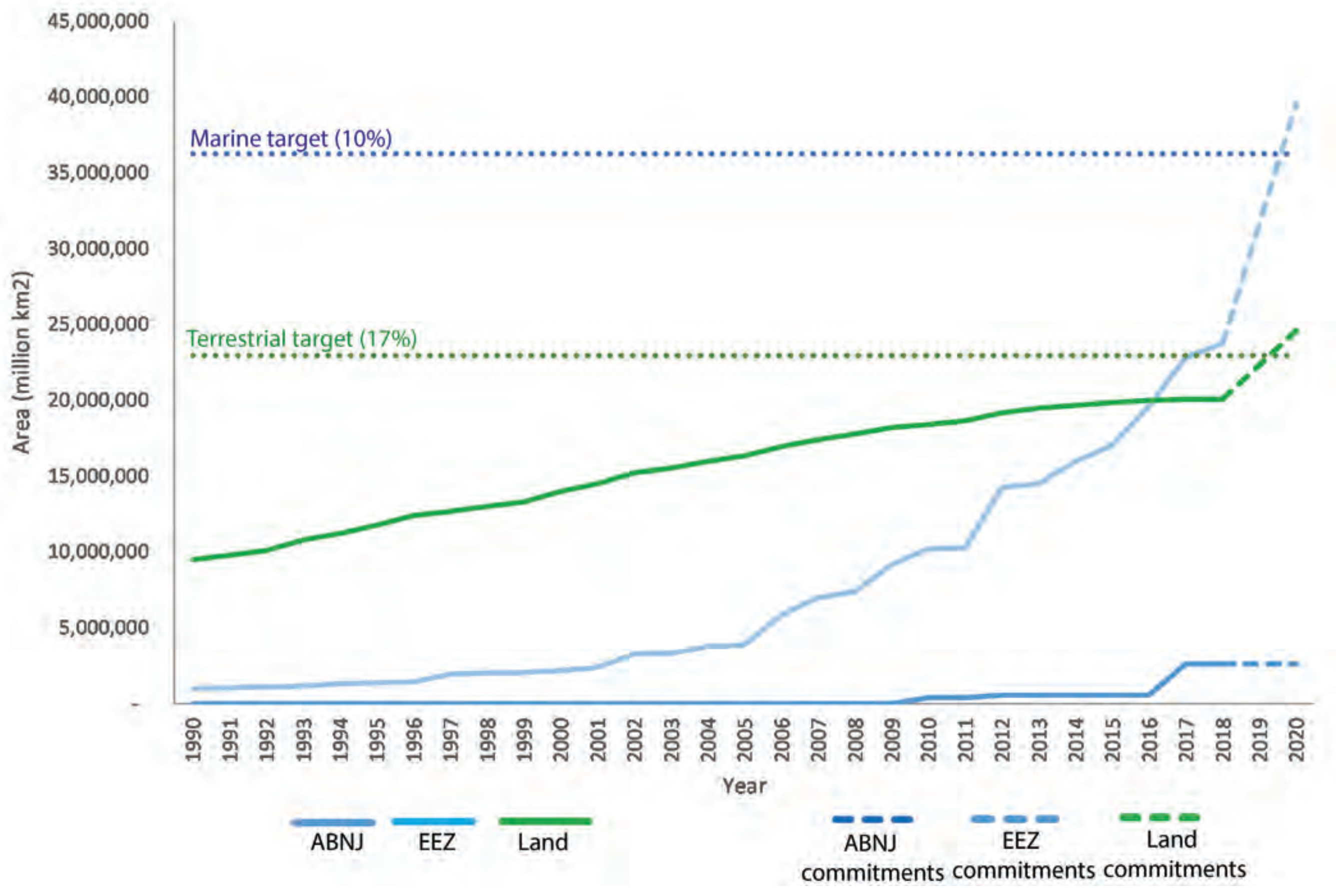


Figure 1. Growth in protected area coverage on land and in the ocean between 1990 and 2018, and projected growth to 2020, according to commitments from countries and territories. ABNJs: Areas Beyond National Jurisdiction (i.e. those more than 200 nautical miles from the coast); EEZs: Exclusive Economic Zones (i.e. marine areas under national jurisdiction that are less than 200 nautical miles from the coast). OECMs are new and therefore not incorporated into the figure. (From UNEP-WCMC, IUCN, and NGS, 2018. Reproduced with permission.)

However, because so much of Earth's terrestrial surface is fragmented, improving or sustaining connectivity among and between protected areas and OECMs is key for the effective conservation and management of biodiversity. Where it is not possible or appropriate to create additional protected areas or OECMs, connecting those already in place can serve to enhance biodiversity conservation. Managing for connectivity in ranching or forestry systems can enhance the conservation estate by increasing the total area within the landscape that is effectively connected, thereby reducing extinction risk (Newmark et al., 2017). In the face of climate change, connectivity becomes even more important, allowing some species to respond with range shifts and others to migrate into protected areas offering newly suitable habitat.

Conservation practitioners and scientists have demonstrated that conservation of species, ecosystems and habitats can only be achieved if protected areas are *functionally* connected (Trombulak & Baldwin, 2010; Resasco, 2019). In intact ecosystems, protected areas are *de facto* connected; in fragmented land, freshwater and seascapes, significant attention must be placed on achieving connectivity. Although connecting protected areas and OECMs has not been proven to strengthen conservation in every situation, connectivity has been demonstrated as an important component of many systems (Hilty et al., 2019).

There is some debate in the literature on negative impacts of corridors (Anderson & Jenkins, 2006; Hilty et al., 2019). Most negative effects appear to be related to increased predator activities, the movement of invasive species and diseases or micro-habitat changes (Weldon, 2006). These negative effects might be significant in individual situations. However, the reported benefits of corridors are far greater than any negative impacts (Hilty et al., 2019). Any potential drawbacks should be considered in corridor design, such as minimising potential edge impacts, exotic and invasive species and potential spread of infectious disease, as well as cost trade-offs of investing in corridors versus core habitat areas (Anderson & Jenkins, 2006; Weldon, 2006; Hilty et al., 2019).

Ensuring that protected areas and OECMs in fragmented systems are functionally connected across terrestrial, freshwater and marine realms and associated airspaces is critically important for many species (Marine Protected Areas Federal Advisory Committee, 2017; Hilty et al., 2019). Examples of organisms that move between these realms include anadromous fish that migrate from the sea to rivers to spawn, amphibians that inhabit multiple ecosystems during different life stages and butterflies (e.g. monarch butterflies, *Danaus plexippus*) that use numerous ecosystem types in their continental-scale, trans-generational migration.

Coral reefs need connectivity at a seascape scale to thrive. *Acropora* sp. shelters a *Linckia* starfish and many fish including *Chromis* sp., Piti Chanel, Guam. © Alisha Gill

Maintaining or restoring ecological connectivity may alsohave temporal aspects; migration can occur on a seasonal, annual or multi-year cycle, as evidenced by monarch butterflies (Runge et al., 2015). Usually, such connectivity movement occurs in all directions, but there are instances of unidirectional movement, such as during long-term climate change when species may shift their ranges poleward or upslope.

It is possible to manage for connectivity from small scales (e.g. streams, coral reefs and seagrass beds) to regional and even continental scales (e.g. chains of islands, mountains, major river systems and deep-sea hydrothermal vent ecosystems). Connectivity conservation is needed at local, regional and global levels and across various degrees of human modification. Many large-scale conservation visions seek to connect protected areas on land, in freshwater and in the ocean (Figure 2) (Worboys et al., 2015). Approaches for implementing these visions have been established in several human-dominated systems (Keeley et al., 2019). Notable examples include Baja to Bering (Mexico, US, Canada), Great Eastern Ranges Initiative (Australia), Amazon Freshwater Connectivity (Pan-Amazon, South America), Yellowstone to Yukon Conservation Initiative (US, Canada), and Vatu-i-Ra Seascape (Fiji).

For more information and examples, see the Annex, 'Approaches to conserving ecological corridors in ecological networks'.

Modelling ecological corridors

The science of measuring, modelling, and mapping the connectivity of land, freshwater and seascapes has grown steadily over the past two decades. This section is a brief overview of key conceptual issues, available tools for modelling connectivity and useful resources to support the definition and delineation of ecological corridors. Many of the conceptual issues (e.g. Crooks & Sanjayan, 2006; Rudnick et al., 2012; Olds et al., 2016; Hilty et al., 2019) are increasingly well understood and practical implementation and management guidance are available (e.g. Beier et al., 2008, 2011; Hermoso et al., 2011; Olds et al., 2016).

There are a number of ways to categorise connectivity. At the highest level, a key distinction relevant to ecological corridors is that connectivity has both *structural* and *functional* components, which are described further below. Although not addressed in depth here, it is worth noting that connectivity

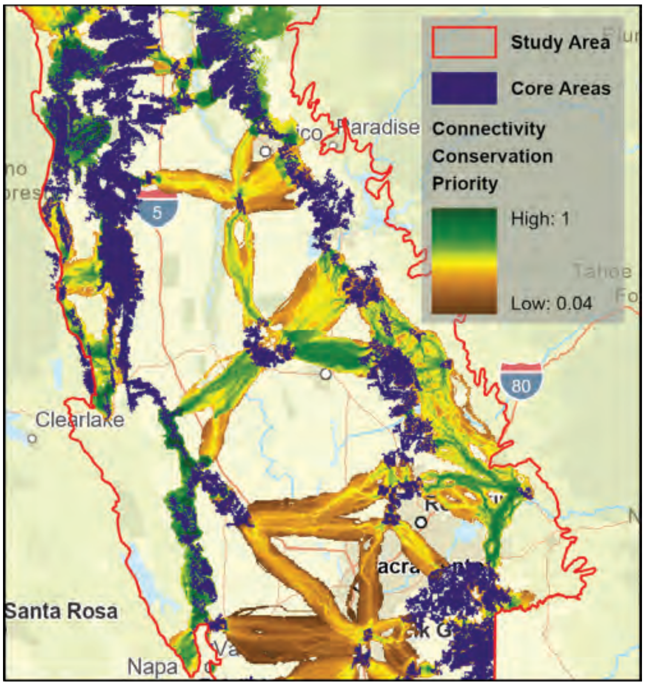
Figure 2. A conceptual representation of an ecological network for conservation. Terrestrial protected areas are in dark green and depicted as surrounded by human activities. Marine protected areas are in dark blue. OECMs are represented in orange. Ecological corridors, both those that are continuous and those that function as stepping stones, are outlined with dashed lines. The ecological network for conservation includes protected areas, OECMs and ecological corridors. © Kendra Hoff / CLLC

Experimental corridors provide a controlled environment to study ecological connectivity. The Savannah River Site Corridor Experiment (South Carolina, USA) is the largest corridor experiment in the world. © Ellen Damschen

Avoiding barriers to species movement is the necessary first step in maintaining connectivity; many barriers can be mitigated by, for instance, installing wildlife-permeable fencing. Whitetail deer (*Odocoileus virginianus*) jumping fence © BG Smith/Shutterstock

can be characterised based on the type of habitat (e.g. marine, freshwater and terrestrial, as described in Chapter 6, 'Applications and Benefits of Ecological Corridors'); the degree of human disturbance (e.g. hedgerows to remnant forest corridors; Theobald, 2013); the scale (local, regional, cross-oceanic, continental); or objectives (daily or seasonal movement, dispersal or habitat, long-term persistence, adaptation to climate change; Crooks & Sanjayan, 2006; Rudnick et al., 2012; Olds et al., 2016; Hilty et al., 2019).

'Functional connectivity' describes how well genes, gametes, propagules or individuals move through land- and seascapes (Rudnick et al., 2012; Weeks, 2017). Identifying areas that provide functional connectivity, either now or in the future, based on the known movements of individuals is an effective way to delineate movement corridors (e.g., Sawyer et al., 2009; Seidler et al., 2015; Hilty et al., 2019 (see Annex, Case Study 15 for details). Because it can be difficult to track a sufficient number of individuals over time, a suite of other approaches to define connectivity has been developed (Rudnick et al., 2012). In some cases, indicator or umbrella species are used to identify connectivity areas for a suite of species (e.g. Weeks, 2017). For long-lived species that are difficult to monitor, indirect approaches that can account for changes over time, such as in genetic make-up, can be effective (Proctor et al., 2012). However, genetic approaches



Modelling software, such as Linkage Mapper, is a tool conservation planners can use for decision-making. A synthesis of four Linkage Mapper outputs (Linkage Priority, Pinchpoint Mapper, Linkage Pathways and Centrality Mapper) provides an initial estimate of connectivity conservation priorities for American badger (*Taxidea taxus*), in the Sacramento Valley, California, USA (Gallo et al., 2019). © John Gallo are generally only a first step to identifying where once-continuous populations are fragmenting. The next step is to delineate potentially important connectivity areas (as per Proctor et al., 2015). Genetic tools can also potentially validate functionality and serve as monitoring tools (Proctor et al., 2018). This approach may be more difficult in marine systems because of data limitations (Balbar & Metaxas, 2019).

'Structural connectivity' is a measure of habitat permeability based on the physical features and arrangements of habitat patches, disturbances, and other land, freshwater or seascape elements presumed to be important for organisms to move through their environment (Hilty et al., 2019). Structural connectivity modelling aims to identify areas through which a variety of species may be able to move. Models often prioritise ecological corridors characterised by a low degree of human modification – areas which are assumed to be permeable to species sensitive to human disturbance (Dickson et al., 2017). In addition, linear areas that provide connectivity, such as river corridors, ocean currents or linear forest fragments, can be identified and prioritised for conservation (e.g. Rouget et al., 2006).

Systematic conservation planning is increasingly incorporating connectivity as a component of planning (e.g., Hodgson et al., 2016; Rayfield et al., 2016; Albert et al., 2017). With a growing number of quantitative approaches, numerous tools are available to map and model connectivity (Table 1). Increasingly, efforts to model connectivity recognise the dynamics of ecological systems, including seasonal or annual dynamics and long-term climate-induced changes (Rouget et al., 2006; McGuire et al., 2016; Simpkins & Perry, 2017).

Table 1. Common approaches to connectivity modelling (Urban & Keitt, 2001; McRae, 2006; Theobald, 2006; Rudnick et al., 2012; http://conservationcorridor.org/corridor-toolbox/).

Model type	Brief explanation
Least-cost	Estimates the surface area of the least-cost movement path from one location (source patch) to another (destination patch) that an individual or process would likely take, assuming knowledge of the destination location, moving across a surface represented by 'costs' (https://corridordesign.org; McRae et al., 2014). Either the single shortest path from one location to another or the full surface area of least-cost distances can be used. Cost-distance surface areas that were created from single, pairwise, factorial or randomly placed locations can be combined.
Circuit theory	Adapted from electrical circuits, circuit theory identifies connectivity by modelling random walkers moving from sources across a surface of resistances to destinations (grounds), allowing multiple pathway options (McRae, 2006; https://circuitscape.org).
Graph theory	Graph theory is the study of graphs that formally represent a network of interconnected objects. Graph theory provides the basis for nearly all connectivity methods, including least-cost and circuit theory. In addition, to prioritise ecological corridors, graph-theoretic metrics can be applied across a 'land- or seascape graph' where patches are nodes and areas of connectivity are edges (Urban and Keitt, 2001; Theobald, 2006; University of Lleida, 2007).
Resistant kernel	Based on least-cost movement from all locations across a land or seascape, implemented using a kernel (moving window) approach (Compton et al., 2007). This approach calculates a relative density of dispersing individuals around source locations.
Reserve design	An approach to guide systematic multi-objective planning to support spatial decision-making about the design of terrestrial, freshwater and marine reserves and management areas (e.g. Moilanen et al., 2008; White et al., 2013).
Individual-based modelling	Simulates movement paths of individuals by following postulated rules. The estimated relative frequency of use is mapped (Horne et al., 2007; Ament et al., 2014; Allen et al., 2016).

Tracking tiger movement along the Nepal–India border in the Himalayan Terai Arc corridor © Gary Tabor

Connectivity conservation also supports human communities by supporting healthy landscapes. A "superbloom" event paints Carrizo Plain National Monument, California, USA. © Emily Pomeroy / Emily Rose Nature Photography

Towards a common language of connectivity conservation

3

Connectivity is important for all domains; terrestrial, freshwater, marine, coastal and aerial. Here, a great egret (*Ardea alba*) patiently hunts in Elkhorn Slough State Marine Reserve, California, USA. © Emily Pomeroy / Emily Rose Nature Photography

A high priority for connectivity conservation policy must be to establish a common set of clearly distinguished terms. A central aim of these Guidelines is to define and explain two such terms, both of which are critical to connectivity conservation: 'ecological network for conservation' and 'ecological corridor'. Providing a clear definition of ecological networks for conservation and guidance on how to identify, establish, measure and report on ecological corridors aids many countries in reaching the goal of identifying, establishing, managing and restoring 'well-connected systems', spelled out in Aichi Target 11 of the Convention on Biological Diversity (CBD), and to achieve other commitments (see Chapter 7 for other examples). It is also critical for the post-2020 global biodiversity framework established to advance progress towards achieving the CBD's 2050 Vision of 'Living in harmony with nature'.

Definition of 'ecological network for conservation'

The idea of an ecological network for conservation is represented by various terms, which are outlined in Table 2. An agreed definition of 'ecological network for conservation' reduces confusion, provides a common standard for global monitoring and database management, and generally improves communication and comparability.

For these purposes, the following definition is used:

> An ecological network for conservation is a system of core habitats (protected areas, OECMs and other intact natural areas), connected by ecological corridors, which is established, restored as needed and maintained to conserve biological diversity in systems that have been fragmented.

Ecological networks are composed of core conservation units – protected areas and OECMs – connected with ecological corridors. The definitions of these areas follow:

- 'Protected areas' are clearly defined geographical spaces, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values (Dudley, 2008; Stolton et al., 2013).
- 'OECMs' ('other effective area-based conservation measures') are geographically defined areas other than protected areas, which are governed and managed in ways that achieve positive and sustained long-term outcomes for the *in situ* conservation of biodiversity with associated ecosystem functions and services, and where applicable, cultural, spiritual, socio-economic and other locally relevant values are also conserved (IUCN WCPA, 2019).

Landscapes are mosaics of interconnected ecological patches which function across spatial scales. The Chignecto Isthmus is the critical landscape gossamer that connects Peninsular Nova Scotia to mainland Canada. © Mike Dembeck

Table 2. Other terms (some of which have been translated into English) that have been applied in practice to describe what these Guidelines call 'ecological networks for conservation'. The presentation of terms in this table is meant to illustrate that the central ideas of 'ecological corridor' and 'ecological network' can be similar and expressed in many ways.

Term	Example
Area of connectivity conservation (ACC)	Used by the Great Eastern Ranges Initiative of Australia, which is an effort to establish connectivity across a large landscape that may encompass a range of land uses, such as agriculture, forestry and human settlements, in addition to protected areas.
Biological corridor	Used by the Mesoamerican Biological Corridor, which was initiated in the 1990s to maintain biological diversity, reduce fragmentation and improve the connectivity of the landscape and ecosystems in Central America and southern Mexico (Ankersen, 1994; Ramírez, 2003).
Conservation lands network	Used in the San Francisco Bay Area of California, USA, as part of a regional prioritisation of connected lands that are important for the protection of biodiversity (Bay Area Open Space Council, 2011).
Conservation management network	Commonly used in Australia in the context of land-based networks for conservation of threatened ecological communities and remnant vegetation. These networks are supported by landowners/land managers and communities (Context Pty Ltd., 2008).
Conservation mosaic of protected areas	Commonly used in South America to refer to a network of protected areas and complementary landscapes/ seascapes, including combinations of formal protected areas (i.e. core conservation areas) and surrounding areas (e.g., production landscapes, privately owned areas, community areas), where the involved entities cooperatively plan and manage the various pieces (Caballero et al., 2015); similar to a biosphere reserve under the UNESCO Man and the Biosphere programme. A Conservation Mosaic of Protected Areas aims to improve ecological connectivity as well as the conservation and sustainable use of environmental goods and services; for an example, see the Brazil Southern Amazon Mosaic (www.wwf.org.br/?29690/Southern-Amazon-Mosaic-facilitates-Protected-Area-management).
Ecological framework	In Russia, commonly used to refer to an 'ecologically continuous system of natural communities', not affected by landscape fragmentation, whose natural communities are ensured legal protection due to their large size and high intensity of matter and energy exchange (Sobolev, 1999; 2003).
Ecological network	Used in nearly all European countries to describe an approach (national and regional) designed to link nature areas more effectively with each other, and with surrounding farmland (Jongman & Bogers, 2008; Miklos et al., 2019).
Flyway sites network	Used, for example, to describe the East Asia–Australasian Flyway; these networks provide various degrees of connectivity and protection for target bird species (Millington, 2018).
Freshwater systems network	Used in South America to refer to freshwater aquatic ecosystems that interact hydrologically, biologically and chemically, and in which a key determinant of these interactions is connectivity, requiring integrated management across ecosystems (e.g. streams, rivers, lakes and wetlands) (Abell et al., 2017; Leibowitz et al., 2018); an example is the Project for Sustainable Management of La Plata River Basin of Argentina, Bolivia, Brazil, Paraguay and Uruguay.
Green infrastructure	Used in the 28 EU Member States and in some regions of the USA. The EU definition: 'Green infrastructure is a strategically planned network of natural and semi-natural areas with other environmental features designed and managed to deliver a wide range of ecosystem services such as water purification, air quality, space for recreation and climate mitigation and adaptation. This network of green (land) and blue (water) spaces can improve environmental conditions and therefore citizens' health and quality of life. It also supports a green economy, creates job opportunities and enhances biodiversity.' The Natura 2000 network constitutes the backbone of the EU green infrastructure.
Marine protected areas (MPAs) network	Used in Australia and the USA to refer to networks of formal MPAs that serve in turn as components of even larger ecological networks for conservation (e.g. the California Marine Protected Areas Network) (Almany et al., 2009; Carr et al., 2017).
Territorial system of ecological stability	In the Czech Republic and Slovakia, used to describe an interconnected complex of both natural and near-natural ecosystems that maintain natural balance (Jongepierová et al., 2012).
Transboundary conservation areas (TBCAs)	Used to define ecologically connected areas that cross international boundaries and contain protected areas. Research on TBCAs has been ongoing for more than 25 years, and the concept has been recognised by both IUCN and the CBD.

- An 'ecological corridor' is a clearly defined geographical space that is governed and managed over the long term to maintain or restore effective ecological connectivity (see detailed explanation below).
- 'Ecological networks for conservation' are more effective in achieving biodiversity conservation objectives than a disconnected collection of individual protected areas and OECMs because they connect populations, maintain ecosystem functioning and are more resilient to climate change. In the context of ecological connectivity, 'connect' refers to the enabling of movement by individuals, genes, gametes and/or propagules.

Definition of 'ecological corridor'

These Guidelines recommend the adoption of a connectivity designation, termed 'ecological corridor', to denote areas within ecological networks that are explicitly devoted to ecological connectivity, and may incidentally also contribute directly to biodiversity conservation. We define the term as follows:

> An ecological corridor is a clearly defined geographical space that is governed and managed over the long term to maintain or restore effective ecological connectivity.

It is worthwhile to elaborate some key phrases and concepts used in this definition to be clear about their intended scope and application in these Guidelines:

- 'Clearly defined geographic space' includes land, inland water, marine and coastal areas or a combination of two or more of these. 'Space' may include the subsurface, the land surface or ocean floor, and the water column and/or airspace including vertical, physical ecosystem structures in three dimensions (adapted from Lausche et al., 2013). 'Clearly defined' means a spatially defined area with agreed and demarcated borders.

Differences between protected areas, OECMs and ecological corridors

Referring back to the definition of 'ecological network for conservation,' note that it is defined as a system composed of two types of core conservation areas, protected areas and OECMs, with ecological corridors being the third element. They are the 'glue' of conservation networks.

Table 3 clarifies the key differences among the elements of an ecological network. Protected areas and OECMs are the fundamental core elements of conservation and of any ecological network. By definition, they *must* conserve *in situ* biodiversity and *may* also conserve ecological connectivity. On the other hand, ecological corridors *must* conserve connectivity. Depending on their condition and management, ecological corridors *may* also conserve *in situ* biodiversity, but this is not a requirement.

Focal species play a key role in determining connectivity conservation priorities, as the jaguar (*Panthera onca*) does across Central and South America.
© Grégoire Dubois

Seabirds play a critical role in marine, inter-island and coastal connectivity. © Dan Laffoley

Table 3. Differences in the role of protected areas, OECMs and ecological corridors. Note that all three terms refer to areas with conservation outcomes. Protected areas and OECMs protect nature as a primary consideration. Ecological corridors play a supporting role for protected areas and OECMs in building ecological networks.

	Protected areas	OECMs	Ecological corridors
MUST conserve *in situ* biodiversity	●	●	
MAY conserve *in situ* biodiversity			●
MUST conserve connectivity			●
MAY conserve connectivity	●	●	

In some cases, ecological corridors can be disjunct patches of habitat, often called ‘stepping stones’, particularly when supporting long-distance migration of wildlife such as marine mammals, sea turtles and birds. For example, for migratory birds, the distance between sites may not need to be minimised unless they are very far apart or the target species has metabolic constraints (Klaasen, 1996). Rather, the sites need to meet a particular species’ natural history requirements (e.g. availability of food, low amounts of disturbance, presence of safe roost sites) at different stages of migration, particularly at staging and stopover sites within the corridors.

Next we turn to an in-depth discussion of ecological networks for conservation.

Tropical forest reserves require connectivity to function as ecological networks for conservation. Sunlight penetrates a shroud of moisture above the cloud forest, Panama. © Marie Read

Corridors can provide the architecture for large-scale conservation in fragmented landscapes. Landholders linking and restoring habitats on rural landscapes with Woomargama National Park, part of the Slopes to Summit alliance, an east–west section of the Great Eastern Ranges ecological corridor in southern New South Wales, Australia. © Ian Pulsford

Ecological networks for conservation

4

Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), Monterey Bay National Marine Sanctuary, California, USA © Emily Pomeroy / Emily Rose Nature Photography

Effective ecological networks for conservation consist of two main elements: 1) areas that protect biodiversity (protected areas and OECMs), and 2) ecological corridors recognised for their contribution to connectivity (refer to Figure 2). Ideally, when designing ecological networks, systematic conservation planning is employed to identify the minimum set of sites needed to protect the most biological diversity in a given region (Margules & Pressey, 2000).

Targets for conservation, which may include focal species, key biodiversity areas, population sizes or habitat areas, are set and the ecological network for conservation is optimised to contain these targets, while also considering their spatial configuration. Socio-economic and political filters may also be considered in systematic conservation planning. Ecological networks are necessary to enhance the integrity, viability and stability of protected areas and OECMs in fragmented systems, making them less vulnerable to all threats, especially in the context of climate change.

In addition to isolation, it is important to consider the size of core habitats (protected areas and OECMs) when meeting the connectivity needs of some species in conservation networks. For large, wide-ranging species, individual protected areas are often not big enough to maintain minimum viable populations. The reality today in many land regions is that creation of new large reserves is not feasible because small habitat fragments are all that remain (Shafer, 1995). Creation of larger reserves is increasingly more common in the ocean. Small protected areas may not be big enough to support populations of even small animals over extended periods (e.g. Henderson et al., 1985; Green et al., 2014). Nevertheless, very small reserves (e.g. those less than 10 ha), even in the most highly fragmented regions, may have critical roles to play in advancing local conservation objectives and community involvement in conservation (Volenec et al., 2020). Moreover, in marine environments, small reserves may in some cases be adequate for specific species and their life-cycle needs. For example, in the sponge reefs off the east coast of Canada, sponge larvae are in the water for just a few days and disperse via currents; they may not go very far, so a marine protected area may readily encompass their dispersal distance. The same is true for invertebrates that are immobile and reproduce by brooding.

Further related to the issue of size, most protected areas and OECMs are not sufficiently large to survive larger-scale ecological disturbances to their biodiversity. For example, natural fires may form part of long-term ecosystem cycles of a protected area, but if it is not large enough the species within will need large tracts of adjacent unburnt habitat to which they can withdraw and recover.

Ideally, protected area and OECM sizes and locations are determined by ecological considerations, but design decisions are often constrained by existing ownership or resource use rights and human activities. To ensure that individuals of species can move between specific core habitats in an ecological network, calculations of appropriate distances between them should be made according to the species' characteristics, such as dispersal range and area required for a minimum viable population. Within these

In many parts of the world, such as East Africa, wildlife populations spend much of their time outside of protected areas, yet utilise protected areas on a seasonal basis. African elephants (*Loxodonta africana*) in Masai Mara, Kenya © Gary Tabor

Free-flowing rivers and their associated riparian corridors link terrestrial and freshwater systems. Aerial view of landscape during flight from Trinidad to Bellavista, Beni Department, Bolivia © World Wildlife Fund (WWF), Photographer Jaime Rojo

parameters, distances ideally should be minimised and the area between core habitats managed so as to maintain ecological connectivity.

Maintaining ecological connectivity, such as through corridors, is important to allow individuals to move among patchy resources and among populations/subpopulations and to facilitate seasonal or periodic migrations. Ecological corridors are also important to facilitate dispersal that ensures genetic diversity and permits recolonisation in areas where populations have gone extinct. These corridors can help increase populations' resilience to large-scale natural disturbances. Ecological corridors also may help extend specific ecosystem services for human use, while serving their main purpose of species movement. Corridors may help maintain ecological processes, such as nutrient cycling, pollination and seed dispersal, across landscapes and seascapes. Finally, even within ecosystems transformed by human activity, ecological corridors provide higher rates of ecosystem recovery in surrounding disturbed areas due to dispersal of seeds and animals from the remaining natural areas (e.g. M'Gonigle et al., 2015; but see also critique from Boitani et al., 2007).

Ecological networks and climate change

Ecological networks for conservation have been recognised as a means to help many species respond to climate change. When well designed, ecological networks, including corridors, can enable species to shift ranges and colonise newly suitable habitats and adapt to climatic conditions. Conservation strategies that make ecological networks more effective to facilitate adaptation to climate change include increasing the number and size of protected areas and OECMs, managing habitats to increase their resilience, establishing or widening connectivity areas, locating reserves in areas of high heterogeneity, and spanning elevational along with other critical gradients (Heller & Zavaleta, 2009; Anderson et al., 2014; Elsen et al., 2018). Of the different climate adaptation strategies, increasing the amount of conserved habitat is one of the most effective (Synes et al., 2015; Table 4). However, conserving a suitable network of habitats should be a priority, rather than increasing the size of a few isolated protected areas and OECMs (Hodgson et al., 2012).

Much of the world faces unprecedented levels of habitat fragmentation. Corridors of high-quality habitat provide the safety net to save biodiversity. Ranchlands near Punta Burica, Panama © Félix Zumbado Morales / ProDUS Universidad de Costa Rica

Table 4. Advantages and disadvantages of strategies to facilitate species range shifts through climate-wise connectivity (adapted from Keeley et al., 2018).

Strategy	Advantages	Disadvantages
Increasing the number of protected and conserved areas throughout the land- and seascape	If properly designed, may increase speed of range shifts in fragmented systems; benefits most species; increases persistence for some species	
Creating few, large protected or conserved areas		Slows speed of range shifts; may result in poor representation of the country/region's full ecosystem diversity
Adding connectivity areas (ecological corridors or additional protected or conserved areas) between existing protected or conserved areas	Increases speed of range shifts in fragmented systems; benefits most species	In rare cases, restoring connectivity could introduce invasive species and harmful alleles (variant forms of a given gene), particularly in freshwater and marine systems
Creating small stepping stones embedded in unsuitable habitat	Increases speed of range shifts in fragmented systems	Only benefits species capable of using stepping stones
Increasing the size of existing protected areas	Increases species persistence; improves temporal connectivity for some species; governance and management structure already exist	May not facilitate connectivity with respect to other resources that wildlife needs; may not provide adequate space for species to move in response to climate change

Ecological networks that collectively encompass temperature gradients can also effectively facilitate species range expansion. This might mean connecting lower- to higher-elevation sites, or inland to coastal areas; sites at different latitudes or ocean depths; or even sites that represent salinity gradients. The Appalachian Mountains in the eastern USA are an example of a mountain range critical for facilitating poleward species movements (Lawler et al., 2013). Likewise, corridor planning in the Albertine Rift region of Africa seeks to ensure elevational and latitudinal connectivity (Ayebare et al., 2013; Plumptre et al., 2016). It should be noted that, in addition to ecological corridors, ecological connectivity can be achieved by expanding existing protected areas and OECMs or adding more of them to a network.

Planning and implementing ecological corridors

5

Arabian oryx (*Oryx leucoryx*), Dubai, UAE © Peter J Hudson

This chapter provides detailed guidelines on how to plan and implement an ecological corridor, starting with fundamental principles that inform a corridor's ecological objectives. The chapter then describes how to document basic information, select objectives, choose a governance model, delineate boundaries and implement management and monitoring plans that reach the corridor's objectives.

Fundamental principles

Every ecological corridor should be founded on a set of objectives that concisely explains why the corridor is being designated and what the expected conservation outcomes are. Keeping a few fundamental principles in mind will be helpful.

1. *Ecological corridors are not a substitute for protected areas or OECMs.* They are meant to complement protected areas and OECMs. The purpose of ecological corridors is to maintain connectivity, especially in regions where additional protected areas and OECMs are not possible, and connectivity is required to retain their elements and processes. As noted earlier, ecological corridors provide specific connectivity value complementary to that of protected areas and OECMs (Table 3). Ecological networks for conservation, as understood in these Guidelines, may contain several corridors identified as part of a specific conservation network. The primary purpose of ecological corridors is to facilitate one or more defined types of ecological connectivity between and among protected areas, OECMS or other core habitats.
2. Ecological corridors should be identified and established in areas where connectivity is required with the aim of building ecological networks for conservation.
3. Each corridor should have specific ecological objectives and be governed and managed to achieve connectivity outcomes.
4. Ecological corridors may consist partly or entirely of natural areas managed primarily for connectivity. Corridors can also cross highly managed areas – such as ranches or commercial forests – provided the area within the corridor is explicitly managed for connectivity. In some cases, a corridor can combine a natural area and an area managed for extraction. *So long as their conservation objectives are supported, ecological corridors may include compatible human activities that practise sustainable resource use.* These might include some forms of human habitation, farming, forestry, grazing, hunting, fishing and ecotourism (see Annex, Case Studies 3 and 12).
5. *Ecological corridors should be differentiated from non-designated areas by the specific uses that are allowed or prohibited within them.* Whereas surrounding lands may look similar, and have similar uses, the uses allowed inside a designated ecological corridor cannot harm its specified connectivity purposes.

In many mountainous regions, valley bottoms contain the greatest biodiversity and provide necessary winter habitat. These are also the areas that people tend to inhabit. Connectivity conservation in these areas relies on coexistence strategies for people and wildlife and coherent multi-jurisdictional approaches to land and freshwater management. Pieniny National Park, Poland & Slovakia © Juraj Švajda

Box 2
Ecological corridor objectives — some examples

1. **Movement of individuals:** To allow for the movement of dispersing tigers (*Panthera tigris*) between India's Dudhwa and Jim Corbett national parks (Seidensticker et al., 2010); to allow wildebeest (*Connochaetes taurinus*) to move between the Serengeti Plains in the United Republic of Tanzania and the Masai Mara Reserve in Kenya in a clockwise manner (Serneels & Lambin, 2001); to aid in the recovery of biota after habitat destruction, e.g. due to mining in deep-sea hydrothermal vent ecosystems (Van Dover, 2014).
2. **Genetic exchange:** To allow for the movement of giant pandas (*Ailuropoda melanoleuca*) in China between population segments that have been separated by a highway and associated development (Zhang et al., 2007); to allow for the diadromous migrations of European eel (*Anguilla anguilla*) through rivers and the North Atlantic Ocean (Kettle & Haines, 2006).
3. **Migration:** To facilitate the annual June passage of wood turtles (*Glyptemys insculpta*) from habitat in Canada's La Maurice National Park to breeding beaches outside of the park (Bowen & Gillingham, 2004); to conserve the pathways of fish, such as the dorado catfish (*Brachyplatystoma rousseauxii*) to breeding sites in the Amazon or green sturgeon (*Acipenser medirostris*) in the Pacific Northwest of the USA (Benson et al., 2007); to conserve one or more of the stopover sites that maintain the migration of spoon-billed sandpipers (*Calidris pygmaea*) and other migratory sandpipers that breed in Russia's Siberia and Kamchatka and migrate along the Pacific coast of Asia, wintering from eastern India to southern China (Menxiu et al., 2012).
4. **Multi-generational movement:** To provide habitat for monarch butterflies migrating over several generations along a central flyway in the states of Minnesota, Iowa, Missouri, Kansas, Oklahoma, and Texas, USA (the 'Monarch Highway', www.monarchhighway.org).
5. **Maintenance/restoration processes:** To restore hydrologic function, such as sediment transport or nutrient cycling, by removing dams from small streams in Wisconsin, USA (Doyle et al,. 2000).
6. **Climate change adaptation:** To facilitate range shifts of species to adjacent mountain ranges through restoring riparian corridors in agricultural landscapes in California, USA (Keeley et al., 2018).
7. **Enhancement of recovery:** To serve as a source of conifer seeds for restoring native trees in logged areas of the mixed forest zone of European Russia (Degteva et al., 2015).
8. **Prevention of undesired flows:** To reduce erosion risk by stopping the increasing velocity of surface water flows downslope in rugged terrain of cultivated steppe landscapes in southern Russia, Ukraine, Moldova, Kazakhstan (Ladonina et al., 2001).

6. To achieve their connectivity objectives, *ecological corridors require their own management plans* (terrestrial, freshwater or marine as the case may be). These may be simple or complex depending on the human activities that are permitted and the tenure issues.

In most instances, ecological corridors will connect protected areas and OECMs, and perhaps other intact natural habitats. However, in some regions, an ecological corridor designation may be needed to funnel migrating species through bottleneck zones that do not necessarily connect to protected areas or OECMs. An ecological corridor could, for example, lead from a protected turtle nesting beach out through a set of islands to the open ocean.

It should be noted that protected areas and OECMs that are already effectively conserving connectivity do not need to be overlaid with an ecological corridor designation.

Objectives

The objectives of an ecological corridor should be clearly stated in its documentation. In addition, it may be useful to show any associated values of the corridor, such as contributions to ecosystem services.

Ecological connectivity objectives: The most critical step in documenting an ecological corridor is defining its objectives for ecological connectivity. Connectivity can be established or maintained for any one or a combination of the following purposes, all of which depend on movements between habitat patches: (1) genetic exchange; (2) movement of individuals to meet life-cycle needs, including migration; (3) provision of habitat for daily to multi-generational movement; (4) maintenance of ecological processes; (5) movement and adaptation responses to global change, including climate change; (6) recovery and recolonisation after disturbance; or (7) prevention of undesirable processes, such as the spread of fire. An ecological corridor should have clear and measurable ecological objectives meeting at least one of the above purposes. Examples of the seven ecological connectivity objectives are provided in Box 2.

Associated ecosystem service values (if applicable): Ecosystem service objectives can often be achieved along with connectivity conservation, and may also be documented. These can include maintaining or enhancing provisioning

Marine connectivity operates across all dimensions of space, within the water column and over the broad reaches of the seas. Scalloped hammerhead (*Sphyrna lewini*) © Adobe Stock

services such as of food and water; regulating services such as regulation of floods, drought, storm surge, land degradation, disease and carbon sequestration; and supporting services such as soil formation and nutrient cycling. While management for specific ecosystem services may be an important objective, so doing should support the ecological corridor's connectivity objectives. Detailed guidance for documenting ecosystem services can be found in the IUCN publication *Tools for Measuring, Modelling, and Valuing Ecosystem Services* (Neugarten et al., 2018).

Associated cultural and spiritual objectives (if applicable): Conservation of important cultural and spiritual values may be associated with an ecological corridor. These values should also be documented in order to maintain support for the corridor.

Contribution to an ecological network for conservation

The contribution of an ecological corridor to the ecological network for conservation in which it is located should be documented. Such documentation can consider multiple metrics (genetic, demographic, community and ecosystem consequences) depending on the conservation objectives of the network. A diversity of empirical and modelling approaches to measure ecological connectivity exist and are the subject of research to refine and expand them. At minimum, documenting the existence of successful movement between protected areas is required. Quantitative estimates of the magnitude of connectivity should be provided. If possible, the contribution of connectivity to population and community metrics (e.g. genetic diversity, population size, species diversity) should be calculated. Evaluating the contribution of ecological corridors and connectivity to network performance should, when possible, include the performance of the network relative to a group of unconnected protected areas (Grorud-Colvert et al., 2011, 2014). Bennett & Mulongoy (2006) provide detailed guidance on how to incorporate many of the considerations of ecological networks.

Social and economic values

While these guidelines are primarily focused on the critical ecological role of ecological corridors, connectivity conservation can have a wide range of social and economic benefits (Hilty et al., 2019, pp. 112–115). Being aware of them can help in corridor design and increase social acceptance, while at the same time maximising their effectiveness. Below are examples of some of the more notable social and economic benefits.

- In some parts of the world, large ecological corridors might be managed for the benefit of mobile peoples, who need connected systems to maintain traditional livelihoods. This is particularly relevant for hunter/

gathering cultures and pastoralist peoples who depend on seasonal movements.

- Ecological corridors can provide a range of co-beneficial recreational values, such as pathways for walking trails (See Annex, Case Studies 10 and 20).
- Corridors established as setbacks, such as forestry or agricultural buffer strips, can protect riparian communities and water quality, and provide flood protection along watercourses.
- Ecological corridors can help define a community's sense of place or distinctiveness, and may help maintain a community's aesthetic preferences or historical grounding.
- Ecological corridors through agricultural areas may serve as a source of pollinators for crops.
- In forest management areas, ecological corridors can provide other benefits, such as acting as wind breaks and sources of seed stock for forest regeneration.

In establishing and managing ecological corridors, it is useful to consider a complete range of social and economic values. If they are to be part of the management plan, the interaction between them and the ecological objectives should be well understood. Any uses of a corridor that support social and economic values should not impair its connectivity (see Annex, Case Studies 16 and 17).

Delineation

An ecological corridor should be clearly delineated. It should have agreed boundaries demarcated by the entity or entities governing and managing it, whether on land, in inland waters, coastal or marine areas, or any combination of these. These boundaries may sometimes be defined by physical features that move over time, such as river banks, ocean currents or sea ice. Given how rapidly the world is changing, provisions for an ecological corridor to move in time and space may be articulated in its management approach. Although the size of an ecological corridor will vary, it should be large enough to achieve its specific ecological connectivity objectives over the long term.

An ecological corridor can be discontinuous (in which case it is often referred to as a 'stepping stone' corridor) provided that the objectives, governance and management are the same across its segments. In order to provide connectivity, stepping stones must be of an appropriate habitat type, align with mechanisms of dispersal (e.g. ocean currents, flyways), and be of a minimum threshold size (see Annex, Case Studies 24 and 25). In cases where there is more than one governance or management entity, management actions should be harmonised and coordinated.

Semi-domesticated reindeer herding is intertwined with the cultural identity and survival of Sami people of northern Scandinavia. Cultural aspects may be appropriate to consider in designing corridor objectives. Sami reindeer herding area, Finland © Juraj Švajda]

In some cases, the delineation of an ecological corridor may need to include a third, vertical dimension if biodiversity is to be effectively conserved. Some protected areas and OECMs already have vertical limits (e.g. they apply only to a certain depth underground or below the water surface). Vertical limits have become particularly controversial in marine protected areas, where vertical zoning for commercial purposes may undermine conservation objectives (e.g. by disrupting ecological connectivity), as it is extremely challenging to monitor or enforce. Examples of vertical-dimension considerations in terrestrial systems include the placement of wind turbines in flyways that intercept and kill migrating avifauna, and, in marine systems, the deployment of fishing gear (e.g. drift nets) at different levels of the water column that intercept and kill migrating pelagic species. Such considerations may also apply to surface freshwater systems, including deep-water lakes with faunal zonation, but also to subterranean freshwater systems, which require management strategies that recognise these systems might be affected by activities at the surface that are relatively remote from them. The height and depth dimensions of an ecological corridor need to allow for effective management to achieve its connectivity objectives.

Gravel bed river systems have riparian corridors that extend well beyond their banks into the subsurface hyporheic zones (see Hauer et al., 2016.) Tusheti, Republic of Georgia © Juraj Švajda

Another aspect of vertical dimensionality is subsurface use rights given that accessing underground resources can harm conservation values. For example, subsurface rights to the seafloor vary greatly based on political jurisdictions and types of human activities (e.g. mining, laying pipelines, or constructing offshore oil extraction facilities). Planners should consider how such modifications affect the movement of species targeted for protection.

Coral atolls may appear as separated islands but are connected across vast distances to form functional marine ecological networks, New Caledonia. © Dan Laffoley

The annual long-distance movement of certain species such as the wood stork (*Mycteria americana*), pictured here in Mato Grosso, Brazil, led to some of the first global and national policies to conserve migratory species. © Grégoire Dubois

The delineation of an ecological corridor should be based on ecological needs for connectivity rather than on land and sea ownership (cadastral) boundaries. However, where cadastral boundaries approximate ecological needs, it may be useful to use these boundaries for management and governance efficiency. For sites crossing political or jurisdictional boundaries for which it is not feasible to have a common governance mechanism, separate ecological corridors may need to be delineated. Otherwise, a governance mechanism comprising more than one entity coordinated under an umbrella decision-making process will be required. Here, harmonisation and coordination can be major challenges. Governance and management must be adapted to individual sites or sets of sites in multiple countries. This can be done through international frameworks, such as the Eastern Asian-Australasian Flyway Partnership, whose Flyway Site Network coordinates the conservation of migratory waterbirds.

Governance

Governance arrangements should be clearly articulated in the documentation. As with protected area and OECM governance, ecological corridor governance has three components: how and by whom decisions are made, and who should be held accountable.

The element of ‘who’ relates to the entities with authority over the ecological corridor. Ecological corridors with complex tenure situations (see next section) may involve many governance authorities (e.g. Indigenous Peoples), along with an agreed mechanism for coordination and oversight (see Annex, Case Studies 6 and 17). The same range of governance types that apply to protected areas and OECMs also apply to ecological corridors (Dudley, 2008; Stolton et al., 2013; Borrini-Feyerabend et al., 2013). These include:

- Governance by government (at various levels);
- Shared governance (sometimes called ‘co-management’), including:
  - Transboundary governance (formal arrangements between one or more sovereign States or Territories (see Annex, Case Study 20);
  - Collaborative governance (through various ways in which individuals and institutions work together (see Annex, Case Study 17);
  - Joint governance (e.g. through a pluralist board or other multiparty governing body);
- Governance by private individuals, organisations or companies (see Annex, Case Study 15); and
- Governance by Indigenous Peoples and/or local communities (see Annex, Case Study 3).

The element of ‘how’ concerns ensuring transparency, accountability, participation and justice in decision-making processes. Governance should strive to be equitable and reflect human rights norms recognised in international and regional instruments and national legislation (see Annex, Case Study 8). Evaluating the ecosystem services associated with proposed ecological corridors helps define the diversity of human benefits associated with them. Any designation of an ecological corridor requires the free, prior

Connectivity conservation provides an avenue to protect biodiversity within the mixed-use landscape matrix. Protected areas are supported by effective conservation outside their boundaries. Homes and agricultural fields in Costa Rica © Félix Zumbado Morales / ProDUS Universidad de Costa Rica

and informed consent of all relevant governance authorities. These principles are applicable to any decision making on allocation, design, establishment, management, redesign, monitoring or evaluation of ecological corridors.

The governance authority may be the same as the landowner or rightsholder of a given portion of an ecological corridor.

There are many mechanisms through which a corridor's ecological objectives might be achieved. An NGO such as a conservancy may do so through a conservation easement, or a written voluntary agreement might be reached in which the landowner/rightsholder agrees to manage a privately owned parcel of land for specific connectivity values (see Annex, Case Studies 13, 14 and 15). Likewise, a group of entities might enter a cooperative agreement, or a local Indigenous or Traditional community may hold legal rights (either by statute or customary law) to certain lands or a defined ocean space within the corridor for sustainable use of a fishery, or conservation and management of an important underwater cultural, historic, sacred or archaeological site.

Effective ecological corridor governance requires building trust, working towards shared values and goals, and developing collaboration across the full range of interests involved (Pullcord et al., 2015).

Tenure

Tenure is a separate consideration from governance (Lausche, 2011) and may take many forms. It involves the conditions and rights under which land, sea, freshwater or air space, or their associated natural resources, are held, occupied or used. While answers to questions of legal and customary tenure (i.e. who holds those rights) are important in determining governance type, they are not the sole determinant. On the contrary, a mix of tenure, whether legally or customarily defined, can be present under all governance types and be represented through a variety of instruments such as formal delegation, leasing, contracts or other agreements (Worboys et al., 2015, p. 181).

For a given ecological corridor, the tenure(s) of the area should be clear and articulated. Tenure rights, particularly for large-scale ecological corridors, may be diverse and complex, requiring a much larger scope of social alliances and cooperation to handle (Worboys et al., 2015). This requires identifying statutory and customary ownership and use rights, and negotiating with all rightsholders on their respective connectivity management roles. The fragmentation of tenure without a collaborative plan for connectivity management can be one of the main drivers of land, freshwater and seascape fragmentation.

Special issues may arise with Indigenous and local community tenure rights if there is lack of legal clarity or if they are in dispute. Sometimes this is because such peoples or communities are not recognised as collective legal entities but only as groups of individuals. This is the case in many places in Africa, Asia and Europe (Worboys et al., 2015, p. 193). In these situations, either a constitutional provision or legislative act may be needed to give collective legal recognition to such entities so they can define and defend access to their rights to use, control and transfer land or resources, as well as take on associated responsibilities.

Special problems also may arise with tenure in marine environments because issues there are often different than on land, where rights may be relatively clear (Day et al., 2012). In Exclusive Economic Zones (EEZs; see caption to Figure 1 for definition) under the UN Convention on the Law of the Sea (UNCLOS), for instance, there generally is no individual ownership of either the seabed or water column; rather, this rests with the nation. In many countries, coastal communities may own or have tenure use rights over certain marine areas or resources. These could include customary rights to traditional fishing grounds, access and management rights over sacred sites of cultural or spiritual value, or rights to sustainably use other renewable marine resources generally or on a project basis (Day et al., 2012).

Documentation of legal or other effective mechanisms

Documentation of the legal or other effective mechanisms that pertain to management of an ecological corridor should describe the governing authority and the legal or customary mechanisms that establish the area's tenure(s). Given the various contexts for the application of ecological corridors around the globe, there will be a diverse array of mechanisms for implementation. These may include:

- Land-use plans and zoning for landscapes;
- Marine spatial plans and zoning for seascapes;
- Covenants and easements;
- Incentives and disincentives;
- Regulatory controls for public health and safety;
- Development controls and building standards; and
- Written voluntary conservation agreements with specific landowners or rightsholders.

In many countries, voluntary conservation agreements are becoming an increasingly popular and effective tool for long-term conservation (see Lausche, 2011 for elaboration of elements and conditions of these agreements). Finally, an emerging area for legal attention is guidance and common rules-of-thumb for design and management of marine ecological corridors (see Lausche et al., 2013).

Longevity of the ecological corridor

Ecological corridors are expected to endure over significant periods of time, so long as the natural attributes and connectivity values for which they are designated remain. Longevity considerations especially pertain to spatially dynamic corridors, such as migration routes of large marine vertebrates (e.g. cetaceans, pinnipeds, sharks, tuna) that track shifting oceanographic patterns. The documentation needs to demonstrate the longevity and succession of the governance arrangements. In the case of written voluntary agreements, a process or mechanism to transfer implementation activities to subsequent owners should be obligatory. However, some governance mechanisms (e.g. hunting, grazing, soil

The future of the Asian elephant (*Elephas maximus*) depends on coherent conservation strategies that work across land-use tenures © Grégoire Dubois

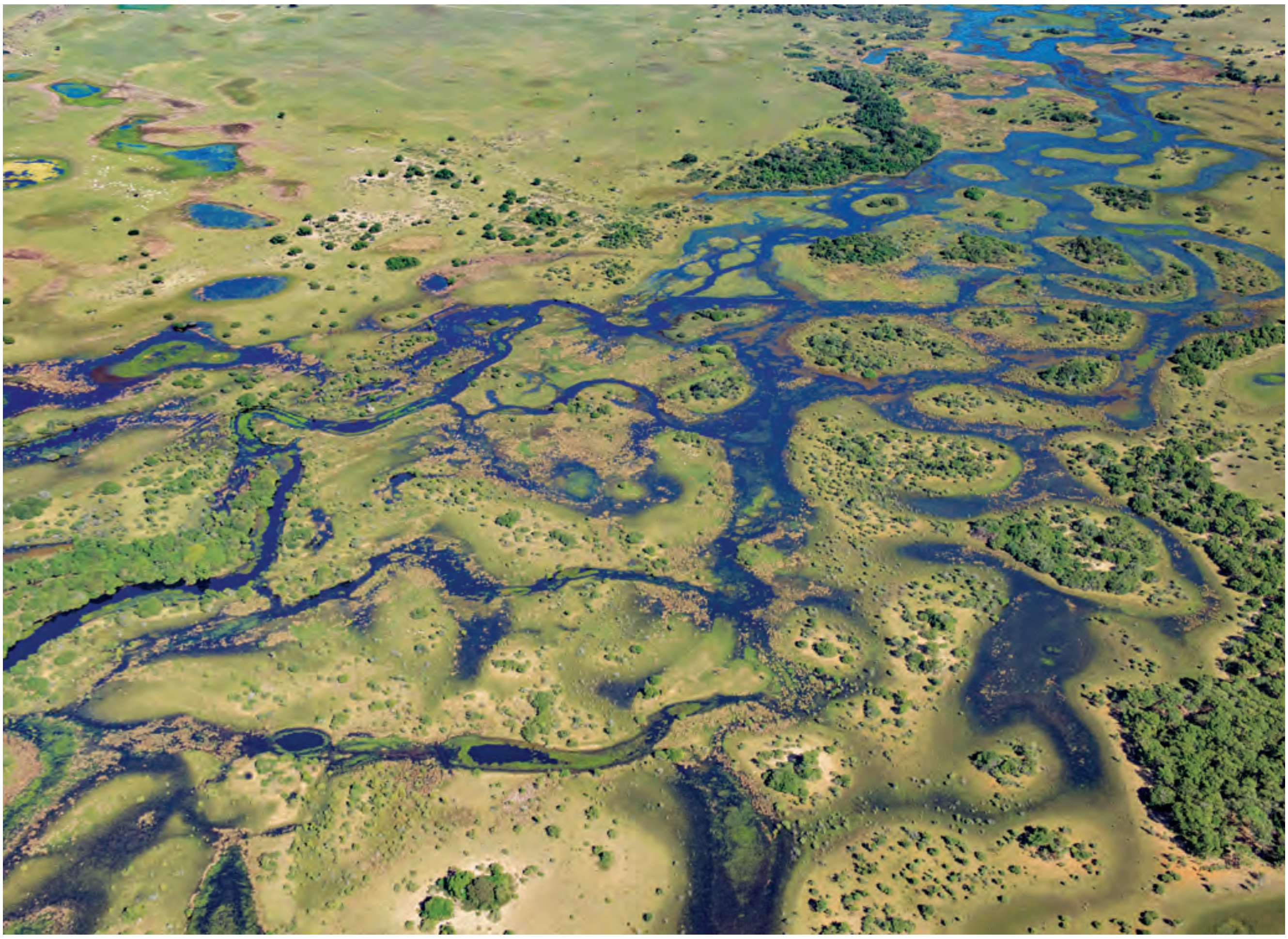
Sea turtle migrations are some of the most wide-ranging in the marine realm, and yet the species are very site specific in their nest habitat fidelity. © Gary Tabor

conservation, fishing regulations, or seasonal use) may be time limited and subject to formal periodic review and renewal. Periodic reviews should include evaluations based on monitoring of ecological, social and economic consequences and performance metrics, when possible.

Management required to achieve objectives

The plan for an ecological corridor should describe management actions required to retain, restore or enhance ecological connectivity. The allowable activities within a corridor should relate directly to its purpose and therefore will be context specific (see Annex, Case Study 23). A multipurpose ecological corridor that is designed to facilitate the movement of all species due to climate change would likely need many more prohibited uses than one that is focused on facilitating the movement of a single species at a specific time of year. The plan should articulate management actions in terms of:

1. **Structural needs.** Are there structural ecological elements that are important to retain or enhance to ensure the corridor meets its objectives? Examples might include maintenance of a percentage of tree cover, restoration of a coral reef, implementation of riparian setbacks or maintenance of in-stream habitat components such as shaded areas, necessary water volume and velocity (see Chapter 2, section on 'Modelling Ecological Corridors' for a discussion of structural and functional connectivity; see also Annex, Case Study 21). Planned management actions should



Ecological communities can be heterogeneous and complex; functional connectivity is a reflection of its ecological context. Capivari River, Pantanal, Mato Grosso do Sul, Brazil © World Wildlife Fund (WWF), Photographer Jaime Rojo

Wildlife crossing structures such as this highway overpass in Croatia, one of 13 in the country, are no substitute for an intact landscape but have value in mitigating the effects of fragmentation for many species. © Djuro Huber

describe practices that achieve sustainable levels of structural ecological elements.

2. **Human activity management.** The management plan should prevent human pressures and threats that would increase fragmentation or undermine restoration efforts undertaken to achieve connectivity (see Annex, Case Study 5). Generally, livelihoods based on compatible activities and incentives that minimise or exclude extractive activities and other modern, industrial-scale activities should be encouraged. Decision makers (e.g. the governance authority) should determine which human activities need to be maintained, and which need to be controlled or prohibited, whether permanently or at specific times, to ensure that the corridor meets its connectivity conservation objectives. These objectives should form the foundation of a corridor's management plan or agreement.

Here are examples of some questions that planners may need to answer. If an ecological corridor includes a river, do human uses include dams, channelisation or other in-stream activities that compromise biodiversity dependent on specific habitats and natural flow regimes? If a corridor includes use by livestock, are there considerations of stocking intensity or fencing? If a corridor allows resource extraction, what management is needed to meet connectivity objectives? Are any human activities occurring that are incompatible with the ecological objectives, such as transportation infrastructure construction or industrial development? Can the design incorporate special wildlife connectivity needs, such as through the creation of wildlife overpasses or tunnels in cases where transportation or other infrastructure may otherwise impede ecological connectivity? Are there any Green Infrastructure plans, projects or methodologies being used or developed?

The management documentation for an ecological corridor should list prohibited or permissible activities and describe any restoration needed to achieve connectivity. For some activities, it may be necessary to specify a level (e.g. 'high', 'medium' or 'low') compatible with the connectivity objectives. One approach could be to create a decision framework for allowable activities (Saarman et al., 2013).

For corridors that traverse areas of poor habitat quality, restoration plans and metrics of success should be encouraged (see Annex, Case Study 11). It will be necessary to determine when an area under restoration is appropriate for inclusion within the corridor.


Corredor Florestal – Pontal do Paranapanema in Brazil demonstrates that large-scale restoration efforts can utilise connectivity conservation strategies.
© IPE / Laury Cullen Jr; reproduced under Creative Commons.


Because some ecological corridors also conserve climate gradients in areas impacted by climate change, monitoring efforts can include specific climate variables in periodic assessments. Pinkwood (*Eucryphia moorei*) in higher-rainfall, moist sites on the Great Escarpment, Monga National Park, Great Eastern Ranges ecological corridor, Australia © Ian Pulsford

Monitoring, evaluation and reporting requirements

The documentation for an ecological corridor should include a monitoring and evaluation plan, along with a strategy for securing resources to implement it. Authorities responsible for an ecological corridor should plan and carry out monitoring to track progress, evaluate effectiveness in achieving stated objectives and adapt management strategies based on results. Monitoring and evaluation should support an adaptive approach to management and take into account climate change impacts. Benefits of a monitoring and evaluation plan include aiding effective resource allocation, promoting accountability and increasing public support (Hockings et al., 2006). The plan should recognise both aspirational and readily feasible components.

'Monitoring' is the collection of information about specific ecological indicators repeatedly over time to discover trends in the ecological status of a corridor and in the effectiveness of management. Monitoring provides data needed to assess the extent to which an ecological corridor is achieving its connectivity objectives (see Annex, Case Studies 6 and 14).

In conjunction with evaluation, monitoring helps assess the adequacy of management and identify necessary adjustments (Hockings et al., 2006). Monitoring and evaluation should be a long-term commitment of an ecological corridor's governance, supported by appropriate resource allocations (see Annex, Case Studies 7 and 10).

Monitoring the effectiveness of an ecological corridor for specific connectivity objectives can take various forms. These range from habitat suitability measures to empirical species movement data to conservation genetics indicators (Bennett, 2003). Where climate mitigation is an anticipated benefit, monitoring variables should include changes in the condition of ecosystems and, when feasible, in the size of carbon stocks and associated stability of storage.

In a growing number of instances, geospatial data technologies such as remote sensing, aerial photographs and satellite imagery may be combined with traditional knowledge and real-time feedback to assist with monitoring. Monitoring approaches may involve time-series collection of information or use of control groups for comparisons. Monitoring methods may be qualitative, quantitative, or both, and must be reliable, cost-effective, feasible and contextually appropriate. A monitoring plan should identify specific, achievable, relevant, time-bound and measurable indicators.

Monitoring data need to be analysed at an appropriate level to meet information needs. Data analysis should be done regularly so that adjustments to management strategies can be made as part of an adaptive management process (Conservation Measures Partnership, 2013).

Because transparency and accountability are essential components of the governance of ecological corridors, monitoring results and their meaning need to be documented and shared with the public. Documentation should include a communication plan indicating how results will be conveyed to key audiences. It is important to note that these audiences are likely to be quite diverse. They may include affected landowners, rightsholders and other stakeholders, such as local communities, project partners, agency staff, policy makers, scientific and technical advisers, and donors (see Annex, Case Study 7).

Basic documentation for reporting

Ecological corridors may be documented and tracked at both national and international levels. Appropriate mechanisms will need to be developed to report this information to global databases for area-based conservation measures, such as the Protected Planet Database managed by the UN Environment Programme World Conservation Monitoring Centre (UNEP-WCMC). In addition to registering ecological corridors and networks, national and global databases will contribute to monitoring and tracking the status of these areas, as well as progress towards conservation commitments.

The basic documentation for reporting on an ecological corridor should include:

- Name of the site;
- Geographic description
- Map of location using a polygon shapefile;
- Year of establishment; and
- Contact information of reporting organisation.

Chilean flamingos (*Phoenicopterus chilensis*) rely on salt lagoons and soda lakes. These habitats are vulnerable to human disturbance. © Marie Read

Across the world, linear transportation infrastructure threatens wildlife via direct mortality and fragmentation of ecological connectivity. Top: A painted turtle (*Chrysemys picta*) makes a perilous crossing in Valentine National Wildlife Refuge, Nebraska, USA © Marcel Huijser; bottom: Greater rhea (*Rhea americana*) crossing the road near Bonito Mato Grosso do Sul Brazil © Marcel Huijser

Applications and benefits of ecological corridors in different environments

6

White-lipped tree frog (*Litoria infrafrenata*), a tropical rainforest inhabitant on Cape York, Australia © Ian Pulsford

Connectivity is relevant across a range of environments from terrestrial and marine to freshwater and airspaces. This chapter elaborates upon ecological corridor applications and benefits in different environments.

In ***terrestrial environments,*** ecological corridors may facilitate daily, migratory or dispersal movements. The last ensures gene flow between populations, such as when a young animal looks for a new home range, or wind disperses seeds. Ecological corridors can also serve multi-generational dispersals, such as climate-related range shifts over time and through space. Ecological corridors may vary greatly in size to facilitate migrations, such as those of caribou (*Rangifer tarandus*), which travel hundreds or thousands of kilometres, to those of a population of Jefferson salamanders (*Ambystoma jeffersonianum*) near Burlington, Ontario, Canada, which move a short distance from upland forests to temporary ponds where they lay their eggs.

A terrestrial ecological corridor may be a continuous space, such as that which connects populations of lions (*Panthera leo*) across communal pastoral lands in the Kavango–Zambezi Transfrontier Conservation Area (Angola, Botswana, Namibia, Zambia, Zimbabwe; see Annex, Case Study 2). Alternatively, an ecological corridor can be a series of discontinuous terrestrial spaces that serve as stopover sites for airborne migratory animals, such as monarch butterflies or red knots (*Calidris canutus*), the latter of which migrates between the Northern and Southern hemispheres. However, such discontinuous corridors function only when aligned with migratory pathways (e.g. flyways) to ensure connectivity.

