DISSERTATION

EFFECTS OF OUTDOOR RECREATION ON WILDLIFE IN PROTECTED AREAS

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ABSTRACT

EFFECTS OF OUTDOOR RECREATION ON WILDLIFE IN PROTECTED AREAS

Biodiversity is undergoing dramatic declines worldwide. Protected areas are the primary strategy used to conserve biodiversity, but they are rarely completely free from threats that imperil ecological communities. The vast majority of protected areas are open to recreation and have a dual mission to conserve natural resources while providing access for outdoor recreation. Many protected areas receive high levels of recreational use, particularly those near large human populations. An increasing body of evidence shows that recreation can have negative effects on animals, but questions remain about the frequency, consistency, and magnitude of the effects of recreation.

To address these knowledge gaps, I conducted a global meta-analysis of the effects of recreation on vertebrate richness and abundance. I reviewed and extracted data from 34 articles that compared vertebrate richness and abundance at sites with low and high levels of recreational use, and estimated that vertebrate richness and abundance are lower in association with higher levels of recreation in over two-thirds (70%) of cases. I observed a moderate negative group-level effect of recreation on bird and mammal abundance, but the group-level effect on fish and reptiles was not significant. Effects were stronger for carnivores and herbivores than for omnivores, and stronger for small-bodied birds and ground-nesting birds than larger and tree- and shrub-nesting birds. Terrestrial and non-motorized activities were associated with reduced vertebrate abundance, whereas aquatic and motorized activities were not.

While categorical comparisons between low and high levels of use can help establish whether recreation effects exist, managers who must plan and regulate recreational use of protected areas need to understand the levels of human activity that trigger animal responses. I assessed shifts in

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mammal habitat use and relative activity over a broad gradient of human activity levels at 92 sampling points located in 14 nature reserves in San Diego County, California, USA. I used camera traps to measure both human and mammal use of reserves, and I modeled mammal habitat use (occupancy and detection probability) and relative activity rates (hours per day with detections) in association with daily counts of total human activity, pedestrians, and cyclists. Human activity was associated with declines in habitat use of several mammal species, particularly bobcats and mule deer, though the strength of these effects was less than the effects of covariates characterizing habitat, topography, and development. Although human activity may not often extirpate mammal species from urban habitat fragments, it can reduce habitat suitability. In particular, bobcat, gray fox, mule deer, and raccoon were less active in areas with higher levels of human activity.

Recreation has negative consequences for many animal species, but its effects on reptiles are largely unknown. I evaluated the effects of non-motorized, non-consumptive recreation on reptiles within urban protected areas in a fragmented landscape in coastal southern California, USA. I surveyed for lizards and snakes, quantified human activity, and modeled species richness, community composition, and occupancy as a factor of human activity along with other variables known to affect reptile distributions. I observed a decline in species richness in association with human activity, which was driven primarily by a decrease in lizard richness. The proportion of specialist species was not affected by human activity. Human activity was associated with a decline in occupancy of the common side-blotched lizard (*Uta stansburiana*), a slight but uncertain decline in occupancy of the orange-throated whiptail (*Aspidoscelis hyperythra*) and no relationship with western fence lizard (*Sceloporus occidentalis*) occupancy. Our study demonstrates that human activity can reduce the ability of urban protected areas to conserve diverse reptile communities.

My study demonstrates the importance of examining the effects of recreation across a wide gradient of human activity and across a broad suite of species to understand which species are sensitive to recreation, to what thresholds of disturbance they respond, and whether their response results in reduced activity, local extirpation, lower species richness, or a change in community composition. These results pose a challenge to natural resource management agencies who must balance recreation access with natural resource protection, and to conservation organizations that rely on outdoor recreation for public support and funding. I recommend that managers plan recreational access at a regional scale and include some areas that are closed to recreation to minimize trade-offs between recreation and species conservation.