Ecological corridors in ***freshwater systems*** should conserve water flows and riparian communities, along with the movement of sediments and other natural materials. They should also allow for movement by native animals and plants. Freshwater ecological corridors may also facilitate daily, migratory or dispersal movements. These corridors provide pathways for movement between habitat patches within a particular freshwater system or across freshwater habitats (e.g. between the main stems of rivers and floodplains, or between rivers, lakes and estuaries) for species that require access to multiple habitats to complete their life cycles. Freshwater corridors may conserve lateral connectivity, for example between a river channel and an adjacent floodplain, such as in gravel-bed ecosystems that require exchanges of matter and energy to sustain viable populations of certain species (Hauer et al., 2016). Particularly in rivers, natural flows of sediment and gravel are also critical for creating habitats upon which many species rely. The vegetation of riparian

The great monarch butterfly migration serves as the iconic continental-scale migration of all invertebrate species. Migrating across long distances and several life generations, monarch butterflies remind us of how vital movement ecology is for species survival. © Adobe Stock

Wetland systems are essential components of any freshwater connectivity conservation strategy. Kings Plains Lake on Kings Plains–South Endeavour Trust Reserve – a wetland in the wet/dry tropics on Cape York, Australia © Ian Pulsford

Rivers are the lifeblood of terrestrial ecosystems. Terrestrial and freshwater systems are inextricably linked. Gravel-bed stream in Costa Rica © Félix Zumbado Morales / ProDUS Universidad de Costa Rica areas and floodplains slows down and reduces peaks in the swellings of rivers while retaining sediments, thus decreasing the energy and destructive power of water flows. Freshwater ecological corridors may also help conserve aquifers and protect groundwater-dependent ecosystems such as springs, karst wetlands and certain types of floodplains (Tomlinson & Boulton, 2010). Such corridors often include and require maintenance of riparian vegetation, which influences the quality of freshwater habitat. The corridors may provide habitat and travel routes for terrestrial species, and may act as filters for pollutants and surface flow runoff. Freshwater ecological corridors with riparian vegetation also protect water bodies from undesired inputs of pollutants in highly developed landscapes (Bastian et al. 2015).

Freshwater ecological corridors may be established for water bodies that flow constantly or intermittently. In both cases, riparian zone restoration and prevention of impairments will often be required. As described above, wetlands and other freshwater areas may be part of a discontinuous terrestrial ecological corridor.

Ecological corridors in ***marine environments*** may connect marine protected areas (MPAs) or other key marine, coastal and estuarine habitats (Day et al., 2012). MPAs are unlikely to encompass the full movements of highly mobile marine mammals, fishes or reptiles, or to accommodate the complete larval stages of sessile fishes, invertebrates, plants and algae. Ecological corridors, as essential elements of marine ecological networks for conservation, can conserve known migration routes and bottleneck zones, such as those between islands that are vulnerable to human activities. Conservation of marine connectivity is also important for juvenile fishes and invertebrate larvae that disperse via ocean currents over periods of days or months before settling on reefs or other substrates (Gotlanders et al., 2003; Cowen & Sponaugle, 2009), as well as for larger animals such as turtles and whales that migrate long distances.

Marine ecological corridors may be especially important for species that use different environments at different stages of their life cycles. For example, marine turtles nest on beaches and may use coastal waters before moving into the high seas, while certain fish may need to migrate to reach a spawning aggregation site. Ecological corridors also facilitate the role of MPAs as sources of species replenishment to populations elsewhere. Marine ecological corridors may need to be quite large given the extent to which oceanic currents, eddies and tides affect processes and the recruitment of organisms. Alternatively, marine ecological corridors could be relatively small to protect migrations of a few kilometres, such as those of red crabs (*Gecardoidea natalis*) on Australia's Christmas Island. Siting of three-dimensional ecological corridors may be affected by water depth; geological features, such as sea mounts; stratification of the water column; or seasonal currents or wind flows (Cowen et al., 2007).

Geophysical processes such as daily tides govern the natural processes that connect and sustain marine and coastal systems. Tropical coral reef on Upolu Island, Samoa © Adobe Stock

Over 50 million red crabs (*Gecarcoidea natalis*) traverse Christmas Island, Australia, to lay their eggs in the ocean. © Adobe Stock

Formal recognition of ecological corridors for marine species such as humpback whales (*Megaptera novaeangliae*) could extend recognised conservation areas from waters under national jurisdiction to the high seas, consistent with the CBD Conference of the Parties decision of 2008 (CBD Guidance on Marine and Coastal Protected Areas and Networks COP 2008 IX/20, Annexes I and II).

Mixed ecological corridors encompass two or all three types of environment (terrestrial, freshwater and/or marine). For example, ecological corridors that span marine and estuarine areas into freshwater reaches may facilitate essential life-cycle movement for anadromous and catadromous fish species (which move from the sea to rivers to spawn and vice versa). Such fish range so widely in marine and freshwater environments that an ecological corridor may not link specific protected or conserved areas but rather conserve critical migration pathways (see Annex, Case Studies 17 and 22).

Likewise, mixed ecological corridors may link MPAs to estuaries to facilitate the movement necessary to sustain species populations and evolutionary processes. These corridors also may connect MPAs with terrestrial protected areas to sustain ecological processes such as migration. There is also an opportunity to maximise the benefits for freshwater and terrestrial species by looking for synergies in migration pathways and habitat needs across realms.

Many birds, insects and other animals move through Earth's ***airspaces.*** The possibility of an air-based or air-column ecological corridor is beginning to be considered due to collisions of birds and bats with wind turbines, high-rise buildings and other human structures (Rydell et al., 2010; Loss et al., 2013). Furthermore, overhead power lines have recently been discovered to produce stroboscopic ultraviolet lights that may act as a barrier to the movement of some bird species (Tyler et al. 2014). Currently, airspace ecological corridors are theoretical, and further work is needed to determine if they are feasible in practice.

In all four of these realms of the biosphere, rapid climate change is increasing the need for ecosystem resilience and for species to adapt to changing conditions. Ecological corridors can contribute to both climate resilience and adaptation. Large, connected terrestrial and aquatic ecosystems are more resilient to climate change because ecological processes important for stability are more likely to be functioning there (Walker & Salt, 2006). Connecting protected areas, OECMs and other important biodiversity areas by means of ecological corridors allows species to adapt to climate change by shifting their ranges to new, suitable habitats and climates. In contrast, habitat loss and fragmentation can prohibit these range shifts. Therefore, protecting and establishing ecological corridors can be an

A toco toucan (*Ramphastos toco*) from Mato Grosso, Brazil, flies across habitat patches in search of food. © Grégoire Dubois

effective strategy to facilitate species persistence (reviewed in Keeley et al., 2018; see Annex, Case Study 8).

Ecological corridors can be designed and managed taking climate considerations into account. Approaches include (see also Gross et al., 2016):

- Ensuring that they contain diverse topography that provides different microclimates for species persistence;
- Establishing them to connect protected areas and conserved areas that can serve as climate refugia;
- Prioritising those that connect protected and conserved areas that together encompass temperature gradients;
- Managing them to account for the rapidity of climate change;
- Managing them to account for animal and plant population dynamics at the leading and trailing edges of ranges;
- Designing them for multiple species redistributions to maintain critical species interactions (e.g. those of mutualists);
- Designing them to facilitate redistribution of genetic diversity in a representative manner;
- Designing them so they can change spatially in sync with climate changes (e.g. those affecting winds, ocean currents, deep-sea chemistry and temperatures, or riparian zones);
- Ensuring that they are sufficiently wide to provide live-in habitat for slow-moving species; and
- Where appropriate, restoring or enhancing vegetation with drought-resistant species to provide resources for wildlife throughout the year.

The emergence of connectivity conservation law and policy

7


Indian rhinoceros (*Rhinoceros unicornis*), Kaziranga National Park, Assam, India © Grégoire Dubois

Most global and regional legal instruments dealing with biodiversity conservation, climate change and environmental sustainability have objectives that will not be met without addressing connectivity conservation effectively over the long term. As a result, at the international level there is growing recognition of ecological connectivity in law and policy. Maintaining connectivity as a core conservation objective can be found in the Aichi Biodiversity Targets of the CBD, the Call to Action for Landscape Connectivity of the World Business Council for Sustainable Development, *A Global Standard for Identification of Key Biodiversity Areas* (IUCN, 2016) and *Guidelines for Applying Protected Area Management Categories* (Dudley, 2008).

In 2010, the Parties to the CBD adopted a 10-year Strategic Plan for Biodiversity that included the 20 Aichi Biodiversity Targets (CBD, 2011). Aichi Target 11 states that by 2020 the planet's area under protection will be increased to at least 17% of terrestrial and inland waters, and 10% of marine and coastal areas, in "effectively and equitably managed, ecologically representative and well-connected systems of protected areas" (CBD, 2011). A recent review of 746 MPAs found that only 11% identified connectivity as a management consideration (Balbar & Metaxas, 2019). Most countries lag significantly behind in implementing the connectivity element of Aichi Target 11.

A principal recommendation of these Guidelines is that the designation 'ecological corridor' be recognised in law and policy internationally. Ecological corridors provide an important mechanism for countries to advance legal obligations and policy commitments, which notably include the CBD, Convention on Wetlands of International Importance especially as Waterfowl Habitat (Ramsar Convention), Convention on the Conservation of Migratory Species of Wild Animals (Bonn Convention) and its ancillary instruments, World Heritage Convention, UNCLOS, UN Framework Convention on Climate Change, and UN Educational, Scientific and Cultural Organization's (UNESCO's) Man and the Biosphere Programme. There are also numerous regional conventions, including the Revised African Convention on the Conservation of Nature and Natural Resources (Maputo Convention) and the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention; promoting the European 'Emerald' Network), the UN Convention on Non-Navigational Uses of International Watercourses, and the Convention on the Protection and Use of Transboundary Watercourses.

At the international level there are also non-treaty conservation networks, such as the European Union's (EU's) Natura 2000, which covers terrestrial, freshwater and marine environments and applies to all EU Member States, and also includes other directives such as the Water, Marine Strategy, and Maritime Spatial Planning Frameworks (Lausche et al., 2013; European Parliament & Council, 2014). In addition, the IUCN WCPA's Transboundary Conservation Specialist Group has developed detailed guidance on transboundary conservation that is highly relevant to connectivity (Vasilijević et al., 2015).

Vicuñas (*Vicugna vicugna*) are found across the high slopes of the Andes. Reserva de Producción de Fauna Chimborazo, Ecuador © Gabriel Oppler

An Assam roofed turtle (*Pangshura sylhetensis*) takes advantage of a connected wetland area within and surrounding Kaziranga National Park, Assam, India.
© Grégoire Dubois

At the national level, a variety of policies, laws, administrative authorities, regulations and plans also require or benefit from connectivity conservation to meet their objectives (Lausche et al., 2013). Government policies and plans such as National Sustainable Development Strategies and National Biodiversity Strategies and Action Plans (NBSAPs) guide overall development. Virtually all national legal systems also have specific laws relevant to ecological corridors that deal with nature, wildlife and biodiversity conservation, and sustainable use (e.g. laws covering forestry, fisheries, grazing lands and water flows) and use direct regulation or voluntary conservation agreements, often with incentives.

Connectivity objectives are increasingly prevalent in national and sub-national planning and policy initiatives. Until recently, connectivity legislation was rare at the national or even sub-national level (Lausche et al. 2013). Now, countries such as Bhutan, Costa Rica and Tanzania, and sub-national jurisdictions such as California and New Mexico (USA), have enacted corridor legislation. Additionally, site-specific legislation has been enacted in some countries. For example, the South Korea Act on the Protection of the Baekdu Daegan Mountain System, 2003 (Act no. 7038), which came into effect in 2005, designates an area of 263,427 ha. Of this, 86% is made up of 183 existing protected areas and 14% consists of new buffer and core areas that create a biodiversity corridor along the main mountain range of the Korean Peninsula (Miller & Hyun, 2011; see also Farrier et al., 2013, and KLRI, 2014, for other case studies of legal actions to protect specific connectivity areas).

For the most part, however, current national and sub-national efforts to conserve connectivity utilise and adapt existing policies and laws. Conservation and sustainable resource use laws are the first tier for this purpose. These include protected areas laws, general biodiversity or nature conservation laws, and resource-specific laws such as those relating to sustainable use of forests, fisheries, soils or water. These instruments normally involve direct regulation and arguably should give attention to connectivity conservation to meet their objectives effectively. Supportive laws may extend to hunting controls, integrated resource management and environmental pollution controls. Major substantive areas of law beyond traditional conservation instruments are also important. These include laws and policies on land-use planning; development controls (e.g. through zoning); marine spatial planning; acquisition of rights by government permits and licences for transportation, infrastructure, mining and energy; conservation easements and voluntary agreements; and strategic and project-focused environmental assessments.

Economic instruments are another suite of available tools that may reinforce direct regulation or serve as an alternative approach to support connectivity conservation. These instruments may encourage certain behaviour that could include actions of landowners and rightsholders to further

Private land incentives are critical in supporting connectivity efforts that span private and public land domains. Intensively managed Naturpark Beverin, Switzerland © Juraj Švajda

Zebras from Masai Mara Reserve, Kenya, range widely into surrounding communal lands. The rise of private conservancies in Africa has potential to support connectivity conservation goals. © Gary Tabor

specific ecological corridor objectives. Such instruments include positive incentives (e.g. technical assistance, subsidies, tax credits, or reduced tax liability); negative incentives (e.g. tax increases or withholding of technical assistance); compensation for conservation actions or loss of economic productivity; payments for environmental services or stewardship (e.g. maintenance of forest cover, restoration of riparian areas, or other green infrastructure); and market-driven tools such as tradeable permits and conservation/bio-banking (see Lausche et al., 2013, for an extensive discussion of such tools for both terrestrial and marine environments).

The formal process of amending or enacting new legal instruments takes significant time and should not delay efforts to protect and secure ecological corridors. While legal approaches will vary, most countries' legal systems – national and sub-national (provincial, state, etc.) – already have a number of tools in place to begin the essential process of recognising and protecting ecological corridors, including through such instruments as NBSAPs and national Climate Change Action Plans (see Annex, Case Studies 1 and 2). These tools should be identified and analysed as soon as possible for key connectivity sites before their conservation is no longer economically or politically feasible, even as the longer-term process of amending or enacting new connectivity-specific legislation is pursued.

The development of ecological corridors contributes to the broader approach known as 'Nature-based Solutions', defined by IUCN as "actions to protect, sustainably manage, and restore natural or modified ecosystems, that address societal challenges effectively and adaptively, simultaneously providing human well-being and biodiversity benefits." Guidance on Nature-based Solutions can be found in Cohen-Shacham et al. (2016).

Nomination of ecological corridors and ecological networks for conservation to the Protected Planet Database

Governance authorities may voluntarily report ecological corridors and ecological networks for conservation to the Protected Planet Database managed by UNEP-WCMC and IUCN, which encourage the practice. At the time of publication, the reporting structure is under development with partners. Check with www.protectedplanet.net to verify if this database is online.

Generally, a given country's focal point for the Protected Planet Database would report the ecological corridor or an ecological network for conservation using the reporting portal. There is also an opportunity for individual governance authorities to report directly to the Protected Planet Database. Landowners or rightsholders retain the right to object to the external nomination or recognition of their area as an ecological corridor in cases in which their free, prior and informed consent has not been obtained. This applies to all four governance types, as set out in the 'Governance' section of Chapter 5.

Inscribing an area as an ecological corridor or an ecological network for conservation in the Protected Planet Database places a heightened responsibility on the governance authority to continue to manage the area over the long term in ways that achieve its specific connectivity goals. The authority is responsible for reporting any changes in boundaries, governance or objectives. While national circumstances differ, it is hoped that national or regional legislation will provide greater support and recognition to existing governance systems and not supplant or unnecessarily alter any local arrangements.

Conclusion

8

Red-shouldered hawk (*Buteo lineatus*), Chesapeake & Ohio Canal National Historical Park, Maryland, USA © Nicholas Tait

Ecological corridors in terrestrial, freshwater and marine ecosystems are a critical conservation designation needed to ensure healthy ecosystems. They are a key component of ecological networks for conservation and complement the objectives of protected areas and OECMs by knitting together these core habitats and other intact natural areas. These Guidelines support the growing demand for connectivity conservation, recognised by scientists, policy makers and practitioners. Connectivity conservation requires innovative implementation approaches to conserve lands and water within the conservation matrix – across patterns of resource use, jurisdictions, cultures and geographies. These Guidelines provide direction on how to conserve vital ecological connectivity values in every conservation situation in a consistent and measurable fashion. The toolbox for connectivity conservation includes various types of formal and informal recognition, national legislation, local and regional zoning regulations, conservation easements, conservancy design and transportation planning. Our world needs such a diversity of actions to maintain and restore ecological connectivity, an essential part of halting biodiversity loss and adapting to climate change.

There are many dimensions of ecological connectivity, including gene flow, movement of individuals, metapopulation dynamics, migration, seasonal dispersal and flows of ecological processes. The terms ecological networks and ecological corridors have been defined and operationalised throughout these Guidelines to establish a common set of terms, principles and approaches that can be consistently applied, yet tailored to the specific contexts of ecological connectivity around the world. Connectivity conservation will be enhanced by speaking this common language and working together toward shared successes.

The science underpinning connectivity conservation clearly supports that larger, well-connected areas are more likely to maintain biodiversity and ecological integrity. Given the current biodiversity and climate crises, there is an urgent need to restore and sustain ecological connectivity among and between protected areas, OECMs and other intact natural areas. By connecting these areas with each other, it is possible to arrest and reverse ecosystem fragmentation.

Well-connected ecosystems support a diversity of ecological functions including migration, water and nutrient cycling, pollination, seed dispersal, food security, climate resilience and disease resistance.

The loss of ecological connectivity is most often a consequence of policy and management decisions made by the development, transportation, agriculture and extraction sectors. These Guidelines and Case Studies provide insights into examples and best practices to demonstrate approaches that can ensure ecological connectivity for different ecosystems and species, and at different spatial and temporal scales. An emphasis on human and technical capacity is required for mainstreaming and accelerating uptake of connectivity conservation measures to buffer and better adapt to the impacts of climate change.

Ecological connectivity often transcends national boundaries and can span different ecosystems within a country. The strategies and approaches outlined here take into careful consideration how national and regional transboundary measures can be formed and contribute to aggregated accomplishments internationally. Planning and implementing ecological networks and corridors require specific objectives to be set, and governance and management mechanisms to be aligned with achieving effective conservation outcomes.

Most global, regional and national targets for biodiversity conservation, climate change and environmental sustainability cannot be met unless ecological connectivity conservation is addressed. The importance of connectivity in achieving the objectives of the Convention on Biological Diversity cannot be overstated. As such, it is highly relevant for accomplishing the current and future objectives of many other Multilateral Environmental Agreements. Ecological connectivity – if further recognised in law and policy around the world – can serve as an integrative and cross-cutting mechanism to advance obligations and commitments within and across national borders. Overall, connectivity conservation, by linking together protected areas, OECMs and ecological corridors, offers scalable solutions for environmental, social and economic challenges. The world needs – and it is in our collective interest — to protect, maintain and restore ecological connectivity.

Glossary

Biodiversity: The variability among living organisms from all sources including terrestrial, marine and other aquatic ecosystems, and the ecological complexes of which they are part; this includes diversity within species, between species, and of ecosystems (CBD Article 2, 1992).

Connectivity

- **Ecological connectivity:** The unimpeded movement of species and the flow of natural processes that sustain life on Earth (CMS, 2020).

  There are various sub-definitions of *ecological connectivity* that are useful in the context of these Guidelines:

  - **Ecological connectivity for species (scientific-detailed definition):** The movement of populations, individuals, genes, gametes and propagules between populations, communities and ecosystems, as well as that of non-living material from one location to another.
  - **Functional connectivity for species:** A description of how well genes, gametes, propagules or individuals move through land, freshwater and seascape (Rudnick et al., 2012; Weeks, 2017).
  - **Structural connectivity for species:** A measure of habitat permeability based on the physical features and arrangements of habitat patches, disturbances and other land, freshwater or seascape elements presumed to be important for organisms to move through their environment. Structural connectivity is used in efforts to restore or estimate functional connectivity where measures of it are lacking (Hilty et al., 2019).

Conservation: The protection, care, management and maintenance of ecosystems, habitats, wildlife species and populations, within or outside of their natural environments, in order to safeguard the natural conditions for their long-term permanence.

Dispersal: The condition of individuals or seeds moving from one site to a breeding or growing site.

Ecological corridor: A clearly defined geographical space that is governed and managed over the long term to maintain or restore effective ecological connectivity. The following terms are often used similarly: ‘linkages’, ‘safe passages’, ‘ecological connectivity areas’, ‘ecological connectivity zones’, and ‘permeability areas’.

Ecological indicator: A measurable entity related to a specific ecological information need, such as the status of a population, a change in a threat or progress toward an ecological objective (Hilty & Merenlender, 2000).

Ecological network (for conservation): A system of core habitats (protected areas, OECMs and other intact natural areas), connected by ecological corridors, which is established, restored as needed and maintained to conserve biological diversity in systems that have been fragmented (see Bennett & Mulongoy, 2006).

Ecosystem: A dynamic complex of plant, animal and micro-organism communities and their non-living environment interacting as a functional unit. It is the sum total of all the abiotic and biotic processes going on in an ecosystem that transfer energy and matter within and between ecosystems (e.g. biogeochemical cycles, primary production, etc.) (CBD Article 2, 1992).

- **Ecosystem functioning:** The collective life activities of plants, animals and microbes and the effects these activities – feeding, growing, moving, excreting waste, etc. – have on the physical and chemical conditions of the environment (Naeem et al., 1999).
- **Ecosystem services:** The benefits people obtain from ecosystems. These include provisioning services such as food and water production; regulating services such as flood and disease control; cultural services such as spiritual, recreational and cultural benefits; and supporting services such as nutrient cycling that maintain the conditions for life on Earth (Millennium Ecosystem Assessment, 2005).
- **Ecosystem structure:** The biophysical architecture of an ecosystem; the composition and arrangement of all the living and non-living physical matter at a location (Russi et al., 2013).

Flyway: The entire range of a migratory bird species, distinct populations of a species, or groups of related species through which individuals move on an annual, seasonal or multi-year basis from breeding grounds to non-breeding areas. The term also includes intermediate resting and feeding places, as well as the areas within which the birds migrate (Boere & Stroud, 2006).

Fragmentation: The breaking up of a habitat, ecosystem or land-use type into smaller and, often, more isolated parcels, thereby reducing the number of species that can be supported.

Governance authority: The institution, agency, individual, Indigenous Peoples or community group, or other body acknowledged as having authority and responsibility for decision making over an area, and whose authority may include management of an area (IUCN WCPA, 2019; Borrini-Feyerabend et al., 2013). It is to be recognised that there may be multiple governance authorities, both formal and informal.

Governed: The condition in which an area is under the authority of a specified entity or entities conducting the actions, policy and affairs of the area. Ecological corridors can be governed under the same range of governance types as protected areas.

Habitat: The place or type of site where an organism or population naturally occurs (CBD Article 2, 1992).

Indigenous Peoples: Tribal peoples whose social, cultural and economic conditions distinguish them from other sections of the national community, and whose status is regulated wholly or partially by their own customs or traditions or by special laws or regulations. The term also includes peoples in independent countries who are regarded as indigenous on account of their descent from the populations that inhabited the country, or a geographical region to which the country belongs, at the time of conquest or colonisation or the establishment of present state boundaries and who, irrespective of their legal status, retain some or all of their own social, economic, cultural and political institutions (Borrini-Feyerabend et al., 2004; following IUCN's use of the International Labour Organization's ILO Convention 169 on Indigenous and Tribal Peoples). Preferred terminology varies around the world, and terms such as 'Aboriginal' or 'Traditional Peoples' are sometimes used instead.

Landscape: A heterogeneous space comprising a cluster of interacting ecosystems, geological features and ecological processes, and often including human influences (Forman & Godron, 1986; Wu, 2008). Landscapes are generally large, but can be defined at a range of spatial scales. Interaction of landscape spatial elements can result in emergent effects not inherent to each element separately (e.g. viability of populations, microclimates, runoff regulation, aesthetic quality, etc.).

Local community: A human group sharing a territory and involved in different but related aspects of livelihoods such as managing natural resources, producing knowledge and culture, and developing productive technologies and practices. Since this definition can apply to a range of community sizes, it can be further specified that the members of a 'local community' are those who are likely to have face-to-face encounters and/or direct mutual influences in their daily lives. In this sense, a rural village, a clan or the inhabitants of an urban neighbourhood can be considered a 'local community', but not all the inhabitants of a district, a city quarter or even a rural town. A 'local community' could be permanently settled or mobile (Borrini-Feyerabend et al., 2004).

Managed: In the context of an ecological corridor, the condition of taking active steps to conserve or restore the natural (and possibly other) values to ensure functionality. Note that 'managed' can include decisions not to intervene in an area.

Migration: The regular annual or seasonal movement of individual animals or populations of animals between distinct habitats, each of which is occupied during different parts of the year (Lindenmayer & Burgman, 2005).

Migratory species: The entire population or any geographically separate part of the population of any species or lower taxon of wild animals, a significant proportion of whose members cyclically and predictably cross one or more national jurisdiction boundaries (CMS Article 1, 1979).

Monitoring: The collecting of information on indicators and/or targets repeatedly over time to evaluate trends in the status of conservation targets, often related to effectiveness of management and/or governance activities (e.g., Hilty & Merenlender, 2000).

OECM (Other Effective Area-Based Conservation Measure): A geographically defined area other than a protected area, which is governed and managed in ways that achieve positive and sustained long-term outcomes for the *in situ* conservation of biodiversity with associated ecosystem functions and services and, where applicable, cultural, spiritual, socio-economic and other locally relevant values are also conserved (IUCN WCPA, 2019).

Populations: All the organisms of the same species that live in a specific geographic area at the same time and have the capability of interbreeding.

Protected area: A clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values (Dudley, 2008; Stolton et al., 2013).

Resilience: In the context of ecological networks for conservation, the capacity of a part or the whole of an ecological network to withstand changes to the processes that control its structures and functions (Holling & Gunderson 2002).

Restoration: In the context of ecological corridors, the recovery of ecological connectivity that has been diminished, impaired or destroyed (modified from Society for Ecological Restoration International Science & Policy Working Group, 2004). Restoration is guided by scientific inputs that help prioritise actions.

Rightsholders, stakeholders: In the context of protected areas and conservation, the term 'rightsholders' refers to people (such as but not limited to landowners) socially endowed with legal or customary rights with respect to land, water and natural resources. By contrast, 'stakeholders' possess direct or indirect interests and concerns about these resources but do not necessarily enjoy a legally or socially recognised entitlement to them (Borrini-Feyerabend et al., 2013).

Seascape: A spatially heterogeneous marine region that can be delineated at a range of scales and which includes physical, geological and chemical aspects of oceans. It can be a combination of adjacent coastline and sea, such as mangroves, coral reefs, seagrass beds, tidal marshes and deep seas. It includes the features of the geology and morphology of the sea floor as well as the living communities of the benthos, water column and surface, and often includes the influence of humans (Pittman, 2017; Fuller, 2013). Seascapes are generally large, but can be defined at a range of spatial scales.

Sustainable use: The use of components of biological diversity in a way and at a rate that does not lead to the long-term decline of biological diversity, thereby maintaining the potential to meet the needs and aspirations of present and future generations (CBD Article 2, 1992).

The Russian River corridor in California, USA, maintains ecological connectivity as the river passes through agricultural, residential and urban landscapes. © Adina Merenlender

References

Abell, R., Lehner, B., Thieme, M., and Linke, S. (2017). 'Looking beyond the fenceline: Assessing protection gaps for the world's rivers'. *Conservation Letters* 10:384–394. https://doi.org/10.1111/conl.12312.

Albert, C.H., Rayfield, B., Dumitru, M., and Gonzalez, A. (2017). 'Applying network theory to prioritize multispecies habitat networks that are robust to climate and land-use change'. *Conservation Biology* 31:1383–1396. http://doi.org/10.1111/cobi.12943.

Almany, G.R., Connolly, S.R., Heath, D.D., Hogan, J.D., Jones, G.P., McCook, L.J., Mills, M., Pressey, R.L., and Williamson, D.H. (2009). 'Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs'. *Coral Reefs* 28:339–351. https://doi.org/10.1007/s00338-009-0484-x.

Allen, C. H., Parrott, L., and Kyle, C. (2016). 'An individual-based modelling approach to estimate landscape connectivity for bighorn sheep (*Ovis canadensis*)'. *Peerj* 4. https://doi.org/10.7717/peerj.2001.

Ament, R., Callahan, R., McClure, M., Reuling, M., and Tabor, G. (2014). *Wildlife Connectivity: Fundamentals for Conservation Action.* Bozeman, MT: Center for Large Landscape Conservation.

Anderson, A.B. and Jenkins, C.N. (2006). *Applying Nature's Design: Corridors as a Strategy for Biodiversity Conservation.* New York: Columbia University Press. https://doi.org/10.1086/513391

Anderson, M.G., Clark, M. and Sheldon, A.O. (2014). 'Estimating climate resilience for conservation across geophysical settings'. *Conservation Biology* 28(4): 959–970.

Ankersen, T.T. (1994). 'Mesoamerican Biological Corridor: The legal framework for an integrated, regional system of protected areas'. *Journal of Environmental Law and Litigation* 9:499–549.

Ayebare, S., Ponce-Reyes, R., Segan, D.B., Watson, J.E.M., Possingham, H.P., Seimon, A., and Plumptre, A.J. (2013). 'Identifying climate resilient corridors for conservation in the Albertine Rift'. Unpublished Report by the Wildlife Conservation Society to MacArthur Foundation.

Balbar, A.C. and Metaxas, A. (2019). 'The current application of ecological connectivity in the design of marine protected areas.' *Global Ecology and Conservation* 17:e00569. https://doi.org/10.1016/j.gecco.2019.e00569.

Barthem, R.B., Goulding, M., Leite, R.G., Cañas, C., Forsberg, B., Venticinque, E., Petry, P., Ribeiro, M.L., Chuctaya, J., and Mercado, A. (2017). 'Goliath catfish spawning in the far western Amazon confirmed by the distribution of mature adults, drifting larvae and migrating juveniles'. *Scientific Reports* 7:41784.

Bastian O., Grunewald K., and Khoroshev A.V. (2015). 'The significance of geosystem and landscape concepts for the assessment of ecosystem services: Exemplified on a case study in Russia'. *Landscape Ecology* 30:1145–1164. https://doi.org/10.1007/s10980-015-0200-x.

Bay Area Open Space Council (2011). *The Conservation Lands Network: San Francisco Bay Area Upland Habitat Goals Project Report.* Berkeley, CA: Bay Area Open Space Council. https://www.bayarealands.org/wp-content/uploads/2017/07/CLN-1.0-Original-Report.pdf (Accessed: 25 March 2019).

Beier, P., Majka, D.R., and Spencer, W.D. (2008). 'Forks in the road: Choices in procedures for designing wildland linkages'. *Conservation Biology* 22:836–851. https://doi.org/10.1111/j.1523-1739.2008.00942.x.

Beier, P., Spencer, W., Baldwin, R.F., and McRae, B. (2011). 'Toward best practices for developing regional connectivity maps'. *Conservation Biology* 25:879–892. https://doi.org/10.1111/j.1523-1739.2011.01716.x.

Bennett, A.F. (2003). *Linkages in the Landscape: The Role of Corridors and Connectivity in Wildlife Conservation.* Gland, Switzerland: IUCN. https://doi.org/10.2305/IUCN.CH.2004.FR.1.en.

Bennett, G. and Mulongoy, K.J. (2006). *Review of Experience with Ecological Networks, Corridors and Buffer Zones,* CBD Technical Series 23. Montreal: Secretariat of the Convention on Biological Diversity.

Benson, R.L., Turo, S., and McCovey Jr., B.W. (2007). 'Migration and movement patterns of green sturgeon (*Acipenser medirostris*) in the Klamath and Trinity rivers, California, USA'. *Environmental Biology of Fishes* 79:269–279.

Boere, G. C. and Stroud, D.A. (2006). 'The flyway concept: What it is and what it isn't'. In: G.C. Boere, C.A. Galbraith, and D.A. Stroud, (eds.). *Waterbirds around the World,* pp. 40-47. Edinburgh: The Stationery Office.

Boitani, L., Falcucci, A., Maiorano, L. and Rondinini, C. (2007). 'Ecological networks as conceptual frameworks or operational tools in conservation'. *Conservation Biology* 21(6):1414–1422.

Borrini-Feyerabend, G., Dudley, N., Jaeger, T., Lassen, B., Broome, N., Phillips, A. and Sandwith, T. (2013). *Governance of Protected Areas: From Understanding to Action.* Best Practice Protected Areas Guideline Series, no. 20. Gland, Switzerland: IUCN. https://portals.iucn.org/library/node/29138.

Borrini-Feyerabend, G., Kothari, A. and Oviedo, G. (2004). *Indigenous and Local Communities and Protected Areas: Towards Equity and Enhanced Conservation.* Best Practice Protected Areas Guideline Series, no. 11. Gland, Switzerland and Cambridge, UK: IUCN. https://portals.iucn.org/library/node/8549.

Brashares, J. S., Arcese, P., and Sam, M.K. (2001). 'Human demography and reserve size predict wildlife extinction in West Africa'. *Proceedings of the Royal Society of London: Biological Sciences* 268:2473–2478. https://doi.org/10.1098/rspb.2001.1815.

Caballero, P., Battaglini, E., and Lagnaoui, A. (2015). 'Project information document: Orinoquia Integrated Sustainable Landscapes.' The World Bank. http://documents.worldbank.org/curated/en/800621561650457648/pdf/Project-Information-Document-Orinoquia-Integrated-Sustainable-Landscapes-P167830.pdf (Accessed: 14 November 2019).

Carr, M., Robinson, S.P., Wahle, C., Davis, G., Kroll, S., Murray, S., Schumacher, E.J., and Williams, M. (2017). 'The central importance of ecological spatial connectivity to effective coastal marine protected areas and to meeting the challenges of climate change in the marine environment'. *Aquatic Conservation*. https://doi.org/10.1002/aqc.2800.

CBD (Convention on Biological Diversity) (5 June 1992). 1760 UNTS 69. https://treaties.un.org/pages/ViewDetails.aspx?src=TREATY&mtdsg_no=XXVII-8&chapter=27 (Accessed: 25 March 2019).

CBD (2008). *CBD Guidance on Marine and Coastal Protected Areas and Networks*. COP 2008 IX/20, Annex I and II.

CBD (2011). *Strategic Plan for Biodiversity 2011–2020 and the Aichi Targets.* Montreal: Secretariat of the Convention on Biological Diversity.

Ceballos, G., Ehrlich, P.R., and Dirzo, R. (2017). 'Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines'. *Proceedings of the National Academy of Sciences* 114(30): E6089–E6096. https://doi.org/10.1073/pnas.1704949114.

CEPF (Critical Ecosystems Partnership Fund). Website: https://www.cepf.net/our-work/biodiversity-hotspots/caribbean-islands/species (Accessed: 23 October 2019).

Citanovic, C. and Hobday, A.C. (2018). 'Building optimism at the environmental science-policy-practice interface through the study of bright spots'. *Nature Communications* 9(1):3466. https://doi.org/10.1038/s41467-018-05977-w.

CMS (Convention on the Conservation of Migratory Species of Wild Animals) (23 June 1979). 1651 UNTS 333. https://treaties.un.org/pages/showDetails.aspx?objid=08000002800bc2fb (Accessed: 25 March 2019).

CMS (2020). *Improving Ways of Addressing Connectivity in the Conservation of Migratory Species,* Resolution 12.26 (REV.COP13), Gandhinagar, India (17-22 February 2020). UNEP/CMS/COP13/CRP 26.4.4. https://www.cms.int/sites/default/files/document/cms_cop13_crp26.4.4_addressing-connectivity-in-conservation-of-migratory-species_e_0.docx.

Cohen-Shacham, E., Walters, G., Janzen, C. and Maginnis, S. (eds.) (2016). *Nature-based Solutions to Address Global Societal Challenges.* Gland, Switzerland: IUCN. https://doi.org/10.2305/IUCN.CH.2016.13.en.

Compton, B.W., McGarigal, K., Cushman, S.A., and Gamble, L.R. (2007). 'A resistant-kernel model of connectivity for amphibians that breed in vernal pools'. *Conservation Biology* 21:788–799. https://doi.org/10.1111/j.1523-1739.2007.00674.x.

Conservation Corridor (2018). 'Corridor Toolbox'. http://conservationcorridor.org/corridor-toolbox/ (Accessed: 14 November 2019).

Conservation Measures Partnership (2013). *Open Standards for the Practice of Conservation Version 3.0*. http://cmp-openstandards.org (Accessed: 15 November 2019).

Context Pty Ltd. (2008). *Strategic Plan for Conservation Management Networks in Victoria: Working Together to Protect Biodiversity.* Brunswick, Victoria: Context Pty Ltd. http://www.swifft.net.au/cb_pages/conservation_management_networks_cmns.php (Accessed: 25 March 2019).

Cowen, R.K., Gawarkiewicz, G., Pineda, J., Thorrold, S.R., and Werner, F.E. (2007). 'Population connectivity in marine systems: An overview'. *Oceanography* 20:14–21. https://doi.org/10.5670/oceanog.2007.26.

Cowen, R.K. and Sponaugle, S. (2009). 'Larval dispersal and marine population connectivity'. *Annual Review of Marine Science* 1:443–466. https://doi.org/10.1146/annurev.marine.010908.163757.

Crooks, K. R. and Sanjayan, M. (eds.) (2006). *Connectivity Conservation*. Cambridge. UK: Cambridge University Press. https://doi.org/10.1017/CBO9780511754821.

Day, J., Dudley, N., Hockings, M., Holmes, G., Laffoley, D., Stolton, S., and Wells, S. (2012). *Guidelines for Applying the IUCN Protected Area Management Categories to Marine Protected Areas.* Gland, Switzerland: IUCN. https://portals.iucn.org/library/node/10201.

Degteva, S.V., Ponomarev, V.I., Eisenman, S.W., and Dushenkov, V. (2015). 'Striking the balance: challenges and perspectives for the protected areas network in northeastern European Russia'. *Ambio* 44:473–490.

Dickson, B.G., Albano, C.M., McRae, B.H., Anderson, J.J., Theobald, D.M., Zachmann, L.J., and Dombeck, M.P. (2017). 'Informing strategic efforts to expand and connect protected areas using a model of ecological flow, with application to the western United States'. *Conservation Letters* 10:564–571. https://doi.org/10.1111/conl.12322.

Doyle, M.W., Stanley, E.H., Luebke, M.A., and Harbor, J.M. (2000). ‘Dam removal: Physical, biological, and societal considerations’. In R.H. Hotchkiss and M. Glade (eds.). *Building Partnerships,* pp. 1-10. Proceedings of the 2000 Joint Conference on Water Resources Engineering and Water Resources Planning and Management, Minneapolis, MN, 30 July–2 August. https://ascelibrary.org/doi/book/10.1061/9780784405178

Dudley, N. (ed.) (2008). *Guidelines for Applying Protected Area Management Categories*. Gland, Switzerland: IUCN. https://doi.org/10.2305/IUCN.CH.2008.PAPS.2.en.

Ellis, E.C., Goldewijk, K., Siebert, S., Lightman, D. and Ramankutty, N., 2010. ‘Anthropogenic transformation of the biomes, 1700 to 2000.’ *Global Ecology and Biogeography* 19(5):589–606. https://doi.org/10.1111/j.1466-8238.2010.00540.x

Elsen, P.R., Monahan, W.B., and Merenlender, A.M. (2018). ‘Global patterns of protection of elevational gradients in mountain ranges’. *Proceedings of the National Academy of Sciences* 201720141. https://doi.org/10.1073/pnas.1720141115.

European Parliament and Council. (2014). *Directive 2014/89/ EU Parliament and Council of the European Union, 23 July 2014: Establishing a Framework for Maritime Spatial Planning.* https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=celex%3A32014L0089 (Accessed: 25 March 2019).

Farrier, D., Harvey, M., Teles Da Silva, S., Diegues Leuzinger, M., Verschuuren, J., Gromilova, M., Trouwborst, A., and Paterson, A.R. (2013). *The Legal Aspects of Connectivity Conservation (Vol. 2) – Case Studies.* Gland, Switzerland: IUCN. https://portals.iucn.org/library/efiles/documents/EPLP-085-002.pdf (Accessed: 15 November 2019).

Foden, W.B. and Young, B.E. (eds.) (2016). *IUCN SSC Guidelines for Assessing Species’ Vulnerability to Climate Change. Version 1.0.* Occasional Paper of the IUCN Species Survival Commission, no. 59. Cambridge, UK and Gland, Switzerland: IUCN Species Survival Commission. https://doi.org/10.2305/IUCN.CH.2016.SSC-OP.59.en.

Forman, T.T., and Godron, M. (1986). *Landscape Ecology.* New York: John Wiley & Sons.

Fuller, B.J.C. (2013). ‘Advances in seascape ecology: Applying landscape metrics to marine systems’. *Ecology of Fragmented Landscapes* 1(5).

Gillanders, B.M., Able, K.W., Brown, J.A., Eggleston, D.B., and Sheridan, P.F. (2003). ‘Evidence of connectivity between juvenile and adult habitats for mobile marine fauna: An important component of nurseries’. *Marine Ecology Progress Series* 247:281–295. https://doi.org/10.3354/meps247281.

Green, A.L., Fernandes, L., Almany, G., Abesamis, R., McLeod, E., Alina, P.M., White, A.T., Salm, R., Tanzer, J., and Pressey, R.L. (2014). ‘Designing marine reserves for fisheries management, biodiversity conservation, and climate change adaptation’. *Coastal Management* 42(2):143–159. https://doi.org/10.1080/08920753.2014.877763.

Grorud-Colvert, K., Claudet, J., Carr, M., Caselle, J., Day, J., Friedlander, A., Lester, S., Lison de Loma, T., Tissot, B., and Malone, D. (2011). ‘The assessment of marine reserve networks: Guidelines for ecological evaluation’. In: J. Claudet, J. (ed.). *Marine Protected Areas: A Multidisciplinary Approach*, pp. 293-321. Cambridge, UK: Cambridge University Press. https://doi.org/10.1017/CBO9781139049382.016.

Grorud-Colvert, K., Claudet, J., Tissot, B.N., Caselle, J.E., Carr, M.H., Day, J.C., Friedlander, A.M., Lester, S.E., Lison de Loma, T., Malone, D., and Walsh, W.J. (2014). ‘Marine protected area networks: Assessing whether the whole is greater than the sum of its parts’. *PLoS ONE* 9(8):e102298. https://doi.org/10.1371/journal.pone.0102298.

Gross, J.E., Woodley, S., Welling, L.A., and Watson, J.E.M. (eds.) (2016). *Adapting to Climate Change: Guidance for Protected Area Managers and Planners.* Best Practice Protected Area Guidelines Series, no. 24, Gland, Switzerland: IUCN. https://doi.org/10.2305/IUCN.CH.2017.PAG.24.en.

Hanski, I. (1999). *Metapopulation Ecology*. Oxford: Oxford University Press.

Hauer, F.R., Locke, H., Dreitz, V.J., Hebblewhite, M., Lowe, W.H., Muhlfeld, C.C., Nelson, C.R., Proctor, M.F., and Rood, S.B. (2016). ‘Gravel-bed river floodplains are the ecological nexus of glaciated mountain landscapes’. *Science Advances* 2:e1600026. https://doi.org/10.1126/sciadv.1600026.

Heller, N.E., and Zavaleta, E.S. (2009). ‘Biodiversity management in the face of climate change: A review of 22 years of recommendations’. *Biological Conservation* 142:14–32. https://doi.org/10.1016/j.biocon.2008.10.006.

Henderson, M., Merriam, G., and Wegner, J. (1985). ‘Patchy environments and species survival: Chipmunks in an agricultural mosaic’. *Biological Conservation* 31:95–105. https://doi.org/10.1016/0006-3207(85)90043-6.

Hermoso, V., Linke, S., Prenda, J. and Possingham, H.P. (2011). ‘Addressing longitudinal connectivity in the systematic conservation planning of fresh waters’. *Freshwater Biology* 56(1):57–70. https://doi.org/10.1111/j.1365-2427.2009.02390.x.

Hilty, J.A., Keeley, A.T.H., Lidicker Jr., W.Z, and Merenlender, A.M. (2019). *Corridor Ecology: Linking Landscapes for Biodiversity Conservation and Climate Adaptation.* 2nd ed. Washington, DC: Island Press.

Hilty, J.A., and Merenlender, A.M. (2000). ‘Faunal indicator taxa selection for monitoring ecosystem health’. *Biological Conservation* 92:185–197. https://doi.org/10.1016/S0006-3207(99)00052-X.

Hockings, M., Stolton, S, Leverington, F., Dudley, N., and Courrau, J. (2006). *Evaluating Effectiveness: A Framework for Assessing Management Effectiveness of Protected Areas.* Best Practice Protected Areas Guideline Series, no. 14, 2nd ed. Gland, Switzerland and Cambridge, UK: IUCN. https://doi.org/10.2305/IUCN.CH.2006.PAG.14.en.

Hodgson, J.A., Thomas, C.D., Dytham, C., Travis, J.M.J., and Cornell, S.J. (2012). 'The speed of range shifts in fragmented landscapes'. *PLoS One* 7. https://doi.org/10.1371/journal.pone.0047141.

Hodgson, J.A., Wallis, D.W., Krishna, R., and Cornell, S.J. (2016). 'How to manipulate landscapes to improve the potential for range expansion'. *Methods in Ecology and Evolution* 7:1558–1566. https://doi.org/10.1111/2041-210X.12614.

Holling, C.S., and Gunderson, L.H. (2002). 'Resilience and adaptive cycles.' In: L.H. Gunderson, and C.S. Holling (eds.). *Panarchy: Understanding Transformation in Human and Natural Systems*, pp. 25–62. Washington, DC: Island Press.

Horne, J.S., Garton, E.O., Krone, S.M., and Lewis, J.S. (2007). 'Analyzing animal movements using Brownian bridges'. *Ecology* 88:2354–2363. https://doi.org/10.1890/06-0957.1.

IPBES (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services) (2019). *Summary for Policymakers of the Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.* Díaz, S., Settele, J., Brondizio E.S., Ngo, H.T., Guèze, M., Agard, J., Arneth, A., Balvanera, P., Brauman, K.A., Butchart, S.H.M., Chan, K.M.A., Garibaldi, L.A., Ichii, K., Liu, J., Subramanian, S.M., Midgley, G.F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., Polasky, S., Purvis, A., Razzaque, J., Reyers, B., Roy Chowdhury, R., Shin, Y.J. Visseren-Hamakers, I.J., Willis, K.J., and Zayas, C.N. (eds.). Bonn: IPBES Secretariat.

International Union for Conservation of Nature (IUCN) (2016). *A Global Standard for the Identification of Key Biodiversity Areas, Version 1.0.* 1st ed. Gland, Switzerland: IUCN. https://portals.iucn.org/library/node/46259.

IUCN World Commission on Protected Areas (WCPA) (2019). *Guidelines for Recognising and Reporting Other Effective Area-based Conservation Measures.* Gland, Switzerland: IUCN.

IUCN (undated). World Commission on Protected Areas (IUCN WCPA). IUCN Definitions – English. https://www.iucn.org/downloads/en_iucn__glossary_definitions.pdf (Accessed: 15 November 2019).

Jones, K.R., Venter, O., Fuller, R.A., Allan, J.R., Maxwell, S.L., Negret, P.J., Watson, J.E.M. (2018). 'One-third of global protected land is under intense human pressure'. *Science* 360:788–791. https://doi.org/10.1126/science.aap9565.

Jongepierová, I., Pešout, P., Jongepier, J.W., and Prach, K. (eds.) (2012). *Ecological Restoration in the Czech Nature Conservation Agency of the Czech Republic, Prague.* http://www.ochranaprirody.cz/en/what-we-do/territorial-system-of-ecological-stability (Accessed: 25 March 2019).

Jongman R., and Bogers M. (2008). *Current Status of the Practical Implementation of Ecological Networks in the Netherlands.* Alterra/European Centre for Nature Conservation. http://www.ecologicalnetworks.eu/documents/publications/ken/NetherlandsKENWP2.pdf (Accessed: 25 March 2019).

Juffe-Bignoli, J., Harrison, I., Butchart, S.H.M., Flitcroft, R., Hermoso, V., Jonas, H., Lukasiewicz, A., Thieme, M., Turak E., Bingham, H., Dalton, J., Darwall, W., Deguignet, M., Dudley, N., Gardner, R., Higgins, J., Kumar, R., Linke, S., Milton, G.R., Pittock, J., Smith, K.G. & Van Soesbergen, A. (2016). 'Achieving Aichi Biodiversity Target 11 to improve the performance of protected areas and conserve freshwater biodiversity'. *Aquatic Conservation: Marine and Freshwater Ecosystems* 26:133–151. https://doi.org/10.1002/aqc.2638.

Keeley, A.T.H, Ackerly, D.D., Cameron, D.R., Heller, N.E., Huber, P.R., Schloss, C.A., Thorne, J.H., and Merenlender, A.M. (2018). 'New concepts, models, and assessments of climate-wise connectivity'. *Environmental Research Letters* 13:073002. https://doi.org/10.1088/1748-9326/aacb85.

Keeley, A.T., Beier, P., Creech, T., Jones, K., Jongman, R.H., Stonecipher, G., and Tabor, G.M. (2019). 'Thirty years of connectivity conservation planning: An assessment of factors influencing plan implementation'. *Environmental Research Letters* 14(1):103001. https://doi.org/10.1088/1748-9326/ab3234.

Kenneth, D., Bowen, J., and Gillingham, C. (2004). 'R9 Species Conservation Assessment for Wood Turtle – *Glyptemys insculpta* (LeConte, 1830)'. Milwaukee, WI: US Forest Service.

Kettle, A.J., and Haines, K. (2006). 'How does the European eel (*Anguilla anguilla*) retain its population structure during its larval migration across the North Atlantic Ocean?'. *Canadian Journal of Fisheries and Aquatic Sciences* 63:90–106.

Klaasen, M. (1996). 'Metabolic Constraints on Long-Distance Migration in Birds'. *The Journal of Experimental Biology* 199:57–64.

KLRI (Korean Legislative Research Institute) (2014). *Baekdu-Daegan Protection Act.* Act No.12414, March 11, 2014. http://extwprlegs1.fao.org/docs/pdf/kor93916.pdf (Accessed: 25 March 2019).

Ladonina, N.N., Cherniakhovsky, D.A., Makarov, I.B., and Basevich, V.F. (2001). 'Managing agricultural resources for biodiversity conservation: Case study of Russia and CIS countries'. *Environment Liaison Center International:* 1–52.

Lausche, B., Farrier, D., Verschuuren, J., La Vina, A.G.M., Trouwborst, A., Born, C-H., and Aug, L. (2013). *The Legal Aspects of Connectivity Conservation: A Concept Paper.* IUCN Environmental Policy and Law Paper, no. 85, volume 1. Gland, Switzerland: IUCN. https://portals.iucn.org/library/node/10421.

Lausche, B. (2011). *Guidelines for Protected Areas Legislation.* IUCN Environmental Policy and Law Paper, no. 81. IUCN, Gland, Switzerland. https://portals.iucn.org/library/node/9869.

Lawler, J.J., Ruesch, A.S., Olden, J.D., and McRae, B.H. (2013). 'Projected climate-driven faunal movement routes'. *Ecology Letters* 16:1014–1022. https://doi.org/10.1111/ele.12132.

Leibowitz, S., Wigington, P., Schofield, K., Alexander, L., Vanderhoof, M., and Golden, H. (2018). 'Connectivity of streams and wetlands to downstream waters: An integrated systems framework'. *Journal of the American Water Resources Association* 54(2):298–322. https://doi.org/10.1111/1752-1688.12631.

Lindenmayer, D.B., and Burgman, M. (2005). *Practical Conservation Biology*. Victoria, Australia: CSIRO Publishing. https://doi.org/10.1071/9780643093102.

Locke, H., Ellis, C.E., Venter, O., Schuster, R., Ma, K., Shen, X., Woodley, S., Kingston, N., Bhola, N., Strassburg, B.N.B., Paulsch, A., Williams, B., and Watson, J.E.M. (2019). 'Three global conditions for biodiversity conservation and sustainable use: An implementation framework'. *National Science Review* nwz136. https://doi.org/10.1093/nsr/nwz136.

Loss, S.R., Will, T., and Marra, P.P. (2013). 'Estimates of bird collision mortality at wind facilities in the contiguous United States'. *Biological Conservation* 168:201–209. https://doi.org/10.1016/j.biocon.2013.10.007.

MacArthur, R.H. and Wilson, E.O. (1963). An equilibrium theory of insular zoogeography. *International Journal of Organic Evolution* 17:373–387. https://doi.org/10.1111/j.1558-5646.1963.tb03295.x.

MacArthur, R.H., and Wilson, E.O. (1967). *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.

Margules, C.R. and Pressey, R.L. (2000). 'Systematic conservation planning'. *Nature* 405(6783):243.

Marine Protected Areas Federal Advisory Committee (2017). *Harnessing Ecological Spatial Connectivity for Effective Marine Protected Areas and Resilient Marine Ecosystems.* https://nmsmarineprotectedareas.blob.core.windows.net/marineprotectedareas-prod/media/archive/fac/products/connectivity-report-combined.pdf.

McCullough, D.R. (1996). *Metapopulations and Wildlife Conservation.* Washington, DC: Island Press.

McGuire, J. L., Lawler, J.J., McRae, B.H., Nuñez, T.A., and Theobald, D.M. (2016). 'Achieving climate connectivity in a fragmented landscape'. *Proceedings of the National Academy of Sciences* 113:7195–7200. https://doi.org/10.1073/pnas.1602817113.

McRae, B.H. (2006). 'Isolation by resistance'. *Evolution* 60:1551–1561. https://doi.org/10.1111/j.0014-3820.2006.tb00500.x.

McRae, B.H., Shah, V., and Mohapatra, T. (2014). *Circuitscape.* http://www.circuitscape.org/linkagemapper (Accessed: 5 February 2018).

Menxiu, T., Lin, Z., Li, J., Zöckler, C., and Clark, N.A. (2012). 'The critical importance of the Rudong mudflats, Jiangsu Province, China in the annual cycle of the spoon-billed sandpiper *Calidris pygmeus*'. *Wader Study Group Bulletin* 119:74.

M'Gonigle, L. K., Ponisio, L., Cutler, K., and Kremen, C. (2015). 'Habitat restoration promotes pollinator persistence and colonization in intensively-managed agriculture'. *Ecological Applications* 25:1557–1565. https://doi.org/10.1890/14-1863.1.

Miklos L, Diviakova, A and Izakovičová, Z. (2019). *Ecological Networks and Territorial Systems of Ecological Stability.* London: Springer Nature. https://doi.org/10.1007/978-3-319-94018-2_1.

Millennium Ecosystem Assessment (2005). *Millennium Ecosystem Assessment. Ecosystems and Human Well-being: A Framework for Assessment.* Washington, DC: Island Press.

Miller, K., and Hyun, K. (2011). 'Ecological corridors: Legal framework for the Baekdu Daegan Mountain System (South Korea)'. In: B. Lausche (ed). *Guidelines for Protected Areas Legislation.* IUCN Environmental Policy and Law Paper, no. 81. IUCN, Gland, Switzerland. https://portals.iucn.org/library/node/9869.

Millington, S. (2018). *The Role of Protected Areas in the Conservation of Migratory Waterbirds in the East Asian–Australasian Flyway (PPT).* http://www.env.go.jp/en/nature/asia-parks/pdf/wg2/APC_WG5-11_Spike%20Millington.pdf (Accessed: 1 November 2019).

Moilanen, A., Leathwick, J., and Elith, J. (2008). 'A method for spatial freshwater conservation prioritization'. *Freshwater Biology* 53:577–592. https://doi.org/10.1111/j.1365-2427.2007.01906.x.

Naeem, S., Chapin III, F.S., Costanza, R., Ehrlich, P.R., Golley, F.B., Hooper, D.U., Lawton, J.H., O'Neill, R.V., Mooney, H.A., Sala, O.E., Symstad, A.J., and Tilman, D. (1999). 'Biodiversity and ecosystem functioning: Maintaining natural life support processes'. *Issues in Ecology* 4:2–12.

Neugarten, R.A., Langhammer, P.F., Osipova, E., Bagstad, K.J., Bhagabati, N., Butchart, S.H.M., Dudley, N., Elliott, V., Gerber, L.R., Gutierrez Arrellano, C., Ivanić, K.-Z., Kettunen, M., Mandle, L., Merriman, J.C., Mulligan, M., Peh, K.S.-H., Raudsepp-Hearne, C., Semmens, D.J., Stolton, S., and Willcock, S. (2018). *Tools for Measuring, Modelling, and Valuing Ecosystem Services: Guidance for Key Biodiversity Areas, Natural World Heritage Sites, and Protected Areas.* Best Practice Protected Area Guidelines Series, no. 28. Gland, Switzerland: IUCN. https://doi.org/10.2305/IUCN.CH.2018.PAG.28.en.

Newmark, W.D. (1987). 'A land-bridge island perspective on mammalian extinctions in western North American parks'. *Nature* 325:430-432. https://doi.org/10.1038/325430a0.

Newmark, W.D. (1995). ‘Extinction of mammal populations in western North American national parks’. *Conservation Biology* 9:512–526. https://doi.org/10.1046/j.1523-1739.1995.09030512.x.

Newmark, W.D. (2008). ‘Isolation of African protected areas’. *Frontiers in Ecology and the Environment* 6:321–328. https://doi.org/10.1890/070003.

Newmark, W.D., Jenkins, C.N., Pimm, S.L., McNeally, P.B., and Halley, J.M. (2017). ‘Targeted habitat restoration can reduce extinction rates in fragmented forests’. *Proceedings of the National Academy of Sciences* 114:9635–9640. https://doi.org/10.1073/pnas.1705834114.

Olds, A.D., Connolly, R.M., Pitt, K.A., Pittman, S.J., Maxwell, P.S., Huijbers, C.M., and Schlacher, T.A. (2016). ‘Quantifying the conservation value of seascape connectivity: A global synthesis’. *Global Ecology and Biogeography* 25:3–15. https://doi.org/10.1111/geb.12388.

Parks, S., and Harcourt, A. (2002). ‘Reserve size, local human density, and mammalian extinctions in U.S. protected areas’. *Conservation Biology* 16:800–808. https://doi.org/10.1046/j.1523-1739.2002.00288.x.

Phillips, A. (2007). ‘A short history of the international system of protected area management categories’. Paper prepared for the WCPA Task Force on Protected Area Categories.

Pittman, S.J. (ed.) (2017). *Seascape Ecology.* Hoboken, NJ: Wiley-Blackwell.

Plumptre, A.J., Ayebare, S., Segan, D., Watson, J., and Kujirakwinja, D. (2016). ‘Conservation Action Plan for the Albertine Rift.’ Unpublished Report for Wildlife Conservation Society and its Partners.

Proctor, M.F., Paetkau, D., Mclellan, B.N., Stenhouse, G.B., Kendall, K.C., Mace, R.D., Kasworm, W.F., Servheen, C., Lausen, C.L., Gibeau, M.L., Wakkinen, W.L., Haroldson, M.A., Mowat, G., Apps, C.D., Ciarniello, L.M., Barclay, R.M.R., Boyce, M.S., Schwartz, C.C., and Strobeck, C. (2012). Population fragmentation and inter-ecosystem movements of grizzly bears in western Canada and the northern United States. *Wildlife Monographs* 180:1–46. https://doi.org/10.1002/wmon.6.

Proctor, M.F., Nielsen, S.E., Kasworm, W.F., Servheen, C., Radandt, T.F., Machutchon, A.G., and Boyce, M.A. (2015). ‘Grizzly bear connectivity mapping in the Canada–United States trans-border region’. *Journal of Wildlife Management* 79:544–588. https://doi.org/10.1002/jwmg.862.

Proctor, M.F., Kasworm, W.F., Annis, K.M., MacHutchon, A.G., Teisberg, J.E., Radandt, T.G., and Servheen, C. (2018). ‘Conservation of threatened Canada-USA trans-border grizzly bears linked to comprehensive conflict reduction’. *Human Wildlife Interactions* 12:248–272.

Prugh, L.R., Hodges, K.E., Sinclair, A.R., and Brashares, J.S. (2008). ‘Effect of habitat area and isolation on fragmented animal populations’. *Proceedings of the National Academy of Sciences* 105:20770-20775. https://doi.org/10.1073/pnas.0806080105.

Pulsford, I., Lindenmayer, D., Wyborn, C., Lausche, B., Vasilijević, M. and Worboys, G.L. (2015). ‘Connectivity conservation management’. In: Worboys, G.L., Lockwood, M., Kothari, A., Feary, S., and Pulsford, I. (eds.). *Protected Area Governance and Management,* pp. 851–888. Canberra: ANU Press.

Ramírez, G. (2003). ‘El Corredor Biológico Mesoamericano’. CONABIO. *Biodiversitas* 47:1–3.

Rayfield, B., Pelletier, D., Dumitru, M., Cardille, J.A., and Gonzalez, A. (2016). ‘Multipurpose habitat networks for short-range and long-range connectivity: A new method combining graph and circuit connectivity’. *Methods in Ecology and Evolution* 7:222–231. https://doi.org/10.1111/2041-210X.12470.

Resasco, J., (2019). ‘Meta-analysis on a decade of testing corridor efficacy: What new have we learned?’ *Current Landscape Ecology Reports* 4:61–69. https://doi.org/10.1007/s40823-019-00041-9.

Rouget, M., Cowling, R.M., Lombard, A.T., Knight, A.T., and Kerley, G.I. (2006). ‘Designing large-scale conservation corridors for pattern and process’. *Conservation Biology* 20:549–561. https://doi.org/10.1111/j.1523-1739.2006.00297.x.

Rudnick, D.A., Ryan, S.J., Beier, P., Cushman, S.A., Dieffenbach, F., Epps, C.W., Gerber, L.R., Hartter, J., Jenness, J.S., Kintsch, J., Merelender, A.M., Perkl, R.M., Preziosi, D.V., and Trombulak, S.C. (2012). ‘The role of landscape connectivity in planning and implementing conservation and restoration priorities’. *Issues in Ecology* 16:1–20.

Runge, C.A., Watson, J.E.M., Butchart, S.H., Hanson, J.O., Possingham, H.P., and Fuller, R.A. (2015). ‘Protected areas and global conservation of migratory birds’. *Science* 350:1266–1258. https://doi.org/10.1126/science.aac9180.

Russi D., ten Brink, P., Farmer, A., Badura, T., Coates, D., Förster, J., Kumar, R., and Davidson, N. (2013). *The Economics of Ecosystems and Biodiversity for Water and Wetlands*. London and Brussels: IEEP; Gland, Switzerland: Ramsar Convention Secretariat.

Rydell, J., Bach, L., Dubourg-Savage, M.J., Green, M., Rodrigues, L., and Hedenström, A. (2010). ‘Bat mortality at wind turbines in northwestern Europe’. *Acta Chiropterologica* 12:261–274. https://doi.org/10.3161/150811010X537846.

Saura, S., Bertzky, B., Bastin, L., Battistella, L., Mandrici, A., and Dubois, G. (2018). ‘Protected area connectivity: Shortfalls in global targets and country-level priorities’. *Biological Conservation* 219:53–67. https://doi.org/10.1016/j.biocon.2017.12.020.

Saura, S., and de la Fuente, B. (2017). 'Connectivity as the amount of reachable habitat: Conservation priorities and the roles of habitat patches in landscape networks'. In S.E. Gergel and M.G. Turner (eds.). *Learning Landscape Ecology*, pp. 229–254. New York: Springer. https://doi.org/10.1007/978-1-4939-6374-4_14.

Sawyer, H., Kauffman, M.J., Nielson, R.M., and Horne, J.S. (2009). 'Identifying and prioritizing ungulate migration routes for landscape-level conservation'. *Ecological Applications* 19:2016–2025. https://doi.org/10.1890/08-2034.1.

Saarman, E., Gleason, M., Ugoretz, J., Airame, S., Carr, M.H., Fox, E.W., Frimodig, A., Mason, T., and Vasques, J. (2013). 'The role of science in supporting marine protected area network planning and design in California'. *Ocean and Coastal Management* 74:45–56. https://doi.org/10.1016/j.ocecoaman.2012.08.021.