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CHAPTER 1 : A META-ANALYSIS OF RECREATION EFFECTS ON VERTEBRATE SPECIES RICHNESS AND ABUNDANCE¹

Summary

Most protected areas globally have a dual mission to conserve natural resources and provide access for outdoor recreation or ecotourism, yet questions remain about the ecological effects of recreation. We conducted a global meta-analysis of the effects of recreation on vertebrate richness and abundance. We estimated that vertebrate richness (n=15 articles) and abundance (n=32) are lower in association with higher levels of recreation in over two-thirds (70%) of cases. We observed a moderate negative group-level effect of recreation on bird and mammal abundance, but the grouplevel effect on fish and reptiles was not significant. Effects were stronger for carnivores and herbivores than for omnivores, and stronger for small-bodied birds and ground-nesting birds than larger and tree- and shrub-nesting birds. Terrestrial activities were associated with reduced vertebrate abundance, whereas aquatic activities were not. Both motorized and non-motorized activities were associated with reduced vertebrate abundance, but the effect for motorized activities was uncertain due to small sample size. These results pose a challenge to natural resource management agencies who must balance recreation access with natural resource protection, and to conservation organizations that rely on outdoor recreation for public support and funding. We recommend that managers plan recreational access at a regional scale and include some areas that are closed to recreation to minimize trade-offs between recreation and animal conservation.

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Introduction

Outdoor recreation is prevalent in protected areas, recently estimated at 8 billion visits per year globally (Balmford et al. 2015). Increasingly, research has demonstrated that recreation can have damaging effects on ecological communities (Monz et al. 2013; Sato et al. 2013; Larson et al. 2016). Though recreation may not be the most severe threat facing global biodiversity, it often occurs in places established to protect species and therefore could have disproportionate impacts. At the same time, nature-based recreation is vital for human health and for building connections with nature that can help foster pro-environmental behaviors (Cooper et al. 2015). For these reasons, we need to address the challenges recreation poses to protected area management.

Short-term responses of animals to even quiet recreation can include increased physiological stress (Arlettaz et al. 2007) and time spent in flight and vigilance behaviors (Naylor et al. 2009). Though habituation to human disturbance can dampen behavioral responses of animals to human presence (Baudains & Lloyd 2007), it may also increase their vulnerability to predation (Geffory et al. 2015) or conflicts with humans (Bejder et al. 2009). Over time, animals may alter their spatial and temporal habitat use to avoid disturbance (Lesmerises et al. 2018), reducing habitat suitability in areas used by recreationists. Elevated stress, energy expenditures, and shifts in activity patterns at the individual level can scale up and affect population and community measures such as abundance or density (Bötsch et al. 2017), species richness (Reed & Merenlender 2008), and community composition (Kangas et al. 2010).

However, findings vary widely among individual studies that focus on a single ecosystem, taxon, or type of impact, including some recent studies that have observed limited effects of recreation on animal communities (Kays et al. 2016; Reilly et al. 2017). Accordingly, questions remain about the magnitude of the effects of recreation and their consistency across taxa and scale. A systematic review focused on frequency of recreation effects revealed that although 93% of

articles documented at least one effect of recreation on wildlife, there was considerable variation among taxonomic groups and types of activities (Larson et al. 2016).

Meta-analysis is increasingly popular in ecology and conservation as a tool to synthesize evidence across studies and explore large-scale patterns. Meta-analyses can combine data from similar studies to estimate overall effect sizes while considering sources of heterogeneity such as differences in methods or study taxa (Haddaway 2015). Previous meta-analyses on recreation effects on wildlife have focused on winter recreation (Sato et al. 2013) and behavioral and physiological measures (Bateman & Fleming 2017). Our analysis complements and builds upon these prior studies by encompassing many types of recreation and focusing on responses at the population and community levels, where decisions about animal conservation and management are typically made. More specifically, we examine differences in vertebrate richness and abundance in response to outdoor recreation. We ask if there are differences among classes of vertebrates, species characteristics, types of recreation, and temporal and spatial patterns of recreational use. Managers of protected areas are increasingly aware of the potential for recreation to impact biodiversity, but little information is available to help them evaluate management options. Examining the findings of individual studies in a synthetic fashion, we provide broader conclusions about recreation effects that can help inform management decisions to reduce impacts from recreational use of protected areas.

Methods

Article selection

Our search protocol, fully described in Larson et al. (2016), was designed for a highsensitivity, low-specificity search (Pullin & Stewart 2006). We used the keywords "tourism" and "recreation" to systematically search for articles published through March 2018 within a list of 196 journals drawn from five Web of Science categories (biodiversity conservation, ecology, zoology, ornithology, and behavioral sciences; Appendix 1.1). Since we relied on the journal category feature within Web of Science to narrow the scope of our search, we did not replicate the search in additional databases or gray literature. We screened titles and abstracts to remove clearly irrelevant articles, then reviewed full-text articles and selected those that met the following inclusion criteria: 1) articles estimated species richness and/or abundance of at least one animal species; 2) articles reported species richness and/or abundance estimates at two or more categorical levels of nonconsumptive recreation while other site characteristics were similar; 3) articles included sufficient data (in results, figures, or supplemental materials) to calculate effect sizes (Fig. 1.1). We define "abundance" to include indices of relative abundance or activity levels, such as detection frequencies of animals or sign. The second criterion ensured that studies had similar designs that compared recreation effects between categorical levels of use (e.g., sites with relatively low and high levels of recreation), while other site characteristics (e.g., habitat, geographic location) did not differ substantially (as assumed or measured by the study authors). While studies measuring recreation as a continuous variable are useful for understanding effects of recreation, they were difficult to include in meta-analyses because authors frequently analyzed such data with multivariate models (i.e., recreation variables along with covariates), meaning that the reported effect of recreation was conditional on the effects of covariates. We therefore excluded these studies from our analysis. The second criterion also filtered out studies examining consumptive forms of recreation such as hunting, fishing, and collecting.

Data extraction

We extracted pairs of estimates ("comparisons") of vertebrate richness or abundance at low and high levels of recreation from each included article. Many articles contained data for multiple species or temporal and spatial scales, which we retained as separate comparisons in the database. For each comparison, we recorded the focal taxa, type of recreation activity (aquatic, winter, or terrestrial; motorized or non-motorized), and type of response variable (species richness or abundance; Table 1.1). We recorded whether the recreation disturbance was a temporal difference, defined as a comparison between recreation levels at the same site(s) at different times, or a spatial difference, defined as a comparison between recreation levels at different sites at the same time. We categorized the recreation disturbance as "novel" to the study system if it differed from the baseline recreation level based on the authors' descriptions (e.g., an experimental hiking treatment in a forest closed to recreation); otherwise, the disturbance was labeled "ongoing." From external databases, we collected the average body mass, diet category, and nesting behavior (for birds) of each species (Jones et al. 2009; Parr et al. 2014; Cornell Lab of Ornithology 2018; Myers et al. 2018). We then extracted the means, standard deviations, and sample sizes of species richness or abundance estimates at low and high recreation levels from the text, supplemental materials, or figures using an online digitization tool (Rohatgi 2017). We used data from the lowest taxonomic grouping available.

We pooled data to increase consistency among articles, including species richness and abundance estimates from individual study sites or sampling seasons within each article. When measurements were taken multiple times before or after a recreation 'treatment' (n=1 article), we used only the time points closest to the treatment to increase similarity among comparisons. Likewise, when articles (n=2) tested three or more levels of recreation (e.g., no, low, and high recreation sites), we used data from the lowest and highest impact sites. Finally, we pooled estimates from population segments such as age class or sex.

Statistical methods

For each comparison, we calculated hedges' g and its variance, a standardized difference of means commonly used as an effect size in meta-analysis (Koricheva et al. 2013). We used means and standard deviations when available; otherwise we converted test statistics such as chi-square or F-statistics to hedges' g. The units of g are standard deviations separating the means of the low and high recreation groups. Negative values of g indicate that vertebrate richness or abundance was greater with lower levels of recreation. We consider absolute values of $g \ge 0.8$ a large effect, 0.5 a moderate effect, and 0.2 a small effect (Cohen 1988). A hypothetical example in which a mean of 12 (SD=3) species were observed at 10 sites with recreation and 14 (SD=3) species were observed at 10 sites with recreation and 14 (SD=3) species were observed at 10 sites with negative effect. Confidence intervals (95%) accompany all hedges' g values; if these do not include zero, we conclude that the means of low and high recreation estimates are significantly different.

We built multi-level mixed-effects models (Nakagawa & Santos 2012) for richness and abundance to calculate the pooled effect size across all included studies, using the R package metafor (Viechtbauer 2010). In each model we included a random effect for article, because some articles contributed multiple data points from the same location and investigator team, and for species since we expected effects of recreation to differ among species. Effect sizes were weighted by inverse variances in all models (Koricheva et al. 2013). We did not separately model relative abundance measures (detections of animals or sign; n=88) from estimates derived from mark-recapture analyses (n=6) or from complete censuses of territories (n=4) because preliminary analysis showed little difference in pooled effect sizes among these measures. We then built models to explore how effect size varied with the following covariates: broad taxonomic group, recreation activity categories, novel or ongoing disturbance, recreation disturbance type (spatial or temporal), body mass, diet, and

nesting location. We present hedges' g estimates for each level of categorical covariates and regression coefficients ($\beta \pm SE$) for continuous covariates. To assess publication bias, which occurs when studies with statistically significant results are more likely to be published than those without (Nakagawa & Santos 2012), we visually inspected funnel plots and used Egger's regression to examine correlations between effect size and sampling variance (Egger et al. 1997). To assess our ability to detect effects of varying magnitudes, we conducted a retrospective power analysis using the mean sample sizes, effect sizes, and effect size variances from the included studies (Valentine et al. 2010).