Scheffers, B.R., De Meester, L., Bridge, T.C.L., Hoffmann, A.A., Pandolfi, J.M., Corltett, R.T., Butchart, S.H.M., Pearce-Kelly, P., Kovacs, K.M., Dudgeon, D., Pacifici, M., Rondinini, C., Foden, W.B., Martin, T.G., Mora, C., Bickford, D., and Watson, J.E.M. (2016). 'The broad footprint of climate change from genes to biomes to people'. *Science* 354:aaf7671. https://doi.org/10.1126/science.aaf7671.

Seidensticker, J., Dinerstein, E., Goyal, S.P., Gurung, B., Harihar, A., Johnsingh, A.J., Manandhar, A., McDougal, C.W., Pandav, B., Shrestha, M., and Smith, J.D. (2010). 'Tiger range collapse and recovery at the base of the Himalayas'. *Biology and Conservation of Wild Felids* 12:305–324.

Seidler, R.G., Long, R.A., Berger, J., Bergen, S., and Beckmann, J.P. (2015). 'Identifying impediments to long-distance mammal migrations'. *Conservation Biology* 29:99–109. https://doi.org/10.1111/cobi.12376.

Serneels, S., and Lambin, E.F. (2001). 'Impact of land-use changes on the wildebeest migration in the northern part of the Serengeti–Mara ecosystem'. *Journal of Biogeography* 28:391–407.

Shafer, C.L. (1995). 'Values and shortcomings of small reserves' *BioScience* 45(2):80–88. https://doi.org/10.2307/1312609.

Simpkins, C. E., and Perry, G.L. (2017). 'Understanding the impacts of temporal variability on estimates of landscape connectivity'. *Ecological Indicators* 83:243–248. https://doi.org/10.1016/j.ecolind.2017.08.008.

Sobolev, N.A. (ed.). (1999). *Criteria for Ecological Network Development*. Moscow: Biodiversity Conservation Center (BCC).

Sobolev, N.A. (2003). *The State of Progress of Ecological Networks in the Russian Federation*. Department of Protected Areas and Biodiversity Conservation of the Ministry of Natural Resources (Russian Federation) in collaboration with Biodiversity Conservation Center. http://www.biodiversity.ru/eng/programs/econet.html.

Society for Ecological Restoration International Science & Policy Working Group (2004). *The SER International Primer on Ecological Restoration.* Tucson, USA: Society for Ecological Restoration International.

Stolton, S., Shadie, P., and Dudley, N. (2013). *Guidelines for Applying Protected Area Management Categories: Including IUCN WCPA Best Practice Guidance on Recognising Protected Areas and Assigning Management Categories and Governance Types.* Best Practice Protected Area Guidelines Series, no. 21. Gland, Switzerland: IUCN. https://portals.iucn.org/library/node/30018.

Synes, N.W., Watts, K., Palmer, S.C.F., Bocedi, G., Barton, K.A., Osborne, P.E., Travis, J.M.J. (2015). 'A multi-species modelling approach to examine the impact of alternative climate change adaptation strategies on range shifting ability in a fragmented landscape'. *Ecological Informatics* 30:222–229. https://doi.org/10.1016/j.ecoinf.2015.06.004.

Tabor, G. (2019).'Ecological connectivity: A bridge to preserving biodiversity'. In *Frontiers 2018/19 Emerging Issues of Environmental Concern,* pp. 24-37. Nairobi: United Nations Environment Programme.

Theobald, D M. (2006). 'Exploring the functional connectivity of landscapes using landscape networks'. In K.R. Crooks and M.A. Sanjayan (eds.). *Connectivity Conservation: Maintaining Connections for Nature,* pp. 416–443. Cambridge, UK: Cambridge University Press. https://doi.org/10.1017/CBO9780511754821.019.

Theobald, D.M. (2013). 'A general model to quantify ecological integrity for landscape assessments and US application'. *Landscape Ecology* 28:1859–1874. https://doi.org/10.1007/s10980-013-9941-6.

Tomlinson, M., and Boulton, A.J. (2010). 'Ecology and management of subsurface groundwater dependent ecosystems in Australia – A review'. *Marine and Freshwater Research* 61:936–949. https://doi.org/10.1071/MF09267.

Trombulak, S.D., and Baldwin, R.F. (eds.) (2010). *Landscape-Scale Conservation Planning*. New York: Springer. https://doi.org/10.1007/978-90-481-9575-6.

Tyler, N., Stokkan, K.A., Hogg, C., Nellemann, C., Vistnes, A.I., Jeffrey, G. (2014). 'Ultraviolet vision and avoidance of power lines in birds and mammals'. *Conservation Biology* 28:630–632. https://doi.org/10.1111/cobi.12262.

UNEP-WCMC (United Nations Environment Programme World Conservation Monitoring Centre), IUCN, and NGS (National Geographic Society) (2018). *Protected Planet Report 2018.* Cambridge, UK: UNEP-WCMC; Gland, Switzerland: IUCN; and Washington, DC: NGS. https://livereport.protectedplanet.net/pdf/Protected_Planet_Report_2018.pdf (Accessed: 15 November 2019).

University of Lleida (2007). Software for Quantifying the Importance of Habitat Patches for Landscape Connectivity through Graphs and Habitat Availability Indices. http://www.conefor.org/files/usuarios/CS22manual.pdf (Accessed: 5 February 2018).

Urban, D., and Keitt, T.H. (2001). 'Landscape connectivity: A graph-theoretic perspective'. *Ecology* 82:1205–1218. https://doi.org/10.1890/0012-9658(2001)082[1205:LCAGTP]2.0.CO;2.

Van Dover, C.L. (2014). ‘Impacts of anthropogenic disturbances at deep-sea hydrothermal vent ecosystems: A review’. *Marine Environmental Research* 102:59–72. https://doi.org/10.1016/j.marenvres.2014.03.008.

Vasilijević, M., Zunckel, K., McKinney, M., Erg, B., Schoon, M., and Rosen Michel, T. (2015). *Transboundary Conservation: A Systematic and Integrated Approach*. Best Practice Protected Area Guidelines Series, no. 23, Gland, Switzerland: IUCN. https://doi.org/10.2305/IUCN.CH.2015.PAG.23.en.

Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., Levy, M.A., and Watson, J.E.M. (2016). ‘Sixteen years of change in the global terrestrial footprint and implications for biodiversity conservation’. *Nature Communications* 7:12558. https://doi.org/10.1038/ncomms12558.

Venter, O., Magrach, A., Outram, N., Klein, C.J., Possingham, H.P., Di Marco, M., Watson, J.E.M. (2017). ‘Bias in protected-area location and its effects on long-term aspirations of biodiversity conventions’. *Conservation Biology* 32:127–134. https://doi.org/10.1111/cobi.12970.

Volenec, Z.M., and Dobson, A.P. ‘Conservation value of small reserves’. *Conservation Biology* 34:1 (2020): 66–79. https://doi.org/10.1111/cobi.13308

Walker, B., and Salt, D. (2006). *Resilience Thinking: Sustaining Ecosystems and People in a Changing World.* Washington, DC: Island Press.

Watson, J.E.M., Venter, O., Lee, J., Jones, K.R., Robinson, J.G., Possingham, H.P. and Allan, J.R. (2018). ‘Protect the last of the wild’. *Nature* 563 7729:27–30. https://doi.org/10.1038/d41586-018-07183-6.

Weeks, R. (2017). ‘Incorporating seascape connectivity into conservation prioritisation’. *PloS One* 12:1–16. https://doi.org/10.1371/journal.pone.0182396.

Weldon, A.J. (2006). ‘How corridors reduce indigo bunting nest success’. *Conservation Biology* 20(4):1300–1305. https://doi.org/10.1111/j.1523-1739.2006.00403.x

White, J.W., Scholz, A.J., Rassweiler, A., Steinback, C., Botsford, L.W., Kruse, S., Costello, C., Mitarai, S., Siegal, D.A., Drake, P.T., and Edwards, C.A. (2013). ‘A comparison of approaches used for economic analysis in marine protected area network planning in California’. *Ocean & Coastal Management* 74:77–89. https://doi.org/10.1016/j.ocecoaman.2012.06.006.

Wittemyer, G., Elsen, P., Bean, W.T., Burton, A.C.O., and Brashares, J.S. (2008). ‘Accelerated human population growth at protected area edges’. *Science* 321:123–126. https://doi.org/10.1126/science.1158900.

Worboys, G.L., Lockwood, M., Kothari, A., Feary, S., and Pulsford, I. (eds.). (2015). *Protected Area Governance and Management.* Canberra: ANU Press. https://doi.org/10.22459/PAGM.04.2015.

Wu, J. (2008). ‘Landscape ecology’. In: S.E. Jorgensen (ed.). *Encyclopedia of Ecology*, pp. 2103–2108. Oxford, UK: Elsevier. https://doi.org/10.1016/B978-008045405-4.00864-8.

Zhang, H.K., Cheng, H.F., Zhuyun, L.I., and Li, D.Q. (2007). ‘Status and conservation strategy of giant panda habitat in Qinling tunnel area of 108 national road’. *Journal of Shaanxi Normal University (Natural Science Edition):* S1.

Annex: Approaches to conserving ecological corridors in ecological networks

Introduction

This compendium of case studies illustrates initiatives around the world that are working toward protecting or restoring ecological connectivity. The case studies offer insight into the breadth of approaches being used to advance conservation of ecological corridors to benefit ecological networks in terrestrial, freshwater and marine realms (Table 5). Each case study describes the context and challenges to connectivity in the study region, explains the approach to conservation, presents an example of an ecological corridor in the network, and shares some results. The case studies were selected to demonstrate a variety of ecological networks for conservation and ecological corridors within them, as well as a variety of approaches to their conservation. These examples can help us understand both the diversity of current efforts and the need to move toward formalising ecological corridors as elements of ecological networks for conservation

Table 5. Schematic overview of the case studies.

Case study title	Type of study region	Greatest threat to connectivity	Approaches to conserving ecological corridors
1. Kilimanjaro Landscape: Ensuring the viability of wildlife populations	terrestrial, rural	habitat loss and fragmentation	• conservation lease programme for private landowners
2. Connectivity conservation in the Kavango Zambezi Transfrontier Conservation Area: The Zambezi-Chobe Floodplain Wildlife Dispersal Area	terrestrial, rural	deforestation, uncontrolled settlements, overgrazing, over-exploitation of fish, uncontrolled fires	• establishment of a five-country transfrontier conservation area • development of integrated development plans • creating awareness and engaging local stakeholders • establishment of community conservancies • promotion of conservation agriculture • establishment of wildlife sanctuaries
3. Conserving six landscapes of the Albertine Rift to ensure connectivity	terrestrial, rural	habitat loss and fragmentation	• facilitating cooperation • developing sustainable-use community areas
4. The Kilombero Valley Ramsar site, United Republic of Tanzania	terrestrial, rural	sustained human immigration and growing settlements and agriculture	• designation as a Ramsar site • transitional governance approach from central management of large protected areas to management of a mosaic of smaller protected areas
5. Ecological corridor for the reunion of giant pandas in the Qinling landscape	terrestrial, rural	highway and human land use	• baseline survey and mapping • habitat restoration • community engagement • traffic management • capacity enhancement • wildlife monitoring
6. Thailand's experience in ecologically connecting its protected areas	terrestrial, rural	deforestation and conversion of forests into plantations	• establishment of non-hunting areas and buffer zones • management of lands for connectivity
7. East Coast Conservation Corridor in Tasmania	terrestrial, rural	land-use change	• restoration • land-use planning • management for connectivity
8. The Great Eastern Ranges: Australia's first continental-scale ecological network for conservation	terrestrial, rural	land degradation	• restoration • conservation by private landowners • community education • biological surveys • research programs

Table 5 (continued). Schematic overview of the case studies.

Case study title	Type of study region	Greatest threat to connectivity	Approaches to conserving ecological corridors
9. COREHABS to BearConnect: Securing ROAMing in the wilderness corner of Europe	terrestrial, rural	rapid infrastructure development	• identification and assessment of ecological corridors • integration of protected areas and ecological corridors into cadastral plans and land registers
10. Ecological connectivity in an urban context: Utrechtse Heuvelrug, Netherlands	terrestrial, urbanised	pressures from infrastructure, urban expansion, intensive agriculture and recreation	• landscape defragmentation through road crossings and open space preservation
11. The Spanish National Network of Drover's Roads (Vías Pecuarias)	terrestrial, rural and urbanised	loss of extensive livestock farming and transhumance	• legal protection • ecological corridor demarcation • fostering of extensive livestock farming, encouragement of young people to transhumance and cattle farming • restoration • education • exploitation of multifunctionality
12. ECONET: Ecological network in the Kostroma Region, Russia	terrestrial, rural	deforestation	• ecological network consisting of protected areas and ecological corridors • protected areas with different regimes of multifunctional activities
13. Sustaining forested landscape connections in the northern Appalachians: The Staying Connected Initiative	terrestrial, rural and urbanised	fragmentation from roads and human development	• focus work in nine highest-priority linkage areas • strategic land protection • land-use planning • community outreach and engagement • habitat restoration • transportation mitigation
14. Yellowstone to Yukon (Y2Y): Connecting and protecting one of the most intact mountain ecosystems	terrestrial, rural	fragmentation from roads and human development	• protection of areas important for biodiversity • restoration and maintenance of areas for ecological connectivity • direction of development away from areas of biological importance • promotion of people and wildlife living in harmony
15. Conserving long-distance migration: The Red Desert to Hoback Mule Deer Corridor, Wyoming, USA	terrestrial, rural	human development	• detailed mapping of migration routes • assessments of land-use patterns and threats along the routes • land protection • land management • road crossings
16. Corridors for life: Improving livelihoods and connecting forests in Brazil	terrestrial, rural	landscape fragmentation from agriculture and settlements	• vision plan for large-scale reforestation • enlargement and eventual connection of forest fragments through reforestation • adoption of biodiversity-friendly land-use options • promotion of change in land-use practices • adoption of sustainable agriculture and agroforestry • improvement of farmers' livelihoods • carbon offsets
17. Connectivity, ecosystem services and Nature-based Solutions in land-use planning in Costa Rica	terrestrial, rural	human development	• municipal land management plans

Table 5 (continued). Schematic overview of the case studies.

Case study title	Type of study region	Greatest threat to connectivity	Approaches to conserving ecological corridors
18. The Jaguar Corridor Initiative: A range-wide species conservation strategy	terrestrial, rural	human land-use changes	• modelled ecological corridors • prioritised populations and ecological corridors • validated modelled corridors using a rapid-assessment interview-based methodology • varied implementation action at local level
19. Grassroots reserves have strong benefit for river ecosystems in the Salween River Basin	freshwater, rural	overfishing	• ecological networks of small riverine reserves
20. The ecological corridor Mura-Drava-Danube and future five-country biosphere reserve	freshwater, rural	human land-use changes	• transboundary cooperation for harmonised conservation, integrated management and restoration • establishment of a transboundary biosphere reserve
21. Pacific salmon watersheds: Restoring lost connections	freshwater, rural	dams hindering fish migrations	• dam removal and mitigation to benefit salmon and other migratory fishes
22. Fragmentation of riparian protections throughout catchments, Oregon, USA	freshwater, rural	human land uses and fragmented land protections along the continuum of the river	• development of an understanding of the mosaic of protective efforts to identify gaps in them
23. Protection of the free-flowing Bita River	freshwater, rural	extractive industries, livestock grazing, large timber plantations, and urbanisation	• formation of an alliance • working with local stakeholders • decision-making framework to choose best conservation actions • protection as a Ramsar site
24. The Great Barrier Reef – Systematically protecting connectivity without connectivity data	marine	recurrent coral reef bleaching, cyclones, invasive species outbreaks, poor water quality, unsustainable fishing, dredging and coastal development	• networks of strategically placed marine reserves • zoning based on systematic planning principles
25. Northern Channel Islands: Connectivity across a network of marine protected areas contributes to positive population and ecosystem consequences	marine	human impacts such as fisheries, invasive species, and climate change	• marine protected area network with resulting ecological corridors

Terrestrial connectivity: Africa

1. Kilimanjaro Landscape: Ensuring the viability of wildlife populations

Kathleen H. Fitzgerald, *African Wildlife Foundation*

Key lesson

Conservation lease agreements support the viability of Amboseli National Park wildlife populations, and could move toward being enduring ecological corridor(s) recognised by the world.

Context and challenge

The transboundary Kilimanjaro Landscape stretches from Amboseli National Park to Chyulu National Park and Tsavo West National Park in Kenya to Mount Kilimanjaro National Park in Tanzania (Figure 1). Amboseli National Park, 392 km^2, forms the core of the ecosystem while six community lands, group ranches, surround the park. Amboseli National Park is world-renowned for its elephants and magnificent views of Mount Kilimanjaro, but the park is too small to support viable populations of wildlife. Wildlife depends on the unprotected areas outside the park. If the ecosystem is to support wildlife in the long term, the areas surrounding the park must be protected.

The greatest threat in the landscape is habitat loss and fragmentation (Figure 2). A majority of the group ranch land surrounding the park was subdivided into 0.8-ha, 4-ha and 24-ha lots allocated to individual Maasai landowners. The subdivision is primarily due to a breakdown in communal systems, failure of the group ranch system to deliver equitable benefits and improve community livelihoods, and a more sedentary way of life. Some Maasai landowners are selling their land for development and agriculture.

Approach

In 2008, the African Wildlife Foundation (AWF, www.awf.org) launched a conservation lease program to:

- Contribute to the sustainability of Amboseli National Park by protecting strategic ecological corridors;
- Prevent conversion of habitat; and
- Provide incentives directly to landowners to keep their land open and passable to wildlife.

AWF worked with individual landowners to help them understand that collectively their land was more valuable than individually, which resulted in the landowners forming associations. This enabled them to make collective decisions while retaining and benefitting from their individual landownership. These associations range in size from 50 to 90 landowners. Through these associations, AWF engaged the landowners in a discussion about conservation leases and payment for ecosystem services (PES). AWF proposed to lease land from the Maasai via a PES arrangement and pay them to keep their land open for wildlife. Different organisations now manage and pay for the leases in the Amboseli ecological corridors, including AWF, Tawi Lodge

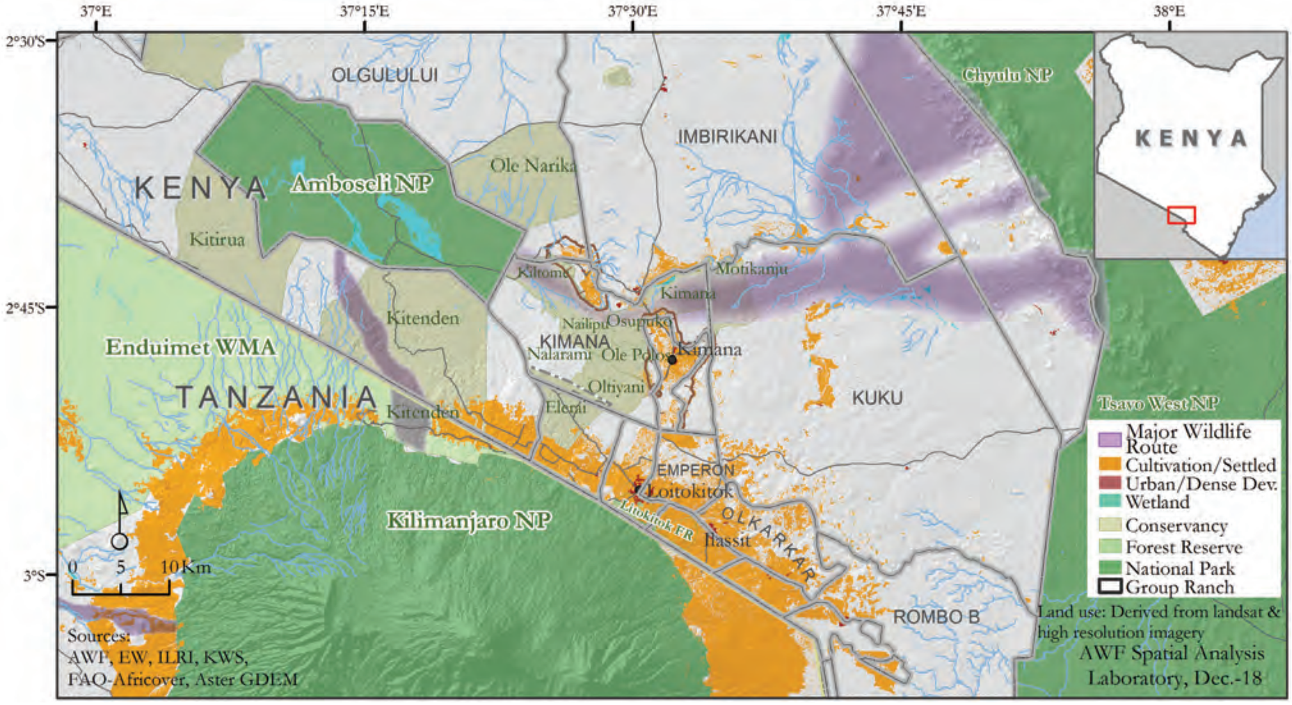


Figure 1. The Kilimanjaro landscapes showing community-owned wildlife conservancies established by AWF to protect key ecological corridors
© African Wildlife Foundation

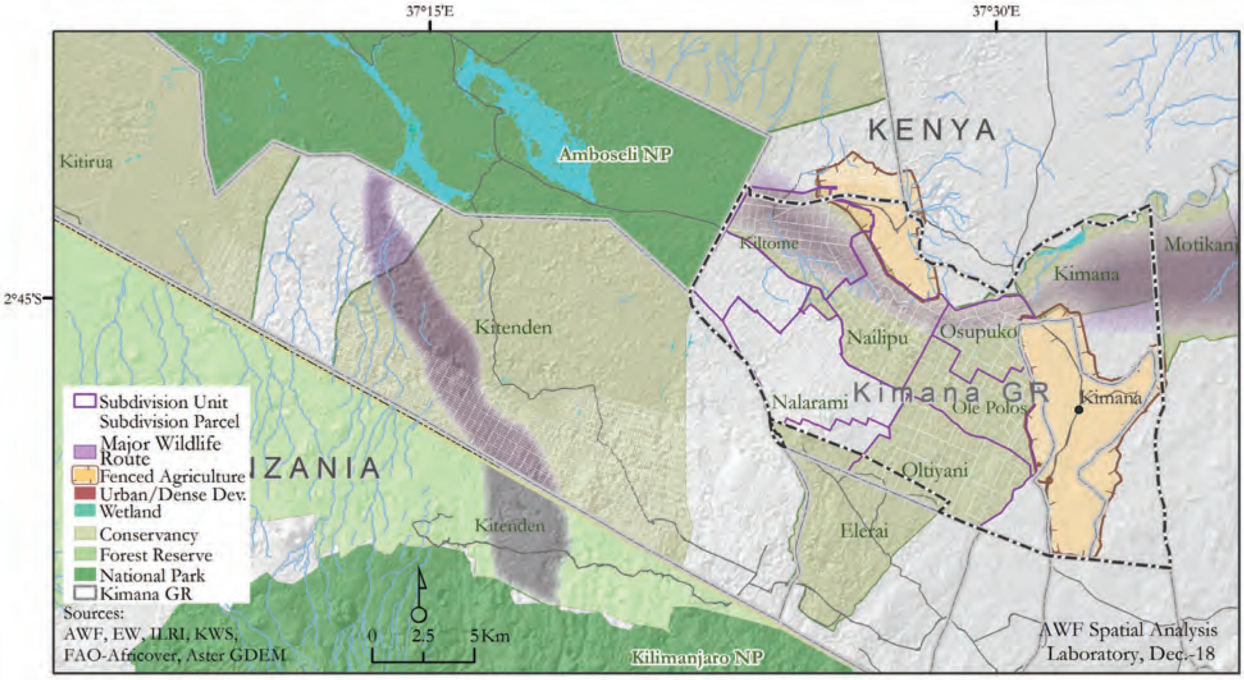


Figure 2. Land subdivision in the Kilimanjaro landscape. The Kimana Group Ranch is located east of Amboseli National Park. © African Wildlife Foundation

(www.tawilodge.com), the Big Life Foundation (www.biglife.org), and IFAW, the International Fund for Animal Welfare (www.ifaw.org).

Example of an ecological corridor

In one specific area, the Kimana Group Ranch, directly east of Amboseli, AWF worked with the landowners and presented a conservation lease agreement in a series of community meetings. Women, youth and men participated in these meetings. They were held in the local language, Kimaasai, with translation as needed into Swahili and English. AWF's community organiser, who was from the Kimana community, was pivotal in organising and facilitating these meetings.

The conservation lease outlines the purpose, terms, land-use restrictions, retained rights, payment requirements, how violations will be addressed, and other relevant issues. The purpose of the conservation lease is to "provide habitat, dispersal and movement areas for wildlife" and to help "connect conservation areas" and "contribute to the survival of wildlife areas in the Amboseli ecosystem as well as the continued existence of ecotourism as a means of poverty reduction and economic development and overall public benefit by ensuring that wildlife species endure for the benefit of future generations."

The conservation lease prohibits building new houses, fencing, logging, mining, dredging, agriculture, resource extraction, non-tourism-related commercial activity, and illegal taking of wildlife. Grazing is permitted in compliance with a management plan. The community selected a Maasai attorney who met with them (in the absence of AWF) to review the lease agreement in its final stage before signing. By having this meeting without AWF, community members were free to voice concerns, and changes were made as a result. AWF paid the fees of the attorney for the community. The extensive community engagement took approximately eight months. AWF determined the value of the lease by doing a market assessment of other leases related to tourism and agriculture in the region. While these leases are not permanent, the hope is that this will be a step toward permanent protection.

Results

Currently there are five community conservancies involving more than 350 individual landowners that protect approximately 8,000 ha of ecological corridors that connect protected areas. With an average household of seven, the lease program is directly benefitting over 2,450 individuals, and this does not include employment beneficiaries, such as scouts.

One of the challenges with PES programs is sourcing the funds. The protected area authority recognises the importance of the ecological corridors, but is unable to pay; thus, the project relies on donors. Because the land is privately owned and the program entirely voluntary, there are landowners who have chosen not to participate. This has resulted in fragmentation and fencing, putting at risk the long-term viability of the program.

2. Connectivity conservation in the Kavango Zambezi Transfrontier Conservation Area: The Zambezi-Chobe Floodplain Wildlife Dispersal Area

Lésa van Rooyen, *Peace Parks Foundation*

Context and challenge

The Kavango Zambezi (KAZA) Transfrontier Conservation Area (TFCA) is situated in the Kavango and Zambezi river basins where the borders of Angola, Botswana, Namibia, Zambia and Zimbabwe converge (Figure 1). It spans an area of approximately 520,000 km^2 and includes 36 proclaimed protected areas. The KAZA TFCA countries support over 200,000 elephants, most of which are found south of the Zambezi River. Due to human activities, the KAZA TFCA faces habitat fragmentation and loss of connectivity. Protected areas could become isolated ecological islands, leading to reduced biodiversity and blocked elephant movement. The major threats to the area are as follows:

- the deforestation of the area to create fields for agriculture and for making charcoal;
- uncontrolled settlements along main roads and watercourses, which cause fragmentation of the landscape;
- overgrazing of the area due to uncontrolled cattle numbers;
- over-exploitation of fish due to unsustainable fishing practices; and
- uncontrolled fires in the Simalaha floodplain wetland ecosystem.

A key objective of the KAZA TFCA is to form a transboundary ecological network to ensure connectivity between key protected wildlife areas and, where necessary, reconnect isolated wildlife areas.

Key lesson

Designated wildlife dispersal areas established in collaboration with local communities are a promising step toward legal agreements to maintain connectivity for wildlife.

Figure 1. Kavango Zambezi Transfrontier Conservation Area. The major threat to biodiversity in the project area is the over-utilisation of resources in the sensitive wetlands of the Simalaha Floodplain, identified in the centre of the figure. The Kasaya River marks the boundary between the two chiefdoms and flows through the middle of the Simalaha Community Conservancy. © Peace Parks Foundation

Approach

The KAZA TFCA commenced in 2006 when a memorandum of understanding was signed by the five partner countries to establish the world's largest transfrontier conservation area. Each of the five countries agreed to create an Integrated Development Plan to indicate how the national development plans will link across borders. The process was also used to create awareness and engage local stakeholders. A Master Integrated Development Plan was created that identifies six transboundary wildlife dispersal areas (WDAs), which are critical to re-establish connectivity and conserve large-scale ecological systems that extend beyond the boundaries of protected areas.

Example of an ecological corridor

The Zambezi-Chobe Floodplain WDA contains several sensitive areas, mainly along the rivers and associated floodplains, which are not formally protected. Located centrally in this WDA is the Simalaha floodplain in Zambia, which was identified by the communities as a critically important area that should be secured to ensure connectivity between Chobe National Park in Botswana and Kafue National Park in Zambia. The communities recalled that the area used to be a haven for animals, and mobile species such as elephant and buffalo used to move through the area.

Peace Parks Foundation has worked with the Sesheke and Sekute chiefdoms over the past ten years to establish and develop the Simalaha Community Conservancies (180,000 ha) in collaboration with the local traditional leadership and communities to secure the land for conservation. The Sesheke and Sekute chiefdoms created a steering committee made up of members of the Kutas, the two traditional councils. A working group was established, with representation from the Kutas and Peace Parks Foundation, to coordinate activities such as acting as liaison with communities and developing a land-use plan. Peace Parks was requested to assist with fundraising to implement the project. The first funds received assisted with an awareness and sensitisation programme during which the working group members visited different villages to explain the community conservancy concept. During this time the boundaries of the conservancy were delineated with input from the community. The two chiefs confirmed the boundary by signing a copy of the map, and submitted it to the Ministry of Land for its records.

The Simalaha Community Conservancy is managed on business principles and registered as a legal entity. A local attorney was appointed to assist with the drafting of a constitution and the establishment of an appropriate legal structure. A community trust was created that is the owner of the assets. The trust established a for-profit company that manages the business side of things and also looks after the wildlife management and tourism development. Any profits made by the company are paid to the trust for distribution to the beneficiaries according to a predetermined formula. Seven Village Action Groups were formed to represent the communities. The Simalaha Community Conservancy was officially launched in 2012.

Results

From the start, there was general acceptance of the project and great enthusiasm from the traditional leadership. However, because the development of a wildlife product takes time and significant resources, it was important also to create alternative livelihood options. Conservation agriculture was successfully introduced and became the preferred farming method, producing higher yields than traditional methods.

A 24,000-ha wildlife sanctuary was fenced and stocked with plains game species (wildebeest, *Connochaetes* spp.; zebra, *Equus* spp.; defassa waterbuck, *Kobus defassa*; impala, *Aepyceros melampus*; red lechwe, *Kobus leche*; puku, *Kobus vardonii*; giraffe, *Giraffa camelopardalis*; and buffalo, *Syncerus caffer*). Initially, around 780 animals were translocated, a number which increased to over 1,400 animals by the end of 2018.

Twenty village scouts were trained to look after the wildlife. In the five years that wildlife has been in the sanctuary, only one poaching incident was recorded – a person from outside the area set snares. The local community reported the incident, showing that the communities have taken ownership of the wildlife. Although fences initially played an important role in containing the translocated wildlife, the long-term plan is to remove them and allow the wildlife to move freely. Seasonal migration of wildlife is already observed, as wildlife move into the woodlands and higher ground during the flooding period and back to the floodplain along the Zambezi River during the dry winter period.

The story of the Simalaha Community Conservancy spread quickly between traditional leaderships and soon other chiefs visited the area to learn more about the project. Other conservancies are being established as a result. Exchange visits with traditional leaders in Namibia may lead to the expansion of existing conservancies on the Namibian side to ensure a link between Chobe National Park to Simalaha Community Conservancy.

The Zambezi-Chobe Floodplain is, at this stage, not a functional WDA. Once existing community conservancies have been expanded and new ones added, the Zambezi-Chobe Floodplain is expected to start functioning as a WDA. Improved law enforcement capacity in Angola and Zambia along the Kwando river is increasing the numbers of elephants moving into Luengue Luiana National Park in Angola because of the increased safety.

3. Conserving six landscapes of the Albertine Rift to ensure connectivity

Andrew J. Plumptre, *Key Biodiversity Areas Secretariat (formerly of Wildlife Conservation Society)*

Context and challenge

The Albertine Rift region spans six countries (Burundi, Democratic Republic of Congo, Rwanda, Uganda, United Republic of Tanzania, Zambia) and is one of the most biodiverse parts of Africa, with more endemic and threatened species of vertebrates than elsewhere on the continent (Figure 1) (Plumptre et al., 2007). It is also a region with one of the highest human population densities in Africa, and as a result has lost 30% of its natural habitat to agriculture and settlement (Ayebare et al., 2018). While relatively well covered by protected areas, many of them are separated from each other and in danger of becoming isolated islands of natural habitat in a sea of agriculture.

Approach

In 2000, the MacArthur Foundation financed a collaborative planning approach for the Albertine Rift that brought together the national governments and many conservation organisations to develop a conservation framework plan.

Key lesson

Local communities are engaged in connectivity conservation by recognising that designating areas for ecological connectivity will also protect their ancestral lands from new settlers. Recognition of local connectivity areas at the federal and/or global level would help local connectivity conservation.

This overarching framework identified six key landscapes in the Albertine Rift that potentially could be managed at the landscape level to ensure connectivity between protected areas (Figure 1).

Detailed conservation plans were developed for each of the six landscapes. The two transboundary landscapes (the Greater Virunga Landscape and the Congo-Nile Divide) each developed a memorandum of understanding (MOU) for

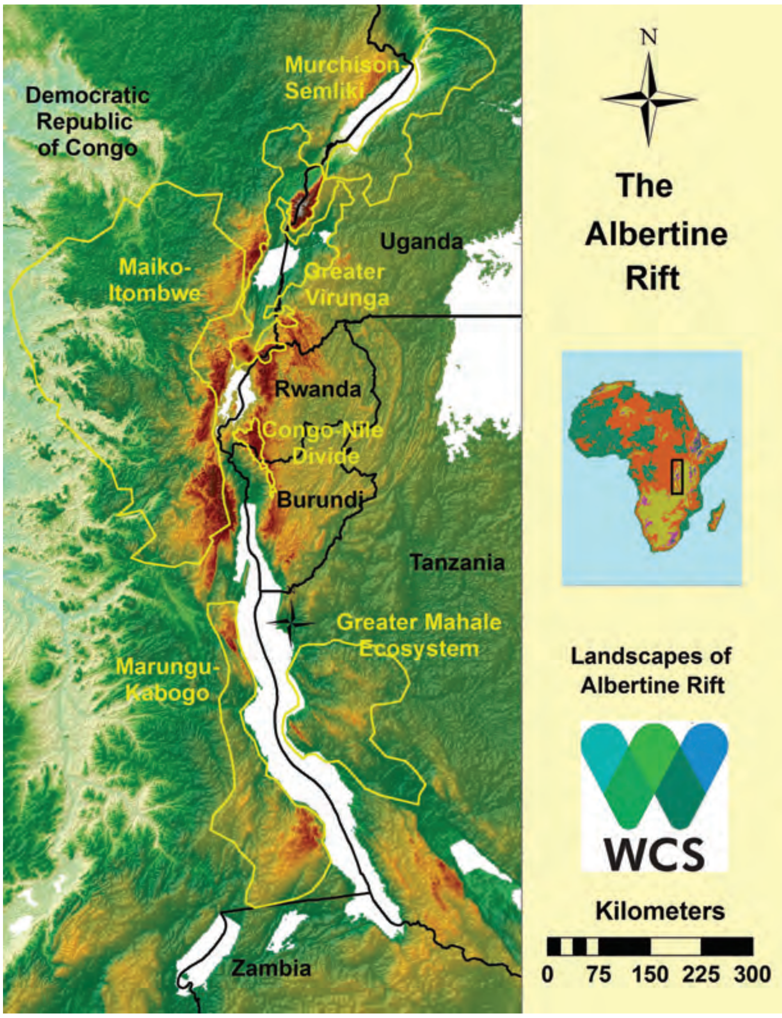


Figure 1. The six landscapes of the Albertine Rift © A.J. Plumptre

collaboration. In the Greater Virunga Landscape the MOU evolved into a transboundary treaty for conservation of the landscape. Funds were then raised to implement the plans. In some regions, biodiversity surveys were conducted, and systematic conservation planning was done using distribution models of endemic species in the region. This analysis identified additional critical areas outside the existing ecological networks for conservation in the six landscapes (Plumptre et al., 2017).

Examples of ecological corridors

Implementation of connectivity conservation in the Albertine Rift varied greatly. In the Murchison-Semliki Landscape, a highly populated, fragmented region with many immigrants looking for land, the focus was on conserving remaining ecological corridors (Figure 2). Forest corridors along streams and rivers and a savannah corridor along the escarpment above Lake Albert were protected. In the Maiko-Itombwe Landscape, large areas of contiguous tropical forest still exist. Therefore, the focus was on working with local people to set aside some of the most important areas as protected areas and linking them with ecological corridors in the form of sustainable-use community areas (Figure 3). Local communities were willing to engage in the process because they realised that it would help them protect their ancestral lands from people migrating into the area from outside their culture.

In the two transboundary landscapes the main focus was on the protected areas because most natural habitat outside of them had already been lost. However, landscape-scale conservation and management are still important for species moving long distances, such as lions, elephants, spotted hyenas, leopards, chimpanzees, mountain gorillas and vultures. Ensuring that the existing connectivity between protected areas will not be severed by park developments and tourism infrastructure is important for these species.

Results

Since 2000, conservation action plans have been developed for each of the six landscapes and are recognised locally, nationally, and for the transboundary landscapes, internationally. Maintaining or restoring connectivity between existing protected areas has been more successful in some landscapes than others.

Biodiversity surveys in parts of the Democratic Republic of Congo led to the creation of four new protected areas: Itombwe Natural Reserve and Tayna Reserve in the Maiko-Itombwe Landscape, and Kabobo and Ngandja reserves in the Marungu-Kabobo Landscape. They ensure maintenance of connectivity and conservation of endemic and threatened species in these two landscapes. To maintain connectivity, several other community reserves were designated and are

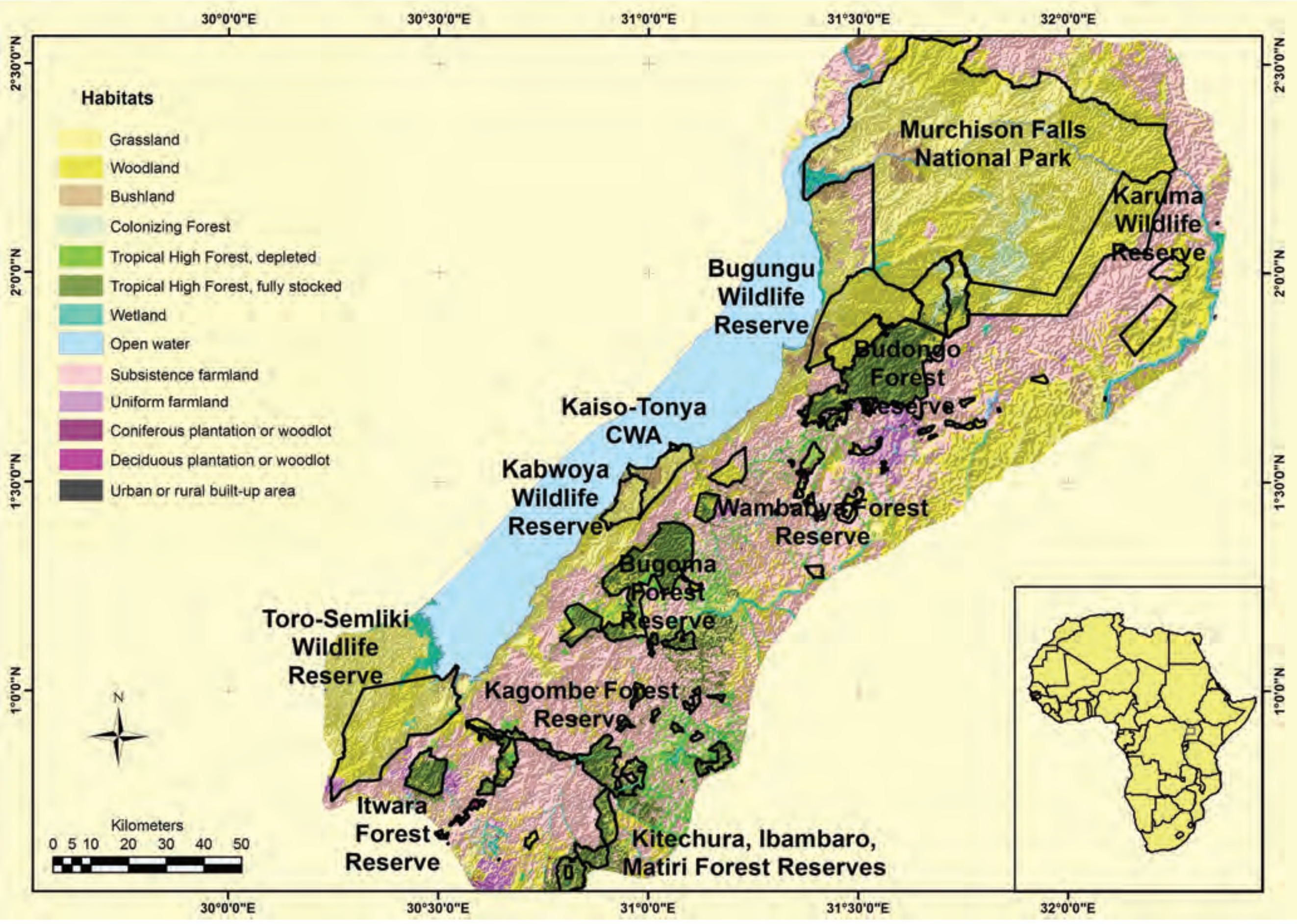


Figure 2. The main protected areas and natural habitats in the Murchison-Semliki Landscape © A.J. Plumptre

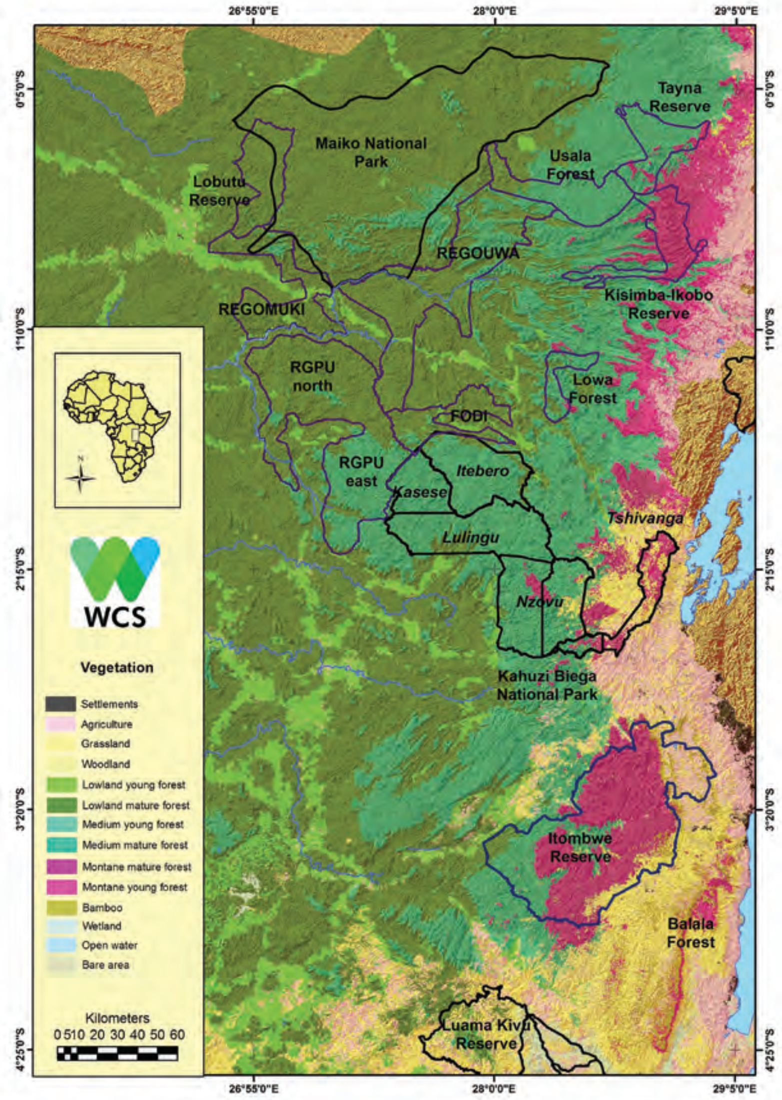


Figure 3. The main protected areas (black borders), community reserves (blue borders) and natural habitat in the Maiko-Itombwe Landscape © A.J. Plumptre

locally recognised in the Maiko-Itombwe Landscape, but have not been legally recognised at the national level. In addition, a fifth protected area, Oku Primate Reserve, is being established by local communities in the same landscape to better connect and conserve Grauer's gorilla and elephant populations.

In the Marungo-Kabobo region, efforts were made to establish these two contiguous protected areas, which represent the largest block of forest along Lake Tanganyika.

While connectivity still exists in the Greater Mahale Landscape, a too-narrow focus on chimpanzees is hindering the conservation of several other endemic species, many of which have different habitat and connectivity requirements. There is a need to develop conservation plans that consider the broader biodiversity of this region. However, the recognition of these large landscapes is helping with their longer-term conservation and management. More resources are needed to implement conservation action, but limited resources are being used effectively to maintain connectivity at the landscape scale.

4. The Kilombero Valley Ramsar site, United Republic of Tanzania

Giuseppe Daconto, *formerly of the Belgian Development Agency / Tanzanian Ministry of Natural Resources and Tourism*

Key lesson

This Ramsar site requires a framework for conservation that includes ecological corridors to guide efforts by the central government and local stakeholders.

Context and challenge

The Kilombero Valley is a floodplain about 220 km long and up to 70 km wide in the Rufiji River catchment in southern Tanzania, sandwiched between the Udzungwa Mountains and the Mahenge Hills (Figure 1). Multiple tributaries converge in the valley, forming the Kilombero River. During the rainy season, water runoff from the steep tributaries rapidly reaches the valley floor and transforms it into a large swamp. The extensive valley used to be a dry-season refuge and offered multiple connectivity routes for wildlife populations moving between the Udzungwa range and the Selous Game Reserve, and thus played a critical role for connectivity at a regional scale in southern Tanzania. The floodplain used to host significant wildlife populations, including elephants and a large number of the near-threatened puku antelope. Starting in the 1990s, the landscape underwent radical change, driven by sustained human immigration and growing settlements, massive expansion of rice farming and livestock grazing, deforestation and development of infrastructure. Rice growing and grazing have drastically reduced the natural wetland habitat. Land-use changes and settlements have almost completely disrupted wildlife connectivity across the valley. Game populations have been decimated (Leemhuis et al., 2017).

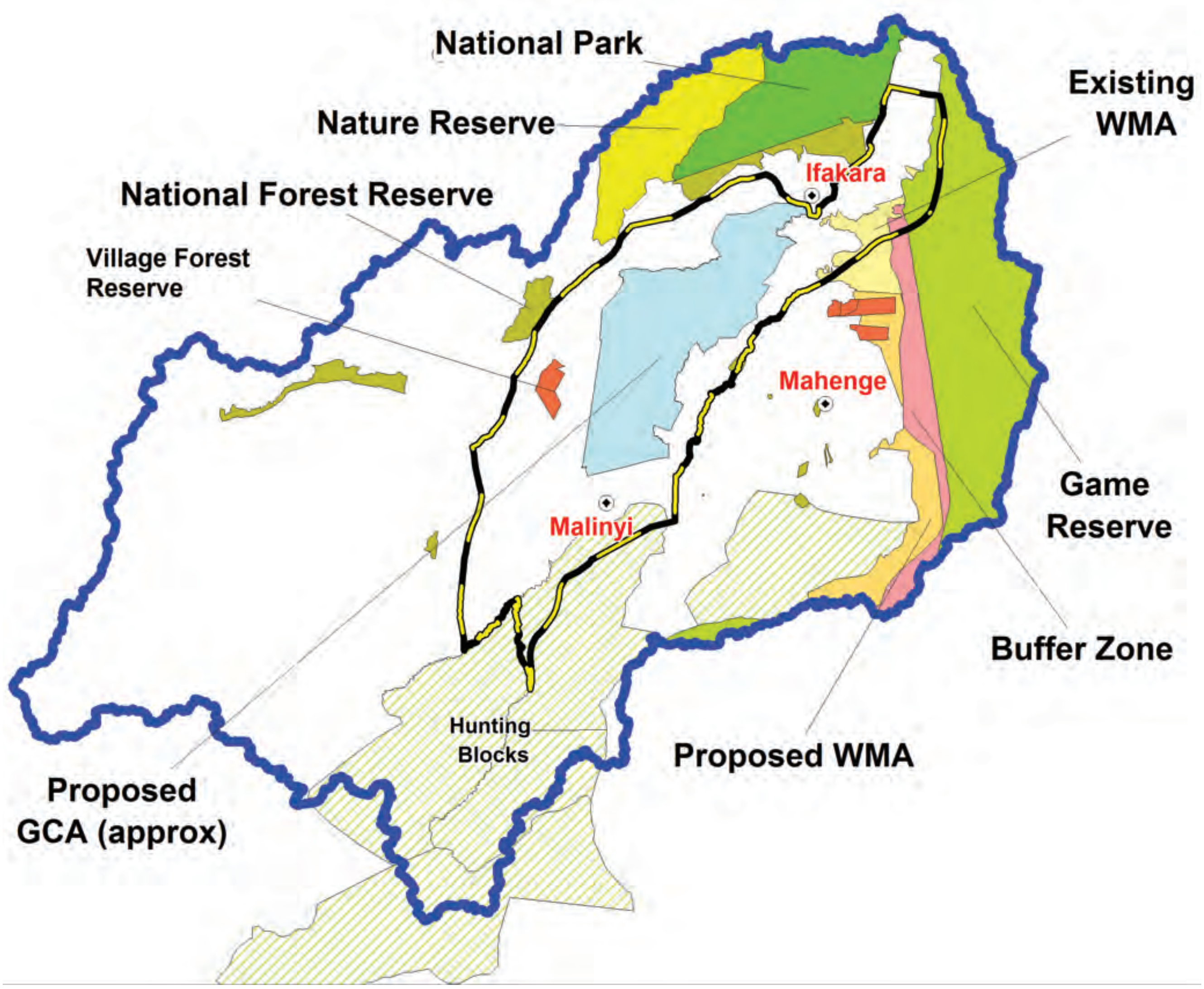


Figure 1. Protected areas in the Kilombero catchment (source: plan document). The Ruipa Ecological Corridor connects Udzungwa National Park and Kilombero Nature Reserve to the Selous Game Reserve, crossing the Kilombero Valley south of Ifakara. The black-and-yellow line outlines the Ramsar site.

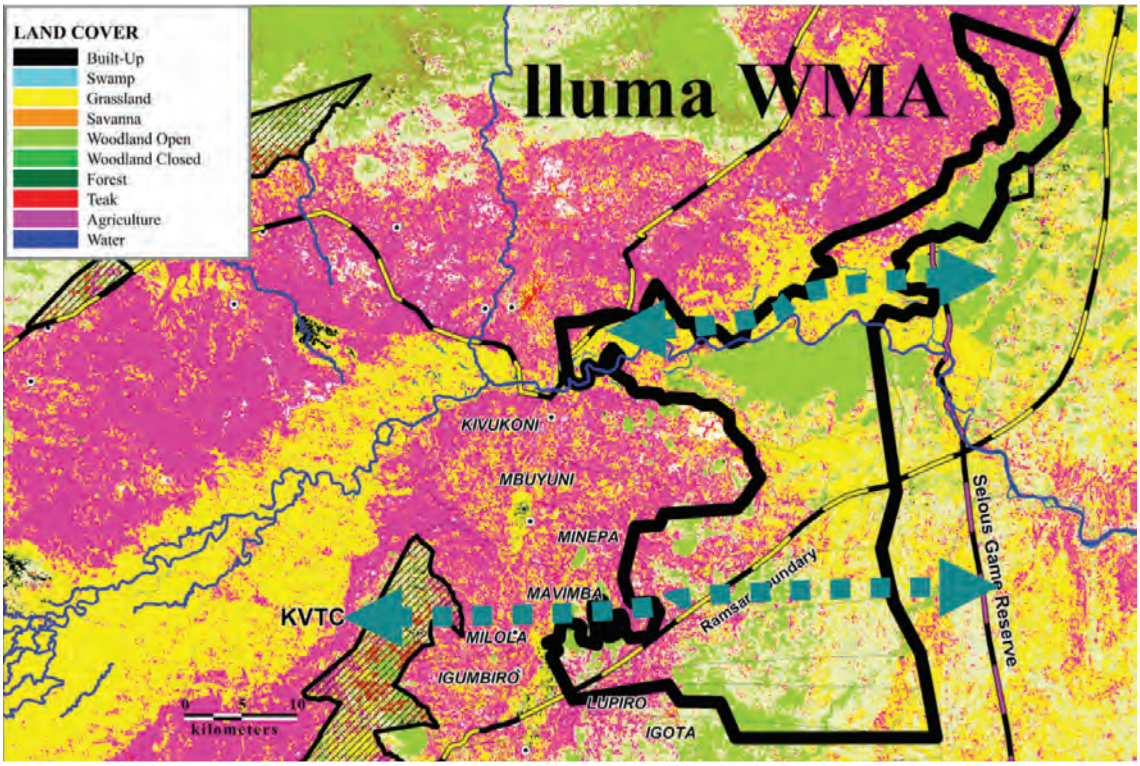


Figure 2. Detailed land-use analysis of the Ruipa-East corridor connecting the valley to Selous Game Reserve. Source: Plan documents.

Approach

The central government has maintained nominal authority over the core area and large tracts of land in the watersheds. The designation of the area as a Ramsar site in 2000 underscored the importance of the landscape. However, social and economic change has been mostly unregulated. Land conflicts abound and are heavily politicised. The management of the landscape, including the conservation of residual wildlife areas, maintenance of connectivity, and the preservation of broader ecological values and functions of the valley requires mediation across several local and national interests. Management of the valley needs to include several sectorial agencies, four district authorities and hundreds of villages, which are the ultimate land management authorities in Tanzania. The governance approach needs to transition from the traditional central management of large protected areas to management of a mosaic of smaller ones embedded in thriving agricultural areas, some under central government, and others under local control. The Integrated Management Plan for the Kilombero Valley Ramsar Site, developed 2016–2018 by the Ministry of Natural Resources and Tourism, is a framework to enable this gradual transition. The preparation of the plan was supported by Belgian Aid and the European Union, through the Kilombero and Lower Rufiji Ecosystem Management Project. Background analysis and planning documents are available from https://kilomberovalley.wordpress.com/.

Maintaining and restoring ecological connectivity will require actions at local, regional and national levels:

1. Consolidation of the core area of the valley (about 2,000 km^2) under central government control.
2. Management of development pressure in the agricultural and settlement belt around the core area. The population of this belt is projected to exceed 1 million by about 2040 at the present trend.
3. Consolidation and effective protection of a constellation of small areas across the landscape. Some of these are owned by villages and managed under the devolved statutes of wildlife management areas or village forest reserves; others are hunting concessions, private land leased for forestry and farming, or areas protected by a local government.
4. Protection and rehabilitation of residual natural habitat on farmland along the tributaries to the main river. This requires effective planning and control over village land use and farming practice, which are mostly very weak, and the coordination of land use across multiple villages, which is almost non-existent.
5. Preservation of the hydrological cycle of the river and its seasonal pulse through effective catchment-scale water resource management.

Example of an ecological corridor

The Ruipa ecological corridor is a link for wildlife moving between Selous Game Reserve in the east and the Udzungwa Mountains in the west (Figure 2). This large-mammal corridor (0.5–6 km wide, 20 km long) crosses a mosaic of habitats, including riverine forest, woodland, scrub, degraded pasture and swamp. Much of the western part of the corridor is degraded but the eastern part still retains limited functionality. Elephants (*Loxodonta* spp.) and buffalo (*Syncerus caffer*) use the corridor annually to migrate between protected areas, although their numbers have declined significantly in recent years. Other animals historically reported

Buffalo (*Syncerus caffer*) © Adobe Stock

from the corridor include the aardvark (*Orycteropus afer*), Angolan black-and-white colobus (*Colobus angolensis*), bushbuck (*Tragelaphus sylvaticus*), crested porcupine (*Hystrix cristata*), Harvey's duiker (*Cephalophus harveyi*), hippopotamus (*Hippopotamus amphibius*), leopard (*Panthera pardus*), lion (*Panthera leo*), puku (*Kobus vardonii*), spotted hyaena (*Crocuta crocuta*), waterbuck (*Kobus ellipsiprymnus*) and the Udzungwa red colobus (*Procolobus gordonorum*), which is endemic to the Udzungwa Mountains. The Ruipa Corridor and several others that cross the Kilombero floodplain have a high conservation significance, as they are perhaps the only viable links remaining between the western and southern Tanzania elephant populations.

Results

The plan provides an overall framework for the very complex undertaking of managing this landscape and rehabilitating its ecological connectivity. Extensive appraisals during the plan preparatory process and other works have identified several action priorities. The implementation requires an institutional mechanism able to:

1. Coordinate many local stakeholders and diverging priorities for land and water use;
2. Establish an effective coordination between the government's sectors of land administration, conservation and water resource management;
3. Bridge central government control and effective devolution and decentralisation (mostly through the national framework for community-based natural resource management, but also by ensuring that local authorities receive some minimum budget transfers from the central government); and
4. Negotiate land-use coordination in priority connectivity areas.

A long-term vision anchored in the conservation agencies could in principle underpin a long-term adaptive management process, but a shared vision, financial resources and institutional capacities are not yet available for the implementation of the plan. The plan proposes a key near-term milestone: the mobilisation of financial resources through central and local government budgets to establish an initial mechanism of local coordination. An appraisal showed that this would be financially feasible. This first step would be independent of external support (which eventually will be required), and would therefore promote local ownership and leadership of managing the landscape for ecological connectivity.

Note: Images produced by the KILOREWMP project, funded by the European Union and Belgian Aid and implemented by the Ministry of Natural Resources and Tourism (via the Wildlife Division and the Tanzania Wildlife Management Authority) and the Belgian Development Agency (Enabel) in collaboration with the districts of Ulanga, Kilombero and Malinyi of Morogoro Region and of Rufiji of Coast Region.

Terrestrial connectivity: Asia

5. Ecological corridor for the reunion of giant pandas in the Qinling Landscape

Hui Wan, *formerly of WWF*

Context and challenge

National Road 108 was built in the 1970s through the Qinling Landscape in central China and over time brought heavy traffic (Figure 1). The road divided an intact forest and caused the fragmentation of previously connected panda habitat. It also gave the local human population access to the forest. Consequent use of wild resources further degraded the habitat. The resident panda population was gradually split in two: the Xinglongling subgroup to the west and the Tianhuashan subgroup to the east.

Approach

In 2000, a tunnel was built by the government to accommodate a new road. The abandonment of the old road and the re-establishment of habitat on land on top of the tunnel provided the opportunity to reconnect the separated panda groups. In 2003, Shaanxi Guanyinshan Nature Reserve was legally established, and in 2005 the World Wildlife Fund (WWF) together with the reserve launched the G108 Qinling vehicle tunnel corridor restoration project (Figure 2). The main strategic activities in the ecological corridor include:

- Baseline survey and mapping to understand the population status of the panda subgroups, the physical distance between them, the socio-economic condition of local communities, the management capacity of the reserve and the forest tenure in the area.
- Habitat restoration through bamboo plantings in gap plots to improve habitat quality, providing connected habitat and thereby a path for panda movement.
- Local community engagement, including providing support to local households, demonstrations of sustainable forest management and education programs about the significance of habitat conservation.
- Traffic management to enforce the ban on humans and vehicles using the abandoned road.

Key lesson

Mitigating fragmentation caused by roads with underground tunnels can be an effective way of restoring connectivity for wildlife; monitoring of the restoration is important to document outcomes.

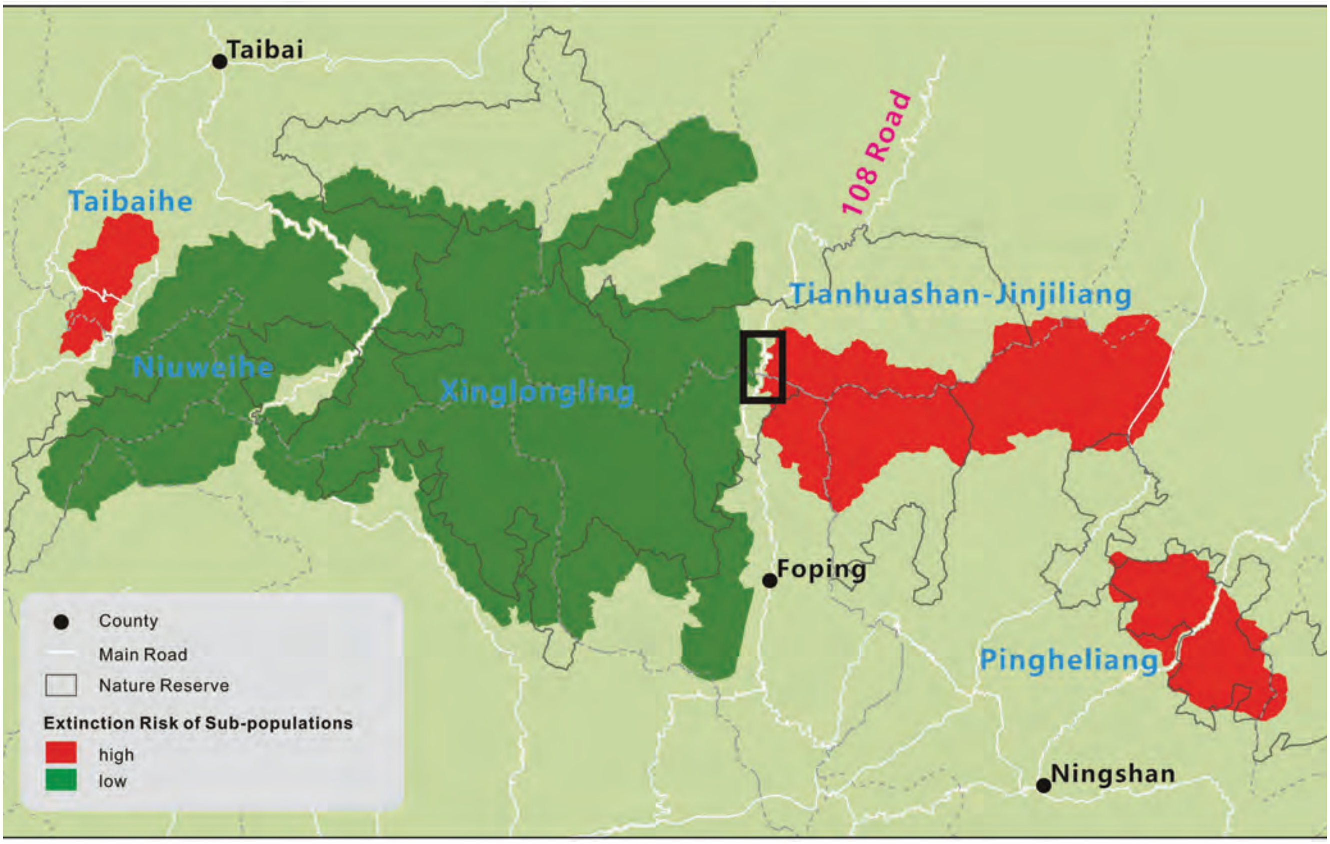


Figure 1. Panda subpopulations in the Qinling landscape. National Road 108 is running from north to south. The black rectangle indicates the location of the ecological corridor. © WWF China

- Capacity enhancement to improve the management effectiveness of Guanyinshan Nature Reserve.
- Wildlife monitoring.

Results

Giant pandas have been documented in the ecological corridor, which includes land on top of the road tunnel and surrounding lands connecting the core areas. The ecological distance between the subgroups has been reduced and is now shorter than the daily activity range of a panda. The number of mammal and pheasant species found in the corridor area has increased from zero to 15.

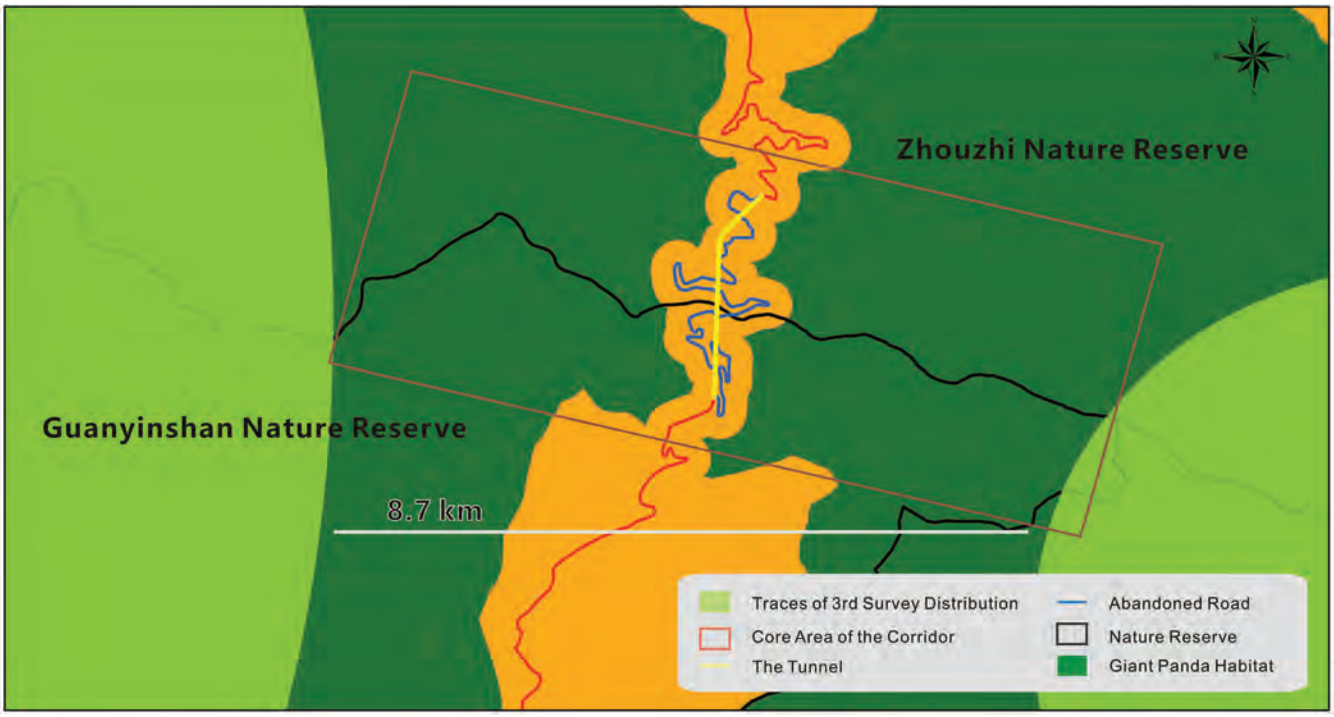


Figure 2. The ecological corridor includes the non-protected area on both sides of the road (orange). The corridor is now connecting the habitat of two panda subgroups. © WWF China

Giant panda (*Ailuropoda melanoleuca*) © Adobe Stock

6. Thailand's experience in ecologically connecting its protected areas

Songtam Suksawang, *Thailand National Parks Office, Department of National Parks Wildlife and Plant Conservation, Ministry of Natural Resources and Environment*

Key lesson

Monitoring and evaluation of identified corridors suggest that some corridors are already working; management of allowable activities in these corridors will be important over the long term.

Context and challenge

In recent years, Thailand has markedly expanded its protected areas system. The kingdom now has 128 terrestrial national parks, 26 marine national parks, 60 wildlife sanctuaries, and 63 non-hunting areas managed by the Department of National Parks, Wildlife and Plant Conservation (DNP). These protected areas cover about 23% of Thailand's territory, a figure justified by the numerous benefits conservation delivers to the Thai people. Where protected areas are adjacent or close together, they can be managed as ecological networks for conservation, but many of them are smaller areas fragmented by highways, railroads and other infrastructure.

Thailand's protected areas are generally effective at curtailing deforestation within their boundaries (a significant exception being the continued poaching of particularly valuable timber such as rosewood). But continued deforestation and conversion of forests into plantations in areas surrounding many of Thailand's protected areas is making them islands of nature in a sea of agriculture, too small to support all the species that occupied the landscape before it became fragmented.

Approach

To promote landscape connectivity, DNP has adopted the concept of ecological networks, which are referred to as 'forest complexes'. National parks and wildlife sanctuaries are ecologically linked to form a larger area that will be able to support viable populations of wide-ranging species of plants and animals, as well as contribute to regional social and economic development through provision of ecosystem services. These areas can be connected by ecological

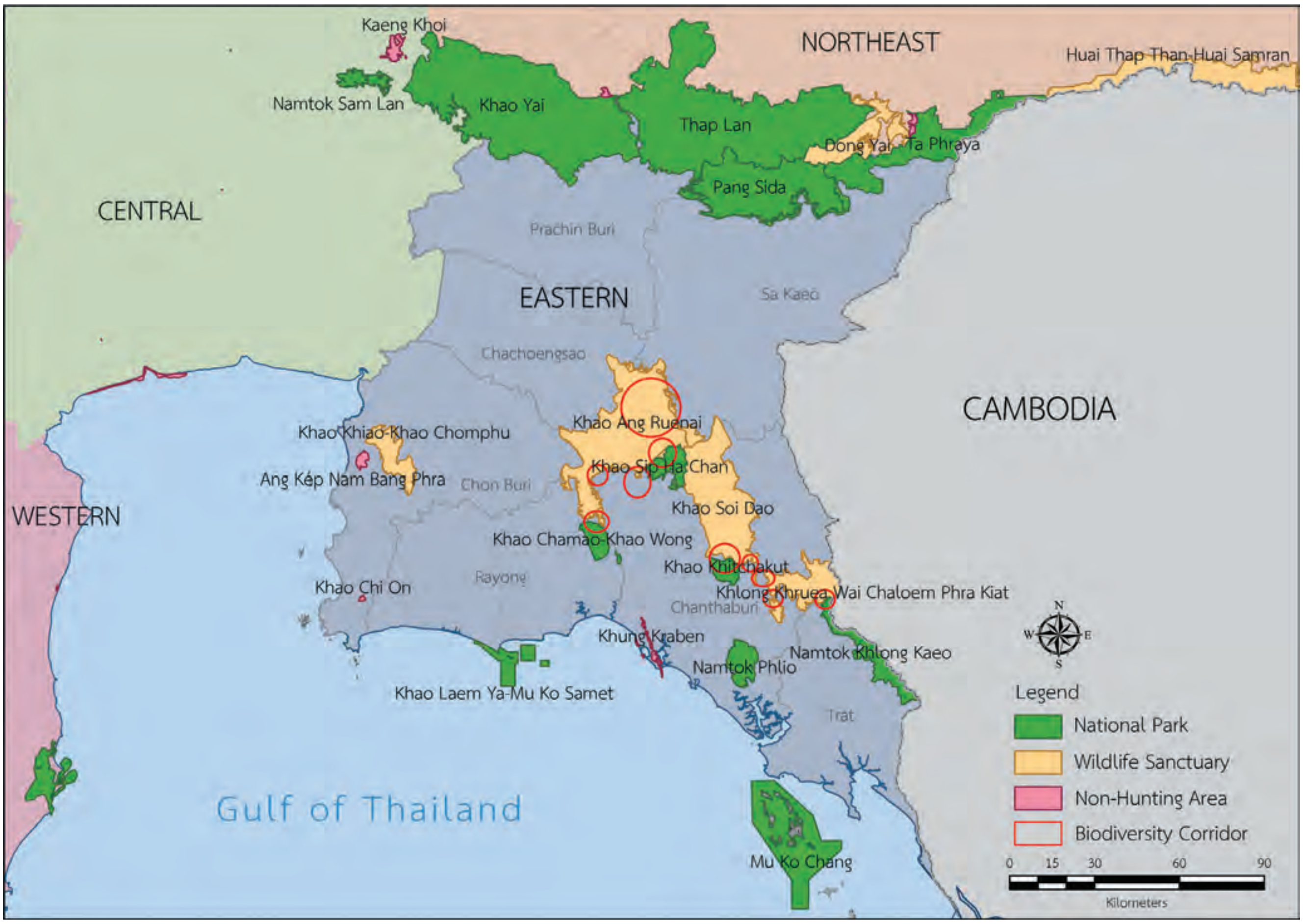


Figure 1. Ecological corridors in the Eastern Forest Complex © Songtam Suksawang / Thailand National Parks Office, Department of National Parks Wildlife and Plant Conservation, Ministry of Natural Resources and Environment

corridors that include non-hunting areas, buffer zones, lands managed by government agencies other than DNP and private lands. This approach requires senior protected area staff to consider managing their sites as parts of larger landscapes.

DNP has been learning lessons about ecosystem complexes by establishing pilot activities in selected sites in two complexes: the Eastern Forest Complex (Figure 1, previous page) and the Western Forest Complex (Figure 2). A forum brought together about 50 of Thailand's most experienced protected area managers and other experts on forest

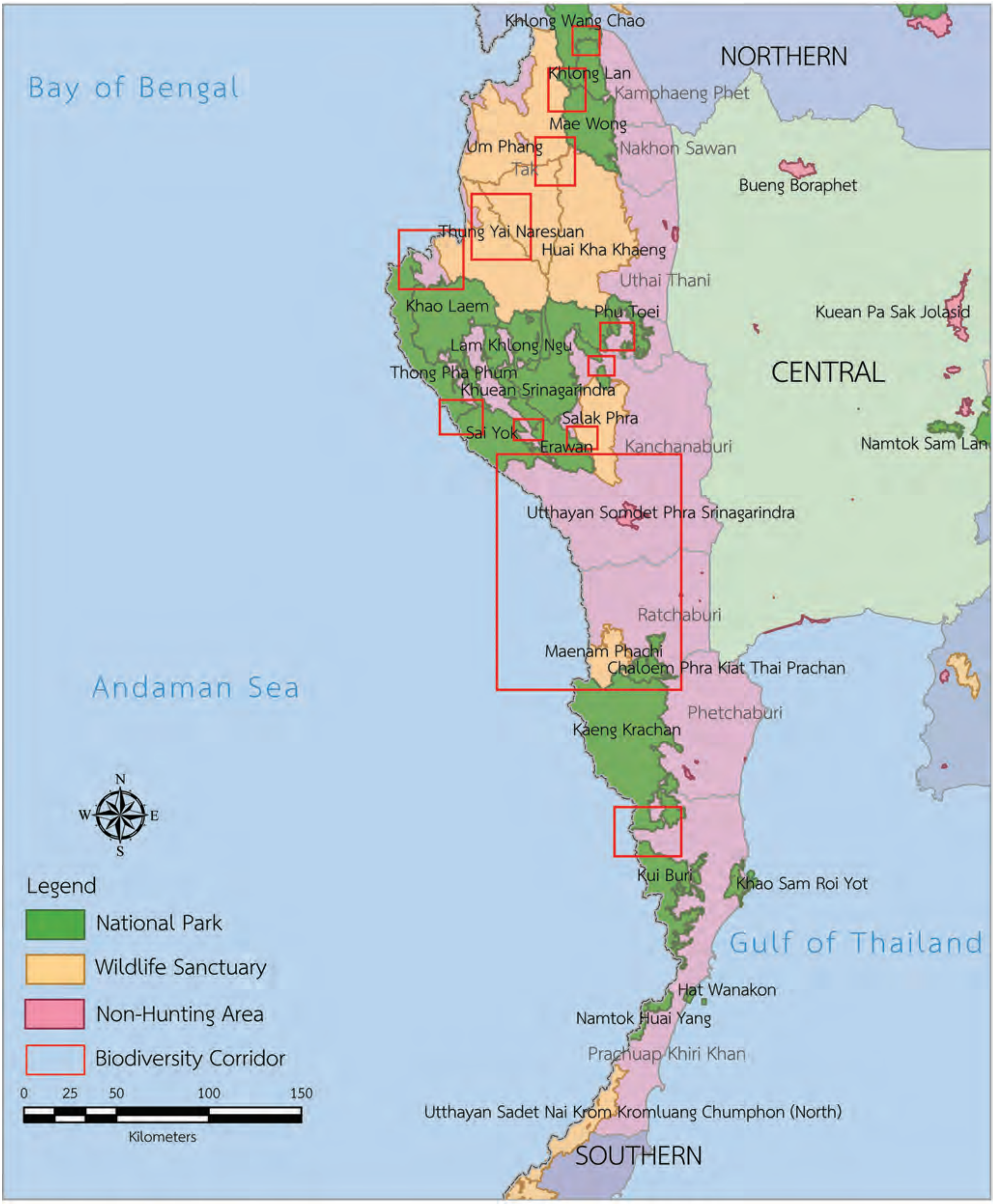


Figure 2. Ecological corridors in the Western Forest Complex. © Songtam Suksawang / Thailand National Parks Office, Department of National Parks Wildlife and Plant Conservation, Ministry of Natural Resources and Environment

Khao Ang Rue Nai Wildlife Sanctuary, Thailand © Adobe Stock

complexes to discuss how ecological corridors can connect protected areas, expanding their effective size to enable the movement of plants and animals between them, physically linking habitats and providing an effective means of adapting ecosystems to climate change.

The forest complexes approach is promising but DNP also needs to consider how to manage any potential negative ecological impacts of connectivity. Without proper management, the connecting corridors could facilitate the spread of disease, invasive alien species, forest fires, and other natural hazards. Ecological corridors may also pose some visitor management challenges. For example, it will be important to ensure that visitors who have paid for admission to a national park do not then expect that they necessarily have the right to enter an adjacent, strictly protected wildlife sanctuary that limits visitation (a potential issue in the case of Huay Kha Khaeng Wildlife Sanctuary).

Examples of ecological corridors

The Eastern Forest Complex includes eight protected areas (Figure 1). Khao Chamao-Khao Wong National Park (84 km^2) is slightly separated from Khao Ang Rue Nai Wildlife Sanctuary (1078 km^2), but an ecological corridor has been shown to be feasible; its establishment depends on the owners of the connecting land being convinced to work with the protected areas. Khao Sipha Chan National Park (118 km^2) is adjacent to Khao Ang Rue Nai and forms part of a naturally connected ecosystem. Similarly, the relatively small Khao Khitchakut National Park (58 km^2) is connected to Khao Soi Dao Wildlife Sanctuary (744 km^2), so they also form a natural unit. Klong Krua Wai Wildlife Sanctuary is connected to Namtok Khlong Kaew National Park, making them part of a long and rather narrow natural unit. They share a boundary with Cambodia, and DNP is working on transboundary protected area conservation with Cambodia's Samlout Protected Area (this is being promoted by the Asian Development Bank).

All the protected areas of the Western Forest Complex are ecologically connected and form Thailand's largest contiguous forest ecosystem complex, covering 14,866 km^2 (Figure 2). Three national parks (part of Khao Laem National Park, Thong Pha Phum National Park, and Sai Yok National Park) are separated from the other sites in the western complex by a highway and various commercial developments along the highway, posing an ecological barrier that will need mitigations with crossing structures, such as broad overpasses covered with vegetation to enable free movement of large mammals.

Results

There is conclusive evidence that tigers, which are well protected in Huay Kha Khaeng Wildlife Sanctuary in the Western Forest Complex, are expanding their population, with "new" tigers dispersing northward to Mae Wong and Klong Lan national parks, where they have become well established. Many other species, including the reintroduced Eld's deer, may also repopulate these national parks from Huay Kha Khaeng, indicating its importance as a source of wildlife for other areas due to the existence of ecological corridors. Local communities have been involved in demarcating boundaries in Mae Wong National Park and have benefitted from multiple-use zones, which can serve as ecological corridors. Communities surrounding Huay Kha Khaeng Wildlife Sanctuary have established community development zones that have been formally recognised as contributing to the objectives of the protected area. More work is clearly needed to develop and implement connectivity conservation in the protected area complexes, but the Eastern and Western forest complexes have shown the practical utility of the approach.

Terrestrial connectivity: Australia

7. East Coast Conservation Corridor in Tasmania

Todd Dudley, *North East Bioregional Network*

Context and challenge

The East Coast Conservation Corridor (ECCC) is a landscape-scale ecological network for conservation extending 280 km north–south from Cape Portland to Cape Pillar, covering 2½ degrees of latitude on the East Coast and hinterland of Tasmania. The existing protected area system and ongoing conservation projects provide a solid foundation for realising what is known as the 'WildCountry vision' of a protected connected landscape in North East Tasmania (Figure 1). In 2012, noted natural heritage expert Peter Hitchcock stated that "the East Coast connectivity corridors have been assessed collectively to have National Heritage significance – one of the more important latitudinally connected tracts of native habitat in Australia."

Key lesson

Finding common interests among many entities and communicating with different types of partners can lead to the ecological restoration of connectivity; long-term efforts, including monitoring, can be ensured through endowments.

While the ECCC still has a high level of landscape connectivity, it is under threat from a variety of impacts, including expansion of intensive agriculture and associated dams, forestry (plantations and native forest), coastal development, invasive plants and feral animals. The challenge is to extend the existing protected area system to limit the extent and impact of threats and to strategically restore areas important for connectivity.

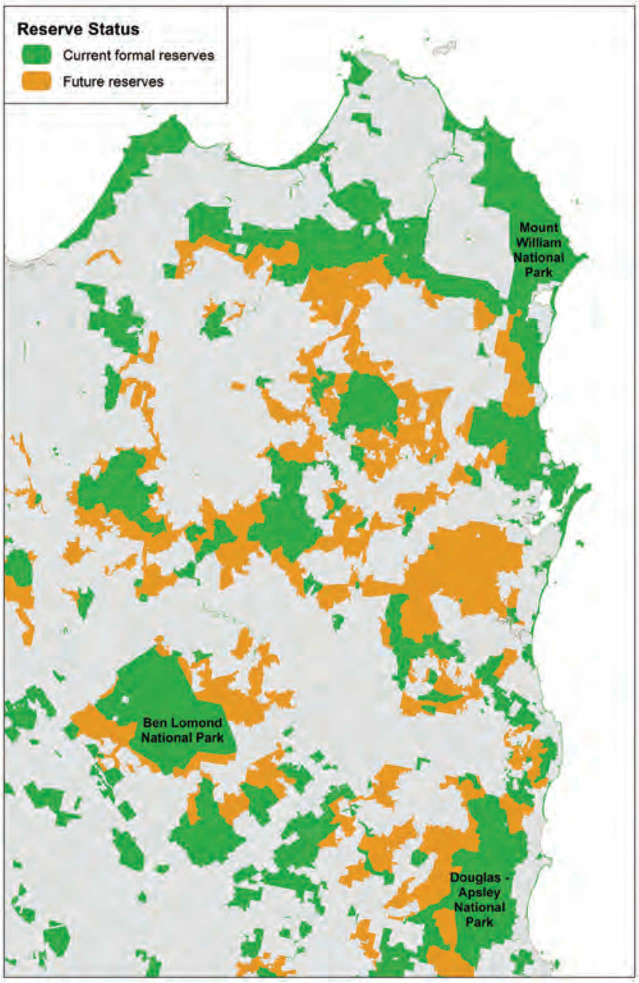


Figure 1. Reserves to improve landscape connectivity in North-East Tasmania © North East Bioregional Network

Approach

The approach is focused on holistic cross-tenure conservation land management with an emphasis on increasing the extent and improving the condition and landscape connectivity of native vegetation and habitat. Identifying and addressing the physical and ethical causes of ecological decline, such as human population growth, consumption and the ideological support of growth economics in a finite world, is part of the strategy.

The North East Bioregional Network is an entirely voluntary organisation that works with about 45 government entities, communities, companies, private organisations and private landholders on issues where common ground can be found. They are in the process of establishing an endowment fund that will enable a long-term commitment to protect and restore the unique flora, fauna and landscapes of eastern Tasmania.

Example of an ecological corridor

The Skyline Tier restoration project is returning 2,000 ha of non-native radiata pine plantation back to biodiverse native forest (Figure 2). By re-establishing the native ecosystem, this ecological corridor will reconnect protected coastal and hinterland areas. The land is owned by the government but leased to a private company, and now co-managed by the company and the North East Bioregional Network.

Results

Activities that have contributed to improved landscape connectivity in the ECCC area since 2005 include:

- Creation of 30 permanent conservation covenants and 60 registrations under the Land-for-Wildlife program on private land.
- Facilitation of the employment and training of over 80 people over the last five years through ecological restoration projects of the North East Bioregional Network, which has had significant ecological, social and

economic benefits and helped consolidate conservation as a highly beneficial activity in remote rural communities.

- Prohibition of new subdivisions within 1 km from the coast in the Break O'Day municipality, thus maintaining an ecological corridor between the coast and hinterland.
- Establishment of a North East Tasmania Land Trust as a non-government organisation to purchase and receive tax-deductible donations of private land for nature conservation.
- Transfer of management of over 100,000 ha of public native forest from the department of Forestry to that of National Parks and Wildlife in North East Tasmania (Figure 1).
- Release of a conservation action plan for the Break O'Day municipality.
- Consideration of connectivity conservation plans in municipal land planning.
- Production of connectivity conservation plans that explicitly seek to protect wildlife corridors and landscape linkages from inappropriate development and are legally binding in municipal planning schemes.

Learn more: www.northeastbioregionalnetwork.org.au

Figure 2. Skyline Tier Ecological Restoration Project. (top) A mature radiata pine plantation was harvested, followed by a hot ecological burn. (bottom) Six years later, intensive restoration work helped regenerate native forest. © North East Bioregional Network

8. The Great Eastern Ranges: Australia's first continental-scale ecological network for conservation

Ian Pulsford, *Connectivity Conservation and Protected Area Consultant*
Gary Howling, *Great Eastern Ranges Initiative*

Challenge

Australia is one of 17 mega-diverse nations globally, with 6,794 vertebrate fauna species – including 1,350 endemic terrestrial vertebrate species, the highest number for any nation – as well as 22,000 species of flora. The greatest concentration of this outstanding biodiversity is found along the rugged eastern mountains and coast. This area comprises a substantial part of Conservation International's "Forests of East Australia" global high-biodiversity hotspot. Substantial sections are conserved in an archipelago of embedded protected areas, including three World Heritage areas, as well as lands used for agriculture, mining, urban development, infrastructure and forestry. Clearing and fragmentation of habitat; land degradation; introduced exotic species of plants, animals and pathogens; and climate change are major threats that degrade and fragment this ecological network for conservation.

Approach

The Great Eastern Ranges (GER) Initiative was established in 2007 with a bold mission to protect, restore and relink habitat to allow nature and people to continue to thrive. The initiative comprises natural lands that extend along the mountainous ranges on the eastern seaboard of Australia for more than 3,600 km from the Grampian Mountains in Victoria, through eastern New South Wales (NSW) and the Australian Capital Territory (ACT), to Cape York in the far north of Queensland (Figure 1). Countless species rely on the Great Eastern Ranges to move and adapt to a climate of extremes. The GER Initiative is an ecological network for conservation that helps people to work together to restore and reconnect nature in areas of high biological importance such as gaps and areas that are fragmented. This work is guided by a vision for the ecosystems of Australia's Great Eastern Ranges to be healthy and connected, which will contribute to the long-term economic, social, cultural and spiritual well-being of the community, and of native plants and animals.

The GER Initiative is one of a very few connectivity conservation initiatives worldwide that have been initiated by government. The initiative began in 2007 with funding from the state of NSW, enabling its Department of Environment, Climate Change and Water to demonstrate a new approach to conservation based on collaborative partnerships. Five 'regional partnerships' were established in five priority connectivity areas. Partners included non-governmental conservation organisations, land care groups, Aboriginal groups, academic institutions, local governments and other government agencies. In 2010, governance devolved to a public–private partnership group of five non-governmental lead partners. Regional groups expanded to ten by 2016. In 2017, governance was transferred to Great Eastern Ranges Ltd. with a board of eight independent directors.

Key lesson

A bold mission to protect, restore and relink habitat to allow nature and people to continue to thrive despite changing climatic conditions can lead to engagement of many parts of society and on-ground conservation activities.

Figure 1. The Great Eastern Ranges ecological network for conservation forms a 3,600-km arc of mostly interconnected natural lands that extends from the Grampians in Victoria to Cape York in far north Queensland. © Great Eastern Ranges Ltd.

Great Eastern Ranges Ltd. is now a not-for-profit entity that operates as an equal partner in a national network of regional partners in 10 partnership areas in Victoria, NSW, the ACT and Queensland.

Examples of ecological corridors

Regional partnership groups consist of public and private organisations and individuals involved in on-ground voluntary conservation activities that come together to collaborate and share resources and capacity (Figure 2). A number of the connectivity partnership areas link north–south along the central mountainous spine and several areas extend east to the coast and west onto the slopes connecting the mountains to the inland. For example, the Slopes to Summit and Kanangra to Wyangala are ecological networks linking alpine and montane forest to the inland. The Kosciuszko2Coast ecological network links the Alps to the east coast. The Victorian Biolinks Alliance works to connect tall-forest landscapes in the central Victorian highlands and the transboundary Border Ranges Alliance works to maintain and improve connectivity of World Heritage-listed rainforests and tall eucalypt forest on the border between NSW and Queensland.

Results

From funding provided by the NSW and Australian governments over 10 years, the GER Initiative and partners coordinated voluntary conservation activities through a suite of instruments. These included whole-of-paddock restoration agreements, voluntary conservation agreements, land for wildlife agreements, grants to fence stream banks, tree planting, habitat restoration, feral animal and weed control, community education through community field days, development of a range of communication products including videos and a web site, biological surveys, and research programs.

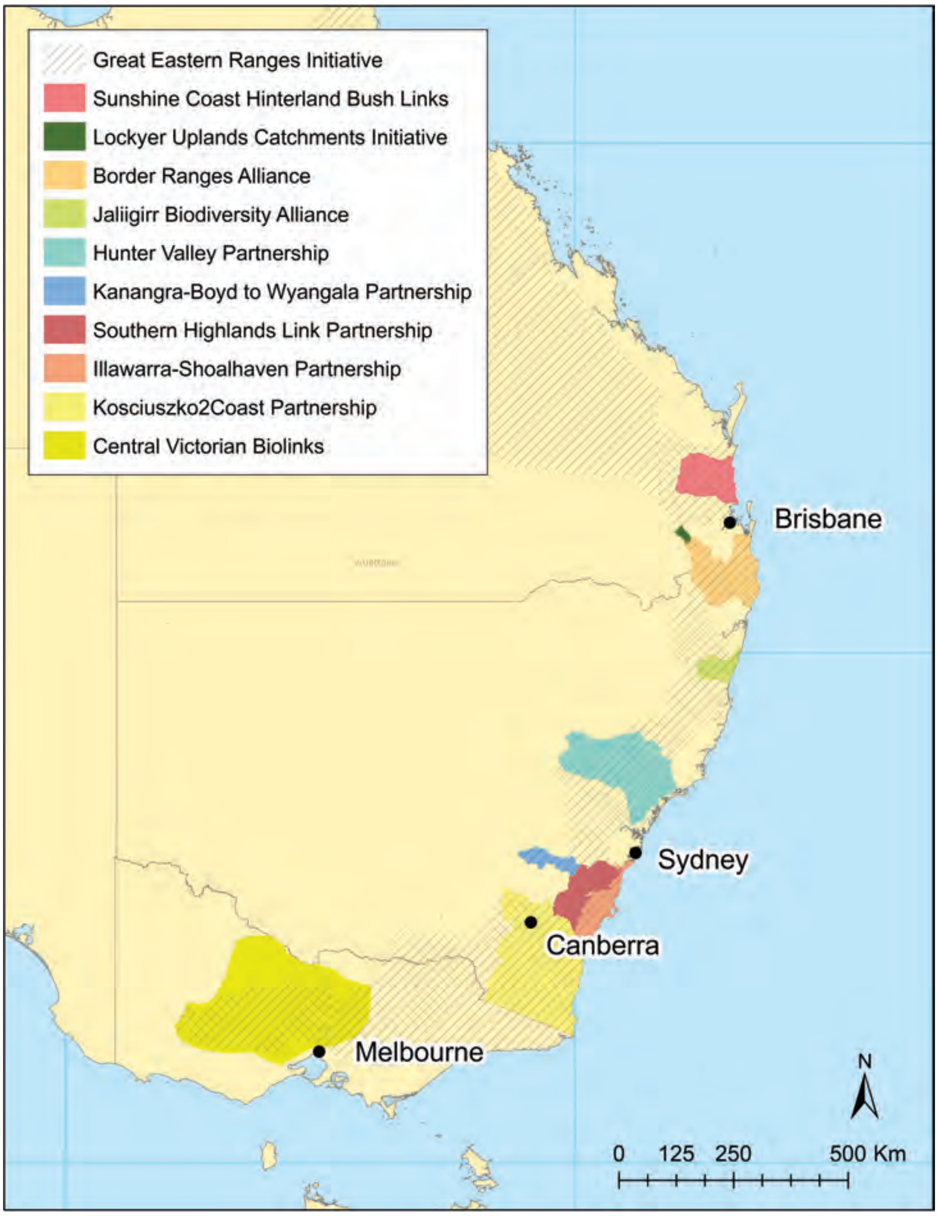


Figure 2. Great Eastern Ranges network of regional partnership areas of connectivity conservation © Great Eastern Ranges Ltd.

Terrestrial connectivity: Europe

9. COREHABS to BearConnect: Securing ROAMing in the wilderness corner of Europe

Ancuta Fedorca, *Transilvania University*

Context and challenge

The Romanian portion of the Carpathian Mountains holds the biggest continuous forest ecosystems in Europe, harbours many well-preserved natural habitats, and is home to large herbivores and carnivores, including brown bear (*Ursus arctos arctos*), wolf (*Canis lupus lupus*) and lynx (*Lynx lynx*) (Figure 1). The mountain range is a biodiversity hotspot situated at the crossroads of several important biogeographic regions. Recent changes in land ownership and rapid infrastructure development (highways, industrial and human settlements, tourist facilities) are threatening the largely intact nature of the Romanian Carpathians. A total of 30.2% of the national territory is covered by forest, including virgin forests and ancient beech forests. While some of the forest is in public ownership, a large proportion is privately owned due to restitution that took place in recent decades. A large number of sites, adding up to 24.46% of the terrestrial national territory, are included in the Natura 2000 network; however, these sites are spatially disconnected.

Key lesson

Romanian legislation requires modelling to identify ecological corridors that can help maintain genetic diversity of wildlife and facilitate adaptation to climate change.

Approach

In 2015, an initiative called COREHABS (Ecological corridors for habitats and species in Romania) brought together six entities (two public universities, one national research institute and three NGOs) to design a national ecological network for ensuring habitat connectivity in tandem with sustainable development. COREHABS is providing corridor modelling as a decision support tool for stakeholders, giving them the opportunity to develop infrastructure while considering the ecological measures necessary to ensure the long-term viability of species and habitats. In 2017, COREHABS combined forces with BearConnect (Functional connectivity

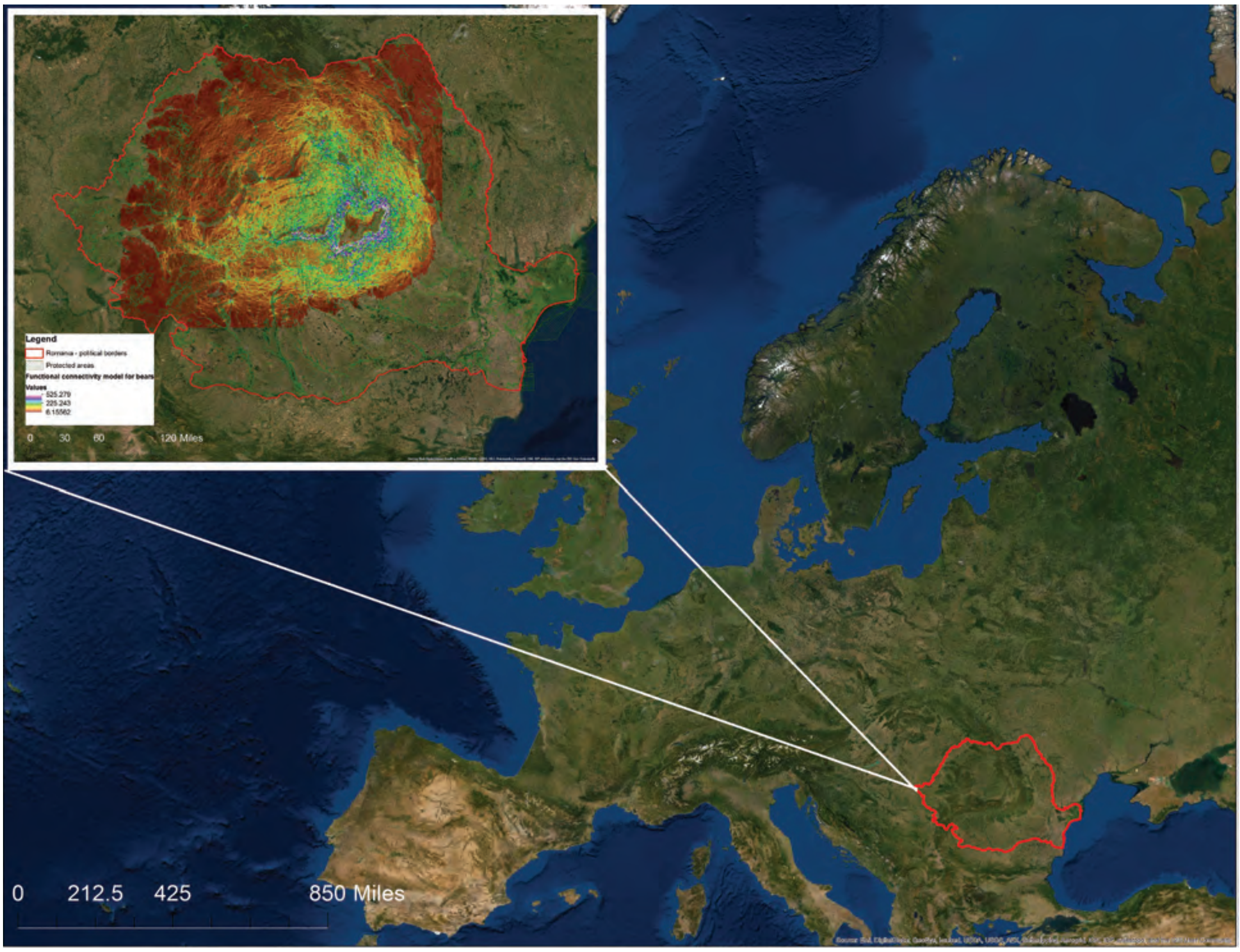


Figure 1. The Carpathian mountain range runs in an arc through the centre of Romania. This map shows modelled values for predicted functional connectivity across brown bear habitat, overlaid with protected areas in Romania. © Ancuta Fedorca

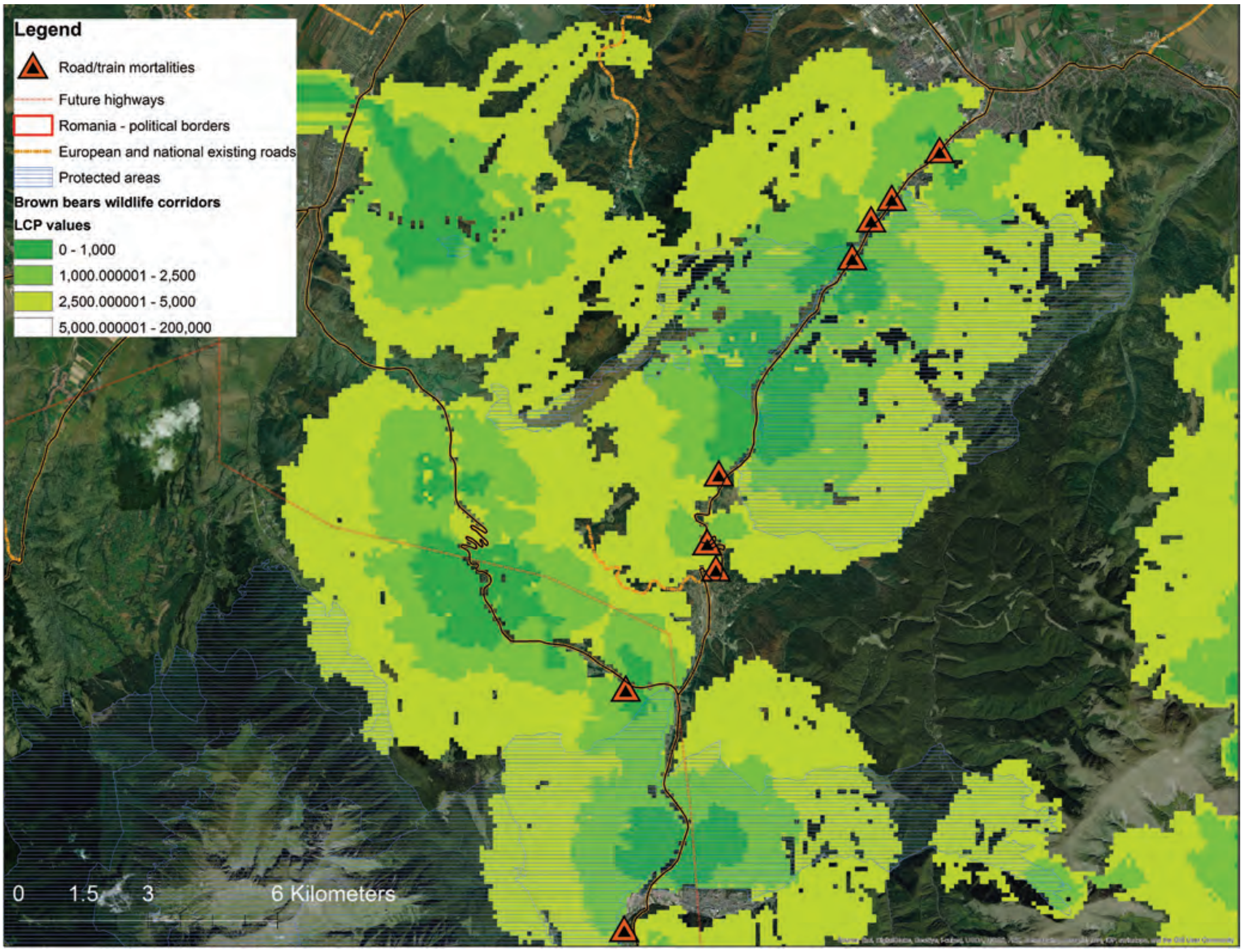


Figure 2. The protected areas in blue need to be connected (Bucegi Nature Reserve, Bucegi Natural Park, and Bucegi Protected Area in the north and Piatra Mare Protected Area and Postavaru Protected Area in the south). The shades of green show highest (darkest green) to lowest (lightest green) areas of predicted connectivity to help prioritise where conservation activities should occur. © Ancuta Fedorca

and ecological sustainability of European ecological networks), an organisation focusing on the brown bear. To achieve ecological corridor conservation and facilitate specific ecosystem processes, the organisations are investigating the degree to which existing ecological networks, which include national protected areas and the Natura 2000 network, ensure landscape functional connectivity and ecological sustainability at different scales, and provide practical recommendations for connectivity conservation.

Romanian legislation on ecological corridor designation (GO 57/2007) mandates the protection of connectivity by designating spatially explicit ecological corridors based on field-informed modelling and empirical validation. Ecological corridors are established on the basis of scientific studies and are designated by an order of the head of the Authority for Forest and the Environment after receiving the acceptance of the Romanian Academy of Science. Protected areas and ecological corridors are integrated into national, regional and local rural and urban planning, cadastral plans and land registers by the National Agency for Cadastre and Real Estate Advertising, and noted in the parcel identification system. Partners for implementation include ministries and agencies responsible for natural resources and infrastructure, Transilvania University of Brasov, and the National Institute for Research and Development, local and regional councils, private forest owners and NGOs.

Examples of ecological corridors

An area of about 10x10 km has been identified as important to connectivity for brown bears between the Bucegi protected areas in the south and the Piatra Mare and Postavaru protected areas in the north (Figure 2). The majority of the land is owned by the state, with small areas being held by the community and private owners.

Results

COREHABS developed an efficient mechanism for identification and assessment of ecological corridors, and is providing specialists in local planning and implementation of a national ecological network for conservation. Romania is on track to protecting a coherent ecological network of protected areas and ecological corridors, which will allow wildlife populations to interbreed, improving long-term genetic viability and climate change resilience.

10. Ecological connectivity in an urban context: Utrechtse Heuvelrug, Netherlands

Rob H.G. Jongman, *Independent Scientist*
Chris Klemann, *Province of Utrecht*

Context and challenge

Netherlands is a largely urbanised country and nature faces pressures from urban expansion, infrastructure, intensive agriculture and recreation. The Utrecht Hills (Utrechtse Heuvelrug) stretch from north-west to south-east and comprise several important nature reserves and a national park. This area is dissected by several motorways and railroad lines, which were making it nearly impossible for fauna to move through the landscape. However, the area is part of the Netherlands Nature Network. Therefore the province of Utrecht and the responsible nature management agencies, Utrechts Landschap (https://www.utrechtslandschap.nl/) and Goois Natuurreservaat (https://gnr.nl/), were mandated to restore connectivity for wildlife.

'The polluter pays' is a basic principle in environmental policy in Netherlands. Therefore, the owner and manager of transportation infrastructure is responsible for financing and implementing all ecopassages (green bridges and culverts); the funds do not come out of the nature conservation budget. This is the main reason why ecopassages were not implemented in the 1990s. The district's mandate to restore connectivity and lack of actions by the national road authorities (which have an implementation budget) created tensions. Coordination between national and provincial authorities was needed for realising necessary connecting measures for provincial roads for an optimal return on investments.

Key lesson

Netherlands offers a model of 'the polluter pays' that helps finance connectivity, such as safe passage across roads, and allows activities compatible with connectivity goals (e.g. recreation) to occur in the corridors.

Approach

A renewed effort was made to speed up the process of landscape defragmentation through the Netherlands Nature Network, which consists of protected areas and the linkages between them, and a national defragmentation plan that came with extra funds. Both programs were scheduled for implementation from 2004 to 2018.

Examples of ecological corridors

For the province of Utrecht, priority measures were planned for the Utrecht Hills to improve wildlife movement across national motorways and railroad lines, which is a national responsibility. The province was expected to contribute to the plan by implementing defragmentation measures for the roads under their responsibility.

Accordingly, the province of Utrecht has elaborated plans and actions for the Utrecht Hills (http://www.hartvandeheuvelrug.nl/projecten/ecologische-verbindingen/). The project 'Hart van

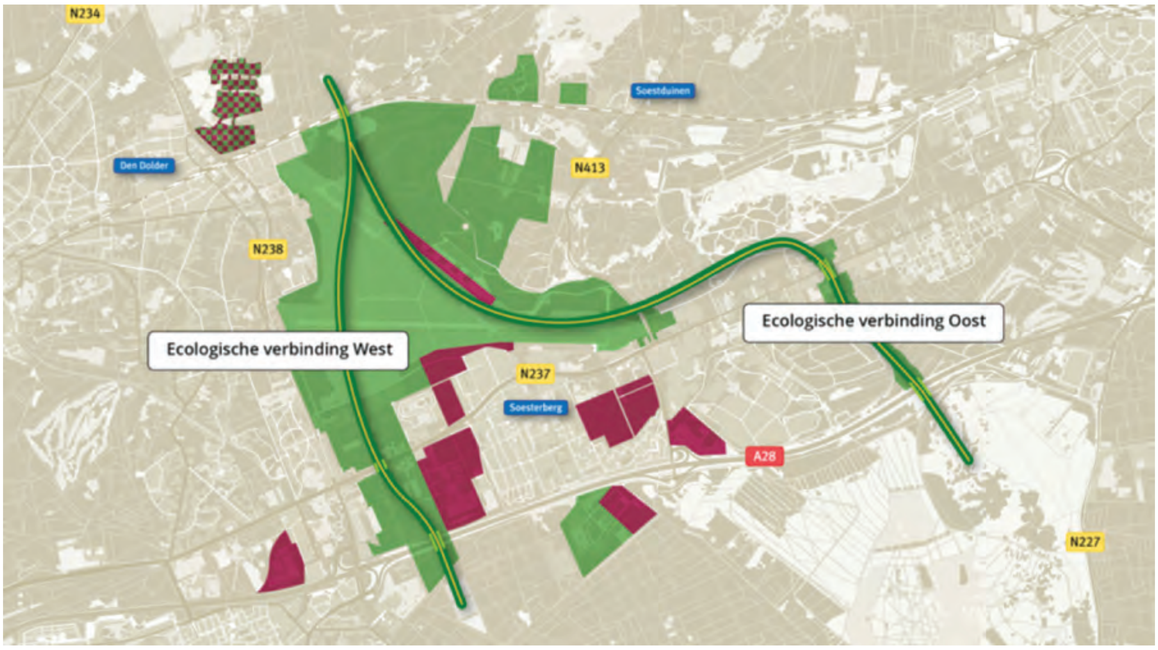


Figure 1. The West and East ecological corridors in the Utrecht hills. The numbers indicate motorways (red) and link roads (yellow). The blue names indicate built-up areas; purple: heathland; green: forest. © Provincie Utrecht

Figure 2. Ecoduct Op Hees, crossing the Utrecht–Amersfoort rail line. The recreation cycle path is situated at the foreground side of the bridge © ProRail

de Heuvelrug' consists of two main ecological corridors that merge in the north (Figure 1).

The western part of the project area is a forest corridor, with the eastern part a heathland corridor. Both corridors contain many small tunnels that cross under roads (such as a tunnel in the south-east of the province under road N225; https://www.youtube.com/watch?v=hHAn-Clwy8Q&feature=youtu.be). To realise connectivity, an additional five ecoducts have been built in these two ecological corridors, including the Ecoduct Op Hees (Figure 2), which was completed in 2013 and crosses a busy railroad line between the cities of Amersfoort and Utrecht. In addition to facilitating wildlife movements, it also serves as a recreation corridor. For this purpose, the ecoduct has been made wider to accommodate cyclists and pedestrians.

Results

The two ecological corridors act as movement routes for mammals (such as roe deer, *Capreolus capreolus*; badger, *Meles meles*; and tree marten, *Martes martes*) and as a temporary living and breeding area for smaller mammal species. Through these ecological corridors, plants and animals can spread and move from Gooimeer (Gooi Lake) in the north-west to the Veluwe National Park in the south-east.

11. The Spanish National Network of Drover's Roads (Vías Pecuarias)

Marcos Pradas, *Independent Forest Engineer*

Key lesson

A transportation network originally established for moving livestock can provide ecological connectivity among protected areas, especially when restored for that function.

Context and challenge

The Spanish National Network of Vías Pecuarias is a network of drover's roads (routes traditionally used to drive livestock on foot from one place to another, e.g. to market or to summer pastures) and additional elements used for transhumance and smaller cattle movements (Figure 1). They criss-cross Spain some 125,000 km in length and covering an area of 400,000 ha, linking a wide variety of protected, unprotected and urban areas. They hark back to prehistory, having been first documented in Roman times and legally protected by decrees issued in AD 654, 1273 and 1995. The Mediterranean region is a biodiversity hotspot where humans are such an integral part of the environment that rural exodus and disappearance of traditional uses are regarded as two of the major ecological threats to the Iberian Peninsula.

Droves are not just trodden and dusty ways, but are open or wooded pastures with a trail in the middle. They often contain trees, hedgerows, dry-stone walls, ponds, wells and watering holes. They can be very biodiverse, many times more so than their surroundings. In addition, they are important for the protection of many ancient breeds of farm animals, many of which are in danger of extinction. They serve as ecological corridors in different ways. Cattle and sheep spread organisms along them. It is estimated that herds of 1,000 sheep or 100 cows spread 3 to 5 million seeds and some 3 tons of dung on a daily basis, thus contributing to species range shifts, a useful adaptation to climate change (Manzano & Malo, 2006). Drover's roads cross protected, conserved and unprotected areas, including urban areas, and

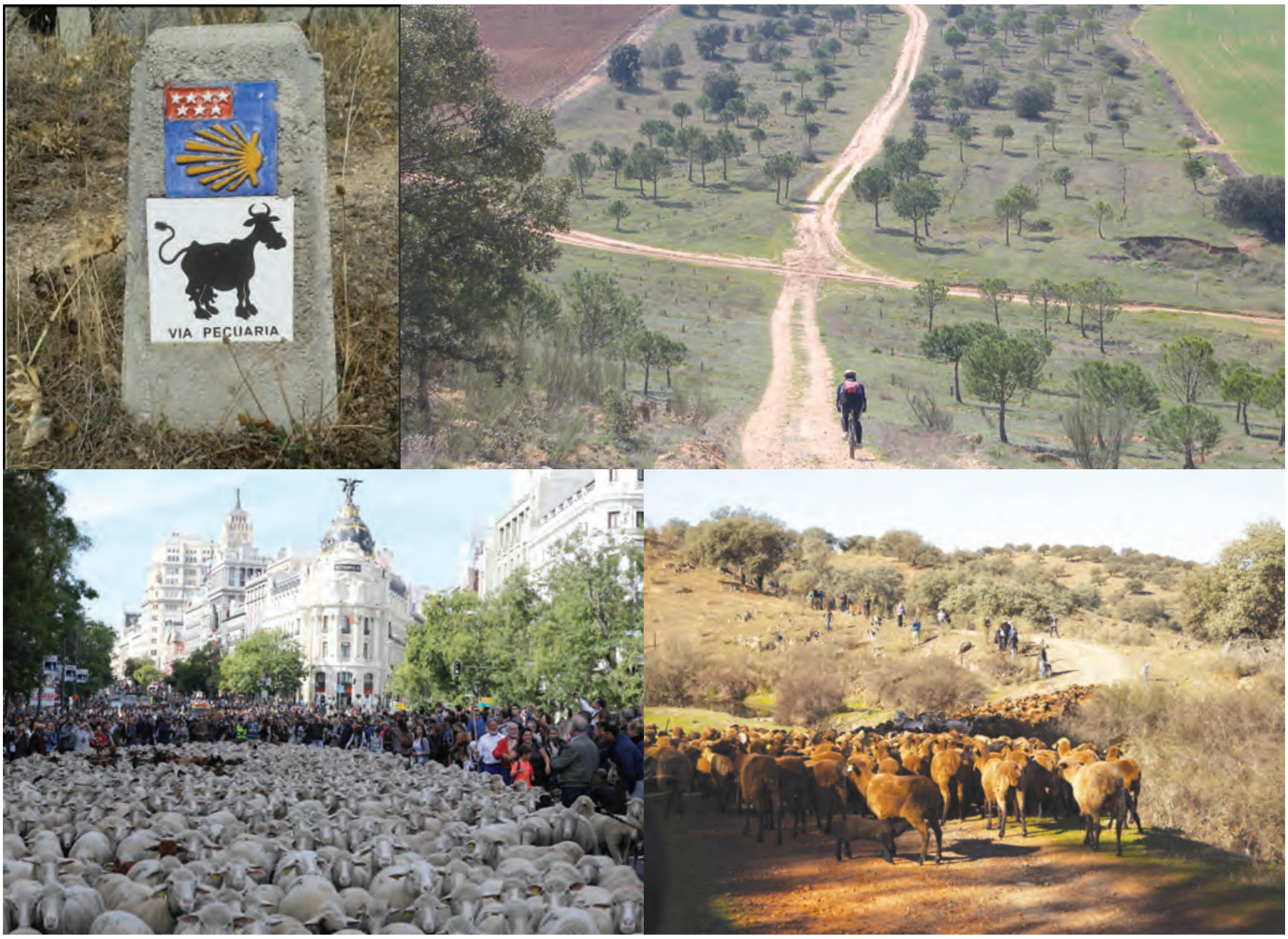


Figure 1. Scenes from drover's roads in Spain.
(upper left) A standard marker (courtesy of Juan Díaz Hidalgo)
(upper right) The Droveway of Salamanca, illustrating its multifunctionality and value as an ecological corridor © Federico Sanz
(lower left) The Fiesta de la Transhumancia in Madrid (courtesy of Diario de Madrid)
(lower right) A road important for four local domestic animal races: the white and black Merina sheep, Verata goat, and Andalusian donkey, which is the oldest donkey breed of Europe and now classified as being in critical danger of extinction © Agustín Pérez, la Siberia Extremeña Biosphere Reserve

are vital for connecting the Natura 2000 network of protected areas. They are particularly important for promoting functional connectivity between isolated grasslands. Because they are linear structures in the landscape, migrating species, including birds, follow them and also use them to rest, drink and feed.

The ecological significance of drover's roads, including their role as ecological corridors, is now being fully acknowledged, and the necessity to protect them has been recognised under Article 8 of the Convention for Biological Diversity, the Sustainable Development Goals, and covenants such as the United Nations Convention to Combat Desertification and the United Nations Framework Convention on Climate Change, among others. The main threat to drover's roads is the decline of extensive livestock farming and transhumance. Other threats include the lack of a true strategy for conservation, reluctance of the government to protect the Vías, illegal settlements, dumping, fencing, resource extraction, pesticides and capping of wells. Many drove ways are now irretrievably occupied and their status as public domain has been or is in the process of being revoked.

Approach

State law 'Ley 3/1995, de 23 de marzo, de Vías Pecuarias' specifies that drover's roads are in the public domain, are unseizable, inalienable and imprescriptible. The law protects an important ecological corridor, and obliges governments to demarcate them. Numerous individuals, agencies, associations, universities, NGOs and working groups are exploring different ways to protect, recover, and foster the droves and bring them to the attention of a wider sector of society. They work toward restoring and fostering extensive livestock farming, attracting young people to transhumance and cattle farming, and rapidly finishing the demarcation of all drove ways. Other actions include pressing governments to enforce the laws; fully exploiting the multifunctionality (livestock transport, ecosystem services, biodiversity conservation, recreation, etc.) of the Vías Pecuarias; and reaching out to a wider sector of society.

Example of an ecological corridor

In Spain, the network of drover's roads is densest in the Autonomous Community of Madrid (Figure 2). Many actions are being taken to protect them. For instance, ecological functionality of the Real Cañada Segoviana (Royal Segovian Droveway) is being improved by the Repsol Foundation and Reforesta through reforestation with native species, fencing of endangered plants, restoration of ponds and creation of new ones, establishment and fencing of refugia for different animal species, habitat improvement for insects, environmental education and monitoring.

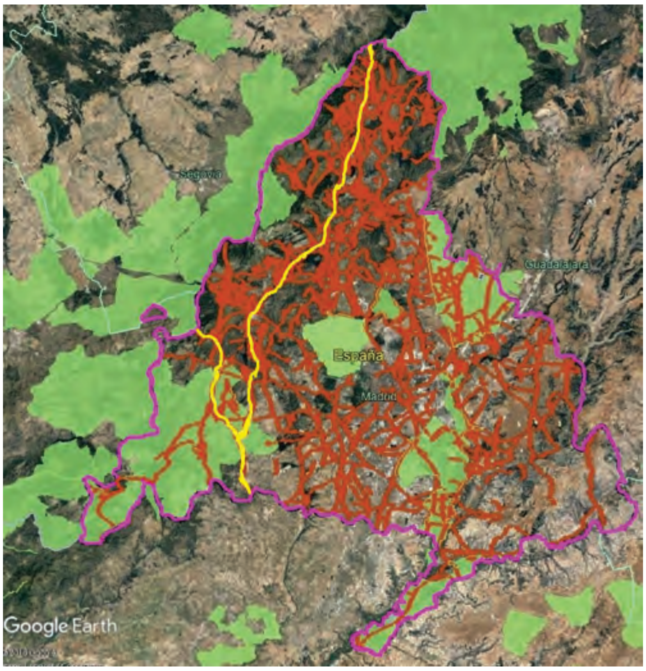


Figure 2. Vías pecuarias of the Autonomous Community of Madrid superimposed on protected areas. Note how they link rural, urban, protected and unprotected areas. In yellow, the Cañada Real Segoviana. Droves outside the Autonomous Community are not depicted. © Marcos Pradas, Spanish Instituto Geográfico Nacional and the Community of Madrid; Base data courtesy of Google Earth

Results

Governments tend to be ambivalent about the issue. On the one hand, of 125,000 km of droves, 40,000 km may already be lost. Governments often permit a change of use of these roads. When their utility for cattle is lost, they decree by law the land-use change and take them out of the public domain. The Autonomous Community of Madrid is no exception and may have lost around 38% of its drover's roads over the past 20 years. One example is the Cañada de Madrid: a linear city was built illegally along 14.2 km of the Galiana's Royal Droveway. On the other hand, many governments are demarcating drover's roads, educating the public, and taking action in the field to protect them and maximise their ecosystem services. In a world that urgently presses to reduce the environmental impacts of meat consumption, a new generation of transhumance practitioners offers the responsible consumer the opportunity to eat animal products that have a positive ecological footprint. Protecting Spain's drover's roads will support this market and, in addition, allow these ecological corridors to continue to deliver their much-needed ecosystem services.

Learn more:
http://www.pastos.es/
https://www.viaspecuariasdemadrid.org/
http://transhumancia.cat/es/inicio/
http://trashumanciadehoy.emiweb.es/paginas/cartografia-y-conocimiento-de-los-caminos.html

12. ECONET: Ecological network in the Kostroma Region, Russia

Alexander V. Khoroshev, *Lomonosov Moscow State University*

Key lesson

Ecological corridors that encompass riparian and forested corridors can have multiple benefits such as decreasing erosion and improving water quality.

Context and challenge

Recent undesirable changes to the landscape of the Kostroma region in central European Russia revealed the need for a strong ecological network for conservation. The region is located in the watershed divide between the Caspian and the White seas. Here, Siberian species transition to European species, and taiga is replaced by broad-leaved forest. Landscape diversity is highest where depressions among morainic hills are combined with post-glacial lakes, fens, bogs, and old-growth and secondary forests that control water runoff and ensure valuable wetland habitats. In recent decades, vast forest areas decreased considerably due to timber harvesting. This harvesting expanded to remote catchment areas, which caused a decrease of runoff volume, loss of opportunities for navigation on rivers, and the degradation of fish resources, all with obvious negative economic consequences for local people. This resulted in the need to preserve the remnants of virgin southern taiga stands within an ecological network.

Approach

The mission of the Kostroma ECONET project, launched in 2003 with strong support of the regional government, was to ensure the protection and connectivity of the most ecologically valuable landscapes as well as to facilitate restoration of lost traditional economic opportunities for local people. The Kostroma ECONET project is based on the idea of critical significance of a connected landscape.

The core areas of the ecological network for conservation are composed of four types of landscapes: (1) intact landscapes representative of the European southern taiga, such as moraine plains with spruce and fir forests (e.g. Kologriv Forest Nature Reserve); (2) fluvioglacial terraces with pine forests, and mires; (3) rare and unique landscapes (e.g. larch forests on sandy terraces); and (4) landscapes with key habitats for migratory birds and mammals (e.g. floodplains used by geese on their spring migration from western Europe to northern Siberia). The full range of typical interfluvial and river valley landscapes is represented in the network (Figure 1), with a higher concentration of protected areas in the upper parts of the river basins that have a higher proportion of mires close to watershed divides. The legal regime of the ECONET prohibits clearcutting in key locations to ensure runoff formation in the interfluves and safeguards the necessary proportion of forests

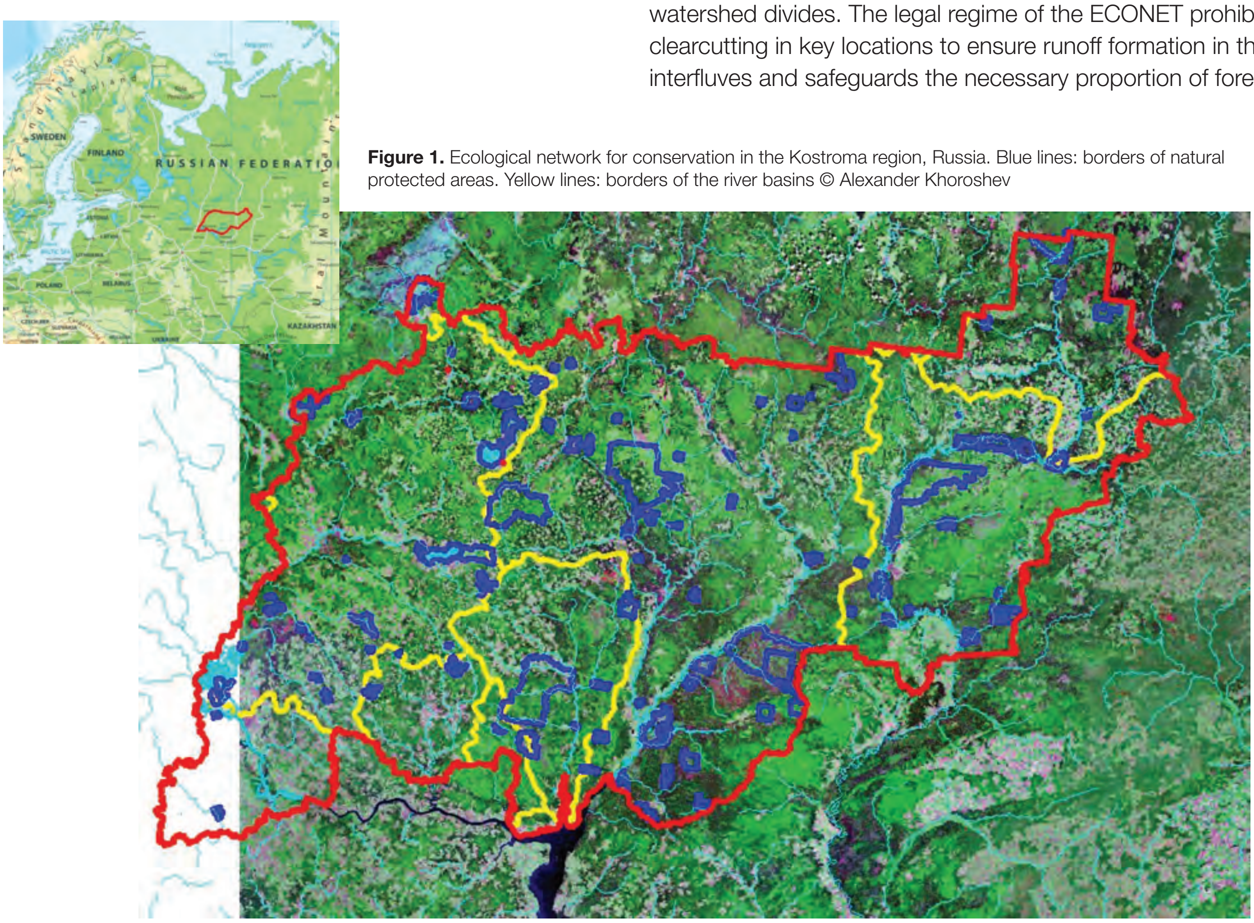


Figure 1. Ecological network for conservation in the Kostroma region, Russia. Blue lines: borders of natural protected areas. Yellow lines: borders of the river basins © Alexander Khoroshev

Kostroma Taiga, Russia © Adobe Stock

in a given basin. The process of planning protected areas included intensive consultations with local stakeholders.

Example of an ecological corridor

The protected areas are connected by ecological corridors consisting either of riparian forests or of zonal coniferous forests embedded in a matrix of timber harvesting areas. The ecological network recognises the crucial contribution of the regional landscapes to the functioning of the larger watershed, the Volga River basin, because the three largest tributaries in its upper reaches come from the Kostroma region. The ecological corridors comprise hydrologically important zones along the slopes of river valleys, terraces and floodplains. Thus, in addition to connecting core protected areas, the ecological corridors decrease erosion, water eutrophication and undesirable surface runoff.

Results

A scheme to develop an ecological network for conservation was adopted by the regional authorities in 2008. Fifty-nine protected areas are being established, with reasonable limitations on timber harvesting, human development, and, if necessary, hunting and fishing embedded in land-use plans. The scheme is now an obligatory part of territorial planning at both the regional and municipal levels.

The experience of the Kologriv Forest Nature Reserve provided evidence that prohibiting hunting in rather small areas can result in an increase of game species populations, their expansion to the adjacent non-protected landscapes and, therefore, an increase in game resources. Some of the established protected areas successfully combine nature protection, recreation and ecological tourism. This is of particular importance to communities in Kostroma's remote districts who struggle with insufficient sources of income. The most serious current challenge to the ECONET project is the delayed designation of protected area borders by state authorities, which results in conflicts with the timber industry and agricultural producers.

Terrestrial connectivity: North and South America

13. Sustaining forested landscape connections in the northern Appalachians: The Staying Connected Initiative

Jessica Levine, *The Nature Conservancy*

Key lesson

In the United States, conservation easements are an important tool to permanently secure connectivity.