Results

Our inclusion criteria filtered the initial list of 2612 articles down to 34, yielding 20 species richness comparisons and 103 abundance comparisons (Appendices 1.2-1.4). Birds were well-represented, with 45 comparisons (37% of 123 total) on 20 species from 15 articles (44% of 34 total). There were a similar number of comparisons for fish (47, or 38% of total) on more species (28), but from fewer articles (6, or 18% of total). Mammals had 27 comparisons (22% of total) on 16 species from 10 articles (29% of total). Reptiles were poorly represented, with 4 comparisons (3% of total) on 3 species from 4 articles (12% of total). There were no articles on amphibians included in the dataset. Across all comparisons for which diet type could be specified, 70% measured responses of carnivores or insectivores, 17% omnivores, and 13% herbivores. For bird comparisons for which nesting behavior could be specified, 50% measured responses of tree-nesters, 42% ground-nesters, and 8% shrub-nesters. Most comparisons assessed responses to terrestrial (59%) or aquatic (38%) recreation activities, with few (2%) assessing responses to winter recreation. Nearly all comparisons focused on non-motorized (97%) rather than motorized (3%) recreation. Most comparisons were

spatial (83%) rather than temporal (17%) and investigated recreation disturbance that was not novel to the system (87%) rather than novel (13%).

We found a moderate negative effect of recreation on vertebrate richness (hedges' g [95% CI]=-0.58 [-1.01, -0.15]; Fig. 1.2a) and a small to moderate negative effect on abundance (-0.45 [-0.72, -0.18]; Fig 1.2b). Retrospective power analysis showed that we could detect a moderate effect on richness with power of 0.64 and on abundance with power of 0.77. Egger's regressions were non-significant, suggesting little evidence of publication bias (richness: z=-1.62, p=0.1; abundance: z=-0.73, p=0.47).

Taxonomic differences and species traits

Effect sizes were large and negative for bird (-0.89 [-1.5, -0.28]; Fig. 1.2a) and mammal (-0.88 [-1.78, 0.01]) richness. Fish richness was similar at low and high recreation levels (-0.02 [-0.69, 0.66]). Insufficient data precluded separate analyses of differences in reptile richness. We observed a moderate negative effect of recreation on bird (-0.58 [-0.97, -0.19]; Fig. 1.2b) and mammal (-0.74 [-1.22, -0.27]) abundance, but no differences in fish (0.1 [-0.48, 0.68]) or reptile (-0.18 [-1.11, 0.75]) abundance between recreation levels.

Bird body mass was positively related to hedges' g for abundance, meaning that small bird abundance was more strongly reduced in association with high recreation than the abundance of larger birds ($\beta \pm SE = 0.36 \pm 0.17$, p=0.04). There was no relationship between mammal body mass and hedges' g for abundance ($\beta \pm SE = -0.08 \pm 0.09$, p=0.41). We observed a moderate negative effect of recreation on carnivore (-0.67 [-1.01, -0.33]) and herbivore (-0.72 [-1.21, -0.23]) abundance, while omnivore abundance (-0.07 [-0.52, 0.38]; Fig. 1.3a) did not differ between high and low levels of recreation. The difference in abundance was especially pronounced for carnivorous birds (-0.79 [-1.32, -0.26]) and mammals (-0.84 [-1.39, -0.28]), whereas the confidence interval of every other combination of diet and taxonomic group included zero. The abundance of groundnesting birds was lower when recreation was higher (moderate effect size of -0.64 [-1.21, -0.07]), whereas tree-nesting (-0.36 [-0.94, 0.21]) and shrub-nesting (-0.36 [-1.47, 0.75]) bird abundance was reduced, but not significantly (Fig. 1.3b).