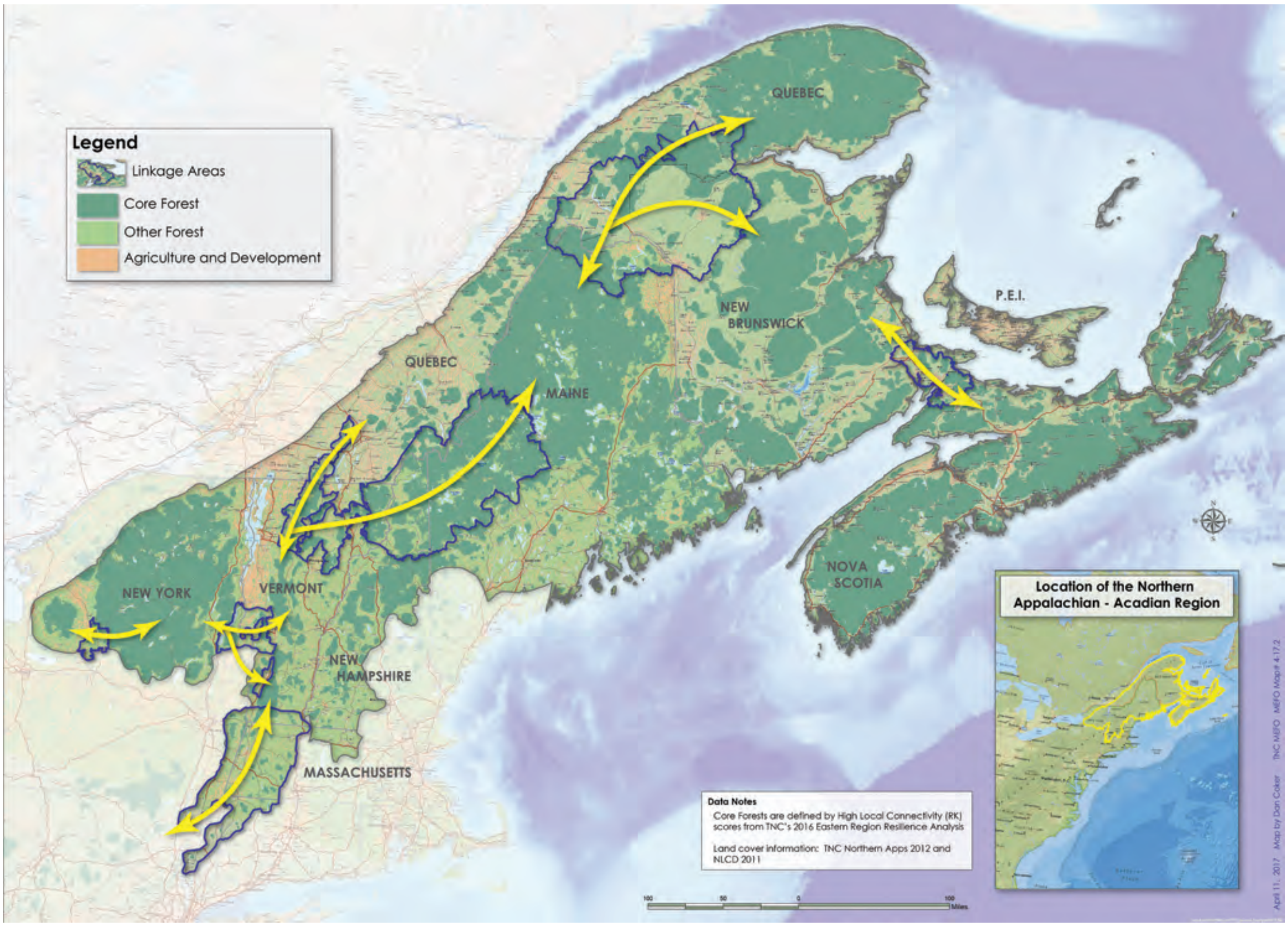
Context and challenge

The 32 million-ha Northern Appalachian–Acadian ecoregion – which includes parts of five US states and three Canadian provinces – contains the largest expanse of temperate broadleaf forest remaining in the world. Protected areas within the region include a national forest, state and provincial parks, national parks and conservation easements. Yet these tracts are nested within a matrix of rural development and human uses. The region is only a half-day's drive from several major urban centres, including New York, Boston and Montreal, and is increasingly in danger of fragmentation from roads and other human development. In 2009, public agencies and private organisations from across the bi-national region formed the Staying Connected Initiative (SCI) to address this challenge.

Approach

The SCI is a partnership of over 55 organisations, including natural resource and transportation departments from the US states and Canadian provinces of the region, conservation organisations and universities. Partners actively collaborate to maintain, enhance and restore landscape connectivity across this large region. On-the-ground efforts are focused on ensuring landscape permeability, today and into the future as the climate changes, in nine highest-priority linkage areas (Figure 1). In these, partners apply a combination of strategies to conserve connectivity, recognising that no single strategy is sufficient and that partners have different areas of influence and expertise. Primary strategies include:

- Strategic land protection of priority parcels for connectivity such as forested pathways and riparian corridors;



Data Notes

Core Forests are defined by High Local Connectivity (RK) scores from TNC's 2016 Eastern Region Resilience Analysis

Land cover information: TNC Northern Apps 2012 and NLCD 2011

April 11, 2017 Map by Dan Coker TNC MEFO MEFO Map# 4-17.2

Figure 1. Staying Connected Initiative region and linkage areas © The Nature Conservancy

- Land-use planning to steer development away from critical connectivity areas;
- Community outreach and engagement to build awareness and appreciation among private landowners and encourage private land management to maintain landscape permeability;
- Habitat restoration in key locations such as wetlands and roadside parcels; and
- Facilitation of the movement of wildlife under roads by means of improved bridges and culverts, signage and fencing.

At the regional scale, partners share best practices and lessons learnt through webinars, meetings and written communications.

Example of an ecological corridor

The Northern Green Mountain linkage area encompasses 2,923 km^2 and is centred on the spine of the Green Mountains. The linkage area stretches from Mt. Mansfield State Forest, which contains Vermont's highest peak, north to Mont Orford National Park in Quebec. Most of the area is forested, with agriculture and small towns and villages in the many valleys that bisect the mountain spine. Within this linkage area, Jackson Valley is an important ecological corridor along the US–Canada border (Figure 2). A 2010 study of the 379-ha parcel found that it served as a key trans-border ecological corridor for a range of animals. Jackson Valley links conserved Atlas Timberlands to the south, Jay State Forest to the east, and a 652-ha preserve in Quebec, protected by Nature Conservancy of Canada, to the north. In 2012, with funding from the US Forest Legacy Program, The Trust for Public Land completed years of work to conserve Jackson Valley. A conservation easement, held by the state of Vermont, prevents development and subdivision in the ecological corridor and requires sustainable management for wildlife, timber, public recreation and soil conservation. The corridor is open to hikers and skiers, and for other forms of non-motorised recreation.

Conservation of this parcel as an ecological corridor is leveraged by the work of many SCI partners on both sides of the border. This work includes land protection in other parts of the linkage (over 12,140 ha to date), technical assistance to municipalities on land-use planning to steer development away from critical ecological corridors, scientific studies along major roadways to identify potential sites for wildlife mitigation measures, and outreach to private landowners on sustainable forest management.

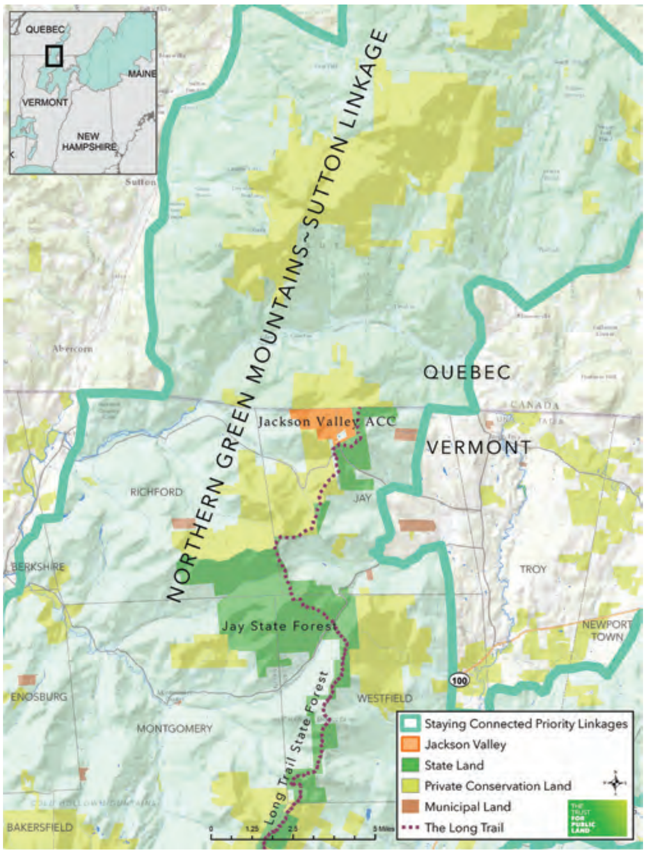


Figure 2. Jackson Valley Ecological Corridor in the Northern Green Mountains linkage area © The Trust for Public Land

Results

Since 2009, SCI government and land trust partners have secured permanent protection of over 222,500 ha in the nine linkage areas. At least 30 land-use plans in the linkage areas, and all five state Wildlife Action Plans in the region, explicitly incorporate wildlife connectivity. Partners from SCI helped to develop and advance the 2016 Resolution on Ecological Connectivity passed by the Conference of New England Governors and Eastern Canadian Premiers, and SCI government agency partners are leading its implementation. The resolution acknowledges the importance of ecological connectivity from a climate adaptation perspective and calls on relevant agencies within the 11 jurisdictions to work together for improved connectivity through transportation improvements, land protection, forest management and other efforts.

Learn more about SCI and the resolution at http://stayingconnectedinitiative.org/ and https://www.coneg.org/wp-content/uploads/2019/01/40-3-Ecological-Connectivity-EN.pdf.

14. Yellowstone to Yukon (Y2Y): Connecting and protecting one the of the most intact mountain ecosystems

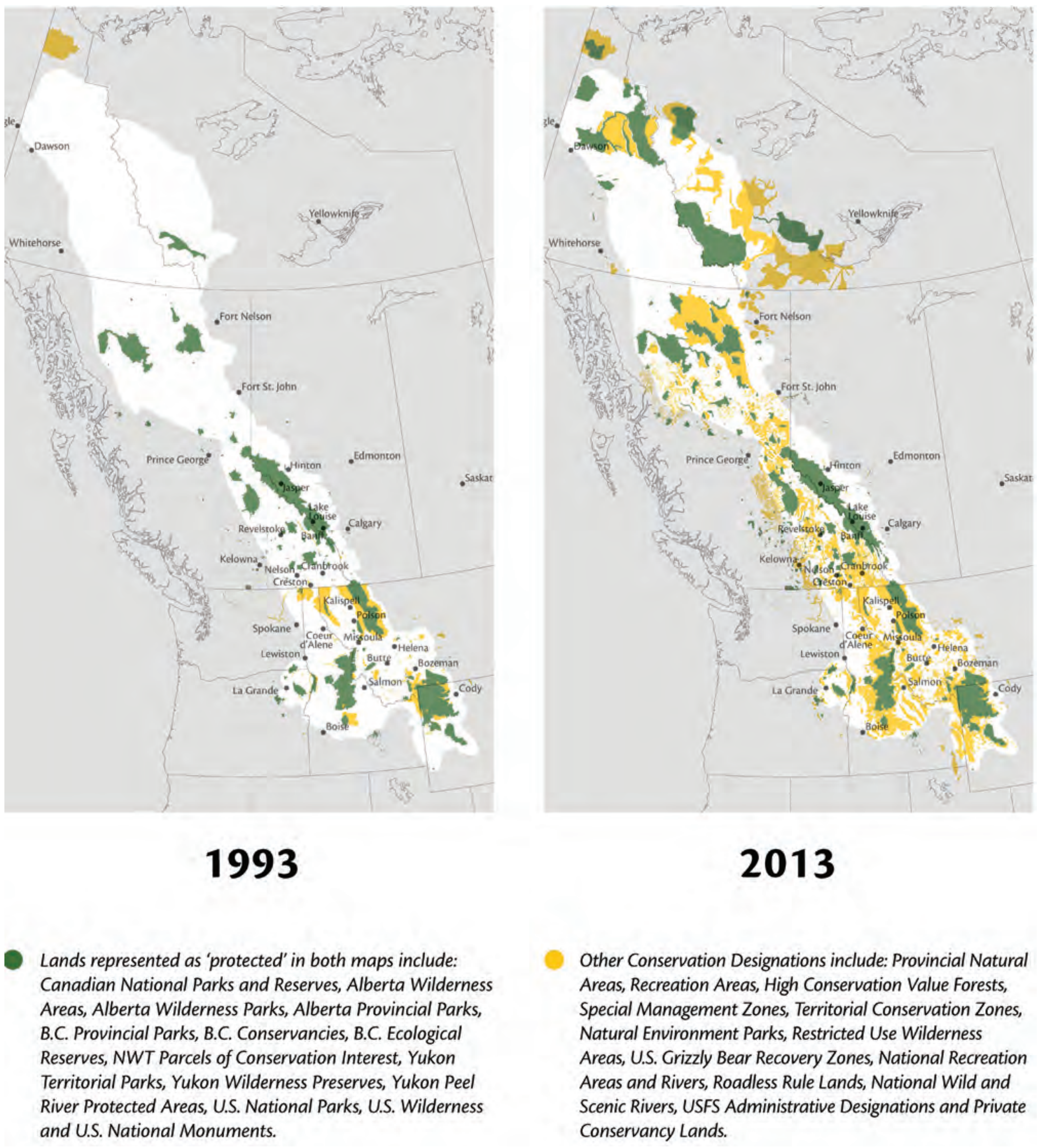
Jodi Hilty, *Yellowstone to Yukon Conservation Initiative*

Context and challenge

Increasing human activities threaten to fragment the 3,200-km-long Yellowstone to Yukon (Y2Y) mountain region in western North America (Figure 1), thus impacting natural processes, wild areas and wildlife, ranging from grizzly bears (*Ursus arctos horribilis*) and mountain caribou (*Rangifer tarandus caribou*) to

Key lesson

Realisation of a larger ecological network vision requires science, on-the-ground action, and monitoring the impact of the collaborative conservation efforts in order to assess whether connectivity goals are ultimately met.



● *Lands represented as 'protected' in both maps include: Canadian National Parks and Reserves, Alberta Wilderness Areas, Alberta Wilderness Parks, Alberta Provincial Parks, B.C. Provincial Parks, B.C. Conservancies, B.C. Ecological Reserves, NWT Parcels of Conservation Interest, Yukon Territorial Parks, Yukon Wilderness Preserves, Yukon Peel River Protected Areas, U.S. National Parks, U.S. Wilderness and U.S. National Monuments.*

● *Other Conservation Designations include: Provincial Natural Areas, Recreation Areas, High Conservation Value Forests, Special Management Zones, Territorial Conservation Zones, Natural Environment Parks, Restricted Use Wilderness Areas, U.S. Grizzly Bear Recovery Zones, National Recreation Areas and Rivers, Roadless Rule Lands, National Wild and Scenic Rivers, USFS Administrative Designations and Private Conservancy Lands.*

Figure 1. Increase in protected areas over two decades in the Y2Y region of North America © Y2Y

jumping slugs (*Hemphillia dromedarius*) and migratory birds. The region has a myriad of jurisdictions, including many Indigenous territories. The US and Canadian governments have classified approximately 80% of Y2Y lands as public and 20% as private or tribal reservation lands.

Approach

Since 1993, a joint Canada–US not-for-profit organisation, the Yellowstone to Yukon Conservation Initiative, has brought partners together to achieve the vision of connecting and protecting the region so that people and nature can thrive within an ecological network for conservation. More than 400 different entities have been or currently are engaged in collaborative conservation that advances the vision across this ecological network. These include conservation groups, local landowners, Indigenous entities, businesses, government agencies, funders and donors, and scientists. The conservation progress across the Y2Y region is due to the collective work of these different groups. Conservation priorities range from protecting areas important for biodiversity and restoring and maintaining areas between protected areas for ecological connectivity, to directing development away from areas of biological importance and promoting people and wildlife to live in harmony across the region. Protected areas include designations such as national, state and provincial parks, and wilderness areas. In the Y2Y region, increased connectivity may be achieved through large and well-placed protected areas, privately conserved lands, or other lands designated for long-term management that allows for connectivity.

Examples of ecological corridors

Within the Y2Y landscape, a variety of groups has been working in the British Columbia, Montana and Idaho trans-border region to identify and reconnect small, isolated grizzly bear populations along the Canada–US border in southeast British Columbia. Using genetics, scientists identified that once-continuous grizzly bear populations had begun to fragment; the scientists then identified the best remnant corridors (Figure 2). Many different groups worked to implement connectivity-friendly management (such as securing private lands and providing tools for coexistence). Ultimately, a decade later, it was possible to demonstrate movements of grizzly bears between previously fragmented ecosystems, accompanied by reproduction (Proctor et al., 2018).

Results

Progress toward protecting a regional ecological network is being made. Protected areas increased more than 50% across the Y2Y region, and a number of ecological corridors and other areas conserving connectivity have been identified, restored and/or maintained between protected areas. Likewise, conservation projects have multiplied across the region to significantly decrease human–wildlife conflicts. Some animals, such as grizzly bears and wolves (*Canis lupus*) in the lower 48 US states, have increased in number and range, but significant conservation remains to be done, as other animals such as mountain caribou have continued to decline in numbers across the region.

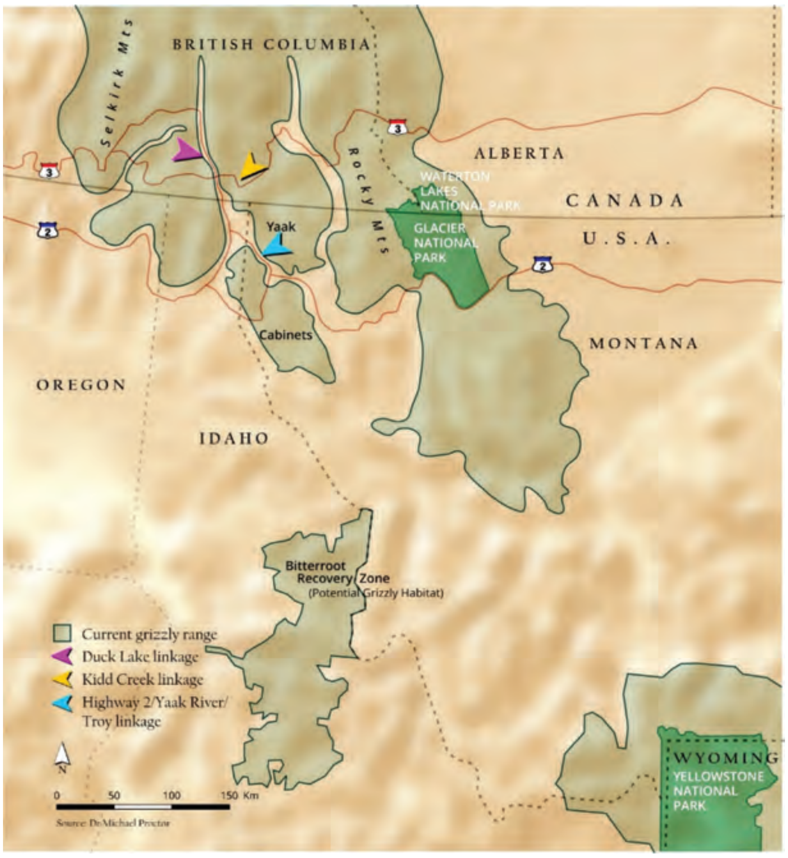


Figure 2. The Y2Y transboundary region including key grizzly bear distribution and linkages. The three arrows point to three different linkages – Duck Lake, Kidd Creek and Yaak River – where private land acquisitions have secured ecological corridors for grizzly bears. © Y2Y

15. Conserving long-distance migration: The Red Desert to Hoback Mule Deer Corridor, Wyoming, USA

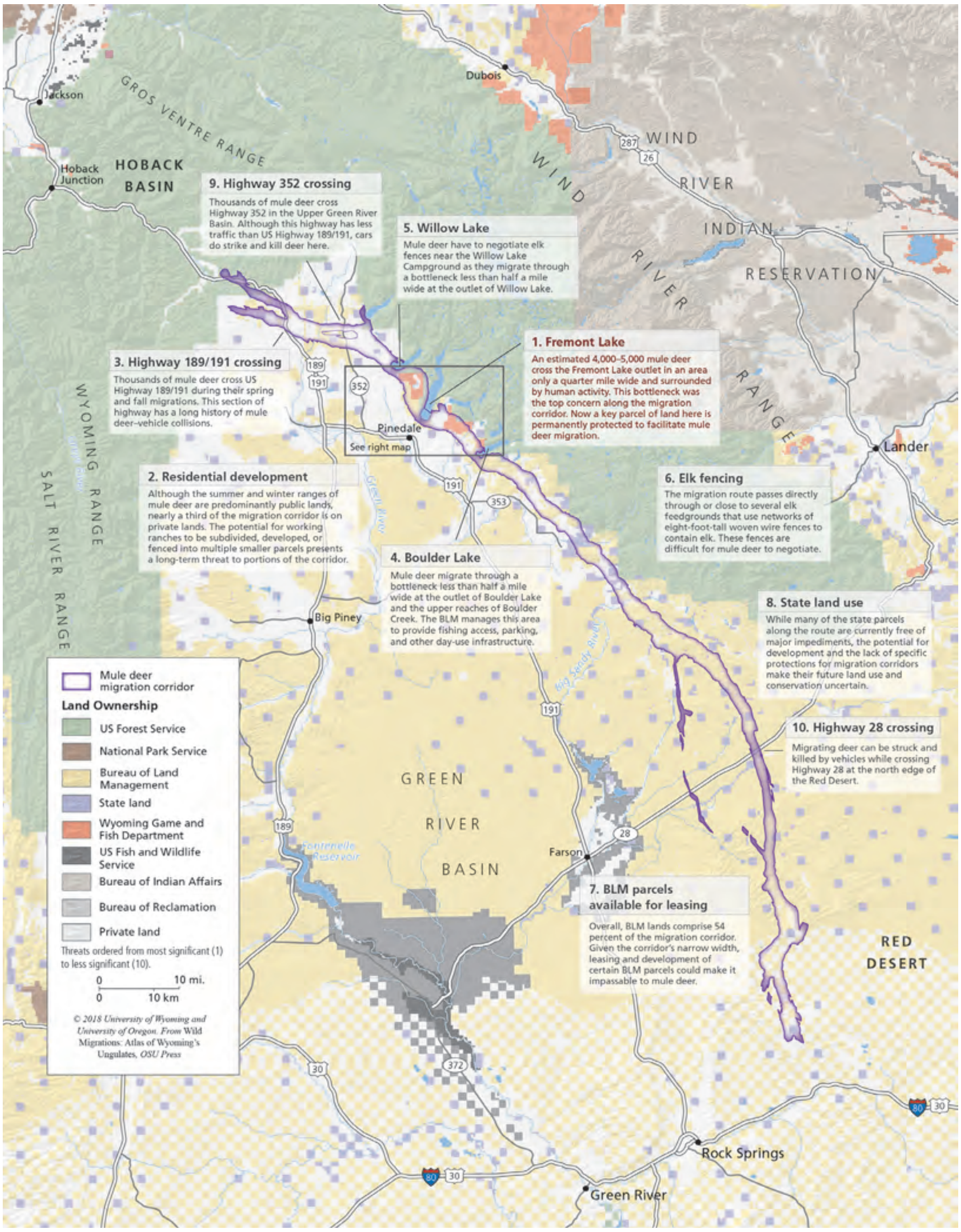
Matthew J. Kauffman, *Wyoming Cooperative Fish and Wildlife Research Unit*
Holly Copeland, *Wyoming Cooperative Fish and Wildlife Research Unit; Hall Sawyer, Western EcoSystems Technology, Inc.*

Key lesson

This work demonstrates how scientific studies documented migratory corridors for wildlife, resulting in the purchase of private lands that otherwise would have been developed.

Context and challenge

Effective protection of landscapes for migratory species is recognised as a global conservation challenge in the face of ever-increasing anthropogenic land-use changes. Ungulates that migrate long distances must move across a variety



1. Fremont Lake
An estimated 4,000–5,000 mule deer cross the Fremont Lake outlet in an area only a quarter mile wide and surrounded by human activity. This bottleneck was the top concern along the migration corridor. Now a key parcel of land here is permanently protected to facilitate mule deer migration.

2. Residential development
Although the summer and winter ranges of mule deer are predominantly public lands, nearly a third of the migration corridor is on private lands. The potential for working ranches to be subdivided, developed, or fenced into multiple smaller parcels presents a long-term threat to portions of the corridor.

3. Highway 189/191 crossing
Thousands of mule deer cross US Highway 189/191 during their spring and fall migrations. This section of highway has a long history of mule deer–vehicle collisions.

4. Boulder Lake
Mule deer migrate through a bottleneck less than half a mile wide at the outlet of Boulder Lake and the upper reaches of Boulder Creek. The BLM manages this area to provide fishing access, parking, and other day-use infrastructure.

5. Willow Lake
Mule deer have to negotiate elk fences near the Willow Lake Campground as they migrate through a bottleneck less than half a mile wide at the outlet of Willow Lake.

6. Elk fencing
The migration route passes directly through or close to several elk feedgrounds that use networks of eight-foot-tall woven wire fences to contain elk. These fences are difficult for mule deer to negotiate.

7. BLM parcels available for leasing
Overall, BLM lands comprise 54 percent of the migration corridor. Given the corridor's narrow width, leasing and development of certain BLM parcels could make it impassable to mule deer.

8. State land use
While many of the state parcels along the route are currently free of major impediments, the potential for development and the lack of specific protections for migration corridors make their future land use and conservation uncertain.

9. Highway 352 crossing
Thousands of mule deer cross Highway 352 in the Upper Green River Basin. Although this highway has less traffic than US Highway 189/191, cars do strike and kill deer here.

10. Highway 28 crossing
Migrating deer can be struck and killed by vehicles while crossing Highway 28 at the north edge of the Red Desert.

Threats ordered from most significant (1) to less significant (10).

© 2018 University of Wyoming and University of Oregon. From Wild Migrations: Atlas of Wyoming's Ungulates, *OSU Press*

Figure 1. The Red Desert to Hoback mule deer migration corridor spans 240 km in southwest Wyoming, USA, crossing a multiple-use landscape. The top ten potential obstacles to the continuity of the corridor are noted. Map from *Wild Migrations: Atlas of Wyoming's Ungulates,* Oregon State University Press. © 2018 University of Wyoming and University of Oregon. Image courtesy of Wyoming Migration Initiative (migrationinitiative.org).

of jurisdictional boundaries, altered or degraded habitats, and human obstacles such as roads, fences, housing and energy development. Globally, long-distance terrestrial migrants continue to decline as a result of these challenges, and ungulates in the American West are no exception. Mule deer (*Odocoileus hemionus*) are an iconic migratory species of the western US, and Wyoming has some of the longest, most intact mule deer migrations in the lower 48 states. In western Wyoming, the Upper Green River Basin is a region known to contain some of the largest mule deer populations in North America. Dozens of long-distance migration routes traveled by mule deer, elk (*Cervus canadensis*) and pronghorn (*Antilocapra americana*) have now been mapped across Wyoming's mountains and plains. As anthropogenic influences increase and migratory ungulates continue to decline worldwide, a focus on landscape connectivity is needed to broaden conservation efforts beyond winter and summer ranges to include migration routes as critical habitat.

Approach

Detailed mapping of migration routes has emerged as a first step towards identifying threats and implementing long-term conservation, aided by new data on ungulate movements from global positioning system (GPS) telemetry studies. The new maps allow assessments of land-use patterns and threats along the routes, which can directly inform conservation action.

Example of an ecological corridor

In 2014, scientists discovered a 240-km-long mule deer migration route, stretching from the desert basins in southwest Wyoming to surrounding mountain ranges. It is known as the Red Desert to Hoback corridor (Figure 1). An estimated 1,000 mule deer travel a one-way distance of 240 km from the Red Desert to the Hoback Basin and surrounding mountain ranges, where they merge with 4,000 to 5,000 other deer that winter in the foothills of the Wind River Range. They all then travel a narrow corridor along the base of the mountains for 96 km before crossing the upper Green River Basin.

Researchers mapped the ecological corridor in detail and then published an assessment analysing land-use patterns and threats for each section (Sawyer et al., 2014). This assessment identified the top ten threats along the length of the corridor and provided conservation organisations with information needed to direct scarce funds to sites where they are most needed, such as specific bottlenecks, road crossings or unprotected segments of private land. At the top of the threats list was the Fremont Lake 'bottleneck', a 400-m-wide constriction created by the lake and the expanding town of Pinedale, where 4,000 to 5,000 deer squeezed through twice a year. The deer were required to either swim (or, when frozen, walk across) the lake, or ford its outlet, which put them on the wrong side of a 2.5-m-high woven wire fence.

Results

The Fremont Lake bottleneck consisted largely of a 145-ha parcel of private lands that was slated for subdivision and conversion to lakeside cottages which, if developed, would have blocked deer migration. Guided by information within the assessment, The Conservation Fund, a national non-profit conservation organisation, identified and purchased the parcel. The land was given to the Wyoming Game and Fish Department, which subsequently protected it through designation as the Luke Lynch Wildlife Habitat Management Area, thereby maintaining in perpetuity the connectivity of the ecological corridor at this key pinch point (Figure 2).

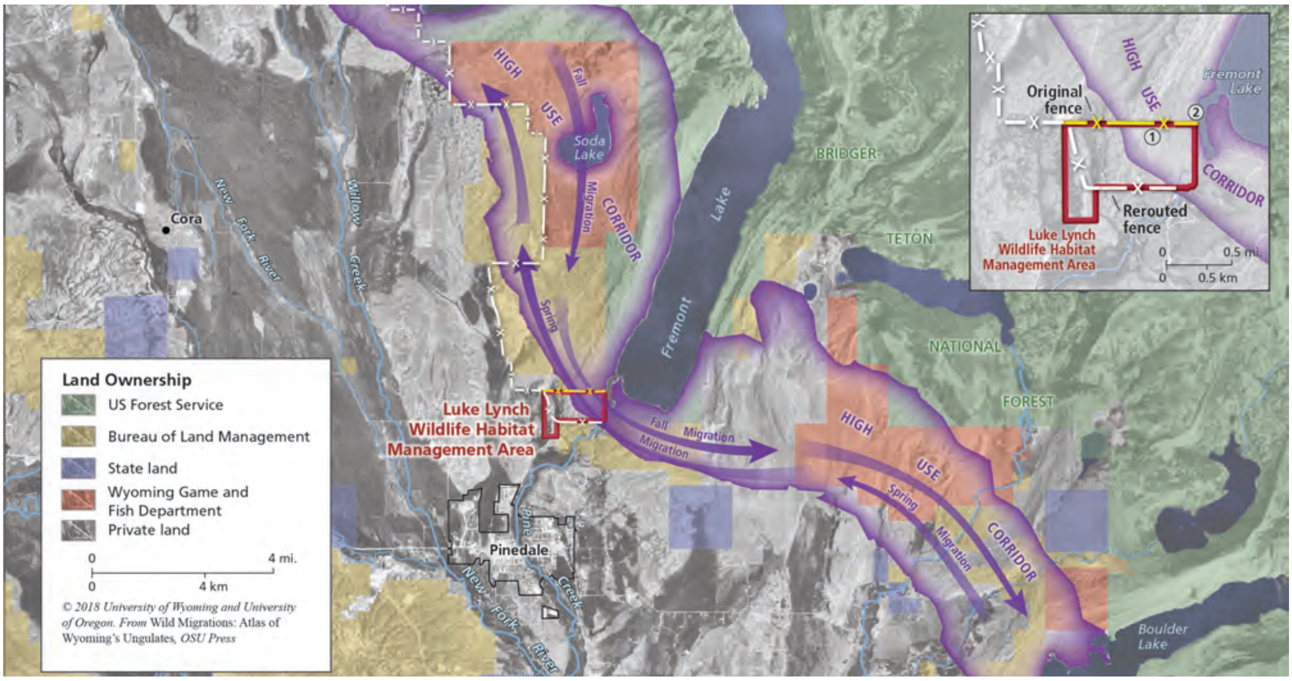


Figure 2. Location of the Fremont Lake bottleneck, now conserved as the Luke Lynch Wildlife Habitat Management Area. Map from *Wild Migrations: Atlas of Wyoming's Ungulates,* Oregon State University Press. © 2018 University of Wyoming and University of Oregon. Image courtesy of Wyoming Migration Initiative (migrationinitiative.org)

16. Corridors for life: Improving livelihoods and connecting forests in Brazil

Laury Cullen, *Instituto de Pesquisas Ecológicas, Brazil*

Key lesson

When working with agricultural communities, focusing on multiple benefits of restoring ecological corridors, such as improving livelihoods and obtaining carbon sequestration funding, is vital.

Context and challenge

In Brazil, the largest Atlantic Forest remnants in the interior lie in the Pontal do Paranapanema area of western São Paulo state. Originally a 124,000-ha public forest reserve was designated, but it was progressively encroached upon during 1960–1990 by large-scale ranching and sugarcane establishments. In the mid-1990s, with pressure for land redistribution from the Landless Rural Workers' Movement (MST) and other groups, many such forests were first occupied by families of MST affiliates and later expropriated for public land reform settlements, dramatically increasing the density of human occupation. After the settlement of many landless households, the pace of land redistribution slowed, and national policies now seek to consolidate existing settlements. Promoting income generation for settlers is urgently needed, as is protecting the remaining fragmented forests within this productive landscape before further pressures ensue. Although agrarian reform settlements and large landowners pose a series of barriers to biodiversity conservation, they also offer important and replicable opportunities for large-scale landscape forest restoration.

Approach

The Corridors for Life project focuses on (1) encouraging the adoption of 'biodiversity-friendly' land-use options; (2) promoting changes in land-use practices of small- and large-scale farmers in rural fragmented landscapes, and enhancing the adoption of sustainable agriculture and agroforestry on their lands; (3) improving the farmers' livelihoods; and (4) providing investors a return in the form of high-quality carbon offsets. Strategically selected areas for agroforestry and restoration will increase habitat viability by means of ecological corridors to increase connectivity between 'core' forest fragments, ensuring genetic exchange. Where corridors are not feasible, this exchange will be achieved through

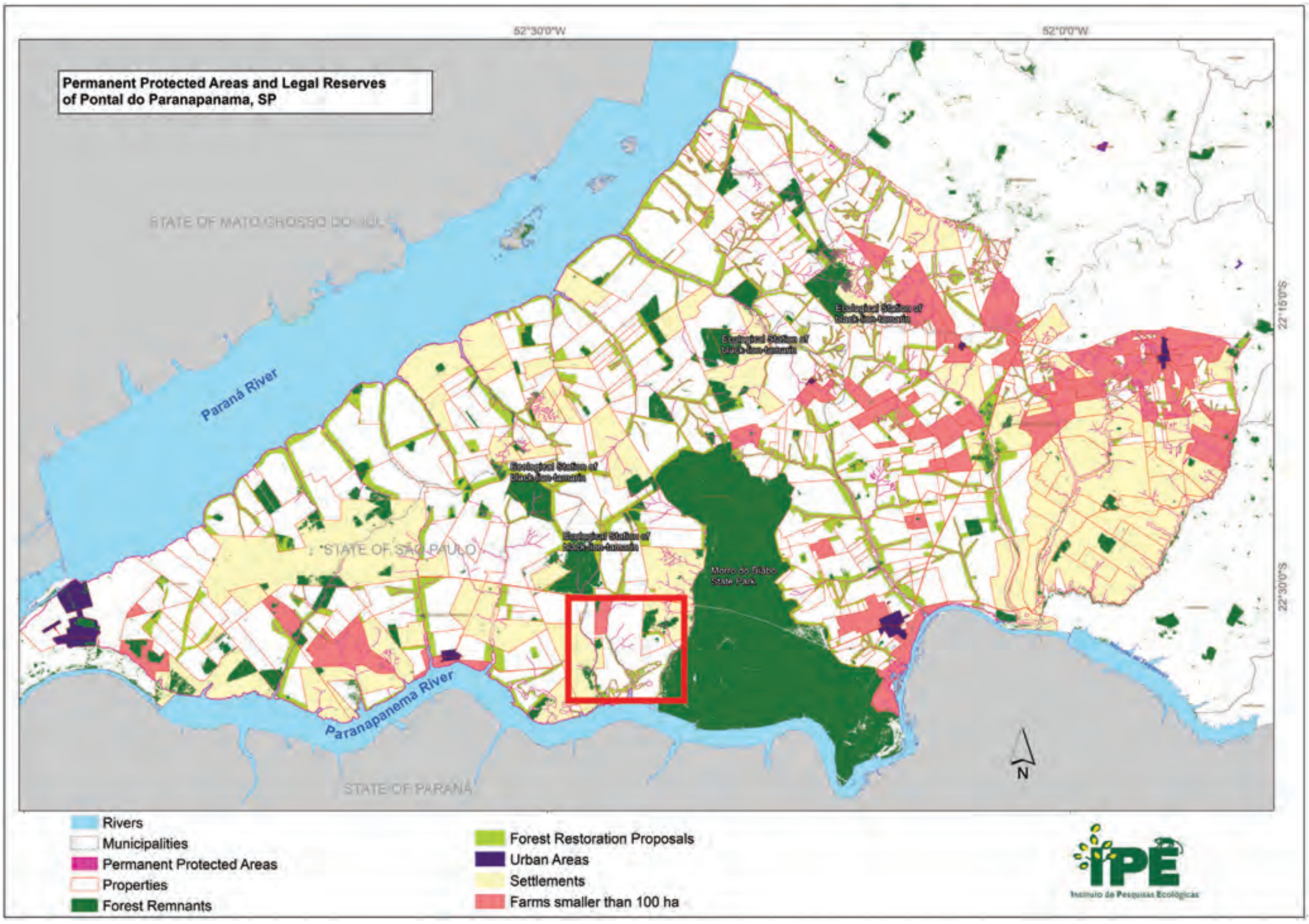


Figure 1. IPÊ's 'dream map' for Pontal de Paranapanema uses ecological and property data in order to create the best approach for reforestation efforts. The red polygon contains the largest ecological corridor (1,200 ha) restored in the Atlantic Forest, linking Morro do Diabo State Park and Black Lion Tamarin Ecological Station. © Instituto de Pesquisas Ecológicas

developing stepping stones. Agroforestry and restoration will also minimise degradation around biologically important landmarks, including Morro do Diabo State Park, as the main reservoir of populations of key and endangered species. Enlarging and eventually connecting forest fragments are two main goals of reforestation projects. From an ecological perspective, this is essential to maintaining viable populations of flora and fauna and mitigating harmful edge effects, such as exposure to light and wind, diseases and invasive species. The Instituto de Pesquisas Ecológicas (IPÊ) developed a 'dream map' for Pontal de Paranapanema, the extreme western municipality of São Paulo, where the institute was founded. This plan for wide-scale reforestation of the Atlantic Forest takes into consideration information on local properties as well as proximity to public protected areas and existing forest fragments to calculate where reforestation efforts would be most effective (Figure 1, previous page). Among the main project partners are state and federal rural extension agencies, private companies interested in the carbon neutralisation market, companies that produce and commercialise ethanol and sugar, and other national and international electric power holding companies.

Example of an ecological corridor

A conceptual map was used to guide the creation of Brazil's largest reforestation corridor (Figure 2), which, after ten years of effort, links two main remnants of Atlantic Forest in the Pontal de Paranapanema region. This ecological corridor is approximately 7 km long with average width of 400 m. It was restored entirely on privately owned lands. It is protected by the Law for Protection of Native Vegetation, passed in 2012, with which the Brazilian National Congress revised the 'old forest code', as the previous version of the law was known. The 2012 law reaffirms the obligation of private landowners to conserve or restore permanent preservation areas and legal reserves on their properties.

Results

To date, approximately 1,800 ha of forest have been restored in Pontal do Paranapanema. This includes the 1,200 ha of the main ecological corridor, another 600 ha in five smaller corridors and 90 agroforestry stepping stones on rural properties. This project consolidates strategies that represent sustainable livelihood alternatives for communities of the land reform movement in Brazil, replicating good practices and policies in income generation and biodiversity conservation. At the policy level, IPÊ, together with other civil organisations in the region, are influencing policies that affect land use and conservation. By using scientific evidence, cooperating with new settlers and large landowners, and collaborating with state and federal agencies, the program is implementing a land-use framework that promotes sustainable agriculture and biodiversity conservation over the long term.

Figure 2. Some 2.4 million trees make up IPÊ's 1,200-ha ecological corridor connecting two main Atlantic Forest fragments, the largest in Brazil.
© Instituto de Pesquisas Ecológicas

17. Connectivity, ecosystem services and Nature-based Solutions in land-use planning in Costa Rica

Félix Zumbado Morales and Jonathan Agüero Valverde, *Research Program in Sustainable Urban Development, University of Costa Rica*

Key lesson

Costa Rica has a three-pronged approach to land conservation: protected areas, ecological corridors and sustainable management of the matrix; different levels of human use are allowed depending on the protection level.

Context and challenge

Costa Rica is a small nation of 51,000 km^2 that contains about 5% of global biodiversity. The sustainable management of biodiversity is one of the pillars of the work carried out by the country. Protected areas are the country's primary conservation strategy, playing a crucial role in the protection of ecosystems. Costa Rica's second most important conservation strategy is the ecological corridor program, managed by the Costa Rican government, but working hand in hand with communities through local ecological corridor committees. Municipal land management plans have emerged as a third tool complementing protected areas and ecological corridors. These management plans generate the guidelines necessary to allow human development activities to be carried out while maintaining sustainable landscapes, taking into consideration the comprehensive use of the regions. Protected areas and ecological corridors are incorporated into the land management plans; the same is true for the principles of ecosystem services and Nature-based Solutions as decision-making tools.

Approach

Land management plans are a tool that local governments can use to generate regulations that complement protected areas and ecological corridors. These three land management tools are complementary and must be developed in an integrated fashion to achieve a systematic approach to planning. Management plans implement ecological corridors through tools such as the establishment of specific areas for focal species; the preservation of agricultural areas that function as biological, conservation and sustainable tourism corridors; the creation of buffer zones around protected

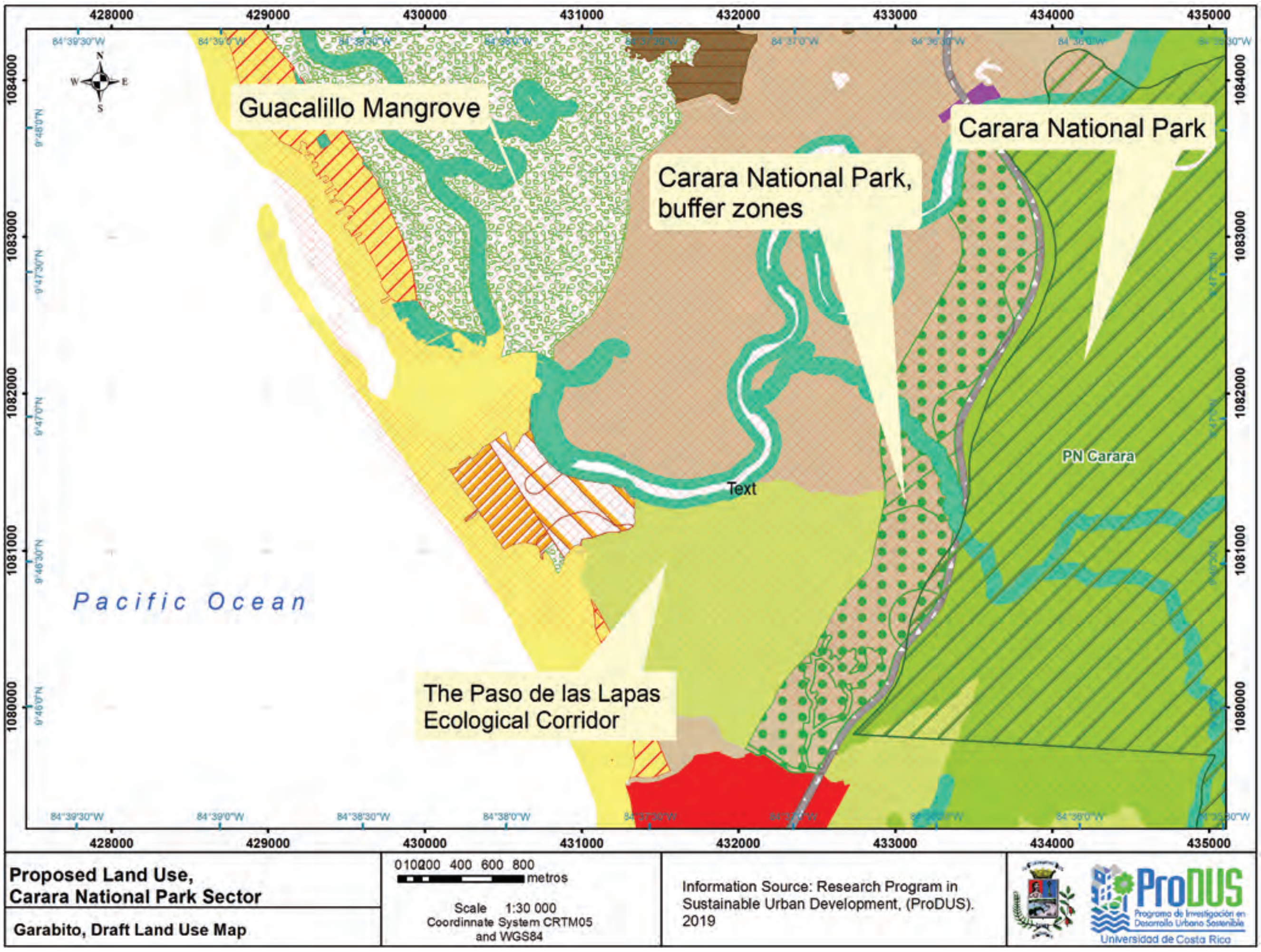


Figure 1. Proposed land uses in the region of Canton of Garabito containing the Paso de las Lapas Ecological Corridor © Research Program in Sustainable Urban Development (ProDUS) Universidad de Costa Rica

Carara National Park, Costa Rica © Adobe Stock

areas; and the zoning of aquifer recharge zones for the protection of water sources for local and regional populations. Through the University of Costa Rica's Sustainable Urban Development Research Program (UCR-ProDUS is the Spanish acronym), land management plans for more than a dozen municipalities have been developed, including the protected areas Corcovado National Park, Piedras Blancas National Park, Ballena Marine National Park, Juan Castro Blanco Water National Park and Carara National Park.

Example of an ecological corridor

UCR-ProDUS developed a land management plan for the Canton of Garabito, which contains the Paso de las Lapas Ecological Corridor (Figure 1). This ecological corridor encompasses 56,200 ha and connects protected areas in the mountains (La Cangraja National Park, Cerros de Turrubares protected area and Carara National Park) with coastal areas. The Paso de las Lapas Ecological Corridor was established in 2007 through an executive order. In Costa Rica, ecological corridors are not state conservation areas, but are a different conservation strategy promoted by the National System of Conservation Areas through the national program of ecological corridors. The ecological corridors connect protected areas, preserve water resources and protect biodiversity. The land plan establishes regulations that ensure the sustainable management of the region. Planning took into account the location of protected areas; the benefit of ecosystem services such as carbon capture, aquifer recharge zones protection and flood regulation; and the value of Nature-based Solutions such as national park buffer zones, river basin management and agricultural land protection. The land management plan strengthens the functionality of the ecological corridors and gives greater control over their management through the input of local governments. Buffer zones and proposed wildlife crossings are important elements of corridor management and implementation. In the land management plan for the Canton of Garabito, measures to protect the Paso de las Lapas Ecological Corridor include zoning of protected areas, low-intensity agriculture and ecotourism areas.

Results

Land management can be an ally of conservation and sustainable development. It can promote ecological connectivity by strengthening ecological corridors that link protected areas. Currently, the Paso de las Lapas land management plan is in the final phase of the approval process. The regulations of the land management plan can help to:

- Reduce conflicts between owners and the municipality;
- Protect ecological connectivity;
- Promote ecotourism and other low-intensity activities;
- Support the ecological corridor's conservation objectives;
- Restrict intensive uses such as residential and industrial development, and other incompatible land uses; and
- Protect fragile ecosystems such as wetlands and mountains.

18. The Jaguar Corridor Initiative: A range-wide species conservation strategy

Kathy Zeller, *Massachusetts Cooperative Fish & Wildlife Research Unit*

Context and challenge

Species conservation efforts are often conducted on discrete populations and are usually envisioned at small scales. Thinking about conservation throughout the entire range of a species allows us to broaden our perspective and identify species' needs across political and jurisdictional boundaries. This perspective also allows for the identification of large-scale patterns of threats and anthropogenic development.

Key lesson

Some large-scale visions for multi-country ecological networks focus on wide-ranging umbrella species such as the jaguar. Ecological corridors in these networks can encompass multiple land uses and different land ownership, from federal entities to individual landowners.

In 1999, the Wildlife Conservation Society and the Universidad Nacional Autonóma de México brought together jaguar (*Panthera onca*) experts to develop a range-wide research and conservation plan for the species. This effort identified 51 jaguar population centres from Mexico to Argentina (Sanderson et al., 2002). Shortly after this plan was developed, a genetic study provided evidence of widespread gene flow across jaguar range (Eizirik et al., 2001), indicating that these populations were still connected and that there was little evidence of geographic barriers to gene flow. These results inspired the Jaguar Corridor Initiative, an approach conceived by the late Dr. Alan Rabinowitz, to maintain connectivity and gene flow across jaguar range.

Approach

To model connectivity, we first updated the 1999 range-wide population data with new information and identified 90 important jaguar populations throughout the species' range,

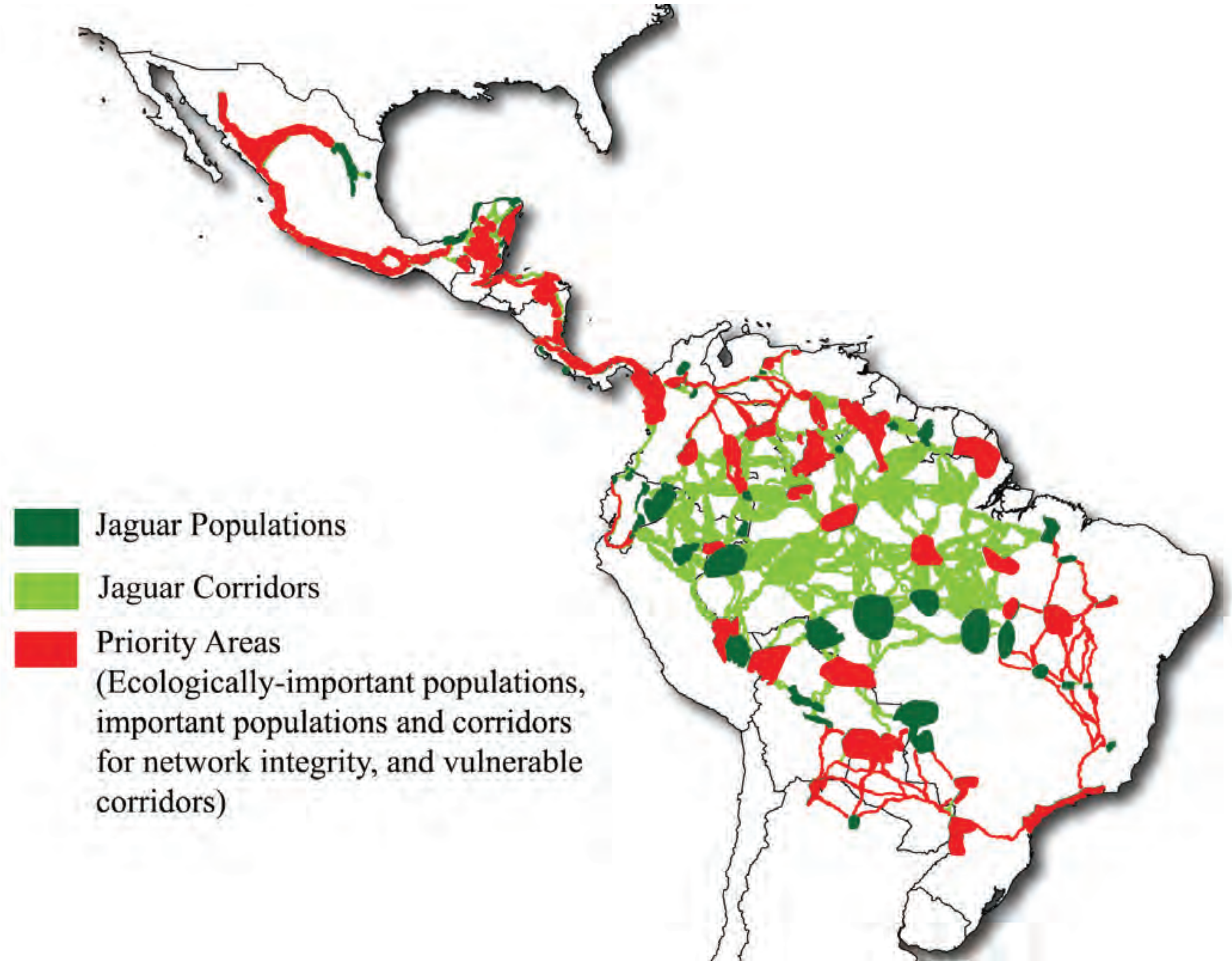


Figure 1. Jaguar populations and corridors across its range. Populations and ecological corridors were prioritised according to ecological importance, network integrity and vulnerability. They were combined to identify all priority areas across jaguar range. © Kathy Zeller

Jaguar (*Panthera onca*) © Adobe Stock

which measured 1.9 million km^2. We then invited 15 jaguar experts to assign cost or resistance values to six GIS layers known to affect jaguar movement. We combined these scored layers into a single resistance surface and modelled least-cost corridors between the 90 populations (Rabinowitz & Zeller, 2010). The resulting 182 corridors measured 2.6 million km^2 for a total conservation network of 4.5 million km^2 (Figure 1, previous page). When compared with the World Database on Protected Areas, 67% of the jaguar populations and 46% of the ecological corridors were under some form of protection.

In order to focus research and conservation efforts across this vast network, we prioritised jaguar populations and ecological corridors using three criteria: ecological importance, network importance and corridor vulnerability (Figure 1) (Zeller et al., 2013). We directed our field-based conservation efforts towards these prioritised areas.

Because the ecological corridors were identified with coarse-scaled GIS data and expert-derived resistance values, we wanted to validate the corridors before conducting site-based conservation activities. This was a challenge, however, because the corridors were often large and comprised numerous landowners. So we developed a rapid assessment, interview-based methodology that allowed us to estimate occupancy for jaguars and their main prey species in the corridors (Zeller et al., 2011; Petracca et al., 2017). All the corridors in Central America have now been validated and adjusted, and validation is currently being conducted in South America. Conservation work across the Jaguar Corridor Initiative is mostly led by the non-profit organisation Panthera (www.panthera.org).

Example of an ecological corridor

The Barbilla-Destierro Jaguar Corridor is located in Costa Rica and links the Talamanca Mountains in the south with the Central Volcanic Range in the north. The corridor, which contains myriad land uses, comprises private, municipal and federal lands. Conservation strategies from the federal to the individual landowner level have been implemented. Examples include:

- Incorporating the corridor into Costa Rica's National Program of Biological Corridors;
- Developing a local corridor council, which brings together landowners once a month to discuss and address threats and opportunities;
- Working with a hydroelectric company to direct its environmental mitigation and restoration projects toward areas that will enhance connectivity across the corridor;
- Training and establishing a Wild Cat Conflict Response Unit to investigate depredations on livestock and implement anti-predator strategies; and
- Providing science-based recommendations to development projects for maintaining connectivity across the corridor.

Results

The Jaguar Corridor Initiative has provided a conservation blueprint across the species' entire geographic range. Panthera is currently leading conservation efforts similar to those described for the Barbilla-Destierro Jaguar Corridor in 11 of the 18 countries where jaguars reside. Jaguar research is ongoing across the ecological network and corridor monitoring plans are being established. Support for the initiative has been steadily growing across jaguar range with the backing of numerous governments, landowners, corporations and scientists. With growing support, the vision of a connected and protected ecological network for jaguars from Mexico to Argentina hopefully will become reality.

Freshwater connectivity: Asia

19. Grassroots reserves have strong benefit for river ecosystems in the Salween River Basin

Aaron A. Koning, *Cornell University*

Key lesson

Recognition and enforcement of river reserves by the local communities, which benefit local fisheries and enhance the health of the river system, is a significant first step to increasing in-stream connectivity in the Mae Ngao River in Thailand.

Context and challenge

In many low-income countries, people depend highly on inland fisheries for daily nutrition, creating strong incentives to access the resource regardless of regulations. Even in protected areas that contain human populations, hunting bans rarely extend in practice to fish. While national fishery regulations and guidelines exist in Thailand, in remote areas such as the Mae Ngao River, enforcement is difficult and rare. Due to their linear nature and the dependence of many sectors upon rivers and their waters, it is a challenge to create ecological corridors covering entire river basins or even individual rivers.

Approach

Throughout Southeast Asia, in response to perceived declines in fish populations, concerns for continued resource security, and encroachment from outsiders using illegal fishing gear (e.g. electric shocking), small no-take reserves on rivers have been created by local communities, established by non-governmental organisations or imposed by national governments. These small reserves are effectively the only management action for these intensive-harvest fisheries. In tributaries of the Salween River in north-western Thailand, ecological networks of small riverine reserves continue to grow, particularly among fishery-dependent communities where overharvest is common.

Example of an ecological corridor

One such ecological network is located in the Mae Ngao River Basin of north-western Thailand, which encompasses 1,000 km^2 and over 8,000 people among more than 70 villages (Figure 1). Over 25 years ago, the first community-created reserve was established following a meeting with a local NGO, which suggested creating small areas closed to fishing as a conservation measure. Initially, only one community took this action, but the practice has slowly spread since to include more than 50 others, which largely act independently and are unsupported by government or other outside entities. Communities individually determine reserve locations, sizes and penalties for non-compliance, which range from the equivalent of 15 USD to over 300 USD. Inside reserves, all harvest activities are prohibited, including harvest of snails and other aquatic invertebrates, which otherwise are commonly eaten, particularly during the extended dry season (November–May). Outside of reserves, harvest effort is high, using a variety of methods (e.g. gill nets, lines, traps, hand spears). Fishing effort often extends from the borders of the reserve for hundreds of meters both upstream and downstream, creating a gauntlet of nets and hooks for fish moving outside of protected areas. Several neighbouring communities have added additional regulations outside reserves, notably banning the use of diving masks in collecting snails and spearfishing. Spearfishing, particularly in the dry season when water temperatures are warm, the water is clear, and local schools are on break, is thought to have a large impact on populations of fish of all sizes.

Results

There is no broader strategic planning among communities regarding the creation of reserves. In fact, there is a general lack of recognition even among community members of the number of reserves in existence throughout the Mae Ngao River Basin. Nevertheless, there are now 52 reserves that, basin-wide, cover 2% of all perennially flowing water, and form a network of protected areas within the larger river network. This network has been entirely created and enforced by individual communities.

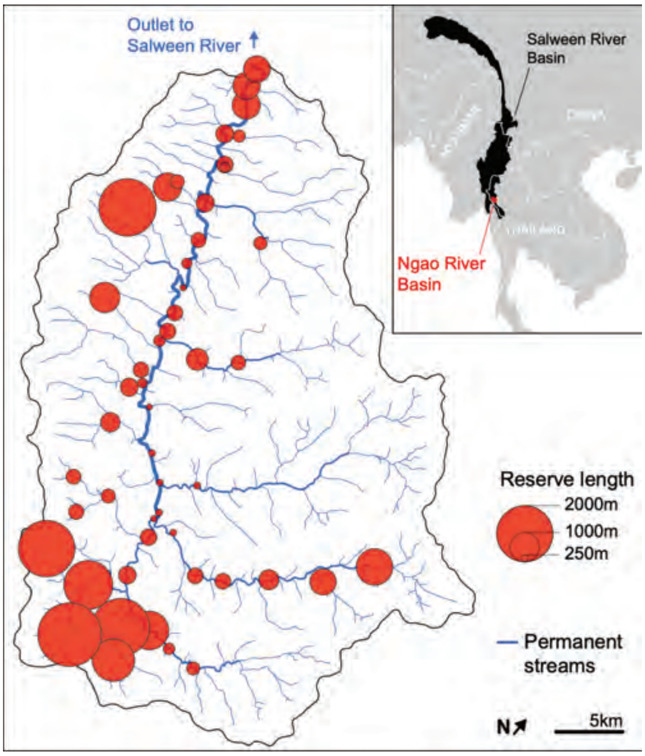


Figure 1. Ecological network of no-take reserves on the rivers in the Mae Ngao River Basin in north-western Thailand © Aaron A. Koning

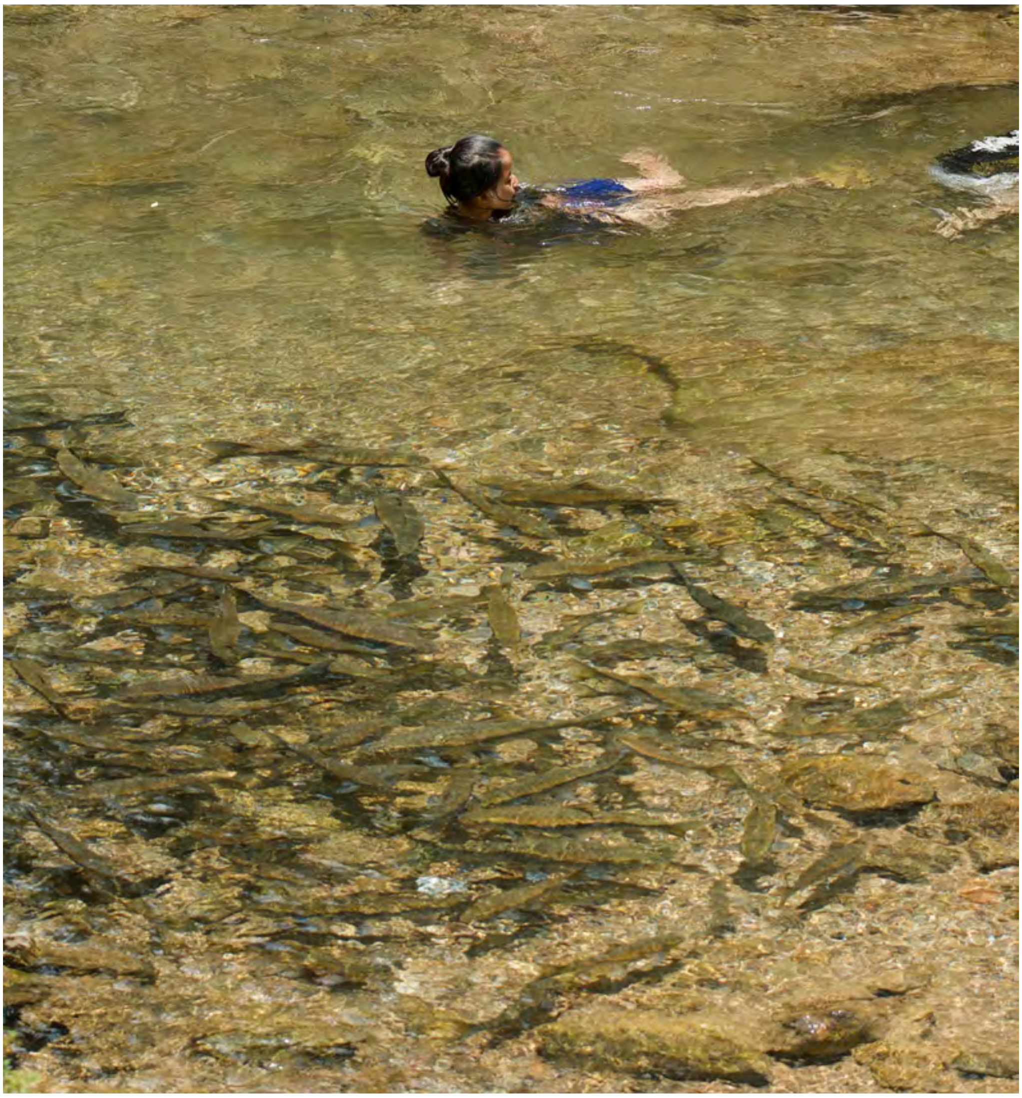


Figure 2. In no-take reserves, large schools of fish can be seen from the riverbank. © Aaron A. Koning

However, intense fishing effort forms a large barrier to connectivity between and among reserves. Viewed at more local scales, though, individual reserves are typically long enough to connect habitats within the river network, including pools that are critical refugia for many species during dry season. In the rainy season, when river levels increase by up to 5 m from dry-season lows, fishing effort goes down and systemwide connectivity goes up, giving fish the opportunity to move for breeding.

Because of the disparity in harvest effort between reserves and other areas, the effects of the conservation action can be seen even from the river bank, where large schools of fish become points of interest for tourists and travellers in the area (Figure 2).

A comparison of 23 of these small reserves with adjacent fished areas showed gains in fish species richness, density and biomass commensurate with reported gains from marine reserves (Koning, 2018; 2019). Specifically, richness increased in reserves relative to fished areas by 27% and density by 124%, and biomass was 23 times higher on average. Although benefits were often observed only three to five years after a reserve was established, gains were sustained through time.

Community members regularly harvest large fish outside of reserves and credit fish movement out of reserves for such catches. It remains unclear whether reserves are sufficiently large to maintain populations over the long term and whether there is regular movement among reserves that would transfer critical genetic diversity among potentially isolated sub-populations. Given the seasonal fluctuations in the river, though, it seems likely that fish movement occurs during the rainy season.

The extent to which these small reserves are able to benefit local fish populations is all the more remarkable given that communities have largely acted independently without a broader coordination of effort. Next steps for this reserve network would be to work with communities, informed by the surveys conducted previously and the body of reserve design theory that has been developed for marine systems, to attempt to optimise reserves individually and collectively for maximum conservation and fishery benefits.

Freshwater connectivity: Europe

20. The ecological corridor Mura-Drava-Danube and future five-country biosphere reserve

Arno Mohl, *WWF Austria*
Ivana Korn Varga, *WWF Adria*
Emöke Györfi, *WWF Austria*

Key lesson
Conserving river connectivity can be achieved through a series of protected areas and a vision that prohibits dams and other developments that would impair the long-term connectivity of river systems, but promotes benefits that are compatible with connectivity.

Context and challenge

For a long time, large parts of the river landscapes along the former Iron Curtain between the Baltic Sea and the Black Sea in Europe remained largely unaffected by serious encroachments. With the end of Communism in Europe in the late 1980s and the subsequent enlargement of the EU eastward, these forgotten river paradises were catapulted into another age. Suddenly, they were in areas of human economic interest. On the one hand, this pressure has threatened to irreversibly destroy the last intact areas. On the other hand, new opportunities for cooperation in nature conservation and sustainable development have emerged. Transboundary Biosphere Reserves (TBRs) are an appropriate tool to tackle this major need for large-scale cross-border river protection, management and restoration. Current examples can be found on the lower reaches of Drava and Mura rivers and in the adjacent floodplains of the middle Danube River between Austria, Slovenia, Croatia, Hungary and Serbia (Mohl et al., 2009).

Approach

As borders between states are political rather than ecological, ecosystems often stretch across national boundaries, and may be subject to different, or even conflicting, management and land-use practices. TBRs provide a tool for common management. A TBR is an official recognition at the international level and by a UN institution, UNESCO, with the political will to cooperate in conservation and sustainable use through common management of a shared ecosystem (UNESCO, 2017). The initiative for the five-country Biosphere Reserve Mura-Drava-Danube between Austria, Croatia, Serbia, Slovenia and Hungary goes back to 1993. It has been developed as a counterproposal to emerging threats of new hydropower dam projects after the fall of the Iron Curtain and as a tool to connect and better protect all national river areas of the corridor under one international management framework (Schneider-Jacoby & Mohl, 2012).

Campaigning against large-scale water management and hydropower dam projects which were threatening the riverine area has been an important approach to achieve protection of this valuable ecosystem. The campaign has increased public and political awareness, created pressure on governments and triggered the establishment of 13 major protected areas, including the 88,000-ha regional park Drava-Mura in Croatia. Mostly part of the Natura 2000 network, these protected areas fall under several categories. Setting up an ecological network for conservation has laid the foundation for transboundary cooperation for harmonised conservation, integrated management and restoration within the future Biosphere Reserve Mura-Drava-Danube.

Since 1993, WWF, EuroNatur and local NGOs have been campaigning to protect the unique landscape of the three rivers in a five-country TBR (Figure 1). Increasingly, governments and NGOs cooperate to jointly achieve, stepwise, the TBR. They are establishing Europe's largest protected river corridor (700 km, 1,000,000 ha) through innovative cross-sector cooperation and harmonised sustainable regional development that also supports cross-border reconciliation (WWF, 2013). Once fully established, the biosphere reserve will form an ecological network for conservation that consists of core zones embedded in buffer zones and transitional zones.

Example of an ecological corridor

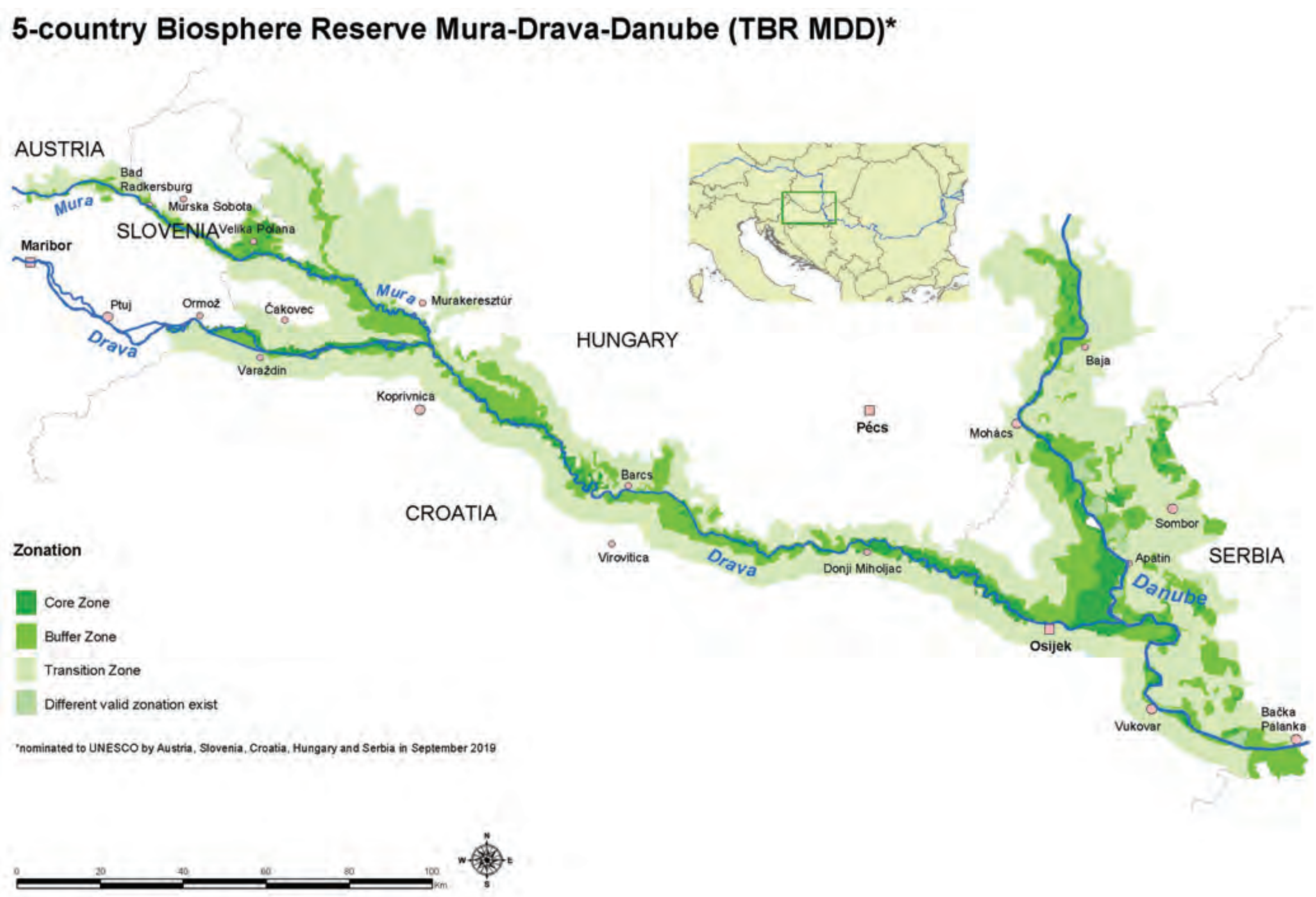
Spanning Austria, Croatia, Hungary, Serbia, and Slovenia, the lower courses of the Drava and Mura Rivers and related sections of the Danube are among Europe's most ecologically important riverine areas – the so-called Amazon of Europe. Despite numerous human-made changes in the past, this region hosts amazing biological diversity and is a hotspot of rare natural habitats, such as large softwood forests, wet meadows, river islands, gravel and sand banks, steep banks, side branches and oxbows (Figure 2).

The area is home to the highest density of breeding pairs of white-tailed eagles (*Haliaeetus albicilla*) in Continental Europe, and other endangered species such as the black stork (*Ciconia nigra*), beaver (*Castor fiber*), otter (*Lutra lutra*) and the nearly extinct ship sturgeon (*Acipenser nudiventris*). Many of the species are indicators of a natural river corridor, including the little tern (*Sternula albifrons*). Every year, more than 250,000 migratory waterfowl use the rivers to rest and feed. The largest and best-preserved floodplains and forests can be found around the confluence of the Danube and Drava, shared between Croatia, Hungary and Serbia. Most parts of this transboundary area are assigned to the core zone of the TBR. In addition to high levels of biodiversity, the river and floodplain areas are vital to the local communities. Local fishers rely upon the fish populations for their livelihoods. The extensive floodplains lower the risks from floods, secure favourable groundwater conditions and provide self-purification of water, which is essential for drinking water, forests and agriculture. People also enjoy recreational activities along the rivers by walking, swimming, fishing and canoeing (WWF Austria, 2014).

Results

Driven by the vision of establishment of the five-country TBR, major progress has been made over the past 30 years toward better protection and management of the river corridor:

- Thirteen major protected areas along the Mura, Drava and Danube, which are forming the TBR's backbone, have been established by the governments of the five countries.
- So far 270 km of natural river stretches have been successfully defended from being destroyed by large-scale water management and hydropower dam projects.
- In 2009, Croatia and Hungary signed a joint declaration to establish the TBR, followed in 2011 by a five-country ministerial declaration. In 2012, the riverine areas in Croatia and Hungary were granted biosphere reserve status, soon followed by those in Serbia (2017), Slovenia



*nominated to UNESCO by Austria, Slovenia, Croatia, Hungary and Serbia in September 2019

Figure 1. The future five-country UNESCO Biosphere Reserve Mura-Drava-Danube © World Wildlife Fund (WWF)

Figure 2. (left) Floodplains of the Danube in Croatia © Mario Romulic. (right) The Drava River in Croatia © Arno Mohl

Black stork (*Ciconia nigra*) © Adobe Stock

(2018) and Austria (2019). The strictly protected core and buffer zone, which consists of those 13 major protected areas, amounts to 280,000 ha. It is surrounded by 650,000 ha of transitional zone.

- Triggered by the TBR, several projects co-funded by the EU are already being implemented across the five countries in the area, aiming to achieve better protection and sustainable development. Within the 'coop MDD' project, the protected area administrations of the Mura-Drava-Danube region have been cooperating since 2017 to jointly focus on common goals and trans-border nature protection measures. The 'Resilient riparian forests as ecological corridors in the Mura-Drava-Danube Biosphere Reserve' project started in June 2019, aiming at preservation and sustainable management of floodplain forests in the TBR. At the same time, the 'Amazon of Europe Bike Trail' ecotourism project started. Furthermore, river restoration is being implemented to create new natural habitats and recreational areas for people to truly experience the stunning landscape along the rivers.

Also in 2019, the dossier was prepared for the five-country TBR nomination, which will harmonise all existing biosphere reserves in the region under one international designation. The next step is for UNESCO to finalise and approve the nomination. Once officially designated, the five-country TBR should take steps to achieve a fully functional biosphere reserve in line with UNESCO requirements. This includes establishing a joint management structure and implementing a joint action plan and projects.

Further information: http://www.amazon-of-europe.com/
http://www.interreg-danube.eu/approved-projects/coop-mdd
http://www.interreg-danube.eu/approved-projects/refocus
http://www.interreg-danube.eu/approved-projects/amazon-of-europe-bike-trail

Freshwater connectivity: North and South America

21. Pacific salmon watersheds: Restoring lost connections

Lauren Law and Jonathan Moore, *Simon Fraser University*

Context and challenge

Coastal watersheds that drain into the northern Pacific Ocean support populations of culturally and economically important migratory salmon. Pacific salmon are born and initially develop in freshwater environments and then migrate to the open ocean, where they forage and grow before returning to natal freshwaters to spawn. Across North America and Asia, 8% of high-value catchments that drain into the northern Pacific Ocean are at least partially protected, predominantly in areas that are higher in elevation and distant from the ocean (Pinsky et al., 2009). However, even if portions of catchments are protected, dams have fragmented many salmon systems. Dams, such as for hydroelectric production, may block or hinder salmon migration, alter hydrological regimes and modify downstream river habitat. As a result of the imperilled or extirpated status of many salmon populations (Gustafson et al., 2007), there have been substantial investments in conservation and recovery.

Key lesson

Even in an otherwise protected watershed, dams impair connectivity of the headwaters to the ocean; dam removal can restore biotic and abiotic processes, as demonstrated in the Elwa River in the USA.

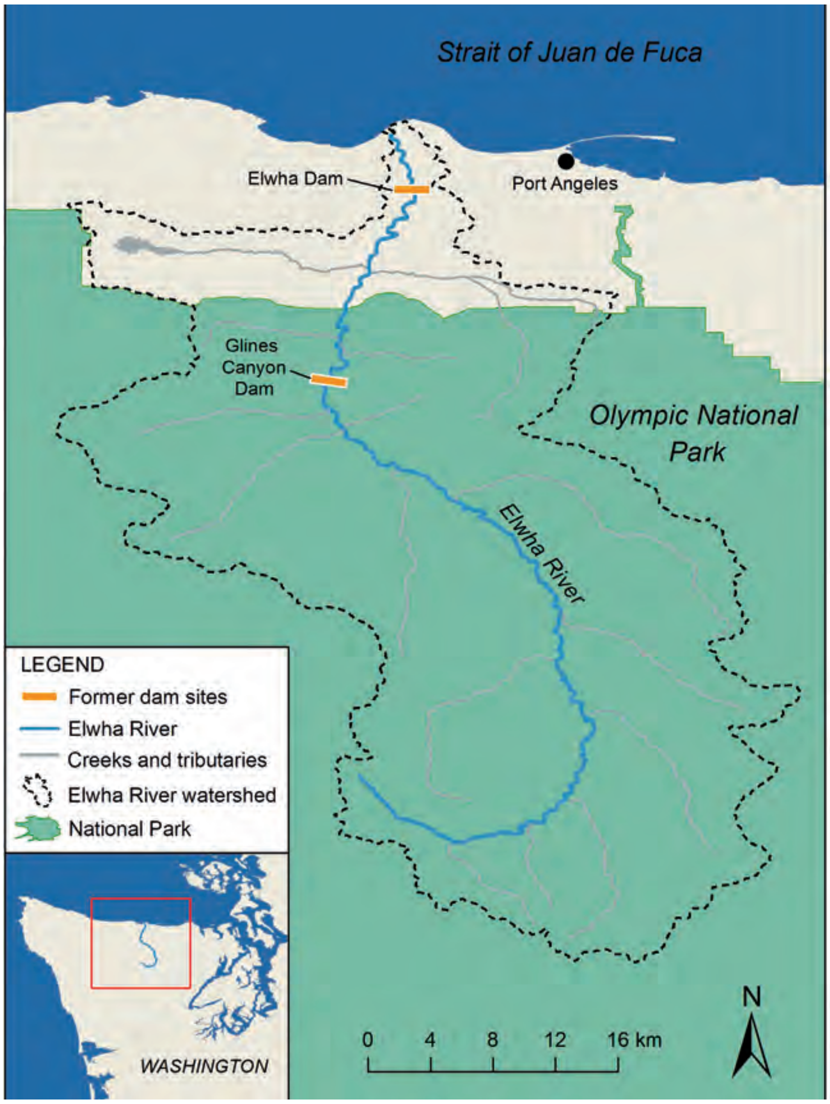


Figure 1. Elwha River watershed within Olympic National Park, Washington, USA. The removal of the Elwha Dam and Glines Canyon Dam restored connectivity between the upper and lower portions of the watershed. © Jonathan Moore

Chinook salmon (*Oncorhynchus tshawytscha*) © Adobe Stock

Approach
Over the last several decades, there has been increasing dam removal and mitigation to benefit salmon and other migratory fishes. Across the USA, more than 1,200 dams had been removed by 2017 (Bellmore et al., 2017). Dam removal generally occurs through a decentralised decision-making process involving numerous stakeholder groups, including federal agencies, state agencies, and private dam owners. Although some dam removals have been voluntary, many have been the result of legal proceedings that fall under the regulatory powers of the Federal Energy Regulatory Commission. Initial removal efforts were focused on older dam structures, which were too costly to maintain and no longer in compliance with modern safety standards. However, in recent years there has been a greater focus on dam removal for environmental protection and habitat restoration. In the USA, the Wild and Scenic River Act (1968) is a legal mandate to preserve rivers having exceptional natural, cultural and recreational values in a free-flowing state.

Example of an ecological corridor
In the USA, one of the largest dam removals that has restored connectivity in a protected salmon watershed was on the Elwha River. The vast majority of the 72-km-long river is within Olympic National Park in the state of Washington. Historically one of the most productive salmon rivers in the Pacific Northwest, the Elwha was disturbed in the early 1900s when two dams were constructed on it, disconnecting the protected upper portion of the watershed from the seascape that migratory salmon rely on. Migration of salmon was blocked, and the movement of sediment and woody debris was disrupted. The building of these large-scale dams led to a 90% reduction in fish populations, a loss of habitat connectivity and decline in habitat complexity (Pess et al., 2008).

In 1992, the Elwha River Ecosystem and Fisheries Restoration Act authorised the removal of the dams to restore the river ecosystem. The US National Park Service removed the dams in phases, starting with the removal of the smaller dam beginning in 2011 and eventually completing the removal of the larger dam in 2014.

Results
The removal of the Elwha River dams led to renewed riverine fluxes of sediments and large woody debris downstream that had been trapped in the dam reservoirs for nearly a century. Approximately 30 million tons of sediment were released, causing some 60 ha of river delta growth (Ritchie et al., 2018). The supply of sediment and large wood to the fluvial system restored channel morphology to its former complexity and resulted in increased river braiding, sediment-bar growth and pool filling.

Renewed connectivity of upstream protected habitat with the seascape in the Elwha River watershed is fostering the return of several salmon species (Chinook, *Oncorhynchus tshawytscha*; coho, *Oncorhynchus kisutch*; chum, *Oncorhynchus keta*; sockeye, *Oncorhynchus nerka*; and pink, *Oncorhynchus gorbuscha*) as well as anadromous trout (e.g. steelhead, *Oncorhynchus mykiss*; and bull, *Salvelinus confluentus*). Scientists have already observed record numbers of Chinook salmon returning to the Elwha, with high returns anticipated to follow for other species. About 30,000 Chinook and coho salmon and 270,000 pink salmon are expected to return annually. Salmon returns will eventually sustain local and regional fisheries.

The Elwha is one of many coastal catchments that has protected salmon habitat in its headwaters but whose connectivity to the seascape was severed. As illustrated by the Elwha project, dam removal and restoration of the free-flowing status of rivers can effectively connect protected headwaters with the seascapes on which migratory fishes such as salmon depend.

22. Fragmentation of riparian protections throughout catchments, Oregon, USA

Rebecca Flitcroft, *USDA Forest Service*
Brett Boisjolie, *Massachusetts Department of Conservation and Recreation*
Mary Santelmann, *College of Earth, Ocean and Atmospheric Sciences, Oregon State University*

Context and challenge

Lotic and lentic environments provide lateral connectivity to floodplain and riparian ecosystems. They can be passages for movement of aquatic organisms to and from headwater areas and marine environments, and are important components of global biogeochemical cycles (Butman & Raymond, 2011). Riparian environments also provide critical buffers between human land uses adjacent to the water's edge by filtering nutrients, retaining sediment and contributing biotic material that constitutes significant food inputs into freshwater food webs.

In many places, protection for freshwater taxa and their habitats is linked to the ribbon of riparian areas that flank rivers and lakes. Riparian protections, in turn, are often linked to land ownership, which changes along the length of a river, from its headwaters to the sea. However, this approach to conservation results in fragmented protections along the continuum of the river.

Key lesson

Maintaining functional habitat can require policy protections and voluntary restoration efforts, both guided by science; monitoring and evaluation are critical to ensure that the actions will indeed result in the desired outcome.

In coastal Oregon, USA, high-gradient headwater streams tend to be located within dense Douglas fir forest where the primary land use is timber harvesting. Downstream of these areas are low-gradient lowland areas that have been converted to agriculture, residential and urban development (Figure 1). Historically, these streams supported thriving

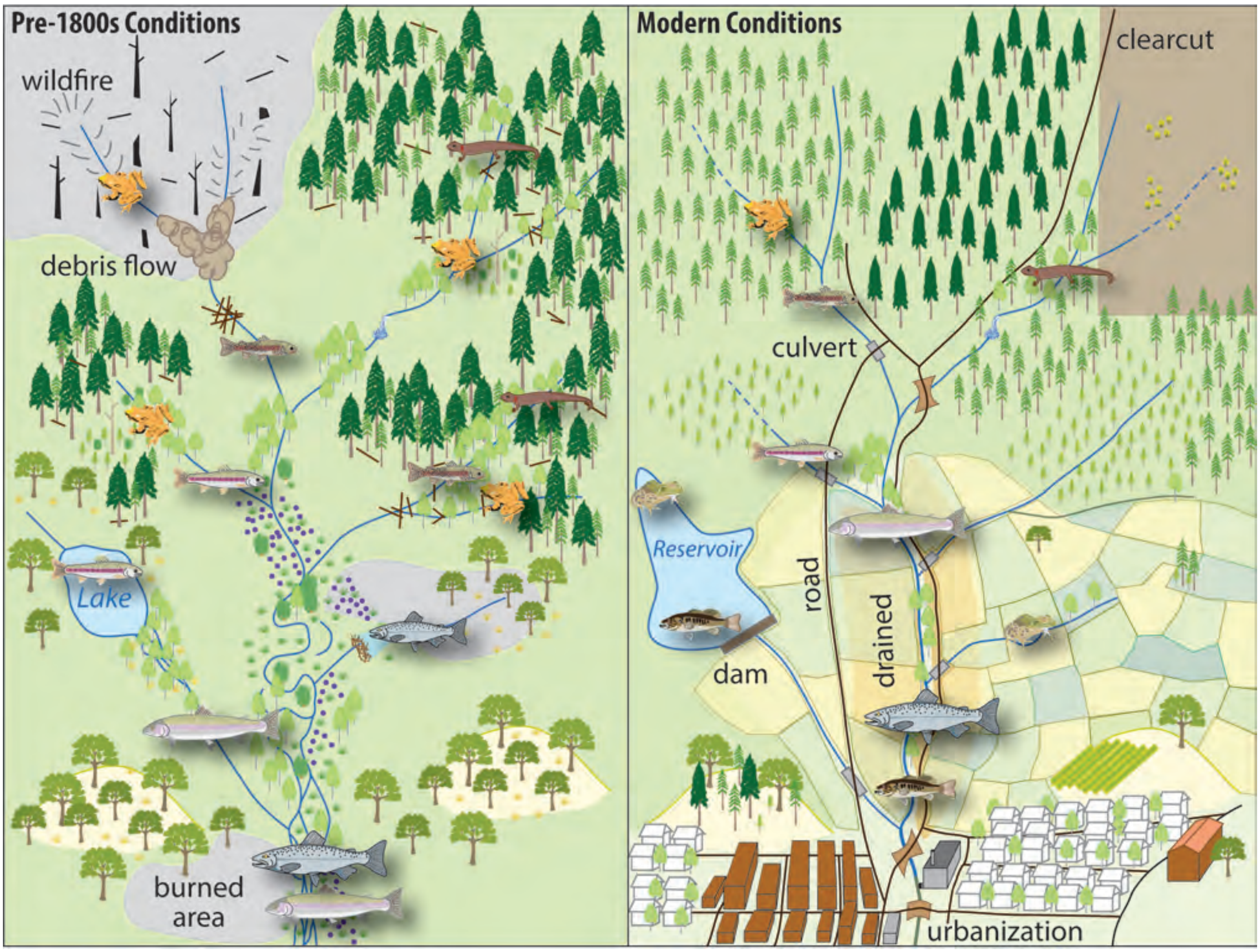


Figure 1. Historically, river systems of the Pacific Northwest connected a diverse array of freshwater and wetland habitats. Over time, development has reduced stream complexity and fragmented landscapes coincident with anthropogenic land uses such as agriculture, timber harvesting or residential development. Figure from Penaluna et al., 2017.

populations of anadromous salmonids that found spawning and rearing habitats throughout the connected corridors of the river network. The extensive floodplain of the Coquille River was a highly productive area for coho salmon (*Oncorhynchus kisutch*). However, this and other flat floodplains were colonised quickly by European settlers and continue to be used for agriculture.

In recent decades, migratory anadromous salmonids, including coho salmon, have been listed as ‘threatened’ or ‘endangered’ under the US Endangered Species Act, making them critical drivers of restoration and habitat protection. Millions of dollars of public funds have been spent on restoration intended to enhance the habitat and population-scale survival of this species. However, fish abundance continues to be lower than historical levels.

Approach

In coastal Oregon, riparian protection measures include a variety of approaches, from voluntary best management practices to legislated prescriptions (Boisjolie et al., 2017). The most rigorous protections are generally associated with extractive natural resource uses such as timber harvest or mining, while the least rigorous are linked with agricultural land uses. Policy approaches include prescriptive policies intended to eliminate pollution to waterways by specifying requirements for riparian areas and explicitly limiting certain management actions. For agricultural lands, outcome-based policy approaches are intended to minimise water pollution, allowing landowners discretion in land management so long as it does not negatively impact water quality standards. The efficacy of these approaches can be difficult to assess at a catchment scale. Prescriptive approaches may constrict

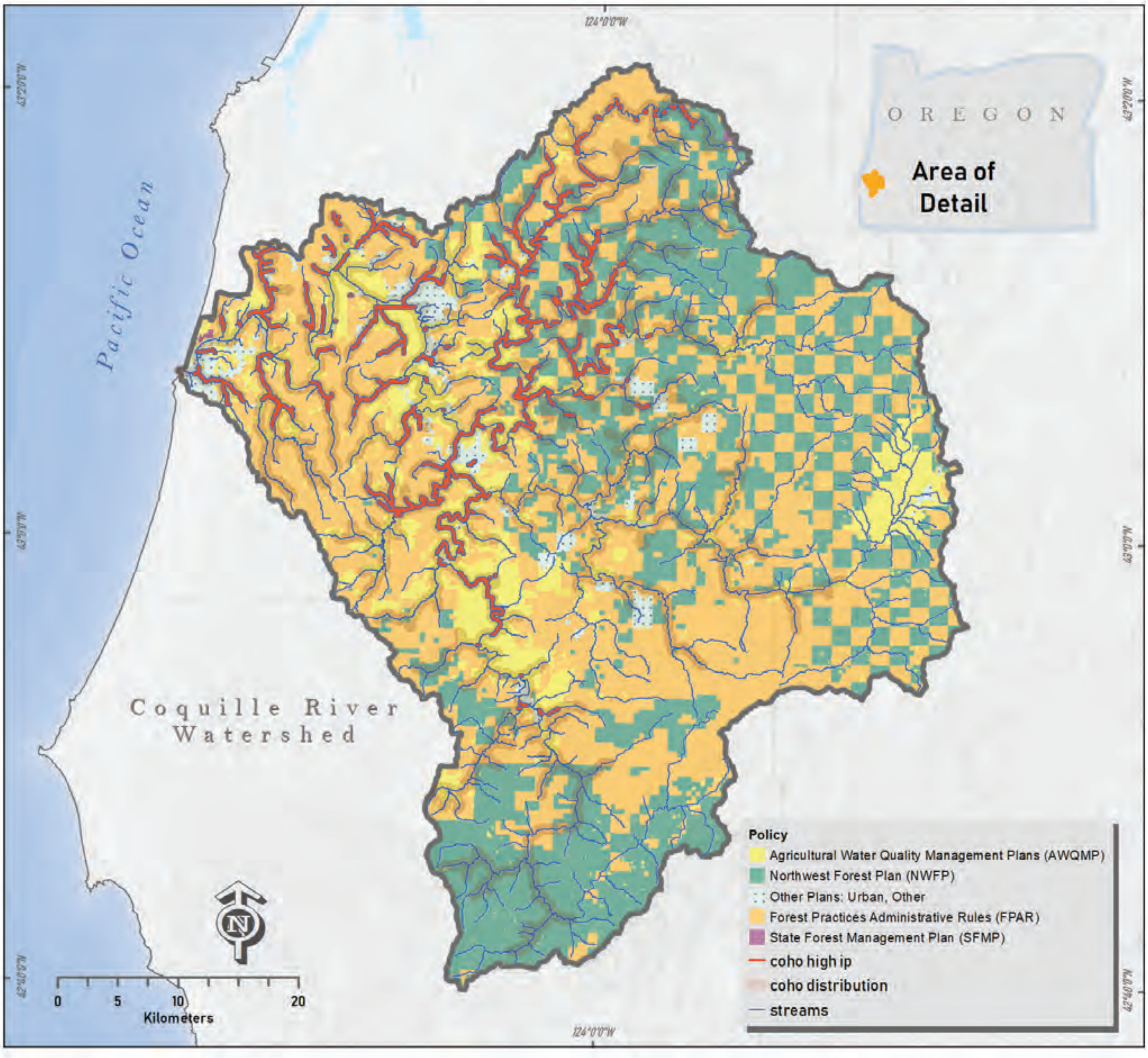


Figure 2. Coho salmon in the Coquille River Basin have historically utilised low-gradient floodplain areas. On the modern landscape, these areas are often associated with agricultural land uses. © Rebecca L. Flitcroft

Juvenile coho salmon (*Oncorhynchus kisutch*) © Adobe Stock

dynamic ecosystems to meet an ideal target condition, while outcome-based policies and a reliance on voluntary efforts can create gaps in protective efforts.

Protective efforts influence habitat conditions in time and space. Consequently, the variability in protective efforts has strong implications for the conservation of riparian ecological corridors. Overcoming fragmented riparian protections can be aided by:

- Legislative efforts;
- Restoration incentives;
- Collaborative restoration projects;
- Conservation designations;
- Technical assistance; and
- The formulation of collaborative governance bodies to address habitat and/or ecosystem degradation.

Understanding the extent of variable protective efforts can inform multi-agency policy responses for species recovery or conservation priorities. Developing an understanding of the mosaic of protective efforts can help identify and quantify gaps in them.

Example of an ecological corridor

For the Coquille River system, maps of riparian policy protections were overlaid with the distribution of coho salmon and areas of high intrinsic potential to support them (Figure 2). The maps show that the majority of riparian areas within the distribution of this fish are managed for agriculture, followed by timber harvesting. Further, areas with high intrinsic potential to support coho salmon are mostly located in agricultural areas. This shows a mismatch between riparian protection of coho salmon streams (which is determined by land ownership) and the location of habitats appropriate for different life stages of these highly migratory fish (which is determined by the hydro-geomorphic context of the river).

Results

Policies intended to protect riparian areas and coho salmon are more specific and enforceable in areas these fishes are less likely to occupy (Boisjolie et al., 2019). This gap in protections has led to the development of voluntary incentives for stream restoration actions and the management of working lands in the Coquille Basin. By mapping protections, their fragmentation along the continuum of the river network can be identified, allowing for targeted restoration or additional protection work. Tracking the effects of voluntary riparian protections, prescribed protections, voluntary approaches to stream restoration and collaborative landscape management are critical in evaluating the success of freshwater recovery throughout the river network. A broader perspective on identifying and quantifying fragmentation, as well as connectivity, is necessary if protections are to be effective for highly migratory fishes that must access habitats throughout a river system.

23. Protection of the free-flowing Bita River

Jose Saulo Usma and Cesar Suarez, *WWF Colombia*
Fernando Trujillo, *Omacha Foundation*
Michele Thieme, *WWF-US*

Context and challenge

The Bita River in Colombia is 520 km long and its basin covers about 822,000 ha (Figures 1, 2). The river begins as a small, spring-fed stream in the middle of the llanos, a network of grasslands and seasonally flooded plains. The river meanders freely through this important and unique ecosystem, creating deep lagoons and beautiful beaches, until it reaches the Orinoco River. Along its path, the still-free-flowing Bita River supports rich biodiversity: freshwater fish, turtles (*Podonecmis* spp.) and crocodiles (*Crocodylus* spp.), river dolphins (*Inia geoffrensis*), jaguars (*Panthera onca*), tapirs (*Tapirus terrestris*), otters, and many other mammals, reptiles and birds.

Despite Colombia's wealth in natural assets, research has revealed that the llanos are one of the most under-protected ecosystems in the country. The country's ecosystems are increasingly under pressure from extractive industries, livestock grazing, large timber plantations and urbanisation. Additionally, the connectivity afforded by the Bita River allows migration of freshwater fish and seasonal movements of dolphins, both of which are critical for local livelihoods, including sustainable tourism, birdwatching and sport fishing.

Key lesson

Management agreements within this Ramsar site are important to maintain connectivity for both freshwater and terrestrial species by managing activities in the watershed such as sport-fishing and agriculture.

Approach

The Alliance for the Bita River was created in 2014 and is composed of the Omacha Foundation, the Alexander von Humboldt Research Institute for Biological Resources, Corporinoquia, the Vichada Government, the Colombian Navy, Colombia's National Parks, the Palmarito Foundation, the Orinoco Foundation, La Pedregoza Corporation, and WWF. Since then, the alliance, fishers, tourism

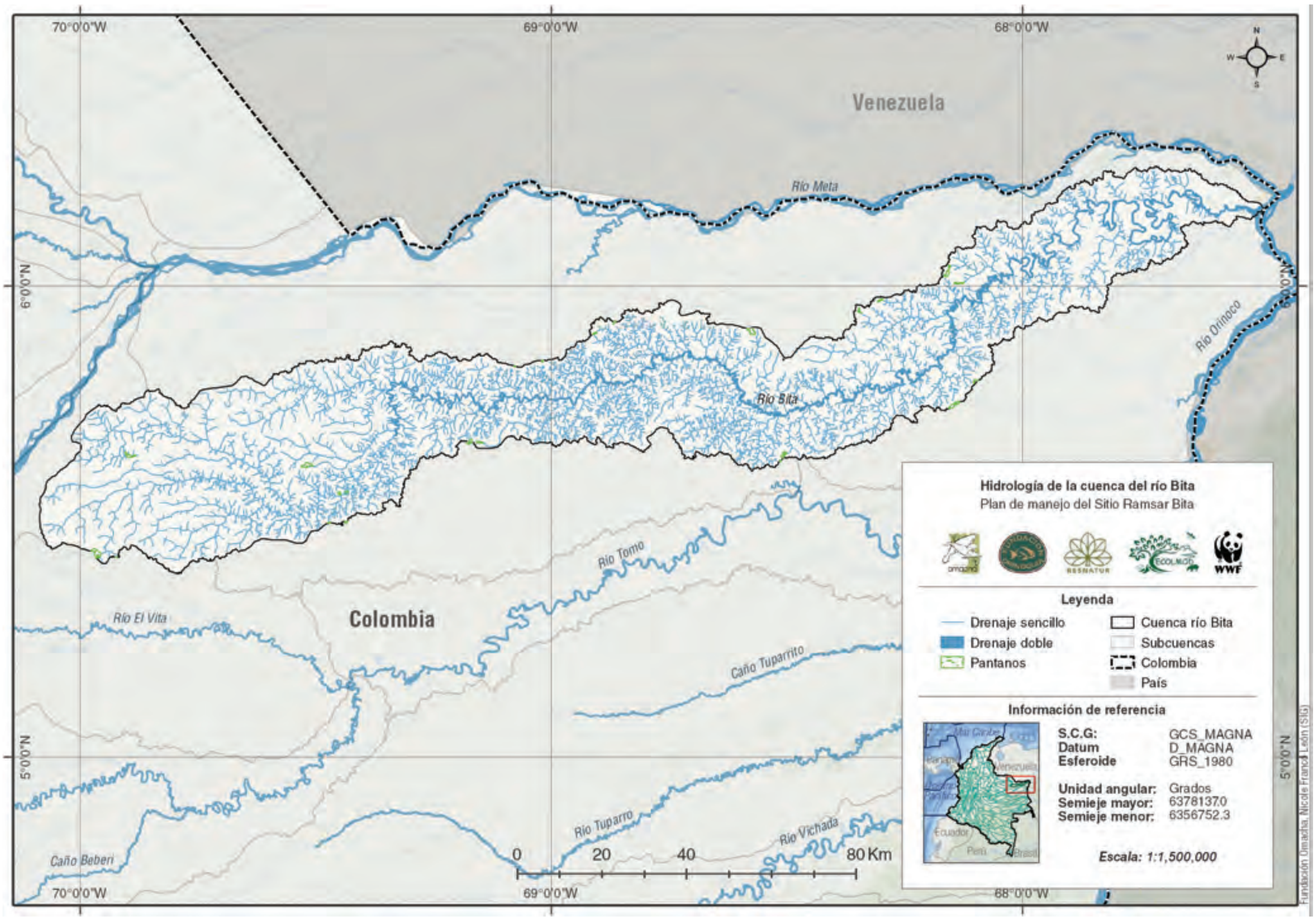


Figure 1. The Bita River Ramsar site in Colombia © Omacha Foundation, Courtesy Fernando Trujillo

Figure 2. Aerial view of the Bita River landscape © Omacha Foundation, Courtesy Fernando Trujillo

representatives, social and environmental organisations, scientists and local people have all been working together to protect the Bita.

To advance conversations about legally protecting the Bita, the alliance hosted a series of workshops with local stakeholders to understand the connections among various activities (such as agriculture and sustainable tourism) and protection. After better understanding the cause-and-effect relationships of these multi-sector activities, the group developed a decision-making framework that uses quantitative data to demonstrate the impacts of certain actions. This framework helped the government, the alliance and other partners choose the best actions to take to conserve the Bita River while meeting the needs of stakeholders.

Example of an ecological corridor

The free-flowing Bita River supports movement and migration of many species, including the following:

- River dolphins: The Bita has one of the best populations of river dolphins thanks to its proximity to the Meta and Orinoco rivers, which supply food (fish) for the dolphins and key habitats for their reproduction.
- Migratory fish: The different types of water and the longitudinal and lateral connectivity between the Bita (black waters), Meta (white waters), and Orinoco (mixed waters) and their wetlands favour the reproduction of many migratory species.
- Tapirs, jaguars, and pumas: It is estimated that 600–700 tapirs, 60–70 jaguars and 100–120 pumas (*Puma concolor*) live in the Bita River Basin thanks to the ecological integrity of its forests and wetlands.
- Other species: The river corridor will support the conservation of other species such as peacock bass (*Cichla* spp.), freshwater stingrays (*Potamotrygon* spp.), giant otters (*Pteronura brasiliensis*), and river turtles.

Results

On June 23, 2018, the Bita River was added to the List of Wetlands of International Importance of the Ramsar Convention. It is the largest Ramsar site in Colombia and one of the first anywhere to protect an entire free-flowing river and its basin (822,600 ha). Since the declaration, a management plan has been developed for the Ramsar site by the Omacha Foundation, Orinoquia Foundation, National University of Colombia, and RESNATUR (a private nature reserve network).

The management plan details actions to conserve and sustainably use the Bita's fisheries because the river is the epicentre for sport fishing in Colombia and important for the ornamental fish trade. Additionally, an agreement has been made to create within the Ramsar site an ecological corridor (228,000 ha) that connects the Upper and Middle Bita rivers and allows movement of 34 species of medium- and large-sized mammals including tapir, jaguar, puma, river dolphins, otters and migratory fishes. Among others, the agreement was signed between the Ministry of Environment, the Omacha Foundation, the Project Design Developers-Folgers Inc., the Tapirs Specialist Group of IUCN SCC, the forestry sector, and the farmers who are located within the ecological corridor in the Ramsar site. These parties committed to undertake sustainable agricultural practices and livestock production, forestry and responsible fruit production within the corridor and support the monitoring of flagship wildlife populations.

Marine connectivity: Australia

24. The Great Barrier Reef: Systematically protecting connectivity without connectivity data

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Jon C. Day, *ARC Centre of Excellence for Coral Reef Studies, James Cook University, Australia*

Key lesson

In barrier reef systems, placement of protected areas and management of activities in buffer zones can promote stepping-stone connectivity, thus maintaining larval movements, migrations from inshore to offshore habitats, and movements of adult benthic and pelagic organisms.

Context and challenge

Australia's Great Barrier Reef (GBR) is the world's largest coral reef ecosystem, and one of the country's most important ecological and economic assets. Most of the GBR is enclosed within the Great Barrier Reef Marine Park (GBRMP), a multiple-use marine park comprising eight different usage zones (Figure 1), with one-third zoned no-take. The Australian government, acting primarily through the GBRMP Authority, is responsible for management, undertaken in conjunction with other federal and Queensland agencies, Indigenous Traditional owners and various other stakeholders.

Although the GBRMP was originally created to protect the reef from mining exploration, its coral reefs are now mainly threatened by recurrent bleaching, cyclones and outbreaks of crown-of-thorns starfish. Large areas, particularly the inshore and northern reefs, have lost large proportions of their live coral cover in recent years. Secondary threats include adverse water quality, unsustainable fishing, dredging and coastal development. Despite these pressures, the condition of the GBR is good compared with that of many other reef systems globally.

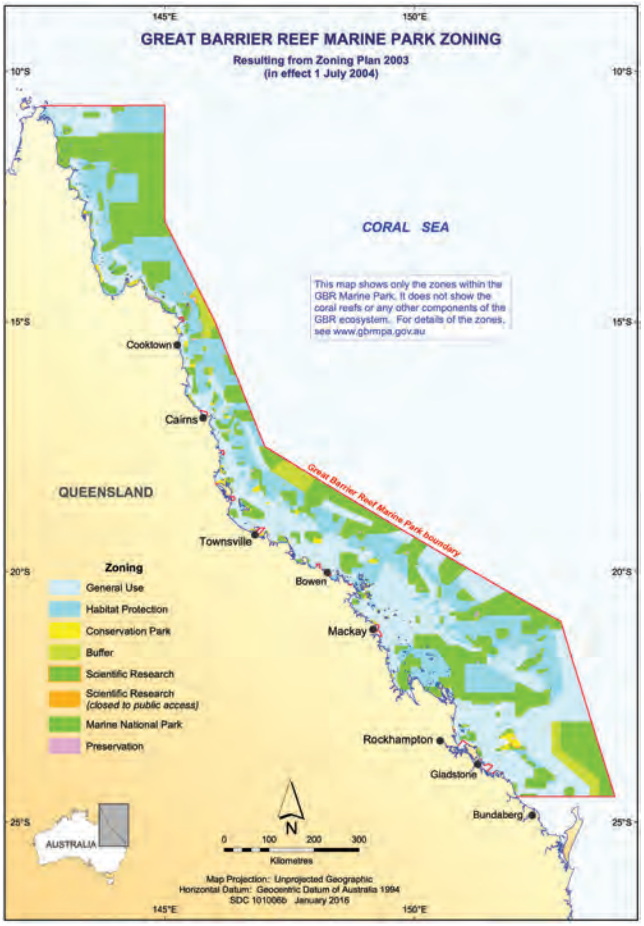

Figure 1. Current zoning for Great Barrier Reef Marine Park (resulting from the 2003 Zoning Plan, in effect since 1 July 2004). Map supplied by Spatial Data Centre, Great Barrier Reef Marine Park Authority, © Commonwealth of Australia (GBRMPA).

Approach

Conservation of the GBR's coral habitat requires three types of connectivity to be protected. The first, and most important, is larval connectivity: most organisms on reefs have an obligate pelagic larval dispersive phase making connectivity a constant demographic necessity. Oceanic currents create spatiotemporally complex larval connectivity patterns that drive population dynamics on the GBR. These connectivity patterns are similar to terrestrial ecological corridors, but the dispersing organisms are not exposed to threats during dispersal, and so marine ecological corridors do not require protection. Instead, conservation outcomes are enhanced by networks of marine reserves that exchange large amounts of larvae, while fishery outcomes are improved when no-take zones are connected to fished areas. The second form of connectivity is ontogenetic migration, typically where species spend their early life-stages in estuarine/inshore habitats, before migrating offshore as adults; Figure 2 shows one example. The third is small-scale movement of adults for foraging or reproducing. Most coral reef species are benthic-associated, and so these movements occur at within-reef scales. However, pelagic species can undertake longer-distance adult movements between reefs.

The GBRMP was substantially rezoned and expanded in 2003, based on systematic planning principles. Eleven biophysical operating principles (BOPs) (GBRMPA, 2002) were devised to protect representative examples of each of the GBR's 70 bioregions (30 reef habitat; 40 non-reef) (Fernandes et al., 2005). The maintenance of connectivity was also an explicit goal of the marine park – both the total size of the no-take marine reserves and their individual locations were taken into account. As an overarching goal, BOP 9 recommended that no-take zones be chosen to maintain connectivity across the GBR. However, minimal data about connectivity were available at the time of the rezoning, and so several of the

BOPs were designed to prioritise potential proxies for each form of connectivity. BOPs 1 and 2 aimed to protect larval connectivity, particularly self-recruitment. For example, BOP 2 recommended that no-take zones be as large as possible, motivated by models indicating self-recruitment increased with reserve dimensions. BOP 4 recommended that no-take zones include whole reefs where possible, to protect connectivity for foraging and migrating adults.

Results

Little information on connectivity was available for the 2003 rezoning, so proxies were used to design networks of no-take zones that would ensure the exchange of larvae between them, as well as the export of larvae to fished areas. Recent empirical studies and biophysical modelling demonstrate that this approach was successful to some extent, with larval dispersal connecting no-take zones at a range of scales, from local self-recruitment (Harrison et al., 2012) to consistent bi-directional exchanges of over 250 km (Williamson et al., 2016; Bode et al., 2019).

There are three possible reasons why a network of no-take zones that was not designed with explicit connectivity data was nevertheless able to achieve connectivity outcomes. First, the GBRMP contains a very large proportion of effective no-take zones (33% of the entire area). We would generally expect that higher levels of protection will achieve superior connectivity outcomes. Second, explicit connectivity proxies form the basis of several BOPs, and these likely improved connectivity outcomes beyond the simple null expectation.

The final reason is less obvious. The GBRMP is a global exemplar of a systematically planned network. Several BOPs (specifically 5 and 7) aimed to create a 'representative' network, with no-take zones distributed across bioregions, latitudes and cross-shelf position. While these goals do not mention connectivity, evidence suggests that representiveness allows no-take networks to effectively protect previously unknown biodiversity features (e.g. mesophotic reefs, as in Bridge et al., 2016). It is entirely possible that representativeness principles are also responsible for the protection of connectivity in the GBR.

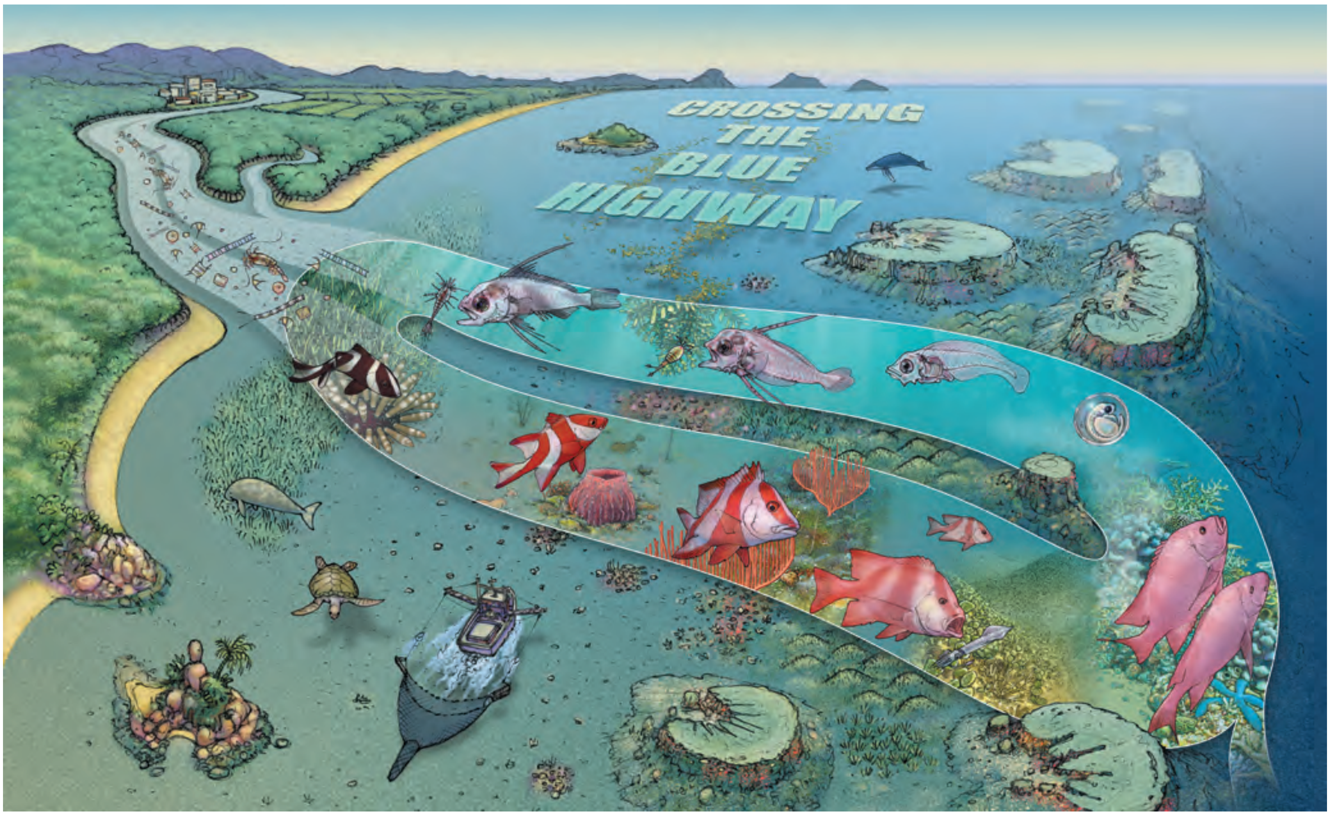

Figure 2. 'Crossing the Blue Highway': The red emperor (*Lutjanus sebae*) spends different stages of its life cycle utilising different habitats across the GBR. © Russell Kelley/Australian Coral Reef Society, http://www.russellkelley.info/print/the-blue-highway/

Marine connectivity: North America

25. Northern Channel Islands: Connectivity across a network of marine protected areas contributes to positive population and ecosystem consequences

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Context and challenge

Temperate coastal marine ecosystems produce a diversity of ecosystem services, including the support of recreationally and commercially important fisheries, economically important ecotourism and other cultural values. One temperate marine ecosystem of particular importance is kelp forests, which support some of the most species-rich and productive ecosystems on Earth. They are subjected to a host of human impacts, particularly from fisheries, invasive species, and various manifestations of global climate change.

Approach

In 1998, a group of fishers, managers and other citizens in southern California, USA, was concerned about declining resources such as abalone, lobsters and rockfishes in nearshore ecosystems, including kelp forests. This group approached the California Fish and Game Commission with a proposal to set aside areas for protection in the northern Channel Islands, a chain of four islands north-west of Los Angeles and separated from the mainland by the Santa Barbara Channel. In 2003, following a multi-year public process, the state of California, in collaboration with Channel Islands National Park (CINP), created 13 marine protected areas (MPAs) within state and national park waters. In 2007, the National Oceanic and Atmospheric Administration extended eight of these MPAs into Channel Islands National Marine Sanctuary (CINMS) waters (Figure 1). Thus, the MPAs encompass both state and federally managed waters. The objectives of the MPAs were to help restore biodiversity, ecosystem health and fisheries species by protecting marine life and habitats. Extending from the intertidal zone to depths of 1,400 m, the MPAs encompass a diversity of ecosystems, distinguished by seafloor type (rock versus sand) and depth.

Key lesson

The creation of an ecological network of marine protected areas has helped to restore species, increased connectivity and made the network more robust to invasive species.

Today's Channel Islands MPA network has a large number of overlapping agency jurisdictions. Eleven federal, state and local agencies have some jurisdiction in the planning region. While both CINMS and CINP overlap around the northern Channel Islands, neither agency regulates commercial or recreational fishing. The California Department of Fish and

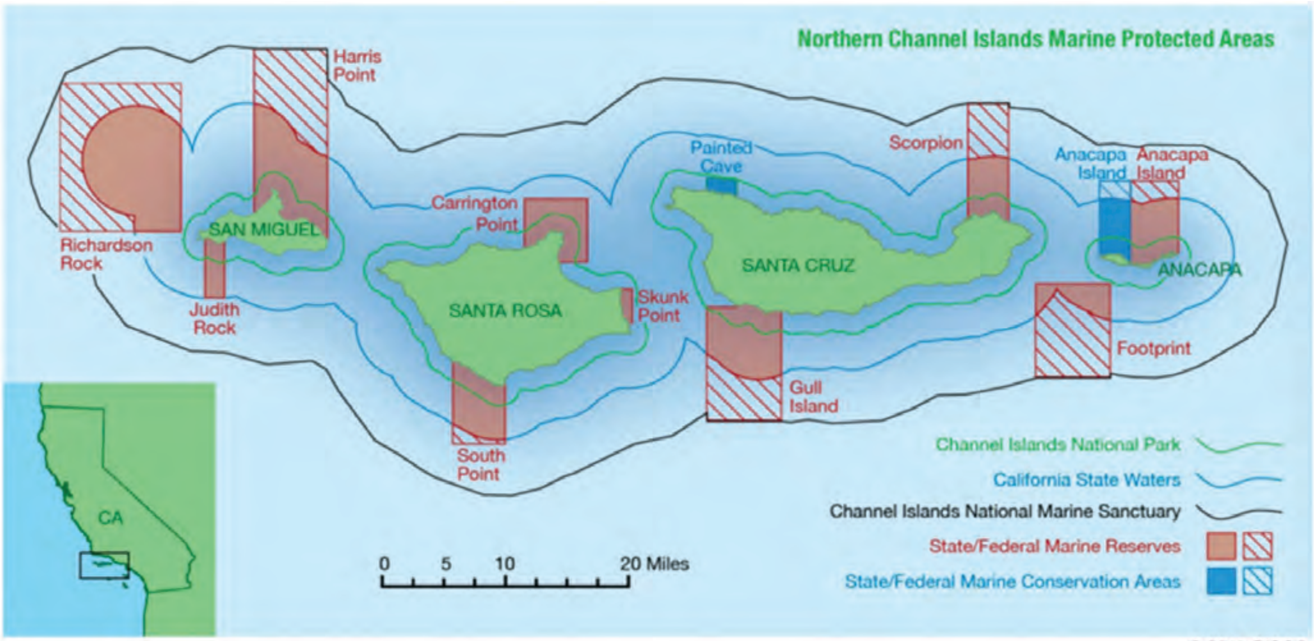

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Figure 1. Map of the distribution of marine protected areas across the Northern Channel Islands archipelago off the coast of southern California, USA (see inset). Map indicates the jurisdictional ranges of state and federal institutions and the two types of protected areas (marine reserves and marine conservation areas) © The Partnership for Interdisciplinary Studies of Coastal Oceans

Kelp forest © Adobe Stock

Wildlife manages all fisheries in state waters (within 5.6 km of the shore), while the California Fish and Game Commission (an appointed body) has authority to set all state fishery regulations, including the creation of MPAs.

Examples of ecological corridors

Though not originally designed as a network of MPAs connected to one another by the dispersal of young (i.e., fish and invertebrate larvae), subsequent analyses of oceanographic currents and larval dispersal patterns indicated that young generated in the MPAs very likely are transported to and contribute to the replenishment of populations and communities in other MPAs, thus forming a *de facto* network. The primary way ecological corridors have been analysed is by simulating the movement of larvae using numerical ocean circulation models that describe currents in the region. For example, Watson et al. (2010) simulated the movement of larvae of two important fishery species – kelp bass (*Paralabrax clathratus*) and kelp rockfish (*Sebastes atrovirens*) – to and from sites throughout southern California, including the Channel Islands MPAs. The simulations calculated the probability of larvae travelling from one location to another; the authors then multiplied those probabilities by estimates of the spawning biomass at each location to predict how many larvae travelled along each potential ecological corridor. The analysis showed that kelp bass larvae produced inside MPAs on Santa Cruz and Anacapa islands likely disperse to other MPAs in the network and to fished areas; the same was true of kelp rockfish larvae produced in MPAs on San Miguel Island (Figure 2). Thus, the MPAs are linked by ecological corridors, but different corridors are used by different species, depending on habitat. In this case, kelp bass prefer the warmer water of the eastern islands while kelp rockfish prefer the cooler western waters.

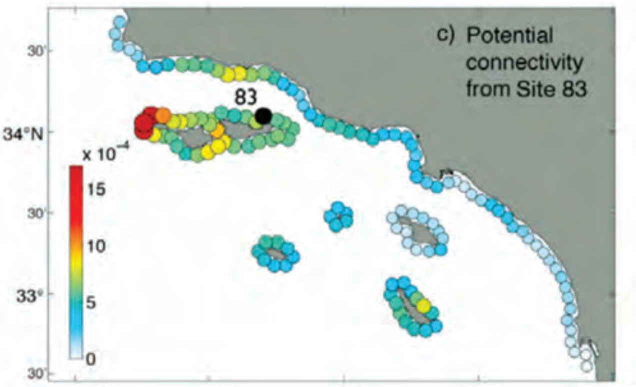

Figure 2. Predicted dispersal of larval kelp bass using an ocean circulation model of the Southern California Bight (Watson et al., 2010). Each coloured circle corresponds to a spatial node (site) in the model from which simulated larvae could be released and to which they can settle. In this example, the connectivity from Site 83 (which overlaps with the Scorpion State Marine Reserve on Santa Cruz Island) is shown. The colour of each dot represents the relative number of larvae that travel along the ocean corridor from Scorpion to the other sites (the numerical values are expressed as a proportion of the total number of larvae released from all sites in the simulation). Thus, there are strong connections to the other MPAs in the Channel Islands, as well as to non-MPA sites.

Results

The ecological network of MPAs implemented in the Channel Islands region contains 21% of the CINMS waters in 11 state marine reserves (no commercial or recreational fishing allowed) and two conservation areas (where some types of fishing are allowed). Following a decade of protection, monitoring of nearshore kelp forests in the Channel Islands MPAs showed increases in the biomass of targeted fish species inside the MPAs relative to fished areas. While the biomass did not increase spectacularly, the dramatic declines that were predicted by some models as a result of potential displacement and compaction of fishing effort did not take place either. More recently, protection of higher-level predators within older, fully protected areas has been shown to prevent invasion of a non-native macroalgae.

Case study references

Ayebare, S., Plumptre, A.J., Kujirakwinja, D., and Segan, D. (2018) 'Conservation of the endemic species of the Albertine Rift under future climate change'. *Biological Conservation* 220:67–75. https://doi.org/10.1016/j.biocon.2018.02.001.

Bellmore, J.R., Duda, J.J., Craig, L.S., Greene, S.L., Torgersen, C.E., Collins, M.J., and Vittum, K. (2017). 'Status and trends of dam removal research in the United States'. *Wiley Interdisciplinary Reviews: Water* 4:e1164. https://doi.org/10.1002/wat2.1164.

Bode, M., Leis, J.M., Mason, L.B., Williamson, D.H., Harrison, H.B., Choukroun, S., and Jones, G.P. (2019). 'Successful validation of a larval dispersal model using genetic parentage data'. *PLoS Biology* 17(7):e3000380. https://doi.org/10.1371/journal.pbio.3000380.

Boisjolie, B.A., Flitcroft, R.L., and Santelmann, M.V. (2019). 'Patterns of riparian policy standards in riverscapes of the Oregon Coast Range.' *Ecology and Society* 24:22. https://doi.org/10.5751/ES-10676-240122.

Boisjolie, B.A., Santelmann, M.V., Flitcroft, R.L., and Duncan, S.L. (2017). 'Legal ecotones: a comparative analysis of riparian policy protection in the Oregon Coast Range, USA.' *Journal of Environmental Management* 197:206–220. https://doi.org/10.1016/j.jenvman.2017.03.075.

Bridge, T.C.L, Grech, A.M., and Pressey, R.L. (2016). 'Factors influencing incidental representation of previously unknown conservation features in marine protected areas'. *Conservation Biology* 30(1):154–165. https://doi.org/10.1111/cobi.12557.

Butman, D. and Raymond, P.A. (2011). 'Significant efflux of carbon dioxide from streams and rivers in the United States'. *Nature Geoscience* 4:839–842. https://doi.org/10.1038/ngeo1294.

Eizirik, E., Kim, J., Menotti-Raymond, M., Crawshaw Jr., P.G., O'Brien, S.J., and Johnson, W.E. (2001). Phylogeography, population history and conservation genetics of jaguars (*Panthera onca,* Mammalia, Felidae)'. *Molecular Ecology* 10:65–79. https://doi.org/10.1046/j.1365-294X.2001.01144.x.

Fernandes, L., Day, J.O.N., Lewis, A., Slegers, S., Kerrigan, B., Breen, D.A.N., Cameron, D., Jago, B., Hall, J., Lowe, D. and Innes, J. (2005). 'Establishing representative no-take areas in the Great Barrier Reef: Large-scale implementation of theory on marine protected areas'. *Conservation Biology* 19(6):1733–1744. https://doi.org/10.1111/j.1523-1739.2005.00302.x.

GBRMPA (Great Barrier Reef Marine Park Authority) (2002). GBRMPA Technical Information Sheet No.6: 'Biophysical Operational Principles as recommended by the Scientific Steering Committee for the Representative Areas Program'. http://www.gbrmpa.gov.au/__data/assets/pdf_file/0011/6212/tech_sheet_06.pdf (Accessed: 20 February 2020).

Gustafson, R.G., Waples, R.S., Myers, J.M., Weitkamp, L.A., Bryant, G.J., Johnson, O.W., and Hard, J.J. (2007). Pacific salmon extinctions: Quantifying lost and remaining diversity'. *Conservation Biology* 21:1009–1020. https://doi.org/10.1111/j.1523-1739.2007.00693.x.

Harrison, H.B., Williamson, D.H., Evans, R.D., Almany, G.R., and Thorrold, S.R. (2012). 'Larval export from marine reserves and the recruitment benefit for fish and fisheries'. *Current Biology* 22:1023–1028. https://doi.org/10.1016/j.cub.2012.04.008.

Koning, A.A., Perales, K.M., Fluet-Chouinard, E., and McIntyre, P.B. (2019). 'Success of small reserves for river fishes emerges from local, network, and cultural contexts'. In review.

Koning, A.A. (2018). 'Riverine reserves: The conservation benefits of spatial protection for rivers in the context of environmental change' (doctoral dissertation). Madison: University of Wisconsin–Madison. Retrieved from University of Wisconsin Digital Collections. OCLC# on1041855468.

Leemhuis, C., Thonfeld, F., Näschen, K., Steinbach, S., Muro, J., Strauch, A., López, A., Daconto, G., Games, I. and Diekkrüger, B. (2017). 'Sustainability in the food-water-ecosystem nexus: The role of land use and land cover change for water resources and ecosystems in the Kilombero Wetland, Tanzania'. *Sustainability* 9(9):1513. https://doi.org/10.3390/su9091513.

Manzano, P. and Malo, J.E. (2006). Extreme long-distance seed dispersal via sheep. *Frontiers in Ecology and the Environment* 4:244–248. https://doi.org/10.1890/1540-9295(2006)004[0244:ELSDVS]2.0.CO;2.

Mohl, A., Egger, G., Schneider-Jacoby, M. (2009). 'Fließende Grenzen – Grenzflusse im Spannungsfeld zwischen Schutz und Nutzung.' ('Flowing boundaries – Tensions between conservation and use of border rivers'.) *Natur und Landschaft* 84(9/10):431–435.