Recreation types and timing

We observed a large negative effect of terrestrial recreation on vertebrate richness (-0.88 [-1.37, -0.4]) and a moderate negative effect on abundance (-0.61 [-0.91, -0.31]; Fig. 1.3c), but no effect of aquatic recreation (richness: -0.01 [-0.66, 0.64]; abundance: 0.1 [-0.46, 0.66]). We detected a small to moderate negative effect of non-motorized recreation on vertebrate abundance (-0.46 [-0.75, -0.18]) whereas the effect of motorized recreation was not significantly different from zero (-0.35 [-1.38, 0.67]; Fig. 1.3d). Studies of temporal differences in recreation levels (richness: -1.08 [-2.06, -0.09]; abundance: -0.67 [-1.21, -0.12]) reported larger negative effect sizes than did studies of spatial differences (richness: -0.46 [-0.94, 0.01]; abundance: -0.38 [-0.71, -0.06]; Fig. 1.3e). Both vertebrate richness and abundance were lower in association with novel disturbances (richness: -1.23 [-1.99, -0.47]; abundance: -0.55 [-1.06, -0.04]) than with ongoing disturbances (richness: -0.48 [-0.94, -0.01]; abundance: -0.43 [-0.73, -0.14]; Fig. 1.3f).

Discussion

Across many vertebrate species, species richness and abundance were lower in association with higher levels of recreation. Differences in vertebrate richness and abundance were approximately half a standard deviation between high and low recreation levels. This means that in approximately 7 out of 10 comparisons, vertebrate richness or abundance is expected to be lower with higher levels of recreation.

Despite substantial knowledge gaps and high variability in wildlife responses to recreation, we identified some traits that may indicate sensitivity to recreation. Bird and mammal richness and abundance were reduced in association with higher levels of recreation whereas fish richness and abundance and reptile abundance were not. However, the near-zero effect sizes for fish and reptiles may be due in part to differential responses to ecotourism operations that involve supplemental feeding versus those that do not. When analyzed separately, recreation involving feeding had a slight positive effect size for fish abundance (0.09 [-0.31, 0.48]) and richness (0.19 [-0.78, 1.16]) whereas recreation without feeding had a slight negative effect size for abundance (-0.11 [-0.46, 0.23]) and a moderately strong negative effect size for richness (-0.67 [-2.25, 0.93]), though all the estimates were imprecise. Just one study involved supplemental feeding of reptiles (Iverson et al. 2006), but when abundance models were run excluding this study, the effect size for reptile abundance was large and negative (-0.81 [-1.92, 0.30]). The change in effect size when this comparison was removed also highlights how limited literature in certain subgroups, such as reptiles, limits inference regarding recreation impacts.

Carnivore and herbivore abundances were reduced in high recreation areas more often than omnivore abundance; this effect was even stronger for avian and mammalian carnivores. Dietary and habitat generalists are known to be more human-tolerant than specialists (Devictor et al. 2008) so it is logical that omnivores would be less sensitive; however, we were not able to examine differences among species with narrow or broad diets within these general categories. For birds, the abundance of small-bodied and ground-nesting species was more frequently reduced with high recreation levels than the abundance of larger-bodied and tree- and shrub-nesting species. This finding is consistent with Samia et al. (2015), who found that smaller birds had reduced tolerance of people compared to larger birds, perhaps because larger animals are more likely to become tolerant to reduce costs associated with regular disturbance. However, our dataset did not include studies on

the abundance of raptors, some of which respond strongly to human disturbance (Spaul & Heath 2016).

Impacts of recreation differed among types of recreational activities. Terrestrial recreation had stronger effects on vertebrate richness and abundance than aquatic recreation. Though just two studies in our analysis examined winter recreation, the authors observed dramatically lower animal densities in areas with recreation (Seip et al. 2007; Slauson et al. 2017). Further, our results imply that non-motorized activities can affect vertebrate abundance just as strongly as motorized recreation, though the small sample size for motorized activities (n=4 articles) suggests that this finding should be considered preliminary. Previous research shows that non-motorized recreation may have more frequent impacts on wildlife (Larson et al. 2016) and it can interact with motorized recreation to facilitate increased disturbance by pedestrians (Spaul & Heath 2016).

Reductions in vertebrate abundance were greater for temporal than for spatial comparisons. Long-term temporal comparisons (multiple years at each level of recreation, n=3) had the greatest effect sizes, perhaps suggesting that repeated human disturbance can have cumulative effects. However, novel disturbances had a stronger effect than ongoing disturbances, suggesting that in some contexts, habituation to recreation may occur. Findings from studies focused on habituation to recreation have been mixed, with some finding evidence for habituation (e.g., Ellenberg et al. 2009; Baudains & Lloyd 2007) and others finding little (e.g., Neumann et al. 2010; Constantine et al. 2004). The apparent contradiction in our results echoes the variability of wildlife responses to recreation documented in the literature; it is not yet clear under which circumstances (e.g., species, landscape factors, intensity of recreational use) recreation effects accumulate or attenuate over time and space, but there is some evidence that habituation potential depends on body size, sex, and temperament of individual animals (e.g., boldness; Ellenberg et al. 2009; Samia et al. 2015). Furthermore, very short

temporary disturbances (≤ 1 day) are rarely studied (n=2) despite the increasing popularity of adventure racing and other high-intensity, short-term events inside protected areas (Newsome 2014).

The shape of the wildlife response curve as recreational use increases remains an open question (Monz et al. 2013). Our low and high recreation categories spanned a wide range of intensities and were relative within studies rather than absolute measures. The large variation in how recreation levels were measured and reported meant we were unable to reclassify and standardize levels across articles or satisfactorily categorize the spatial scale of the recreation comparison. Future studies should provide clear empirical estimates of recreation levels at all study locations to aid comparisons across studies and allow identification of thresholds of recreational use at which effects become more severe. Further, we encourage the publication of full results for all species and population segments measured in the study, including those with non-significant results, to help assess sensitivity within and among animal taxa.

Our findings show that recreation has an overall negative effect on vertebrate species richness and abundance. Despite variability in animal responses to recreation and remaining knowledge gaps, we believe our findings underline the importance of managing recreation on conservation lands. The trade-offs between recreation and conservation pose a problem for conservation organizations and natural resource managers, given participation in outdoor recreation has been linked to interest in conservation easements (Farmer et al. 2016), financial contributions to conservation organizations (Zaradic et al. 2009), and pro-conservation behaviors (Cooper et al. 2015). Funding sources for land acquisition (e.g., the U.S. Land and Water Conservation Fund) often mandate public access, limiting managers' ability to restrict recreation for conservation objectives. While publicly-owned protected areas are the cornerstone of global conservation efforts, an estimated 94% of them are open to recreation (Eagles et al. 2002; IUCN & UNEP 2014). This includes the strictest IUCN categories (1a and 1b), which allow "non-intrusive" recreation (Dudley

2008), although the types and intensities of recreation considered to be non-intrusive is not specified.

Despite the need to manage recreation, management agencies rarely have enough resources to adequately monitor recreational use given considerable spatial and temporal variability in visitation (Cessford & Muhar 2003; Larson et al. 2018). Thus, even if researchers had a clear understanding of threshold levels of recreational use that result in negative outcomes for wildlife, managers may struggle to ascertain where or when recreational limits are exceeded. Public opposition to trail closures, caps on daily visitation, or reservation systems can be strong and could damage the support for conservation agencies and organizations. Therefore, we believe that the best option to minimize trade-offs between recreation and species conservation is to maintain some areas that are closed to recreation. If planning for recreational access is done at the regional level, managers could ensure that protected area networks include some areas that are closed to recreation, balancing the dual land uses of conservation and recreation at the scale of the protected area network instead of each individual protected area.

Variable	Description or list of categories
Taxonomic group	Amphibian, bird, fish, mammal, reptile
Species	
Recreation substrate	Aquatic, winter, terrestrial
Recreation motorized	Motorized, non-motorized
Response variable	Species richness, abundance
Comparison type	Spatial, temporal
Disturbance type	Novel, ongoing
Body mass ^a	Average body mass (g)
Dieta	Carnivore, omnivore, herbivore
Nesting behavior ^a	Ground-nesting, shrub-nesting, tree-nesting

Table 1.1. Covariates extracted from the included studies.

^a Sources: Jones et al. (2009); Parr et al. (2014); Cornell Lab of Ornithology (2018); Myers et al. (2018)



Figure 1.1. PRISMA flow diagram showing the number of articles that were located, retained, and excluded at each stage of the systematic review and meta-analysis process.



Figure 1.2. Effect sizes comparing differences in a) species richness and b) abundance between low-recreation and high-recreation groups, broken down into broad taxonomic groups. The dot size is proportional to the sample size in each sub-group (the size of the diamond is not meaningful for the 'all vertebrates' group. Error bars show 95% confidence intervals.