Penaluna, B.E., Olson, D.H., Flitcroft, R.L, Weber, M.A., Bellmore, J.R., Wondzell, S.M., Dunham, J.B., Johnson, S.L., and Reeves, G.H. (2017). 'Aquatic biodiversity in forests: A weak link in ecosystem services resilience'. *Biodiversity and Conservation* 26:3125–3155. https://doi.org/10.1007/s10531-016-1148-0.

Pess, G.R., McHenry, M.L., Beechie, T.J., and Davies, J. (2008). ‘Biological impacts of the Elwha River dams and potential salmonid responses to dam removal’. *Northwest Science* 82:72–91.

Petracca, L., Frair, J., Cohen, J., Calderón, A.P., Carazo-Salazar, J., Castañeda, F., Corrales-Gutiérrez, D., Foster, R., Harmsen, B., Hernández-Potosme, S., Herrera, L., Olmos, M., Pereira, S., Robinson, H., Robinson, N., Salom-Pérez, R., Urbina, Y., Zeller, K.A., and Quigley, H. (2017). ‘Robust inference on large-scale species habitat use using interview data: The status of jaguars outside protected areas in Central America’. *Journal of Applied Ecology* 55:723–734. https://doi.org/10.5061/dryad.jk6rf.

Pinsky, M.L., Springmeyer, D.B., Goslin, M.N. and Augerot, X. (2009). Range-wide selection of catchments for Pacific salmon conservation. *Conservation Biology* 23:680–691. https://doi.org/10.1111/j.1523-1739.2008.01156.x.

Plumptre, A.J., Ayebare, S., Segan, D., Watson, J. and Kujirakwinja, D. (2017) *Conservation Action Plan for the Albertine Rift.* Wildlife Conservation Society Report to Governments of Uganda, Rwanda, Burundi, Tanzania and Democratic Republic of Congo. https://www.researchgate.net/publication/322722311_Conservation_Action_Plan_for_the_Albertine_Rift (Accessed: 20 February 2020).

Plumptre, A.J., Davenport, T.R.B., Behangana, M., Kityo, R., Eilu, G., Ssegawa, P., Ewango, C., Meirte, D., Kahindo, C., Herremans, M., Kerbis Peterhans, J., Pilgrim, J., Wilson, M., Languy, M. and Moyer, D. (2007). ‘The biodiversity of the Albertine Rift’. *Biological Conservation* 134:178–194. https://doi.org/10.1016/j.biocon.2006.08.021.

Proctor, M.F., Kasworm, W.F., Annis, K.M., MacHutchon, A.G., Teisberg, J.E., Radandt, T.G., and Servheen, C. (2018). ‘Conservation of threatened Canada–USA trans-border grizzly bears linked to comprehensive conflict reduction’. *Human Wildlife Interactions* 12:248–272. https://doi.org/10.26077/yjy6-0m57.

Rabinowitz, A. and Zeller, K.A. (2010). ‘A range-wide model of landscape connectivity and conservation for the jaguar, *Panthera onca*’. *Biological Conservation* 143:939–945. https://doi.org/10.1016/j.biocon.2010.01.002.

Ritchie A.C., Warrick, J.A., East, A.E., Magirl, C.S., Stevens, A.W., Bountry, J.A., Randle, T.J., Curran, C.A., Hilldale, R.C., Duda, J.J., Gelfenbaum, G.R., Miller, I.M., Pess, G.R., Foley, M.M., McCoy, R., and Ogston, A.S. (2018). ‘Morphodynamic evolution following sediment release from the world’s largest dam removal’. *Nature Scientific Reports* 8:13279. https://doi.org/10.1038/s41598-018-30817-8.

Sanderson, E.W., Redford, K.H., Chetkiewicz, C.B., Medellin, R.A., Rabinowitz, A.R., Robinson, J.G., and Taber, A.B. (2002). ‘Planning to save a species: The Jaguar as a model’. *Conservation Biology* 16:58–71.

Sawyer, H., Hayes, M., Rudd, B., and Kauffman, M. (2014). *The Red Desert to Hoback Mule Deer Migration – A Migration Assessment.* Laramie: University of Wyoming. https://migrationinitiative.org/content/red-desert-hoback-migration-assessment (Accessed: 20 February 2020).

Schneider-Jacoby, M., Mohl, A. (2012). ‘Mura-Drava-Danube: Five countries – three rivers – one biosphere reserve’. *Danube News* 25:5–8.

UNESCO (United Nations Educational, Scientific and Cultural Organization) (2017). Transboundary Biosphere Reserves (TBRs). http://www.unesco.org/new/en/natural-sciences/environment/ecological-sciences/biosphere-reserves/regional-and-subregional-collaboration/transboundary-biosphere-reserves-tbr/ (Accessed: 20 February 2020).

Watson, J.R., Mitarai, S., Siegel, D.A., Caselle, J.E., Dong, C., and McWilliams, J.C. (2010). ‘Realized and potential larval connectivity in the Southern California Bight’. *Marine Ecology Progress Series* 401:31–48. https://doi.org/10.3354/meps08376.

Williamson, D.H., Harrison, H.B., Almany, G.R., Berumen, M.L., Bode, M., Bonin, M.C, Choukroun, S., Doherty, P.J., Frisch, A.J., Saenz-Agudelo, P., and Jones, G.P. (2016). ‘Large-scale, multidirectional larval connectivity among coral reef fish populations in the Great Barrier Reef Marine Park’. *Molecular Ecology* 25(24):6039–6054. https://doi.org/10.1111/mec.13908.

WWF (World Wildlife Fund) Austria (2014). ‘Saving the Amazon of Europe. Mura-Drava-Danube: Rivers at the crossroad between protection and destruction’. Vienna: WWF Austria. [Leaflet].

WWF (World Wildlife Fund) (2013). 2013 IRF European Riverprize Application, Mura – Drava – Danube (Austria, Croatia, Hungary, Serbia, Slovenia). Vienna: WWF on behalf of the five countries.

Zeller, K.A., Nijhawan, S., Hines, J., Salom-Perez, R., and Hernandez, S. (2011). ‘Integrating site occupancy modeling and interview data for identifying jaguar (*Panthera onca*) corridors: A case study from Nicaragua’. *Biological Conservation* 144:892–901. https://doi.org/10.1016/j.biocon.2010.12.003.

Zeller, K.A, Rabinowitz, A., Salom-Perez, R., and Quigley, H. (2013). ‘The Jaguar Corridor Initiative: A range-wide conservation strategy’. In: M. Ruiz-Garcia and J.M. Shostell (eds.). *Molecular Population Genetics, Evolutionary Biology and Biological Conservation of Neotropical Carnivores*. Hauppauge, NY: Nova Science Publishers. 629–658.

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Stephen Woodley PhD has worked in environmental conservation as a field biologist, researcher, consultant, University Research Centre Director, and first Chief Scientist for Parks Canada. In 2011, Stephen began working as Senior Advisor to the Global Protected Areas Program of the IUCN and continues that work as Vice Chair for Science and Biodiversity of IUCN's World Commission on Protected Areas. The work focus is to understand the role of protected areas as solutions to the current global conservation challenges.

Barbara Lausche JD is an international environmental law and policy advisor with more than 30 years in conservation law and policy, nationally and internationally. Since 2010, she has served as Director of the Marine Policy Institute (MPI), Mote Marine Laboratory, Florida. As an active member of the IUCN World Commission on Environmental Law and WCPA, she began working with the project early on as part of Graeme Worboys' team, focusing on governance, law, policy, and marine content. Among publications relevant for this project are the IUCN *Guidelines on Protected Areas Legislation* (2011), and *The Legal Aspects of Connectivity Conservation, A Concept Paper* (coauthor, 2013). In 2019, she was appointed Chair of the IUCN WCPA-CCSG Marine Connectivity Working Group, comprising some 80 marine professionals worldwide. Prior positions have included senior staff at the World Bank, World Wildlife Fund-US and numerous legal drafting consultancies in developing countries.

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PLANNING FOR CONNECTIVITY UNDER CLIMATE CHANGE:

USING BOBCAT MOVEMENT TO ASSESS LANDSCAPE CONNECTIVITY ACROSS SAN DIEGO COUNTY'S OPEN SPACES

Photo Credit: Shouqin Huo

SAN DIEGO STATE
UNIVERSITY

FINAL REPORT

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PREPARED FOR THE SAN DIEGO FOUNDATION

GRANT NUMBER C-2011-00177

BY:

MEGAN JENNINGS

REBECCA LEWISON

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EXECUTIVE SUMMARY

Our assessment of connectivity using bobcat movement and habitat use through camera, mortality, telemetry, and genetic data indicate that while functional connectivity is intact in some areas of the San Diego MSCP preserve network, data revealed that connectivity is impaired in other areas. Our connectivity assessment suggests:

- Overall, there is evidence of connectivity in the inland and coastal areas of the MSCP network that we sampled.
- Genetic analysis showed some degree of genetic differentiation between coastal bobcats west of I-15 and inland animals to the east, but did not indicate subpopulation differentiation has occurred. This supports the assertion that the coastal and inland areas have some level of connectivity.
- Movement analyses (camera and telemetry) showed direct use of five of seven linkages that were monitored. Detected movement was highest in Linkage 6-7, Linkage 8-10, and Linkage 5-6.
- For linkages not directly monitored, results from landscape models suggest that at least five other areas identified as putative linkages may have limited to no current connectivity, and another nine may only function partially. These limitations will likely increase under projected land use.
- Habitat alteration and recreation, in addition to other ecological variables, are currently affecting wildlife occupancy. These effects may increase under projected land use shifts.
- Heavily traveled secondary roads with traffic moving at high rates of speed may pose the largest threat to medium-wide ranging wildlife species attempting to move between core conserved areas, especially from coastal to inland areas. Roadkill mortality appears to increase with seasonal increases in animal movement.
- Projected habitat shifts resulting from climate change did not lead to substantial changes in habitat suitability or effective distance between preserves. However, future land use plans that lead to increased areas of altered use categories are likely to reduce habitat suitability in and around inland preserves.

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INTRODUCTION

Current land management plans throughout the U.S. and Europe are designed to protect biodiversity by establishing a network of core habitat areas that are connected via linkages (Nelson *et al.* 2003). The central principle of this large-scale conservation planning is that viable populations and natural communities can be supported by a connected landscape network (Beier *et al.* 2006, Crooks and Sanjayan 2006, Boitani *et al.* 2007, Barrows *et al.* 2011), particularly as the landscape becomes altered by anthropogenic features like roads and housing developments. Landscape connectivity allows for movement among patches of suitable habitat, reduces the chance of extinction and effects of demographic stochasticity on small populations (Brown and Kodric-Brown 1977), and maintains gene flow between populations in patchy landscapes (Simberloff *et al.* 1992). Over longer time scales, and in the face of changing abiotic conditions, connectivity may also prove critical for range shifts in response to landscape changes caused by changing climate and altered disturbance regimes (Hannah *et al.* 2002, Heller and Zavaleta 2009).

In southern California, this landscape-scale network approach has been adopted in response to the widespread habitat conversion and fragmentation that has resulted from intense development (Riverside County 2003, Ogden 1996). Although the direct effects of anthropogenic landscape alteration, namely habitat loss and fragmentation, are paramount in this region (Crooks 2002, Beier *et al.* 2006, Soulé 1991), the potential for large scale shifts in vegetation and habitat types as a result of climate change may present an equally large risk to ecological networks.

General predictions from numerous climate models for the western United States suggest that temperatures will increase, there may be an increase in aridity (Westerling *et al.* 2003), and an overall reduction in rainfall (Hannah *et al.* 2002). These conditions are likely to extend fire seasons and increase fire frequency (Swetnam and Betancourt 1998, Brown *et al.* 2004). These predicted shifts in vegetation distribution and more frequent and/or severe wildfires driven by drier summers and earlier Santa Ana seasons (Miller and Schlegel 2006) may result in large-scale vegetation type conversion to non-native annual grasslands (Bachelet *et al.* 2001, Lenihan *et al.* 2003) and reductions in standing water availability.

All of these projected changes may have direct and indirect (*i.e.* food web) effects on wildlife. Temperature shifts may drive migration upslope to cooler climates (Hughes 2000) or westward to areas with greater marine influence and lower temperatures. Some species or individuals, such as females rearing young, may need improved access to water sources in the form of dense riparian areas and perennial streams, which are found in western portions of San Diego County. Whatever the response, shifts in distribution and habitat use can present a fundamental challenge to the currently designated landscape conservation network.

One of the central sources of uncertainty regarding how wildlife will respond to climate change is the lack of baseline data on current connectivity. In this study, we use bobcats as a model species to establish a foundation of knowledge on the present status of connectivity. Among wildlife species in southern California, bobcats respond negatively to habitat fragmentation, particularly when it results in smaller or more isolated habitat patches (Crooks 2002, Lyren *et al.* 2006, 2008, 2009). As a result, bobcats have been identified as a priority focal species for connectivity monitoring in southern California (Ogden 1996, Crooks 2002, County of San Diego 2004, South Coast Wildlands 2008). Bobcats also have the potential to function as an umbrella species, whereby conservation of viable populations and suitable habitat would confer protection to other species using similar habitats and movement corridors. Because bobcats are medium-ranging habitat generalists, studying their movement ecology and genetic diversity allows insight into landscape connectivity on a sub-regional scale. Because of their sensitivity to anthropogenic impacts to their habitat, bobcats also present an ideal system to study the effects of human recreation activities on wildlife. Understanding how this species responds to the complex interaction between human development and shifting habitats resulting from climate change is essential to preserve long-term connectivity and efficacy of the ecological network in this landscape.

Quantifying or assessing landscape connectivity, however, is non-trivial (Fagan and Calabrese 2006) given the context-dependent nature of connectivity (Crooks and Sanjayan 2006). Spatial and temporal scales may be different for wide-ranging species with a home range of tens of kilometers that responds to large-scale ecosystem processes versus a non-vagile species with a limited home range. Crooks and Sanjayan (2006) suggest connectivity assessments consider both physical and structural connectivity of an area, *i.e.* the physical arrangement of habitat on the landscape, as well as the response to that arrangement by individuals or species (Taylor *et al.* 1993, Tischendorf and Fahrig 2000a, 2000b). While conceptually this is intuitive, measuring both physical and functional connectivity is logistically difficult. There is a general lack of knowledge of how animals are currently using the landscape, and how landscape use changes in response to dynamic landscape processes over time. Most recent efforts in connectivity assessment and planning utilize the concepts of resistance and cost (*sensu* Adriaensen *et al.* 2003) in evaluating functional connectivity. The former refers to the friction, or difficulty, in moving through each individual cell in the landscape and the latter represents the cumulative resistance encountered traveling through a linkage.

To assess the status of connectivity in a landscape-scale conservation network in southern California like the San Diego MSCP, this study was designed to collect robust, multi-faceted data to evaluate habitat use, response to human recreation, use of landscape linkages, and gene flow using bobcats as a focal species. The goal of the project was to establish the current state of landscape connectivity as well as connectivity under projected future conditions resulting from land use and climate shifts. Using bobcats as an indicator, we compared the use of urbanized and more natural habitats and determined how landscape features influenced home range size and distribution. Using these multiple, complementary datasets we asked the research questions: ***1) What is the current state of physical and functional connectivity in the MSCP? 2) Are there barriers to movement through linkages? If so, what and where are those barriers? 3) Does human recreational activity affect wildlife use in habitat cores? 4) How is movement across the landscape likely to change under climate change and land use projections?***

METHODS

Data Collection

Study Area

This study was conducted within the San Diego Multiple Species Conservation Plan Area in southern California across three sites, the Peñasquitos /SR56 area representing fragmented, coastal habitats, the SR67 Corridor between Lakeside and Poway, and the Ramona/SR78 area (Figure 1). The natural habitats and protected open space in the area are primarily publicly-owned, and include Los Peñasquitos Canyon Preserve, Black Mountain Open Space, Sycamore Canyon and Goodan Ranch Preserves, Boulder Oaks Preserve, San Vicente Highlands Preserve, Iron Mountain, San Dieguito River Park lands, and a portion of the Cleveland National Forest in Pamo Valley, north of the town of Ramona. These areas are also centered on major transportation corridors that cross the preserve networks, specifically SR56 near the coast, SR67 inland, and SR78 to the north.

Elevation across the three study sites ranged from sea level at the coast to 1000 m in the inland foothills. Habitat type in the study area varied with both elevation and distance from the coast, but was predominantly a shrubland ecosystem. Habitats across these areas included coastal sage scrub dominated by California sagebrush (*Artemesia californica*), chaparral habitat types generally dominated by scrub oak (*Quercus berberidifolia*) or chamise (*Adenostoma fasciculatum*), oak woodland with coast live oak (*Quercus agrifolia*), grasslands dominated by non-native annual grasses, riparian zones with an oak (*Quercus agrifolia*) or sycamore (*Platanus racemosa*) overstory and herbaceous understory, as well as urban and altered areas. The Mediterranean-climate of the study region is characterized by hot, dry summers and mild, wet winters with precipitation often less than 300 mm.

Remote Cameras

To measure animal distribution, quantify occupancy across the MSCP, and consider the effect of recreation on animal distribution, remote camera stations were established across the study area in locations ranging from internal preserve cores to linkage areas and road crossings (Figure 2). Placement of the 36 camera stations was established on a 2 km grid, based on the minimum expected home range for a bobcat in urbanized landscapes in southern California. Locations for 12 cameras in each of the three study areas were selected to represent an equal sampling of the landscape features listed above, as well as a range of recreational use intensity (Table 1). We primarily utilized two types of cameras, the Cuddeback Expert white-flash camera (Cuddeback, Green Bay, WI, USA) and the LTL Acorn 5210A940 infrared camera (Old Boys Outdoors, Stone Mountain, GA, USA). As a result of theft, vandalism, and equipment failure, some of the older model Cuddeback Expert cameras were eventually replaced with Cuddeback Attack cameras. Cameras were deployed between November 30, 2011 and March 16, 2012 and were run for periods ranging from nine to 12 months. Cameras were set to capture images 24 hours per day, logging over 300,000 images from the 36 stations. Images were manually processed to identify species in each photo and entered into the program Camera Base 1.6 (Tobler 2012), an Access-based database for camera data and photo management.

Mortality Assessment

During the project, we identified and mapped any roadkilled bobcats reported by the public, cooperators, or project staff. Roadkill locations identified prior to the project period were also incorporated into our mapping. If possible, the carcass was collected and stored for necropsy where we collected a variety of samples to be stored for genetic analysis and for possible future use (*e.g.* anticoagulant screening of blood samples). We also collected a number of bobcat carcasses provided by the wildlife rehabilitation center, Fund for Animals Wildlife Center in Ramona, CA. Any patients that arrived and did not survive were stored for us, which included a number of animals that succumbed to notoedric mange. For all carcasses, we recorded cause of death (if known or identifiable), date of collection, sex, weight, body condition, and size. These data are now incorporated into the long-term bobcat mortality database managed by collaborators Lisa Lyren and Erin Boydston, United States Geological Survey – Western Ecological Research Center.

Animal Capture and Telemetry

Bobcats (n = 17) were trapped in baited cage traps (61cm x 43cm x 109cm) and sedated with a combination of ketamine HCl and xylazine HCL. All trapping, collaring, and tracking efforts were conducted by San Diego State University project staff (California Department of Fish and Game Scientific Collecting Permit #SCP-009632, SDSU Animal Protocol # 10-09-027L) between 2009 and 2012. Animals were weighed, measured, ear tagged, and fitted with one of two GPS collar brands (TCG181 or TCG271, Sirtrack Ltd., Havelock North, New Zealand; Quantum 4000, Telemetry Solutions, Concord, California, USA). During animal processing, we opportunistically collected all samples with the potential for future beneficial use. Blood, tissue, and buccal swab samples were taken from captured individuals for genetic testing to examine genetic connectivity across the project area.

Collars were set to collect fine-scale movement, gathering locational fixes eight times per day 5 days/week and 48 times per day 2 days/week, to track individual movement in relation to cores, linkages, potential barriers, human development over the course of six to nine months. Data were retrieved from collars with remote download, or stored-on-board until retrieval through recapture or a timed remote drop-off component in the collar. Data were checked and filtered for inaccurate and erroneous locations prior to analysis, and all locations with poor quality, undefined location (1-dimension or 1d) fixes were removed.

Genetic Sampling

To evaluate the functional connectivity (*i.e.* gene flow) across the sampled area of the MSCP, we collected tissue samples from a total of 62 bobcats gathered from a combination of live trapping, roadkill, and from assembling samples collected opportunistically by collaborators from areas in San Diego County. Genetic samples collected in the field were stored frozen at -20°C until they could be processed in the laboratory. All genetic lab work was conducted in the lab of Dr. Holly Ernest at UC Davis using microsatellite markers that had previously been tested on bobcat samples by Dr. Jennings in 2007 and 2008. Genomic DNA was extracted from blood and tissue using the QIAamp DNeasy blood and tissue kit, and from buccal swabs using the QIAamp DNA Mini and Blood Mini Kit (Qiagen Inc., Valencia, CA, USA), all following the manufacturer's protocols. We amplified 22 microsatellite loci (Table 2) for polymerase chain reaction (PCR). After initial optimization and testing, primers were grouped into multiplexes and prepared for PCR using the Qiagen Multiplex PCR Kit (Qiagen Inc., Valencia, CA, USA). PCR protocols followed the manufacturer's recommendations for the Multiplex PCR Kit. Thermal cycling parameters included an initial denaturing step at 95° C for 15 minutes, followed by 35 cycles of 94° C for 30 seconds; 54-60° C for 90 seconds; 72° C for 90 seconds, and then a final extension step at 72° C for 10 minutes. PCR product was analyzed using an ABI 3730 DNA Analyzer (Applied Biosystems, Foster City, CA, USA) and STRand software (Toonen and Hughes 2001). All PCR and genotyping was duplicated until two consistent results were obtained to reduce genotyping errors that can result in false alleles or allelic dropout.

Data Analysis

Remote Cameras and Occupancy Modeling

We analyzed all camera data using an occupancy modeling approach to identify the occupied rates within the monitored area. An occupancy approach does not monitor abundance;

rather it is used to establish the covariates that affect detection rates as well as the likelihood of species presence at each station. To analyze the camera data using this occupancy framework, we identified all photos of bobcats at all camera stations and created a capture history based on two week time intervals. If a bobcat was detected at a station within the selected two week period, it was recorded as a presence (1), and if not, as a non-detection (0). If the camera was not functioning or not present for a given time frame, a no-data value was recorded. Due a high level of missing values at four camera stations (78-BV, PV-SYC, 56-BV, and PQ-805) resulting from malfunctioning equipment, only 32 camera stations were included in the occupancy modeling. The time period analyzed included 18 two week periods between January and September 2012. These data were input in program PRESENCE 3.1 (Hines 2010) along with covariates for each camera station, including site type (core, bridge, culvert, or any linkage), recreation level (low or high), elevation, distance to major and local roads, and distance to water. We also recorded the proportional area in a 30m buffer around each camera station of each land use type and habitat type described in the habitat modeling section above. Survey covariates, or factors that may influence detection, included camera model at each station and whether the time period was during the wet or dry season. Models were run as single-season, assuming a closed population with no colonization or extinction. Model selection was based on the information theoretic approach using AIC, ΔAIC, and model weights (Burnham and Anderson 1998).

Mortality Assessment

We evaluated our mortality database to determine common causes of mortalities from the carcasses we salvaged during the study period. To visualize vehicle-caused mortalities for bobcats, we mapped all sites where mortalities occurred and identified common features of roadkill sites. With increasing numbers of mange mortalities during the project, we also established a database of incidences of mange reported to us by colleagues in the County, identified on remote cameras, or diagnosed during necropsy.

Home Range

Bobcat habitat use and range was calculated with a 95% adaptive local convex hull method (LoCoH, Getz and Wilmers 2004), using a=18,000 for bobcats. The LoCoH method is well-suited for constructing home ranges in landscapes with features that result in a distribution of point locations exhibiting sharp boundaries, corners, or holes, as is the case for the study area in southern California. The open spaces that make up the bobcat habitat in the study area are intersected by freeways, highways, and secondary roads, and abutted by housing developments and business parks, features generally avoided by bobcats. In addition to calculating the overall home range area with the LoCoH methods, we also calculated the proportion of home range area overlapping urban areas for an estimation of the degree to which animals may be constrained by unsuitable habitat adjacent to open space preserves.

Habitat Models

One component of our connectivity assessment was developed using habitat models. To model bobcat habitat suitability relative to the human landscape and other environmental factors, we used the telemetry data from bobcat GPS collars and evaluated the areas used relative to four different habitat categories: habitat features (habitat type and distance to water), anthropogenic landscape features (land-use type, distance to major roads, and distance to local roads), shifting fire-frequency (fire-return interval departure) and topographic variables (elevation). Habitat covariates were developed from the San Diego Association of Government's (SANDAG) vegetation data which were reformatted into seven groupings, water and wetlands (WAT), altered habitat (ALT), grasslands (GRS), shrublands (SHB), riparian areas (RIP), forested areas (FOR), and other (OTH), which included small areas of desert scrub. Additional information on methods employed can be found in Appendix A.

Based on the results of the habitat selection models, we evaluated the current state of landscape connectivity and the predicted state under projections of future climate and land use changes. There were three components to this assessment: habitat suitability, landscape resistance, and effective distance (*i.e.* cost-weighted distance). We followed established methods (Singleton *et al.* 2004, Beier *et al.* 2007, Spencer *et al.* 2010, Beier *et al.* 2011), and first identified landscape permeability by assigning habitat suitability values, based on empirical values from generalized linear mixed models (GLMMs), between ten (least suitable) and 100 (most suitable) to categories in the GIS raster layers based on the results of univariate modeling and the multivariate model for each species. The biological interpretation of these values, as suggested by Beier *et al.* (2007) is that 100 is equivalent to the best habitat with highest survival and reproductive success, 80 is the lowest value with successful breeding, 60 is associated with consistent use and breeding, 30 represents occasional use for non-breeding activities and anything below 30 is avoided (see Appendix B for more information on methods).

We calculated these surfaces both under current and future conditions, incorporating habitat shifts and land use changes to provide a comparison. Planned land use data from SANDAG's Series 12 Regional Growth Forecast (2050) provided input for projected shifts in land use. We also employed current and future habitat data developed from models established by Stralberg *et al.* (2009). The projected future vegetation classification models used Random Forest algorithms and were based on projections from two different climate models: NCAR CCSM3.0 (National Center for Atmospheric Research Community Climate System Model) averaged from 2038-2069 (478-610 ppm CO_2), and the GFDL CM2.1 (Geophysical Fluid Dynamics Laboratory Coupled Climate Model) averaged from 2038-2070 (478-615 ppm CO_2). When analyzed in our connectivity assessment, the difference between the two climate models was negligible, thus only results from the GFDL CM2.1 model are presented in comparison to the current vegetation condition. The vegetation projection models, like all climate models, are not perfect; the highest spatial resolution is 800 m grid cells and there is inherent uncertainty in modeling future scenarios. However, these vegetation classification models are a published and peer-reviewed product and represent the best available data at the present time.

Genetic Assessment

Data were initially assessed in the Excel Microsatellite Toolkit (Park 2001). Based on published findings of restricted gene flow in southern California (Riley *et al.* 2006, Lee *et al.* 2012), data were split into two putative subpopulations, coastal and inland, for analysis. The data were evaluated in Microchecker 2.2.3 (Van Oosterhout *et al.* 2004) to test for issues of stuttering, null alleles and allelic drop-out. GENEPOP on the Web (Raymond and Rousset 1995, Rousset 2008) was used to test populations for Hardy-Weinberg equilibrium and linkage disequilibrium. F_{ST} and population differentiation was calculated in GENEPOP, and followed by tests to estimate subpopulation differentiation (D_{est}) using Software for Measurement of Genetic Diversity (Crawford 2010) given recent criticisms of F_{ST} (Jost 2008). To evaluate the putative subpopulation structure we defined, we ran program STRUCTURE 2.3.3 2 (Prichard *et al.* 2000, Falush *et al.* 2003) to identify genetically distinct subpopulations (K). We ran a burn in of 10,000 and ran 1,000,000 Markov Chain Monte Carlo iterations. We tested K from 1 to 5 populations, and repeated the analysis 100 times for each K to verify the consistency of likelihood values between runs. In order to choose which value of K best fits our population we analyzed ln P(X|K) as suggested by the STRUCTURE manual (Prichard *et al.* 2000) as well as the ΔK method (Evanno *et al.* 2005).

RESULTS

During the course of the project, we handled 19 bobcats and collared 17, collected over 300,000 photos from camera stations, identified 24 roadkill locations, and processed 62 genetic samples.

Remote Cameras and Occupancy Modeling

Photos processed from the remote camera stations identified bobcats at all but two camera stations during 28 two-week sampling periods. An additional four stations only detected bobcats once during the camera monitoring. Stations with the lowest detection of bobcats included Iron Mountain, Mount Woodson, San Vicente Highlands, Upper Beelor Canyon, three crossings under SR78, Carmel Valley Road at Black Mountain, and Santa Luz at Camino del Sur. Stations with the greatest detections of bobcats (22-26 detections out of 28 sampling periods) included Goodan Ranch, McGonigle Canyon, and Boulder Oaks (see Appendix C for more information on model selection and results). Models suggested that bobcat detection was lower with the older model Cuddeback cameras, and occupancy was negatively associated with bridges, altered habitat, and camera stations within putative linkage zones compared to those in core conserved areas. Although not significant, we also found that bobcat occupancy rates were lower at stations with high recreation and at lower elevation (*i.e.* coastal) stations. Occupancy rates ranged from 0.66 at the Black Mountain Road bridge over Los Peñasquitos Creek to 0.91 at Boulder Oaks Open Space Preserve with higher occupancy rates overall in the inland study areas (Figure 3).

Although we have not yet quantitatively analyzed the patterns of species co-occurrence at remote camera stations, through our image processing, we observed a number of other species that were often detected at stations with frequent detection of bobcats, suggesting bobcats may serve as an indicator of connectivity for these species. Not surprisingly, species known to be tolerant of or associated with urbanized habitats and human activity, *e.g.* coyotes (*Canis latrans*), raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), and Virginia opossums (*Didelphis virginiana*), were detected at most stations, including those where bobcat detections were high. In addition, less common species like greater roadrunner (*Geococcyx californianus*), Western spotted skunk (*Spilogale gracilis*), long-tailed weasel (*Mustela frenata*), gray fox (*Urocyon cinereoargenteus*), mule deer (*Odocoileus hemionus*), and Cooper's hawk (*Accipiter cooperii*) were all observed at many of the stations with frequent bobcat detections. Of these, images of mule deer were repeatedly captured at many of the stations except for the culvert crossings under SR67 where there were only occasional images of mule deer. Beyond these commonly co-occurring species, we also obtained a number of puma images at several of our camera stations in the inland portions of our study area east of SR67.

Mortality Assessment

The primary sources of mortality we identified were vehicle collisions, followed by mange, caused by the felid-specific mange mite, *Notoedris cati*. We identified 24 roadkill locations (Figure 4) across San Diego County. Upon review of the data collected for each roadkill, we determined that the majority of these occurred on undivided, secondary roadways. Vehicles on these roadways often travel at high speeds but through terrain that may make detecting oncoming traffic difficult for animals attempting to cross over the roadway, as opposed to an underpass or culvert. In fact, a number of the roadkilled animals we collected were found near crossing structures, which they may have used rather than going over the road, if the structures had been better placed, not blocked with vegetation, or had appropriate wildlife fencing to direct animals into the crossing structure. Our data also suggest that many of the vehicle-caused mortalities occurred between late September and early March, during the bobcat breeding season. Increased movement activity and exploration out of home ranges in an attempt to find a mate may result in a greater number of crossing attempts resulting in the increased mortalities during this time period.

During the course of this study, we also identified mortality caused by what appeared to be a mange epizootic in the greater Ramona/SR67 area. From detection on cameras, reports from the public, and calls for assistance into the Fund for Animals Wildlife Center rehabilitation center, we counted approximately 21 unique individuals affected by moderate to severe mange between 2010 and 2012 between SR67, the San Diego Country Estates, and SR78 in San Pasqual Valley. Without intervention, all of these animals would eventually die from emaciation or secondary infection resulting from the mange. We provided these data to collaborators focused on studying the prevalence and impact of mange in southern California at University of California - Los Angeles, University of California – Davis, and the Santa Monica Mountains National Recreation Area (Foley *et al.*, in review).

Telemetry and Home Range Analysis

We handled a total of 19 bobcats (14 males, 5 females; Table 3), collared 17, and have retrieved data from eight of the collars. The duration of tracking lasted between 11 and 465 days. Over 12,000 point locations were gathered from seven male and one female bobcat (Figure 5). Radio collar loss or malfunction limited the data we were able to retrieve, although there are still three animals we will attempt to recapture in June 2013 after the kitten season has ended. Additional locations collected through manual triangulation of the VHF signal from each collar are still being processed to incorporate data from the individuals that experienced collar failure.

We calculated the Local Convex Hull (LoCoH) home ranges for each individual (Table 4, Figure 6) utilizing all points available for each animal, and found that the mean home range size was 5.15km^2. Home range size varied greatly between individuals with some animals traveling long distances between core areas. Overall, we found that the majority of landscape used by bobcats was classified as natural habitat. However, animals were found to move relative to the constraints of their surroundings, *e.g.*, bobcats in Los Peñasquitos Canyon had smaller home ranges than in other areas. Similarly, animals in this and other developed areas were found to use more urban habitat than average. In comparison, the animals tracked in Pamo Valley had almost no urban association, showing a link between habitat use and environmental constraints.

Habitat Models

We created 15 different *a priori* models of bobcat presence incorporating combinations of habitat, land use, human development, and topography to identify which variables were most influential in explaining bobcat presence (Table 5). Models including elevation, all habitat variables, and all land use variables outperformed all other models ($AICw_i > 0.999$; Table 6).

The model output indicates that bobcat presence was most closely associated with water/wetland habitats, low elevation, and distance from major and local roads, as well as avoidance of shrublands and urban habitat (Table 7). Although our fire-return interval departure variable did not provide significant explanatory power in our models to predict bobcat presence, our previous research has found this to be a critical variable in analysis of movement data from Orange County that is often overlooked, resulting in overestimations of connectivity (Jennings 2013). Although we did not carry this variable forward in our analyses, it would be useful to continue monitoring fire-return intervals and the potential for vegetation type conversion across the preserve network.

Connectivity Assessment

To assess connectivity, we created three different raster layers based on the empirical data from our modeling efforts: suitable habitat, landscape resistance, and cost-weighted distance. Initially, habitat suitability values for each variable category that was determined to be significant predictor of bobcat presence (land cover, elevation, distance to roads, distance to water, and habitat) were established based on our modeling results (Table 8). Under current climate and land use conditions, our analyses suggest that habitat suitability is relatively high in and around core areas, more so in inland areas than the more fragmented coastal portions of the preserve network. Through our cost-weighted distance connectivity analysis, we found that connectivity among core areas is likely limited in a number of locations, *e.g.* Linkage 1-2b, Linkage 2-3a, Linkage 4-5, Linkage 6-7, Linkage 12-13, and Linkage 5-13 (all linkage designations are those identified in the Connectivity Monitoring Strategic Plan for the San Diego Preserve System 2011). Through our camera and GPS telemetry, we also found that some linkages, or segments of designated linkages do appear to serve as true conduits of animal movement among core areas. This includes Linkage 8-10, the eastern segment of Linkage 11-12, the western segment of Linkage 5-8, and to some degree, Linkage 5-6 under SR67.

In response to projected climate change (GFDL model between 2038 and 2070) and planned land use changes projected by SANDAG (Figure 7), we found little evidence of significant changes in the amount or distribution of suitable habitat resulting from climate conditions. However, the shifts in projected land use, particularly to altered categories of use in inland backcountry areas caused declines in suitable habitat, both within preserve cores, as well as in the areas between protected lands identified as putative landscape linkages.

When we calculated the effective distance between protected lands, the average effective distance for bobcats to travel between protected lands did not appear to change significantly in geographic position or overall value (Figure 8). However, current choke points that are already locations of concern necessary for connecting core preserve lands are likely to become more impacted in the future, further limiting connectivity through these linkages. In particular, several linkage zones identified by the MSCP Connectivity Strategic Plan (2011), *e.g.* Linkage 10-11, Linkage 12-13, Linkage 6-7, Linkage 5-13, Linkage 4-5, Linkage 1-2b, and Linkage 2-3a, may become impassable under future land use development. These linkages represent important connections both north to south and east to west and likely represent highly restricted movement from core preserves in more fragmented urban areas to larger blocks of intact habitat.

Genetic analysis

A total of 62 genetic samples were processed and genotyped and then separated into two putative bobcat subpopulations, a coastal and an inland unit, for analysis (Figure 9).

Microchecker analysis identified that there was no evidence of null alleles in the coastal population, but potential evidence for four loci in the inland population (FCA45, FCA90, Lc110, FCA35). Tests for linkage disequilibrium identified 22 potentially linked loci pairs. FCA35, FCA8, FCA90, and Lc111 were found to be in linkage disequilibrium in both subpopulations, so were eliminated from further analyses. Tests to determine whether each population was in Hardy-Weinberg equilibrium revealed that the coastal population was in equilibrium ($p = 0.0654$) and that the inland populations may be out of equilibrium ($p < 0.001$). This finding may be a result of skewed data, with a larger number of related individuals in inland areas sampled during live captures within a small geographic area. Analysis of relatedness is necessary to test this hypothesis. Tests of genotypic variation suggested that the coastal and inland populations are genetically distinct ($X^2 = 70.20$, df = 36, $p < 0.001$), and that distribution of alleles at all 18 loci differed significantly between coastal and inland populations. We also observed lower allelic richness in coastal bobcat populations, suggesting isolation in fragmented coastal preserves may be limiting gene flow. However, further analyses indicate that the samples tested were not from two distinct subpopulations. Both analyses of subpopulation differentiation ($D_{est} = 0.003$, $F_{ST} = 0.006$) indicate low genetic differentiation between the putative subpopulations. The analysis of the results from our STRUCTURE runs from K= 1 to K=5 also reveal that the samples tested were from a single panmictic population (Figure 10).

DISCUSSION

Our assessment of connectivity using bobcat movement and habitat use through camera, mortality, telemetry, and genetic data indicate that while functional connectivity is intact in some areas of the San Diego MSCP preserve network, data revealed that connectivity is impaired in other areas. Our connectivity assessment suggests:

- Overall, there is evidence of connectivity in the inland and coastal areas of the MSCP network that we sampled.
- Genetic analysis showed some degree of genetic differentiation between coastal bobcats west of I-15 and inland animals to the east, but did not indicate subpopulation differentiation has occurred. This supports the assertion that the coastal and inland areas have some level of connectivity.
- Movement analyses (camera and telemetry) showed direct use of five of seven linkages that were monitored. Detected movement was highest in Linkage 6-7, Linkage 8-10, and Linkage 5-6.
- For linkages not directly monitored, results from landscape models suggest that at least five other areas identified as putative linkages may have limited to no current connectivity, and another nine may only function partially. These limitations will likely increase under projected land use.
- Habitat alteration and recreation, in addition to other ecological variables, are currently affecting wildlife occupancy. These effects may increase under projected land use shifts.
- Heavily traveled secondary roads with traffic moving at high rates of speed may pose the largest threat to medium-wide ranging wildlife species attempting to move between core

conserved areas, especially from coastal to inland areas. Roadkill mortality appears to increase with seasonal increases in animal movement.

- Projected habitat shifts resulting from climate change did not lead to substantial changes in habitat suitability or effective distance between preserves. However, future land use plans that lead to increased areas of altered use categories are likely to reduce habitat suitability in and around inland preserves.

Current levels of connectivity

Genetics and movement data (camera and telemetry) suggest that there is some level of connectivity between the inland and coastal areas of the MSCP we studied, and varying levels of connectivity between core conserved areas within both the east and west (Figure 11, Table 9).

Genetics

Our analysis of genetic samples revealed some level of genetic differentiation between coastal and inland bobcats (Figure 9) at the loci we analyzed, but this level of differentiation has not led to subpopulation structure. This disparity could be the result of two factors, one related to our sample size and distribution, the other associated with population size and genetic drift. We sampled approximately 30 individuals in coastal (closest to coast) and inland (animals east of Interstate 15), however, it is possible that we did not have sufficient sample sizes to detect subpopulation structuring between these areas. It is also possible that the preserves closest to the coast (and farther from I-15) are smaller and more isolated and may in fact, have limited gene flow with outside areas.

The disparity in our results for genetic differentiation may also be the result of limited genetic drift in San Diego County’s coastal preserves. Smaller populations are likely to experience higher rates of genetic drift and may show differentiation in fewer generations. In San Diego’s coastal areas where we collected genetic samples, the preserves are larger blocks of land and are slightly less isolated than the sampling locations from the previous research in the Santa Monica Mountains (Riley *et al.* 2006) or Orange County (Lee *et al.* 2012). Previous research (Riley *et al.* 2006, Lee *et al.* 2012) has found bobcat subpopulation structuring and limited gene flow across major freeways in southern California. In both these studies, the preserves on at least one side of the freeway are small and relatively isolated from other preserves, differing from the slightly larger and more connected preserves in San Diego’s coastal preserves.

Movement data

We have direct camera and telemetry evidence that some movement is occurring between coastal and inland preserves. We documented bobcats moving under I-15 (Figure 5), which may be enough to allow for gene flow between preserves to the east and west of this potential barrier. However, the flow from that point to areas farther inland, such as Sycamore Canyon, appear to be limited by development and altered habitat between I-15 and preserves just west of SR67, with only one bobcat detection at Upper Beelor Canyon, one of the few corridors of open space between coastal and inland zones. We observed a number of animals crossing SR67 through culverts (Figure 3), but also collected roadkilled animals in the area (Figure 4), which represent a barrier to connectivity if the crossings are not fenced and improved, especially as traffic is likely to increase along this transportation corridor in the future. Along the northern east-west linkage, some movement was documented through our Pamo Valley/SR78 study area (Figure 5). In this case, we observed individuals moving along the eastern part of the linkage within San Pasqual Valley, but were not able to monitor the zone to the west through Lake Hodges that is necessary to link eastern to western preserves in this area. Numerous crossings of SR78 were documented in at least one of the four underpasses monitored (Figure 3), but poor placement of culverts, agricultural habitat, and high levels of human movement appeared to restrict movement through the other three crossings.

Within the coastal study area, our data indicate that there is functional movement, at least between preserves on either side of SR56. We observed not only numerous crossings under the three bridges we monitoring along SR56, but movement and behavior (*e.g.* adults with kittens, foraging individuals) suggesting bobcats are utilizing the natural habitat under these bridges as part of their home ranges rather than just as movement corridors. VHF telemetry documented the movement of one individual from Los Peñasquitos Canyon to the Black Mountain Open Space region, but until we retrieve GPS collar data, we will not know which of the bridges he used and whether it was through the putative linkage identified through McGonigle Canyon.

Connectivity between the north and south inland areas appears to be the most problematic for wildlife movement. We were only able to monitor one culvert along SR67 in the region of Mount Woodson, because there is only one available for crossing. This camera station had almost no bobcat activity documented (Figure 3), and we detected at least one roadkill along this section of roadway. While movement to the south through the Scripps-Poway Parkway wildlife tunnel was regularly documented, there is still a large amount of unprotected and developed habitat for animals to move through to get to northern conserved lands. In particular, the crossing of Poway Road appears to be a challenge with multiple roadkills (Figure 4) observed along the winding stretch of road just west of SR67. One animal was tracked as he moved from the northern preserves in San Pasqual Valley up to the Ramona Grasslands, but he did not proceed south to Mount Woodson or to cross SR67 toward Iron Mountain (Figure 5).

Habitat models

Our habitat suitability models, as well as the cost-weighted distance connectivity assessment provide a means of comparing the likelihood of connectivity across the landscape. We found evidence of lower quality habitat both within core areas of the MSCP and in associated putative linkages, namely, Linkage 8-10, 5-8, 2-3a, and 1-2b (Figure 7). While some animals may be willing to use and traverse these unsuitable areas, there are still questions of whether enough animals will do so, whether those that attempt the crossing will be successful, and whether they will find suitable and unoccupied habitat at the other end of the linkage. The cost-weighted distance analysis similarly identified a number of areas where additional linkages are needed as the resistance/cost between one preserve to the next likely limits connectivity (see notations on Figure 8).

Potential impediments to connectivity

Our analyses reinforce the idea that development (current and projected), human use, and road crossings may limit movement in certain areas of the San Diego MSCP preserve network.

Recreation

The occupancy modeling of the remote camera stations across the study area revealed that bobcat occupancy was lowest in areas outside of core conserved areas, in altered habitats, and in the coastal area of our study. While the effect of recreation was not identified as a primary factor, this may have been the result of limited power to detect these effects. We did find overall fewer total detections of bobcats at the camera stations with the highest recreation like Iron Mountain, Los Peñasquitos Canyon, and at the San Dieguito River trailhead at Bandy Canyon Road and SR78 (Figure 3). In fact, only three photos of bobcats were taken at the Iron Mountain station, where tens to hundreds of people passed daily, over the course of the year-long sampling. In contrast, 32 bobcat detections were gathered at camera 67-C4 at the culvert along SR67 just below the hiking trail at Iron Mountain. It is likely that our coarse categorization of recreation into high and low levels to assess its impact on species occupancy oversimplified a more complex interaction between wildlife and human recreation, which has been documented in other studies of the effects of recreation on mammalian carnivore species (George and Crooks 2006, Reed and Merenlender 2008). A more detailed analysis of the recreation data we gathered, including rates, types, and temporal patterns of both recreation and animal detections, could yield results that provide more guidance on the effect of recreation in and around linkages.

Road mortality

Our mortality assessment determined that a high number of mortalities occurred on highly traveled secondary roads where vehicle speeds are often > 50 mph (Figure 4). A number of roadkilled bobcats we collected were found along guardrails near culverts or tunnels suggesting that the animal elected to attempt to cross over the road, rather than go through the crossing. This may be related to crossing type, placement, or simply a result of inadequate or inappropriate wildlife fencing to direct the animal into the crossing. We observed poorly placed (*e.g.* not connected to the crossing structure) and broken fencing, barbed wire fences, and no fencing at a number of the camera stations along SR67. In fact, the SR67 study area faces the greatest challenges for road crossings with high roadkill numbers along secondary roads in an area bounded by highways, virtually on all sides.

Other mortality sources

In addition to limitations on movement across or under roads, there appear to be additional stressors to animals in this area as evidenced by the mange epizootic observed during the study. Our assessment indicated that, as in other areas of southern California (Riley *et al.* 2007), mange is a concern for San Diego bobcat populations. While we were not primarily focused on assessing this disease in our bobcat populations, there is a need for continued cooperation and collaboration with other researchers to provide information about ongoing issues related to mange in San Diego County. It is worth noting that this and other disease outbreaks may be related to connectivity as disease may spread more readily in constrained, highly developed areas, *e.g.* Los Peñasquitos Canyon, as has been observed in other areas of southern California (Riley *et al.* 2007, Foley *et al.*, in review). Research on the prevalence of mange in southern California has detected a correlation between incidences of mange and bobcat exposure to anticoagulant rodenticides which may occur both in highly urbanized areas as well as areas of exurban development where housing and wildlands are intermixed to a greater degree. The apparent mange epizootic we observed during our study supports this relationship. The large projected increase in altered land use categories from the SANDAG models may have indirect effects on the health of wildlife populations beyond the immediate impacts of habitat fragmentation and a decline in habitat suitability.

Development

Bobcat movement and activity in more heavily impacted and fragmented areas of the MSCP network (Los Peñasquitos Canyon into Carmel Valley/Rancho Santa Fe) indicate that connectivity may be particularly constrained in these areas (Table 4, Figure 6). No tracked bobcats traveled beyond the bounds of open space into urban neighborhoods on the edges of Los Peñasquitos Canyon. Indeed, the large number of males captured in this area suggests that urban animals may be experiencing home range pile-ups (*sensu* Riley *et al.* 2006) and occur at higher densities when alternatives for dispersing are limited. Although many bobcats appeared to be tolerant of or adapted to the high level of human activity and urbanized landscape in the coastal cores, this response may be a result of limited options to avoid these areas. Certainly, dispersal remains a concern for bobcats and for the viability of protecting populations of a variety of species in this highly fragmented area. In comparison, bobcats in the north inland area around Pamo Valley, San Pasqual Valley, and SR78 have ample habitat to move through, and as a result, these animals successfully avoided development and areas with increased levels of human activity.

Connectivity under climate change and land use projections

When we evaluated connectivity under potential future climate conditions, we did not see a substantial change in habitat suitability. This may be a result of the coarse scale at which the habitat models were developed, similar to most current climate change models. More notably, when we incorporated data on planned land use for 2050, we saw a marked decline in suitable habitat, particularly in the inland areas surrounding the SR67 study area. There were six linkages identified that displayed the most obvious changes in suitability, which also happened to be areas already experiencing limited movement, *e.g.* Linkages 6-13, 5-13, 6-7, 2-3a, 2-3b, and 1-2b (see notations on Figure 7).

The assessment of connectivity using cost-weighted distance revealed a slight increase in the effective distance required to traverse certain areas under future conditions. The areas of greatest concern with regard to connectivity appear to be Linkages 10-11, 12-13, 6-13, 5-8, 5-13, 4-5, 1-2b, and 2-3a (see notations on Figure 8). Identifying site-specific corridors in these areas with potential alternatives is the first step to re-establishing connectivity at these locations. Then, on a case-by-case basis, steps to improve each linkage can be developed. As higher resolution climate models are released for the MSCP region, these analyses should be repeated. By continuing to monitor both the change in habitat and in land use, local land management agencies will have a greater ability to successfully create and protect connectivity.

Future Directions

The first steps to begin addressing current issues with connectivity include early corridor identification based on empirical data, rather than mapping exercises or expert opinion. We have taken this important first step in analyzing connectivity for San Diego County's ecological network with this synoptic assessment. However, further investigation prior to developing concrete management recommendations is warranted. There are many methods available and in use to assess connectivity, and there is no scientific consensus as to the ideal method (Beier *et al.* 2011). Instead, many experts recommend an ensemble approach, whereby several methods are applied, *e.g.* CircuitScape, MaxEnt, and Zonation programs. Results from these analyses can then be compared to identify areas of agreement that require management action to protect or re-establish connectivity. Integrating data from other ongoing connectivity studies in the region that use both empirical and analytical approaches, it would be possible to evaluate connectivity for a wider range of organisms. While bobcats serve as an indicator for connectivity, a synthetic analysis that incorporates connectivity from other organisms into a comprehensive assessment is an important next step. Utilizing a robust and diverse data set to identify site-specific corridors will also allow us to assess the remainder of MSCP and MSHCP (planned and in-progress) where site-specific data are not currently available.

Once these thorough assessments have been completed, planning efforts can identify and prioritize action for each given corridor. These actions may be to acquire land, restore habitat, protect habitat, and even create corridor redundancy to allow for a changing landscape given uncertainty of future conditions. Considering the potential impact of recreation on bobcat activity patterns, as well as what has been encountered by other studies (George and Crooks 2006, Reed and Merenlender 2008), limiting recreation either temporally or spatially in critical crossing and linkage areas may be another step to consider in re-establishing and protecting connectivity. As this work is being conducted in an ever-changing environment with new and improved information and ways of assessing information constantly evolving, it is important that connectivity assessments be seen as an iterative process. We recommend that monitoring and direct management action be taken in locations that were identified as areas where connectivity was impaired. These areas should continue to be re-evaluated based on projected future change, as well as continued monitoring data, as more information becomes available. Taking a proactive and empirically-based approach to assessing connectivity at this sub-regional scale will allow San Diego’s preserve network to continue moving forward as a functioning land, habitat, and species conservation plan, while allowing for future change in a planning environment challenged by the nature of fixed spatial extents and a dynamic landscape.

REFERENCES

Aarts, G., J. Fieberg, and J. Matthiopoulos. 2012. Comparative interpretation of count, presence-absence and point methods for species distribution models. Methods in Ecology and Evolution 3: 177–187.

Adriaensen, F., J. Chardon, G. deBlust, E. Swinnen, S. Villalba, H. Gulinck, and E. Matthysen. 2003. The application of 'least-cost' modeling as a functional landscape model. Landscape and Urban Planning 64: 233–247.

Bachelet, D., R.P. Neilson, J.M. Lenihan, and R.J. Drapek. 2001. Climate change effects on vegetation distribution and carbon budget in the United States. Ecosystems 4: 164-185.

Barrows, C.W., K.D. Fleming, and M.F. Allen. 2011. Identifying habitat linkages to maintain connectivity for corridor dwellers in a fragmented landscape. The Journal of Wildlife Management 75(3): 682-691.

Beier, P., K. Penrod, C. Luke, W. Spencer, and C. Cabañero. 2006. South Coast missing linkages: restoring connectivity to wildlands in the largest metropolitan area in the United States. Pages 555–586 in K. R.Crooks and M. A.Sanjayan, editors. Connectivity conservation. Cambridge University Press, Cambridge , United Kingdom .

Beier, P., D. Majka, J. Jenness. 2007. Conceptual Steps for Designing Wildlife Corridors. <www.corridordesign.org> (accessed October 2012).

Beier P., W. Spencer, R.F. Baldwin, and B.H. McRae. 2011. Toward best practices for developing regional connectivity maps. Conservation Biology 25: 879–892.

Beyer, H.L. 2012. Geospatial Modelling Environment (Version 0.7.1.0). (software). URL: http://www.spatialecology.com/gme.

Boitani, L., A. Falcucci, L. Maiorano, and C. Rondinini. 2007. Ecological networks as conceptual frameworks or operational tools in conservation. Conservation Biology 21(6): 1414-1422.

Bolker, B.M., M.E. Brooks, C.J. Clark, S.W. Geange, J.R. Poulsen, M.H.H. Stevens, and J.-S.S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution 24: 127–135.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58: 445-449.

Brown, T. J., B. L. Hall, and A. L. Westerling. 2004. The impact of twenty-first century climate change on wildland fire danger in the western United States: An applications perspective. Climatic Change 62:365-388.

Burnham, K.P., and D.R. Anderson. 2002. Model selection and model inference. Second edition. Springer-Verlag, New York, New York, USA.

Burdett, C.L., K.R. Crooks, D.M. Theobald, K.R. Wilson, E.E. Boydston, L.M. Lyren, R.N. Fisher, T.W. Vickers, S.A. Morrison, and W.M. Boyce, W.M. 2010. Interfacing models of wildlife habitat and human development to predict the future distribution of puma habitat. Ecosphere 1: 1–21.

Carmichael, L.E., Clark W., Strobeck C. 2000. Development and characterization of microsatellite loci from lynx (*Lynx canadensis*), and their use in other felids. Molecular Ecology 9:2197-2198.

Clark, R.G., and T.C. Stevens. 2008. Design and analysis of clustered, unmatched resource selection studies. Journal of the Royal Statistical Society, Series C, Applied Statistics 57: 535–551.

County of San Diego. 2004. "MSCP 2003 Annual Report." San Diego: Multiple Species Conservation Program, Department of Planning and Land Use, County of San Diego.

Crawford, N.G. 2010. SMOGD: software for the measurement of genetic diversity. Molecular Ecology Resources 10:556-557.

Crooks, K.R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology 16: 488-502.

Crooks, K.R. and M.A. Sanjayan. 2006. Connectivity Conservation. Cambridge University Press, Cambridge, UK.

Evanno, G., Regnaut S., Goudet J. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Molecular Ecology 14:2611-2620.

Fagan, W.F. and J.M. Calabrese. 2006. Quantifying connectivity: balancing metric performance with data requirements. Connectivity Conservation (eds K.R. Crooks & M. Sanjayan), pp. 297–317. Cambridge University Press, Cambridge.

Faircloth, B.C., Reid A., Valentine T., *et al.* 2005. Tetranucleotide, trinucleotide, and dinucleotide loci from the bobcat (*Lynx rufus*). Molecular Ecology Notes 5:387-389.

Falush, D., Stephens M., Pritchard J.K. 2003. Inference of population structure using multilocus genotype data: Linked loci and correlated allele frequencies. Genetics 164:1567-1587.

Foley, J., Serieys L., Stephenson N., Riley S., Foley C., Woods L., Jennings M., Wengert G., Vickers W., Boydston E., Lyren L., Crooks K., Moriarty J., and Clifford D. In Review. The ecology of notoedric mange. Journal of Wildlife Management and Wildlife Monographs.

George, S.L. and K.R. Crooks. 2006. Recreation and large mammal activity in an urban nature reserve. Biological Conservation 133: 107-117.

Getz, W.M. and C.C. Wilmers. 2004. A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. Ecography 27: 489-505.

Gillies, C.S., M. Hebblewhite, S.E. Nielsen, M.A. Krawchuk, C.L. Aldridge, J.L. Frair, D J. Saher, C.E. Stevens, and C.L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75: 887–898.

Hann, W.J., and D.L. Bunnell. 2001. Fire and land management planning and implementation across multiple scales. International Journal of Wildland Fire 10: 389-403.

Hannah, L., G.F. Midgley, and D. Millar. 2002. Climate change-induced conservation strategies. Global Ecology and Biogeography 11: 485–495.

Hines, J.E. 2010. PRESENCE3–software to estimate patch occupancy and related parameters. Version 3.1. USGS--PWRC. Available from URL: http://www.mbr--pwrc.usgs.gov/software/presence.html

Jennings, M. K. 2013. Landscape dynamics in Southern California: understanding mammalian carnivore response to fire and human development. [Ph.D. Dissertation]. University of California, Davis and San Diego State University.

Jost, L. 2008. G_{ST} and its relatives do not measure differentiation. Molecular Ecology 17(18):4015-4026.

Lee, J.S., E.W. Ruell, E.E. Boydston, L.M. Lyren, R.S. Alonso, J.L. Troyer, K.R. Crooks, S. VandeWoude. 2012. Gene flow and pathogen transmission among bobcats (*Lynx rufus*) in a fragmented urban landscape. Molecular Ecology 21(7):1617-1631.

Lenihan, J. M., R. Drapek, D. Bachelet, and R. P. Neilson. 2003. Climate change effects on vegetation distribution, carbon, and fire in California. Ecological Applications 13:1667-1681.

Lyren, L. M., R. S. Alonso, K. R. Crooks, and E. E. Boydston. 2009. Evaluation of functional connectivity for bobcats and coyotes across the former El Toro Marine Base, Orange County, California: Administrative report delivered to cooperator Jan. 20, 2009, 179 p.

Lyren, L. M., R. S. Alonso, K.R. Crooks, and E. E. Boydston. 2008. GPS telemetry, camera trap, and mortality surveys of bobcats in the San Joaquin Hills, Orange County, California. U.S. Geological Survey Report, 134 p.

Lyren, L. M., G. M. Turschak, E. S. Ambat, C. D. Haas, J. A. Tracey, E. E. Boydston, S. A. Hathaway, R. N. Fisher, and K. R. Crooks. 2006. Carnivore activity and movement in a Southern California protected area, the North/Central Irvine Ranch. U.S. Geological Survey Technical Report, 115 p.

Menotti-Raymond, M., David V.A., Lyons L.A., *et al.* 1999. A genetic linkage map of microsatellites in the domestic cat (*Felis catus*). Genomics 57:9-23.

Menotti-Raymond, M.A., David V.A., Wachter L.L., Butler J.M., O'Brien S.J. 2005. An STR forensic typing system for genetic individualization of domestic cat (*Felis catus*) samples. Journal of Forensic Sciences 50:1061-1070.

Miller, N. L. and N. J. Schlegel. 2006. Climate change projected fire weather sensitivity: California Santa Ana wind occurrence. Geophysical Research Letters 33.

Ogden Environmental and Energy Services. 1996. Biological Monitoring Plan for the Multiple Species Conservation Plan. San Diego, CA.

Park, S.D.E. 2001. Trypanotolerance in West African Cattle and the Population Genetic Effects of Selection [Ph.D. thesis] University of Dublin.

Pearce, J.L. and M.S. Boyce. 2006. Modelling the distribution and abundance with presence-only data. Journal of Applied Ecology 43: 405-412.

Pritchard, J.K., Stephens M., Donnelly P. 2000. Inference of population structure using multilocus genotype data. Genetics 155:945-959.

Reed, S.E. and A.M. Merenlender. 2008. Quiet, nonconsumptive recreation reduces protected area effectiveness. Conservation Letters 1(3): 1-9.

Riley, S.P.D., Pollinger, J.P., Sauvajot, R.M., York, E.C., Bromley, C., Fuller, T.K., and Wayne, R.K. 2006. A southern California freeway is a physical and social barrier to gene flow in carnivores. Molecular Ecology 15:1733-1741.

Riley, S.P.D., Bromley, C., Poppenga, R.H., Uzal, F., Whited, L., and Sauvajot, R.M. 2007. Anticoagulant exposure and notoedric mange in bobcats and mountain lions in urban southern California. Journal of Wildlife Management 71(6):1874-1884.

Riverside County. 2003. Western Riverside Multiple Species Habitat Conservation Plan Documents.

Rousset, F. 2008. GENEPOP ' 007: a complete re-implementation of the GENEPOP software for Windows and Linux. Molecular Ecology Resources 8:103-106.

Safford, H.D., K. van de Water, and D. Schmidt. 2011. California Fire Return Interval Departure (FRID) map, 2010 version. USDA Forest Service, Pacific Southwest Region and The Nature Conservancy-California. URL: http://www.fs.fed.us/r5/rsl/clearinghouse/r5gis/frid/

SanGIS/SANDAG Data Warehouse. December 2010. PlanLU. San Diego Geographic Information Source - JPA/San Diego Association of Governments (SANDAG). Downloaded May 2013. http://www.sangis.org/Download_GIS_Data.htm

Singleton P.H., W.L. Gaines, and J.F. Lehmkuhl. 2004. Landscape permeability for grizzly bear movements in Washington and southwestern British Columbia. Ursus 15: 90-103.

Soulé, M.E. 1991. Conservation: Tactics for a constant crisis. Science 253: 744-750.

Spencer, W. D., P. Beier, K. Penrod, M. Parisi, A. Pettler, K. Winters, J. Strittholt, C. Paulman, and H. Rustigian-Romsos. 2010. California Essential Habitat Connectivity Project: a strategy for conserving a connected California. Report. California Department of Transportation and California Department of Fish & Game, Sacramento, California. Available from http://www.dfg.ca.gov/habcon/connectivity/ (accessed October 2012).

Stralberg, D., Jongsomjit D., Howell C.A., Snyder M.A., Alexander J.D., *et al.* 2009. Re-Shuffling of Species with Climate Disruption: A No-Analog Future for California Birds? PLoS ONE 4(9):e6825.

Swetnam, T. W. and J. L. Betancourt. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. Journal of Climate 11:3128-3147.

Taylor P.D., L. Fahrig, K. Henein, G. Merriam. 1993. Connectivity is a vital element in landscape structure. Oikos 68: 571–73

Tischendorf L., and L. Fahrig. 2000a. How should we measure landscape connectivity? Landscape Ecology 15: 633–41.

Tischendorf L., and L. Fahrig. 2000b. On the usage and measurement of landscape connectivity. Oikos 90: 7–19.

Tobler, M. 2012. Camera Base 1.6. http://www.atrium-biodiversity.org/tools/camerabase/

Toonen R.J. and Hughes S. 2001. Increased Throughput for Fragment Analysis on ABI Prism 377 Automated Sequencer Using a Membrane Comb and STRand Software, Biotechniques, 31:1320-1324. http://www.vgl.ucdavis.edu/informatics/strand.php

Van Oosterhout, C., Hutchinson W.F., Wills D.P.M., Shipley P. 2004. MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data Molecular Ecology Notes 4:535-538.

Westerling, A. L., A. Gershunov, T. J. Brown, D. R. Cayan, and M. D. Dettinger. 2003. Climate and wildfire in the western United States. Bulletin of the American Meteorological Society 84:595-604.