Figure 1.3. Effect sizes comparing differences in abundance between low-recreation and highrecreation groups, broken down by a) diet type, b) nesting behavior (bird data only), c) aquatic or terrestrial recreation activities, d) motorized or non-motorized activities, e) spatial or temporal comparison of recreation levels, and f) novel or ongoing disturbance from recreation. The dot size is proportional to the sample size in each sub-group. Error bars show 95% confidence intervals.

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CHAPTER 2 : EFFECTS OF NON-MOTORIZED RECREATION ON MAMMALS IN URBAN PROTECTED AREAS²

Summary

Protected areas are the primary strategy used to conserve biodiversity, but the vast majority of areas are open to recreation and many receive high levels of recreational use. An increasing body of evidence suggests that recreation can have negative effects on animals, but the levels of human activity that trigger animal responses are not well understood. We addressed this knowledge gap by assessing shifts in mammal habitat use and relative activity over a broad gradient of human activity levels at 92 sampling points located in 14 nature reserves in San Diego County, California, USA. We used camera traps to measure both human and mammal use of reserves, and we modeled mammal habitat use (occupancy and detection probability) and relative activity rates (hours per day with detections) in association with daily counts of total human activity, pedestrians, and cyclists. Human activity was associated with declines in habitat use of several mammal species, particularly bobcats and mule deer, though the strength of these effects was less than the effects of covariates characterizing habitat, topography, and development. Although human activity may not often extirpate mammal species from urban habitat fragments, it can reduce habitat quality. In particular, bobcat, gray fox, mule deer, and raccoon were less active in areas with higher levels of human activity. Our study demonstrates the importance of examining a broad gradient of human activity, including locations with no recreation and very high levels of recreation, to understand which species are sensitive to recreation, to what thresholds of disturbance they respond, and whether their response results in reduced activity or in local extirpation.

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Introduction

Protected areas are the foundation of global conservation efforts to combat biodiversity declines, and they now cover nearly 15% of the earth's terrestrial land area (UNEP-WCMC & IUCN 2016). Yet once the boundaries are drawn, protected areas are not free from threats. Globally, fewer than half (42%) of protected areas are unmodified by humans, and one-third of protected lands are under intense human pressure from agriculture, grazing, urbanization, light pollution, and transportation (Venter et al. 2016; Jones et al. 2018). Sustainable management of protected areas is an ongoing issue that can hinder their ability to effectively conserve biodiversity (Leverington et al. 2010).

Protected areas can promote sustainable development of local communities and help alleviate poverty (Naughton-Treves et al. 2005), primarily through economic opportunities provided by recreation and ecotourism. In the United States outdoor recreation accounts for \$887 billion in consumer spending annually and provides 7.6 million jobs (Outdoor Industry Association 2017). Outdoor recreation fosters connections with nature and sense of place (Cleary et al. 2018) and has been linked to increased pro-environmental behaviors (Cooper et al. 2015) and support for conservation organizations (Zaradic et al. 2009). Accordingly, the dominant narrative regards recreation and ecotourism as a "win-win" for humans and biodiversity.

However, many studies have documented negative effects of recreation on animals (Monz et al. 2013; Sato et al. 2013; Larson et al. 2016; Larson et al. 2019), ranging from physiological and behavioral responses of individual animals (Arlettaz et al. 2007; Naylor et al. 2009) to declines in population abundance (Garber & Burger 1995; Bötsch et al. 2017) and changes in community composition (Reed & Merenlender 2008; Kangas et al. 2010). Animals often shift their spatial and temporal activity patterns to avoid humans (Gaynor et al. 2018; Lesmerises et al. 2018). The spatial effect zone of recreation can be substantial when species respond to disturbance at greater distances,
and when trails and recreation infrastructure are distributed broadly across a landscape (Coppes et al. 2017). For example, about 32% of the area within national parks in the continental United States is within 400 m of a recreational trail, which is within the documented effect distance for mammalian predators and birds of prey (Dertien et al. 2018).

Because recreation infrastructure typically involves minimal physical habitat change, the impacts of recreation activities are difficult to detect and measure, and they cannot be incorporated easily into metrics such as the human footprint (Venter et al. 2016) that are primarily based on remotely-sensed data. The impacts of recreation at an individual site or trail may seem small, but cumulative impacts over time and space can be significant (e.g., Garber & Burger 1995). Recreation can also have secondary impacts such as facilitating the spread of invasive species that alter ecological functioning (Anderson et al. 2015). Consequently, recreation can be considered an "enigmatic" ecological impact, described by Raiter et al. (2014) as an impact that is easily and regularly overlooked in impact evaluations, often because other impacts are more obvious (e.g., Wickham et al. 2013). Failure to account for the ecological effects of recreation is a potentially dramatic oversight given that the vast majority of protected areas globally are open to recreation (Eagles et al. 2002; IUCN & UNEP 2014) and many receive high levels of human visitation (Manning 2002; Balmford et al. 2015).