FIGURES AND TABLES

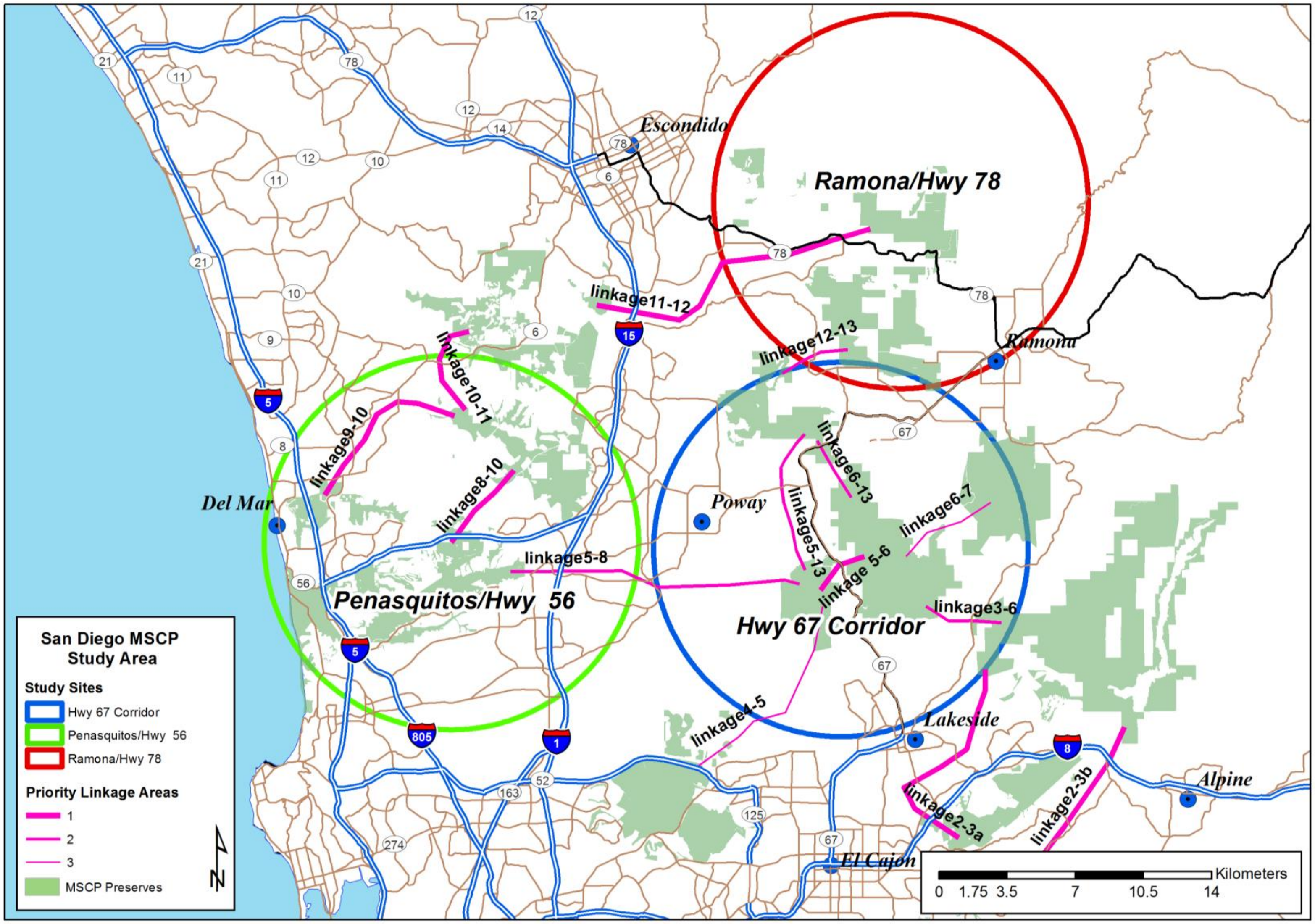

Figure 1. Map of study areas monitoring San Diego County MSCP open space network with core preserves in green. Pink lines represent putative linkage areas previously identified by the MSCP Connectivity Monitoring Strategic Plan. Large circles identify three primary study areas in coastal and inland sites along three major transportation corridors.

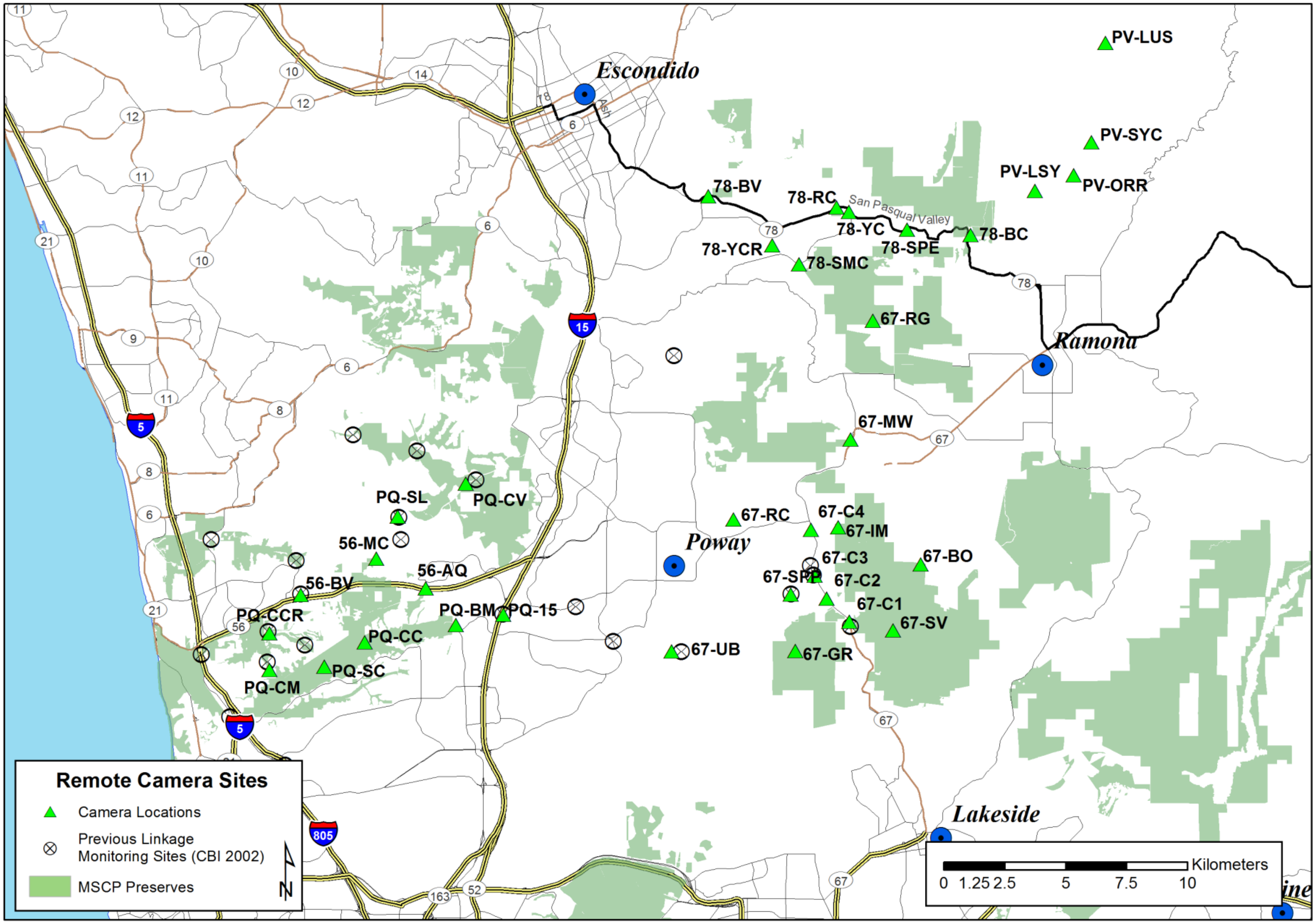

Figure 2. Map of study area with remote camera station monitoring locations (green triangular symbols) with respect to preserve lands. Recommended linkage monitoring sites previously identified (CBI 2002) are represented by circles with an X.

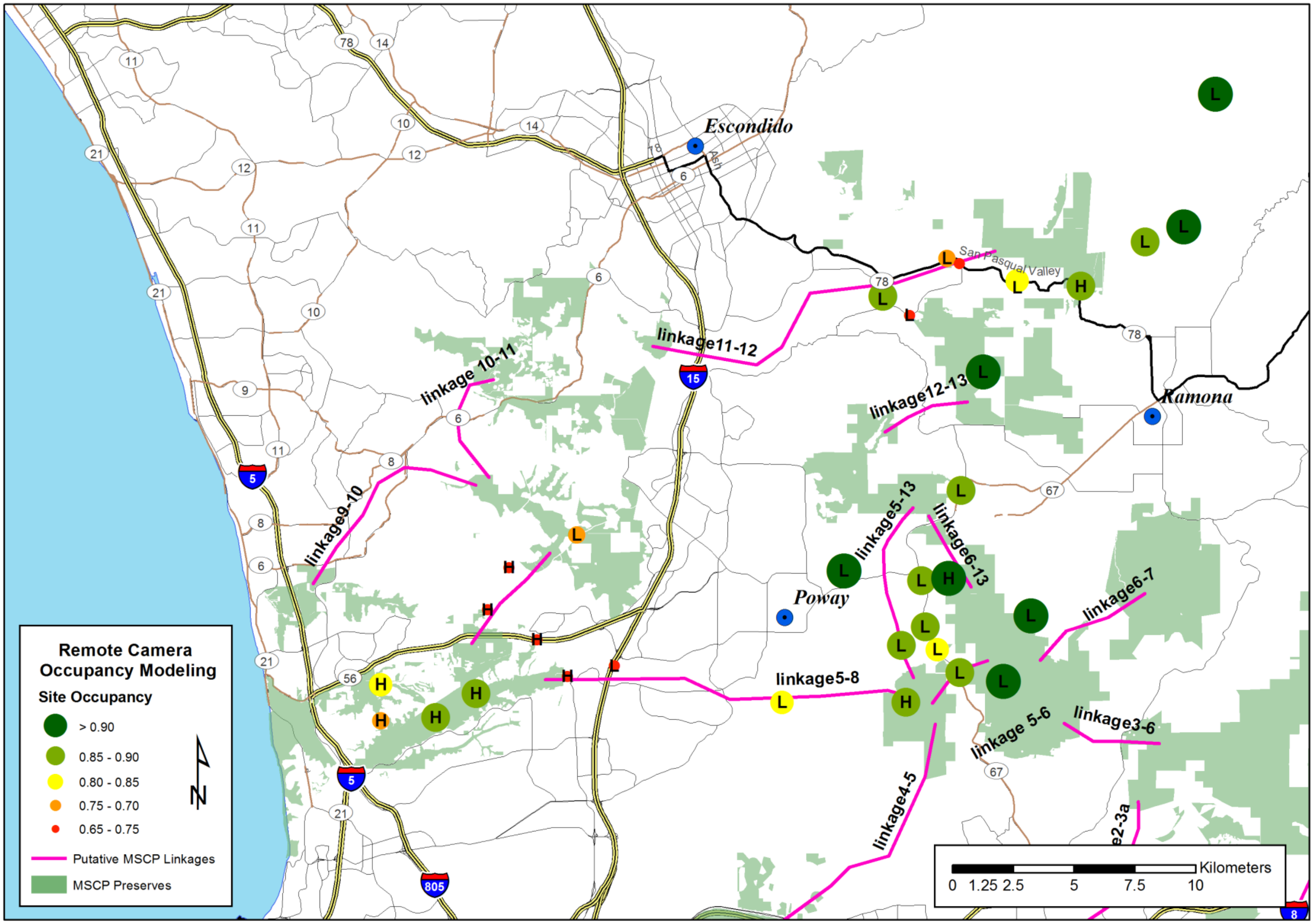

Figure 3. Map of bobcat occupancy rates at remote camera stations (n = 32) determined by occupancy modeling. Rates range from 0.66 to 0.907, represented by smaller red shades at lower occupancies to larger, green shades at the highest occupancy rates. Recreation level at each station is denoted as high (H) or low (L).

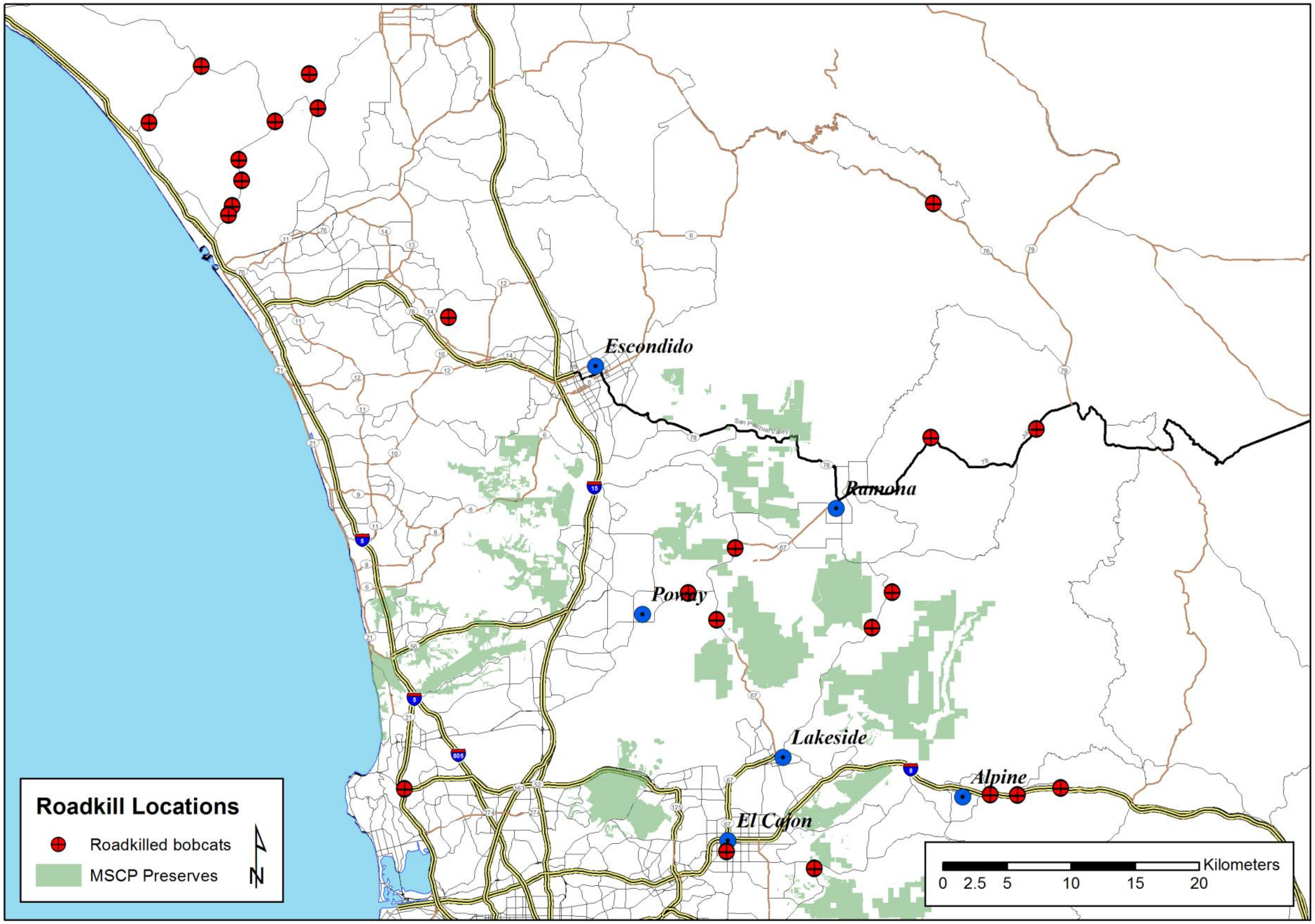

Figure 4. Locations of roadkill bobcats (n = 24) collected or recorded in San Diego County between 2010 and 2013, with the exception of one roadkill location at Marine Corps Base Camp Pendleton collected in 2007.

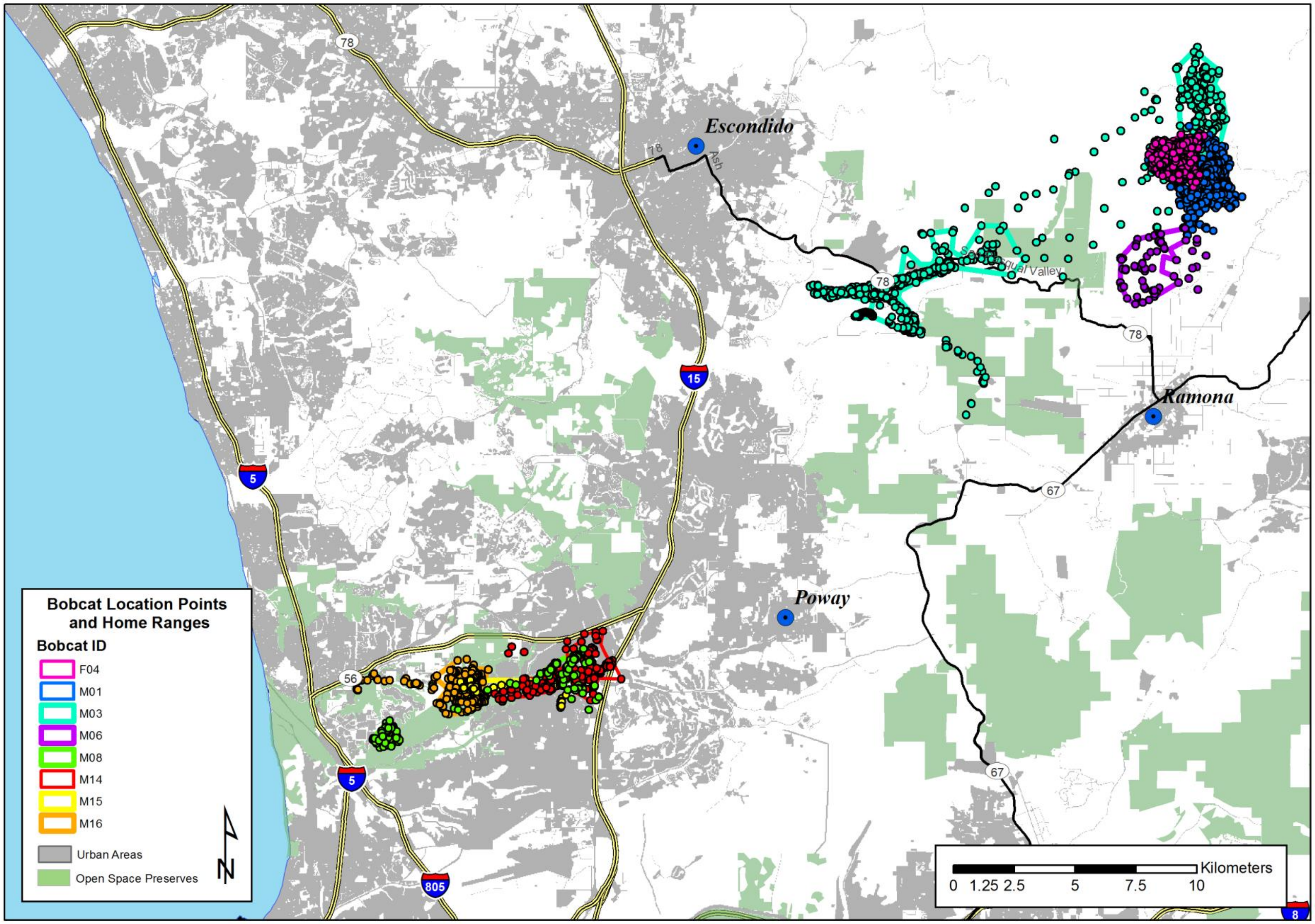

Figure 5. GPS point locations and LoCoH home range estimates for tracked bobcats. Each individual (n = 8) is represented by a different color. Locations are depicted with respect to urban areas, shaded in gray.

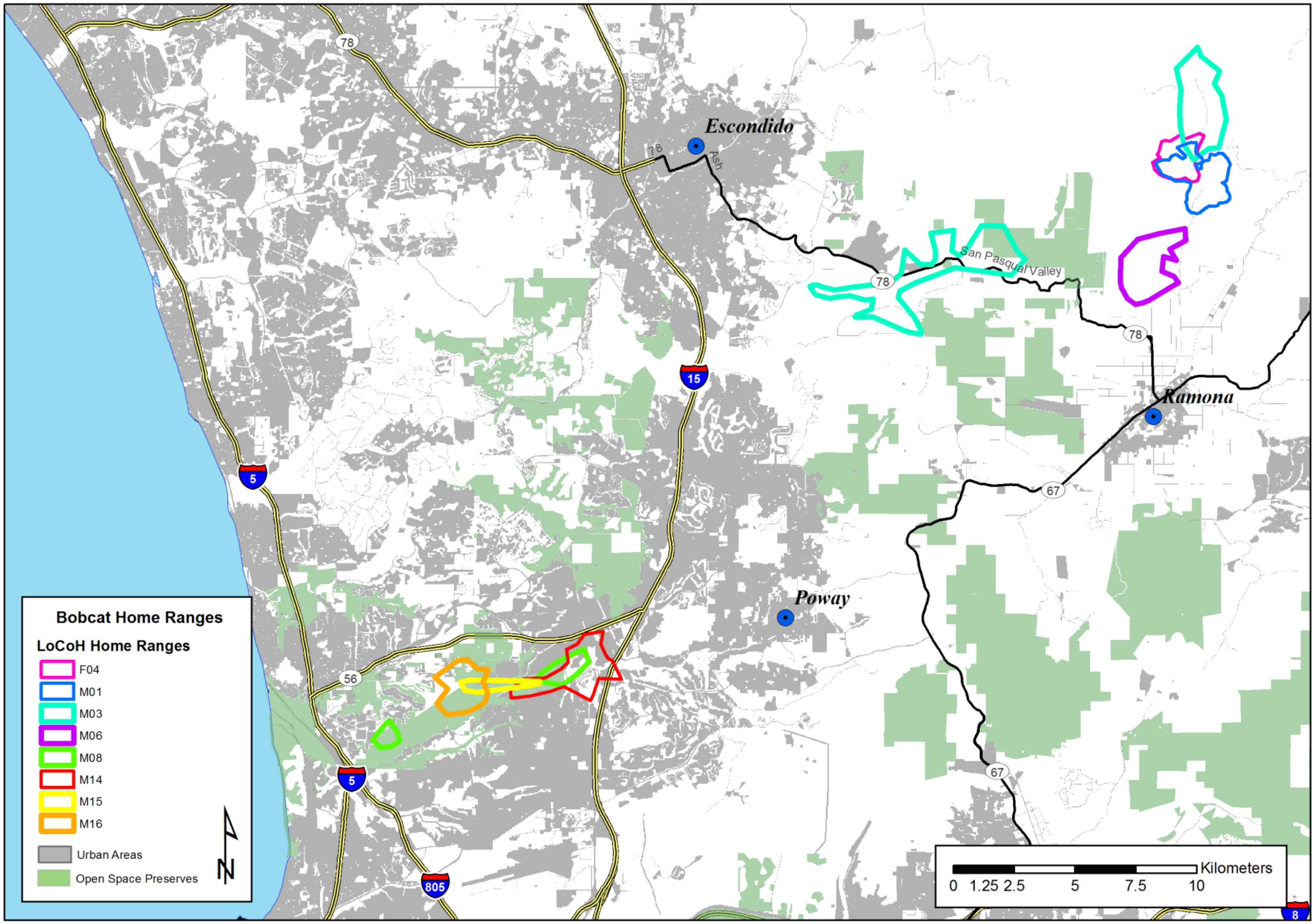

Figure 6. Local Convex Hull (LoCoH) home ranges for all bobcats with GPS collar data retrieved (n = 8). Home ranges are shown with respect to open space preserve boundaries (in green), and areas of urban development (in gray).

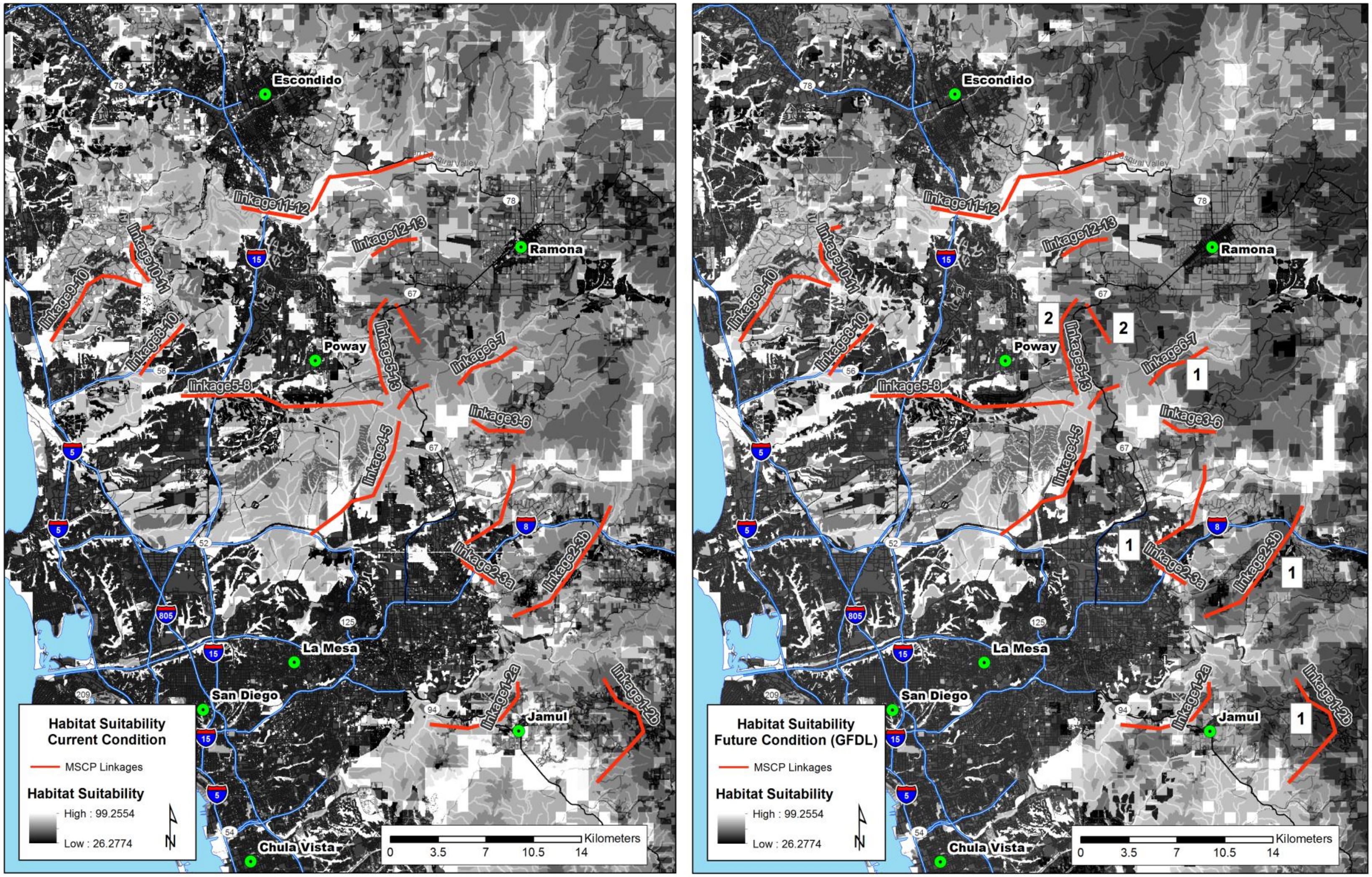

Figure 7. Habitat suitability for the MSCP area under current climate and land use conditions (left panel), and under future climate scenario GFDL and 2050 planned land use conditions (right panel). Lighter areas indicate high habitat suitability. Putative linkage areas are identified by red lines. Numbered squares in right hand panel indicate locations with decreased habitat suitability: 1) due to habitat alteration; 2) due to habitat alteration and roads.

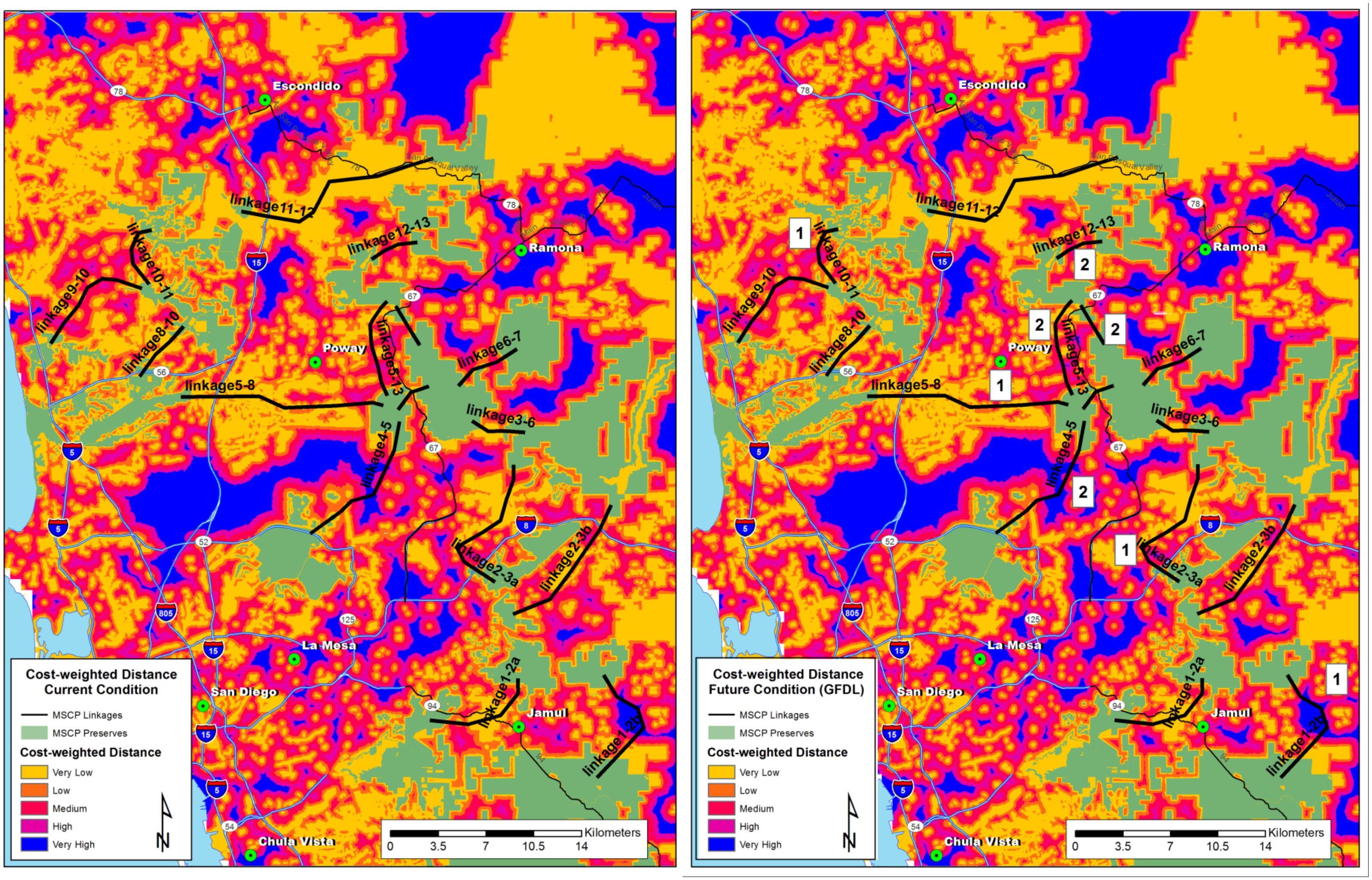

Figure 8. Landscape connectivity assessed by cost-weighted distance for the MSCP area under current climate and land use conditions (left panel), and under future climate scenario GFDL and 2050 planned land use conditions (right panel). Warmer colors indicate areas of lowest effective distance, increasing to highest distances in cooler colors. Putative linkages are identified by black lines. Numbered squares in right hand panel indicate locations with decreased connectivity: 1) due to habitat alteration/development; 2) due to habitat alteration and roads.

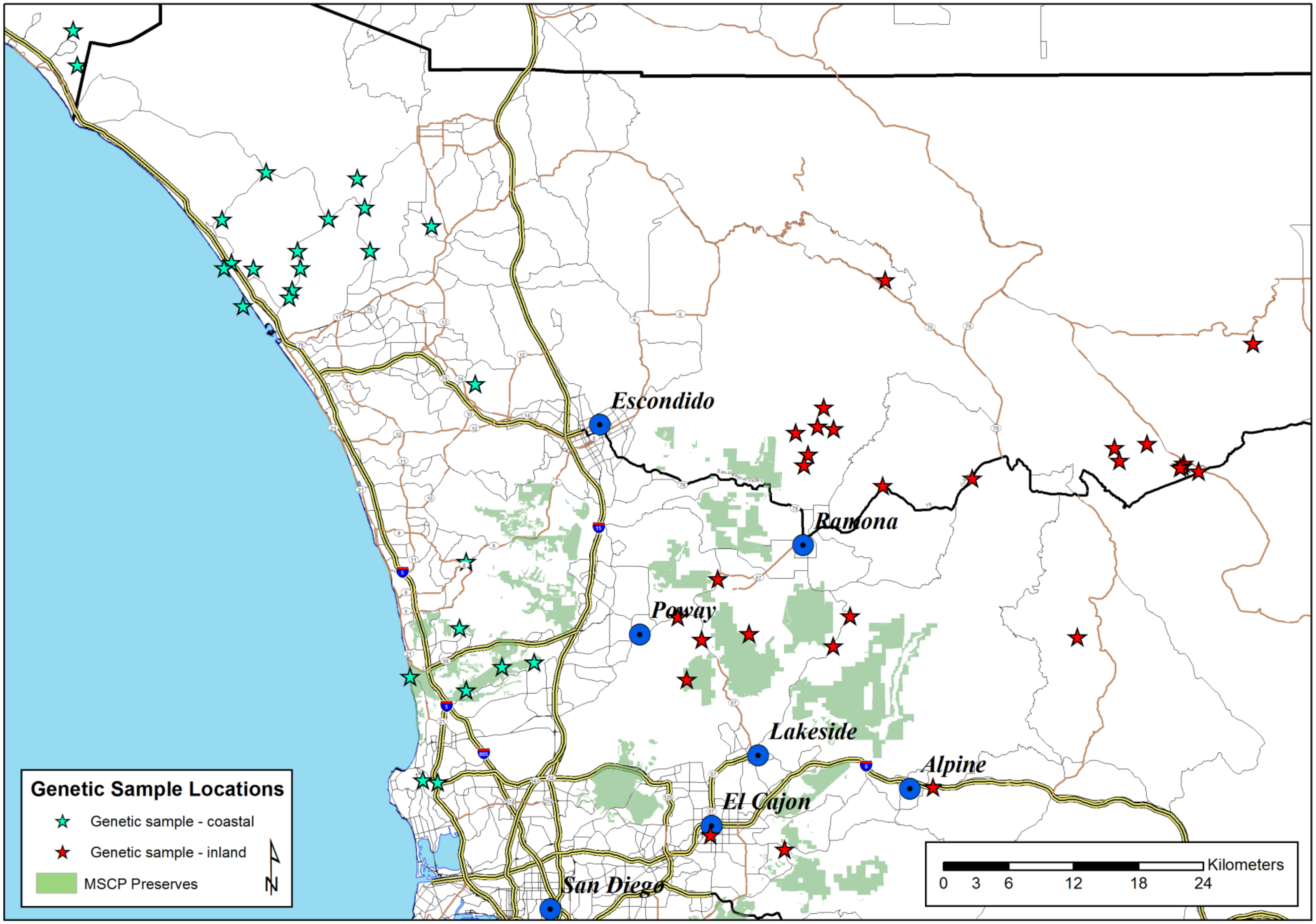

Figure 9. Map of sampling locations for genetic data analyzed (n = 62) and putative subpopulation assignment. Individuals assigned to the coastal population (west of I-15 freeway) are in turquoise, and those in the inland population (east of I-15) are in red.

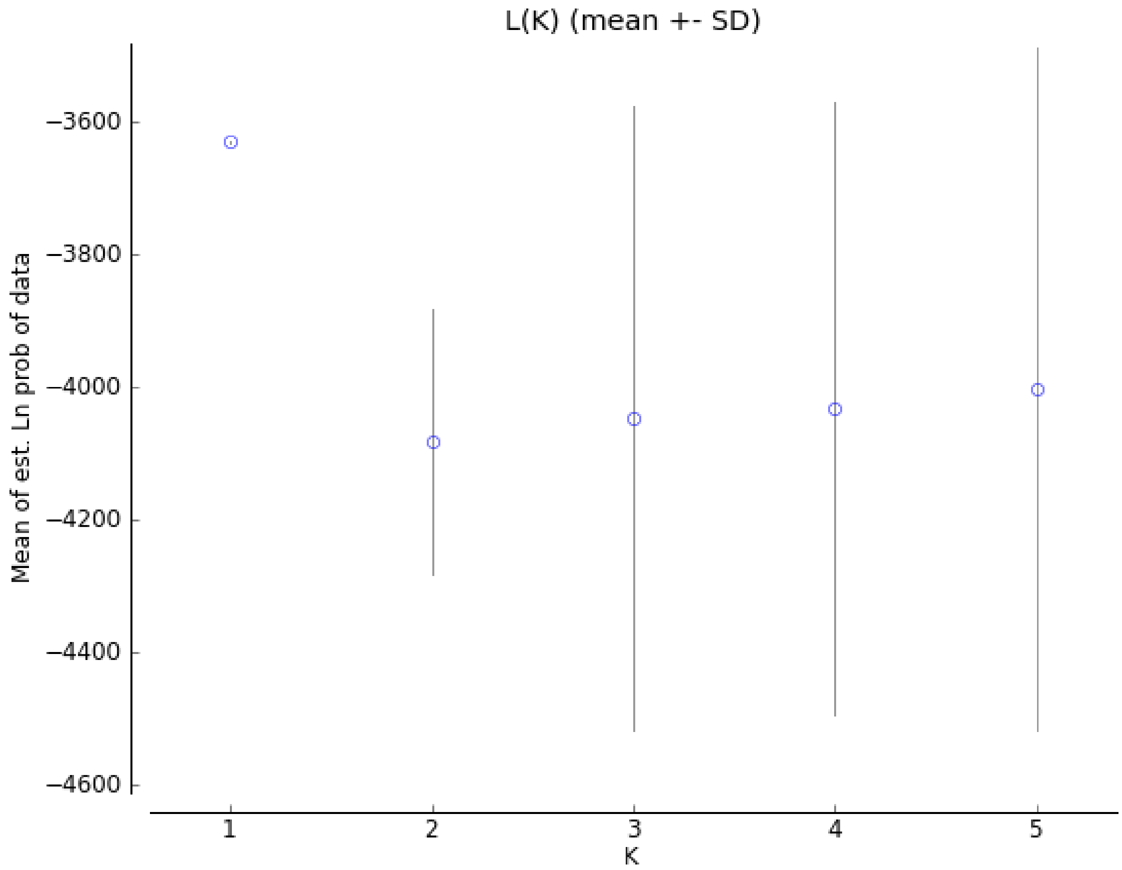

Figure 10. Mean estimated (± SE) probability of the number (K = 1 to 5) of subpopulations of bobcats supported by STRUCTURE analysis. Results support identification of one, panmictic population.

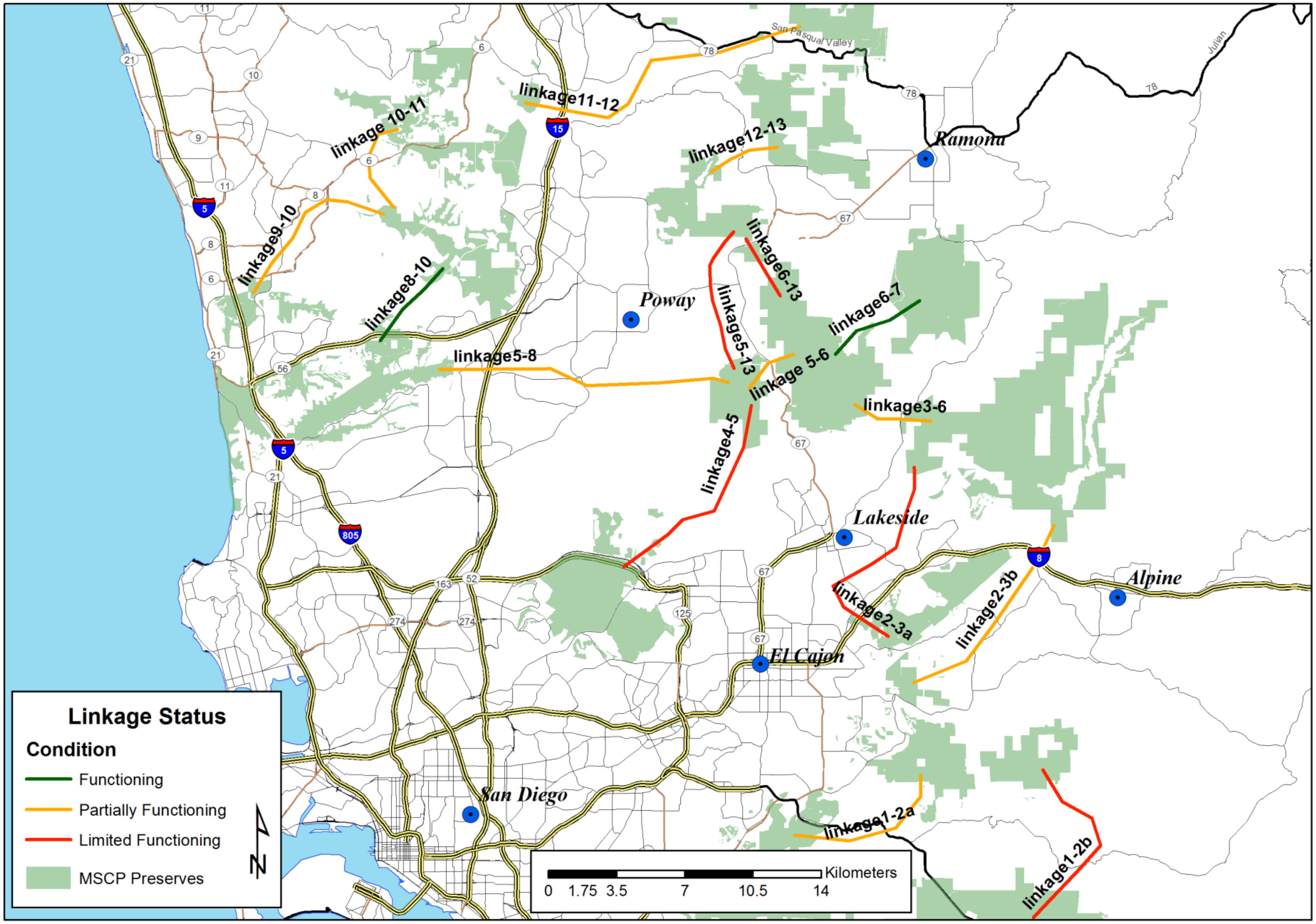

Figure 11. Linkage status map. Status was assessed based on empirical data and modeling results. Red indicates only limited linkage functioning, orange - partial functioning, and green represents functioning linkages.

Station ID	***Study Area***	***Site Type***	***Recreation***	***Camera***
56-AQ	Los Peñasquitos/SR56	Bridge	M	Cuddeback
56-BV	Los Peñasquitos/SR56	Bridge	L	Cuddeback
56-MC	Los Peñasquitos/SR56	Bridge	M	LTL Acorn
67-BO	SR67	Core	L	LTL Acorn
67-C1	SR67	Culvert	L	Cuddeback
67-C2	SR67	Culvert	L	LTL Acorn
67-C3	SR67	Culvert	L	LTL Acorn
67-C4	SR67	Culvert	L	Cuddeback
67-GR	SR67	Core	M	LTL Acorn
67-IM	SR67	Core	H	LTL Acorn
67-MW	SR67	Culvert	L	LTL Acorn
67-RC	SR67	Core	M	LTL Acorn
67-RG	SR67	Core	L	LTL Acorn
67-SPP	SR67	Tunnel	M	LTL Acorn
67-SV	SR67	Core	L	Cuddeback
67-UB	SR67	Linkage	L	LTL Acorn
78-BC	Pamo Valley/SR78	Core	M	LTL Acorn
78-BV	Pamo Valley/SR78	Bridge	L	Cuddeback
78-RC	Pamo Valley/SR78	Bridge	L	LTL Acorn
78-SMC	Pamo Valley/SR78	Bridge	L	Cuddeback
78-SPE	Pamo Valley/SR78	Tunnel	L	LTL Acorn
78-YC	Pamo Valley/SR78	Bridge	H	Cuddeback
78-YCR	Pamo Valley/SR78	Linkage	L	LTL Acorn
PQ-15	Los Peñasquitos/SR56	Bridge	M	Cuddeback
PQ-805	Los Peñasquitos/SR56	Bridge	M	Cuddeback
PQ-BM	Los Peñasquitos/SR56	Bridge	H	LTL Acorn
PQ-CC	Los Peñasquitos/SR56	Core	H	Cuddeback
PQ-CCR	Los Peñasquitos/SR56	Tunnel	H	LTL Acorn
PQ-CM	Los Peñasquitos/SR56	Bridge	M	LTL Acorn
PQ-CV	Los Peñasquitos/SR56	Bridge	L	LTL Acorn
PQ-SC	Los Peñasquitos/SR56	Core	H	Cuddeback
PQ-SL	Los Peñasquitos/SR56	Bridge	H	Cuddeback
PV-LSY	Pamo Valley/SR78	Core	M	LTL Acorn
PV-LUS	Pamo Valley/SR78	Core	L	LTL Acorn
PV-ORR	Pamo Valley/SR78	Core	L	Cuddeback
PV-SYC	Pamo Valley/SR78	Core	L	Cuddeback

Table 1. Remote camera location identifiers and designation by study area, site type, recreation level, and camera type.

Primer	*Species*	*Repeat*	*Size range*	*Number of alleles*	*Ho*	*He*	*PIC*	*Reference*
BCD8T	Bobcat	tetra	156-180	5	0.26	0.35	0.33	1
BCE5T	Bobcat	tetra	256-280	6	0.77	0.71	0.66	1
BCG8T	Bobcat	di	275-299	12	0.89	0.85	0.83	1
FCA126	Domestic cat	di	132-154	7	0.70	0.80	0.76	2
FCA132	Domestic cat	di	182-194	7	0.79	0.83	0.80	2
FCA149	Domestic cat	di	133-149	8	0.74	0.77	0.73	2
FCA23	Domestic cat	di	144-158	6	0.79	0.73	0.69	2
FCA26	Domestic cat	di	138-166	13	0.82	0.87	0.84	2
FCA31	Domestic cat	di	237-255	9	0.79	0.87	0.84	2
FCA35	Domestic cat	di	120-150	16	0.80	0.91	0.89	2
FCA391	Domestic cat	tetra	210-236	5	0.55	0.67	0.61	2
FCA43	Domestic cat	di	131-139	5	0.74	0.74	0.69	2
FCA45	Domestic cat	di	147-173	7	0.65	0.83	0.79	2
FCA559	Domestic cat	tetra	115-135	5	0.70	0.64	0.57	2
FCA742	Domestic cat	tetra	104-134	5	0.62	0.71	0.65	3
FCA77	Domestic cat	di	130-140	8	0.63	0.73	0.69	2
FCA8	Domestic cat	di	140-156	9	0.81	0.74	0.71	2
FCA82	Domestic cat	di	246-266	10	0.90	0.85	0.83	2
FCA90	Domestic cat	di	108-126	7	0.66	0.77	0.73	2
FCA96	Domestic cat	di	189-209	10	0.71	0.84	0.82	2
Lc110	Lynx	di	92-104	7	0.51	0.60	0.55	4
Lc111	Lynx	di	157-217	7	0.79	0.76	0.72	4

Table 2. Locus name, species developed from, repeat motif of microsatellite markers used in genetic analysis. Size range, number of alleles, expected and observed heterozygosity and PIC were based on analysis of 62 bobcat samples. Reference indicates initial publication of markers by: 1. Faircloth *et al.* 2005; 2. Menotti-Raymond *et al.* 1999; 3. Menotti-Raymond *et al.* 2005; Carmichael *et al.* 2000.

Individual	***Capture Date***	***Status***	***Location***	***Comments***
M01	5/13/2009	Collared	Pamo Valley	
M02	1/2/2010	Collared	Pamo Valley	Collar not retrieved
M03	8/22/2010	Collared	Pamo Valley	
F04	9/23/2010	Collared	Pamo Valley	Mortality – suspected puma
F05	10/13/2010	Collared	Pamo Valley	Collar failure
M06	11/9/2010	Collared	Pamo Valley	
M07	10/15/2011	Collared	Los Peñasquitos	Collar not retrieved
M08	10/27/2011	Collared	Los Peñasquitos	Mortality – suspected coyote or domestic dog
M09	10/29/2011	Collared	Los Peñasquitos	Collar not retrieved
M10*	11/29/2011	Collared	FFAWC rehab release – Black Mtn.	Animal missing
F11*	11/22/2011	Ear tagged	FFAWC rehab release - Tenaja	
M12*	11/29/2011	Collared	FFAWC rehab release – Los Peñasquitos	Attempting to recapture
F13*	11/22/2011	Ear tagged	FFAWC rehab release – Torrey Pines	
M14	1/1/2012	Collared	Los Peñasquitos	
M15	1/7/2012	Collared	Los Peñasquitos	
M16	1/8/2012	Collared	Los Peñasquitos	
M17	2/4/2012	Collared	Goodan Ranch	Collar being inspected for data retrieval
F18	2/12/2012	Collared	Boulder Oaks Preserve	Animal missing
M20	3/3/2012	Collared	Boulder Oaks Preserve	Rehabbed for mange first; Attempting recapture

Table 3. Data for all bobcats sampled (n = 19), including individual identifier, date of capture or processing*, tracking status (collar or ear tag only), location of capture, and notes on animal or collar fate. *Four animals were rehabilitated animals from the Fund for Animals Wildlife Center in Ramona. Only two of those animals were collared prior to release back into the wild.

Animal	Urban	Altered	Natural	HR Area (km^2)
M01	1%	8%	92%	4.79
M03a	5%	42%	54%	10.12
M03b	1%	31%	68%	6.37
F04	1%	1%	98%	2.79
M06	0%	9%	91%	5.13
M08a	3%	0%	97%	0.72
M08b	31%	7%	61%	1.55
M14	40%	5%	55%	5.26
M15	14%	0%	86%	1.05
M16	8%	0%	92%	3.43

Table 4. LoCoH home range information for each bobcat with GPS collar data available. Data include total home range area (km^2) and percentage of home range in land use categories urban, altered, and natural.

Variable	*Coefficient*	*SE*	*p-value*
Fire			
Fire return interval departure (6 classes)			
-999	1.323	0.837	0.114
-3	0.518	0.838	0.537
-2	0.529	0.837	0.528
-1	1.598	0.84	0.057
1	0.987	0.841	0.241
2	1.608	0.84	0.056
Habitat			
Herbaceous	0.492	0.057	0
Shrubland	-0.521	0.039	0
Hardwood	0.656	0.067	0
Agricultural	0.089	0.087	0.307
Urban	-0.205	0.077	0.008
Water/Wetland	3.188	0.397	0
Distance to water/100	-0.237	0.013	0
Land Use			
Urban (LU URB)	-1.179	0.119	0
Altered	0.137	0.062	0.027
Natural	0.186	0.055	0.001
Distance to local road/100	-0.042	0.005	0
Distance to major road/100	0.004	0.001	0
Topography			
Elevation/100	-0.322	0.015	0

Table 5. Univariate logistic regression results for each model variable from bobcat telemetry point modeling.

Model	*AIC_c*	*ΔAIC*	*$AICw_i$*
All Habitat, All Land Use, and Topography (HERB + HDW + WAT + SHB + URB + DIST WAT + LU URB + MAJRD + LOCRD + ELEV)	**15520.22**	**0**	**>0.999**
Avoided Land Use and Topography (LU URB + ELEV)	15672.69	152	<0.001
All Habitat, Avoided Land Use and Topography (HERB + HDW + WAT + SHB + URB + DIST WAT + LU URB + ELEV)	15995.97	476	<0.001
All Habitat and Topography (HERB + HDW + WAT + SHB + URB + DIST WAT + ELEV)	16114.3	594	<0.001
Topography (ELEV)	16316	796	<0.001
All Habitat and All Land Use (HERB + HDW + WAT + SHB + URB + DIST WAT + LU URB + NAT + MAJRD + LOCRD)	16517.46	997	<0.001
All Vegetation and Water (HERB + HDW + WAT + SHB + URB + DIST WAT)	16621.26	1101	<0.001
All Vegetation (HERB + HDW + WAT + SHB + URB)	16863.75	1344	<0.001
Avoided Vegetation (SHB + URB)	17013.01	1493	<0.001
Selected Vegetation (HERB + HDW + WAT)	17044.07	1524	<0.001
Avoided Land Use and Roads (URB + MAJRD + LOCRD)	17127.4	1607	<0.001
All Land Use and Roads (LU URB + NAT + MAJRD + LOCRD)	17128.84	1609	<0.001
All Land Use (URB + NAT)	17263.78	1744	<0.001
Avoided Land Use (LU URB)	17265.31	1745	<0.001
Selected Land Use (NAT)	17370.26	1850	<0.001

Table 6. Models of bobcat presence with regard to landscape variables, ranked by Akaike's information criteria for small samples (AIC_c) with ΔAIC, and model weights $AICw_i$. Variables for each model can be found in Table 5. Bold indicates model with greatest support.

Effect	*Coefficient*	*Odds ratio*	*95% confidence limit odds ratio*	
Intercept	1.391			
HERB	-0.334	0.716	0.503	1.018
HDW	-0.001	0.999	0.850	1.174
WAT	**2.031**	**7.624**	**2.947**	**19.719**
SHB	**-0.566**	**0.568**	**0.335**	**0.963**
URB	0.064	1.066	0.385	2.951
DISTWAT	-0.062	0.940	0.788	1.120
LU_URB	**-1.323**	**0.266**	**0.160**	**0.444**
LOCRD	**0.073**	**1.076**	**1.013**	**1.144**
MAJRD	**0.034**	**1.035**	**1.018**	**1.051**
ELEV	**-0.921**	**0.398**	**0.281**	**0.565**

Table 7. Beta coefficients, odds ratios, and 95% confidence limits for odds ratios for variables in the final selected GLMM. Bold indicates variables with the greatest influence on predictions of bobcat presence.

Land Cover		*Elevation*		*Distance to Road*		*Distance to Water*		*Habitat*	
Class	*Score*	*Class*	*Score*	*Class*	*Score*	*Class*	*Score*	*Class*	*Score*
Urban	20	<200 m	100	20 m	20	20 m	100	Wetland	100
Altered	50	200 - 400 m	80	40 m	40	40 m	80	Altered	50
Natural	100	400 - 600 m	50	> 40 m	100	60 m	60	Grassland	60
Water	80	> 600 m	30			>60m	40	Riparian	60
								Shrub	30
								Forest	50
								Other	40
Weight	0.3		0.2		0.1		0.1		0.3

Table 8. Assigned habitat suitability values based on empirical results from univariate and GLMM modeling of bobcat habitat selection. Bottom row indicates weight assigned to each variable type, based on strength of response in models.

Name	Condition	Primary Concerns	Data Used for Assessment
Linkage 6-7	Functioning	Future habitat alteration	Cameras, Habitat suitability and connectivity modeling
Linkage 8-10	Functioning		Cameras, Telemetry, Habitat suitability and connectivity modeling
Linkage 1-2a	Partially Functioning	Road crossing and altered habitat	Habitat suitability and connectivity modeling
Linkage 2-3b	Partially Functioning	Road crossing and altered habitat	Habitat suitability and connectivity modeling
Linkage 5-6	Partially Functioning	Road crossing and altered habitat	Cameras, Roadkill, Habitat suitability and connectivity models
Linkage 5-8	Partially Functioning	Development/altered habitat, secondary roads, total distance	Cameras, Telemetry, Habitat suitability and connectivity modeling
Linkage 9-10	Partially Functioning	Development/altered habitat, secondary roads	Habitat suitability and connectivity modeling
Linkage 10-11	Partially Functioning	Development/altered habitat, secondary roads	Habitat suitability and connectivity modeling
Linkage 11-12	Partially Functioning	Road crossing and altered habitat	Cameras, Telemetry, Habitat suitability and connectivity modeling
Linkage 12-13	Partially Functioning	Development/altered habitat, secondary roads	Habitat suitability and connectivity modeling
Linkage 3-6	Partially Functioning	Secondary roads	Roadkill, Habitat suitability and connectivity modeling
Linkage 1-2b	Limited Functioning	Road crossing and altered habitat	Habitat suitability and connectivity modeling
Linkage 2-3a	Limited Functioning	Road crossing and altered habitat	Habitat suitability and connectivity modeling
Linkage 4-5	Limited Functioning	Development/altered habitat, secondary roads, total distance	Habitat suitability and connectivity modeling
Linkage 6-13	Limited Functioning	Road crossing and altered habitat	Cameras, Habitat suitability and connectivity modeling
Linkage 5-13	Limited Functioning	Development/altered habitat, secondary roads	Cameras, Roadkill, Habitat suitability and connectivity modeling

Table 9. Assessment of linkage status across the MSCP preserve network, with primary concerns for connectivity.

APPENDIX A: HABITAT MODELING METHODOLOGY

For the habitat models developed from bobcat GPS collar data, we identified the proportional area of each of these types within a 30 meter buffer around each location point. We also calculated a distance to water variable (DIST WAT), measuring the Euclidian distance to blue line streams from the USGS National Hydrology Dataset stream layer. Land-use variables were developed from the Southern California Association of Government's (SCAG) land-use data layers, which were categorized into four groups of urban (URB), altered (LU ALT), natural (NAT) and water (LU WAT) and calculated as the proportional area within 30 meters of each point. Euclidian distances from major (DIST MAJRD) and local roads (DIST LOCRD) were also incorporated into the models, and were developed from the CalTrans TIGER data. Topographic data consisted of elevation data (ELEV) from digital elevation models. To assist in interpretation of model results, the distances to water, major and minor roads, and elevation were scaled by dividing each value by 100 m. The fire-return interval departure data is a measure of the shifting fire regime (meanCC FRI), which is a categorical variable with seven classes representing the condition class, or the degree of departure from the natural fire regime with respect to the fire-return interval (Hann and Bunnell 2001, Safford *et al.* 2011). For this last variable, increasingly negative values (-1 to -3) equate to areas that have burned more frequently than the natural fire-return interval (FRI) and are at increasing risk of type conversion. Increasing positive values (1 to 3) reflect areas that have not burned as often as expected when compared to historic FRI. The remaining category represents urban or altered areas that do not have the vegetative structure to carry fire and therefore, do not have a condition class or FRI.

We ran binary generalized-linear-mixed models (GLMM) of bobcat presences and pseudoabsences (Pearce and Boyce 2006, Aarts *et al.* 2012) using the PROC GLIMMIX function in SAS. GLMMs are a robust tool to analyze habitat-selection with telemetry data because the random effects resulting from serial correlation in location data from each individual can be estimated to allow for more accurate and appropriate analysis of population-level effects (Gillies *et al.* 2006, Bolker *et al.* 2009, Burdett 2010). To create binary data, we generated pseudoabsences in proportion to the number of presences for each individual within the 100% MCP using the Geospatial Modelling Environment command to generate stratified random points (Beyer 2012). All variables were first tested using binary logistic regression to determine which were significant on their own and whether the response to each indicated selection or avoidance, which was then factored into GLMM development. Models calculated random effects with the random intercept method with an autoregressive covariance structure and the Huber-White Sandwich variance estimator to calculate empirical standard errors that are robust to the lack of independence in the telemetry data due to both the spatial autocorrelation of locations and correlation of points from each bobcat (Clark and Stevens 2008). GLMMs were fit using the random intercept method and Laplace likelihood approximation, which is a less biased method for fitting GLMMs than pseudo-likelihoods (Bolker *et al.* 2009). We created a correlation matrix of predictor variables with Spearman rank coefficients to determine which variables were correlated at $r > |0.6|$ and these variables were run separately to avoid multicollinearity.

We took a stepwise approach to determine which variables in the GLMM model best explained bobcat response to landscape features. In this stepwise approach, all significant, uncorrelated variables were entered into the model according to the variable categories described above (vegetation, land-use, terrain, and fire). We based model selection on an information theoretic approach using the small sample correction of Akaike's Information Criteria (AIC_c)

and compared overall differences between models with ΔAIC to determine which model best fit the data. We also calculated model weights, AICw_i, or the likelihood of a model, according to Burnham and Anderson (2002). To better understand which variables in the best models were influencing patterns of bobcat presence, we recorded the odds ratios for each variable, as well as the 95% confidence limits for those odds ratios. Odds ratios with confidence limits that bound one are considered less influential in the model.

APPENDIX B: HABITAT SUITABILITY AND CONNECTIVITY MODELING METHODOLOGY

The development of bobcat habitat suitability models and the cost-weighted connectivity assessment were based on the empirical data from our habitat use modeling and developed using raster datasets in GIS. To ensure model comparability, we determined which environmental rasters to use based on whether it included one or more variables that contributed to a significant improvement in predicting bobcat presence in the selected GLMM. For bobcats, habitat suitability was based on values assigned to rasters of habitat type, land-use, Euclidian distance from roads and water, and elevation. After assigning habitat suitability values within each category, we then needed to combine all rasters into a single landscape permeability raster by using the weighted geometric mean, which is recommended over the arithmetic mean (Beier *et al.* 2011). We weighted each raster type according to the relative influence in the models, so that the total of the weights for all rasters would equal 1.0. Habitat suitability was assessed at a 30-m pixel scale and clipped to the region where we had collected telemetry locations for bobcats.

After calculating habitat suitability, which is assumed to represent permeability of the landscape, we then used the inverse of this value to reflect landscape resistance (Singleton *et al.* 2002). Given that 100 was the maximum habitat suitability value, we subtracted the calculated habitat suitability value of each pixel from this maximum to get the complement, resistance. This resistance layer was then used as the cost value to assess the effective distance for each species to move between protected lands using the cost-weighted distance tool from the GIS Spatial Analyst toolbox. Because bobcat movement in this region is likely concentrated between areas of protected, natural lands, we used a state-wide database of conserved lands, California Protected Areas Database (CPAD 1.8, 2012) as the source features between which we calculated the cost-weighted distance. The output of this analysis represents the effective distance, or lowest cost of traveling between source locations, or in this case, protected lands.

APPENDIX C: OCCUPANCY MODEL SELECTION AND RESULTS

To eliminate modeling issues associated with missing data values, the camera sampling period analyzed in Program PRESENCE (Hines 2010) included 18 of the sampling periods, ranging from January 11, 2012 to September 19, 2012. To determine the effects of survey covariates on detection of bobcats, we first ran models with no covariates and tested for the effect of camera type and wet/dry season on probability of detection and determined that only cameras (estimate ± SE; 1.308 ± 0.229) appeared to be an important covariate for detection probability, with a lower detection probability resulting from the use of the older Cuddeback Expert model cameras, which reduced detection rates by approximately half (0.3509 compared to 0.6667). For all subsequent occupancy models, we used this detection model. We ran numerous models of occupancy testing for the effects of site type (core, bridge, culvert, or any linkage), recreation (low and high), land use, habitat type, elevation, distance to major and local roads, and distance to water on bobcat occupancy across all stations. No single model outperformed the others, and therefore, the top seven ranked models were averaged (Table C1). From our modeling efforts, several important covariates emerged for predicting bobcat occupancy at camera stations: lower occupancy rates at stations placed at bridge crossings (-2.193 ± 1.240), lower rates at stations with a greater proportion of altered habitat (-1.759 ± 1.150), and lower occupancy at stations within putative linkage zones (-1.38 ± 1.220), compared with core conserved lands. Although two other variables were identified in the top-ranked occupancy models, neither was significant. These covariates were high recreation (-0.576 ± 1.08) with lower occupancy at high recreation stations, and elevation (0.005 ± 0.010) with higher occupancy rates at the higher elevation stations in the inland study area.

Model	*AIC*	*ΔAIC*	*AICw$_i$*	*Model likelihood*	*Parameters*
Psi (bridge) , p (camera)	538.04	0.00	0.3203	1.0000	4
Psi (altered habitat), p (camera)	539.55	1.51	0.1505	0.4700	4
Psi (bridge+altered habitat), p (camera)	539.71	1.67	0.1390	0.4339	5
Psi (.), p (camera)	539.77	1.73	0.1348	0.4211	3
Psi (linkage area), p (camera)	540.29	2.25	0.1040	0.3247	4
Psi (elevation), p (camera)	540.49	2.45	0.0941	0.2938	4
Psi (high recreation), p (camera)	541.48	3.44	0.0573	0.1791	4
Psi (.), p (.)	572.51	34.47	0.0000	0.0000	2

Table C1. Top occupancy models ranked by Akaike's information criteria with ΔAIC, and model weights AICw_i. As no model clearly outperformed the others, all models were included in model averaging of occupancy rates for each camera station. Covariates included were used to model detection rates (p), and occupancy rates (Psi).