Despite increasing evidence that recreation affects animals, the timing, intensity, and spatial extent of human disturbance that may cause animals to alter their habitat use or activity patterns is not well understood (Monz et al. 2013). Protected area visitation is increasing rapidly (Cordell 2012) and new recreation activities are proliferating (e.g., Newsome 2014), but few studies measure levels of recreation as a continuous variable, relying instead on proxy measures or expert opinion to assign categorical levels of use (Larson et al. 2016). The resulting comparisons among categories make it difficult to assess the sensitivity of species responses to changes in the intensity of human use or

make comparisons among reserves or regions. Nonetheless, studies that do quantify recreation still may not capture the full range of variation in human activity – from no use to very high use – especially since visitation rates can be highly variable within a single reserve (Taczanowska et al. 2014), and even reserves with high total visitation rates likely have low-use areas within them. However, understanding species responses across variable visitation levels is critical for managers, allowing them to assess when and where recreational use exceeds thresholds of human activity that alter animal behavior, habitat use, or persistence on the landscape.

Our goal was to address these knowledge gaps by assessing shifts in mammal habitat use and relative activity over a broad range of recreational use in the highly urbanized landscape of coastal southern California. We used our prior work in the region (Larson et al. 2018) to stratify sampling across a wide gradient of human activity to capture the full variability of mammal responses to disturbance from recreation. Specifically, we ask: 1) how does non-motorized recreation affect habitat use and relative activity of mammals? 2) how strong is the effect of recreation on habitat use and relative activity in comparison to other factors known to affect mammals, such as habitat characteristics and residential development? 3) are there thresholds of recreational use above which mammal habitat use and relative activity decline rapidly? Our findings help establish the relative importance of recreation in comparison to other threats facing biodiversity, and support managers in evaluating trade-offs between recreation and conservation in protected areas.

Methods

Study sites

Our study was conducted within 14 publicly-owned nature reserves in coastal San Diego County, California, USA that are part of the San Diego County Multiple Species Conservation Program. The reserves are managed by city, county, and state agencies as well as private

organizations, and they vary in distance from densely populated areas. We used predictions from an existing landscape-level spatial model of human use intensity (Larson et al. 2018) to choose reserves along a gradient of expected human visitation, as well as sites that are popular for different recreation activities (e.g., hiking, mountain biking, horseback riding). Two reserves closed to the public were included to ensure our study design encompassed areas with little to no human use. Reserves ranged from 301-3369 ha in area, and vegetation communities included chaparral, coastal sage scrub, native and nonnative grasslands, oak and sycamore woodlands, and riparian habitats.

We located 92 sampling points along official and unofficial trails within the study reserves. Points were allocated to reserves proportionally based on length of the total trail network and reserve area, such that a minimum of 3 and a maximum of 12 points were located within each reserve. The point locations were selected using a spatially balanced random design using the RRQRR algorithm on the rasterized trail network (Theobald et al. 2007). To ensure that our study included sampling points with high levels of human use, we gave higher weight to cells expected to receive higher use, based on a) distance from the nearest trailhead and b) estimates of daily human use at trailheads from Larson et al. (2018). We removed trail cells within 100 m of a road or residential parcel. We generated 296 points and screened potential points using aerial imagery and initial field visits, removing point locations that were not located on human trails (e.g., ridgelines, streambeds). In closed reserves, we ensured that sampling points were located on service roads or animal trails similar in width to recreational trails.

Sampling methods

To monitor human activity and mammal habitat use and relative activity, we installed one motion-triggered camera (Bushnell TrophyCam HD Aggressor) at each sampling point. Cameras were housed in locked metal security boxes and affixed to metal poles pounded into the soil facing recreational trails. We did not bait the cameras to avoid influencing animal activity patterns and behavior (Wearn and Glover-Kapfer 2019). Cameras were programmed to take two photos per trigger with a five second delay between triggers. Sampling periods were four weeks, with a check after approximately two weeks, repeated four times between January 2017 and February 2018 to capture seasonal variability in human and animal activity.

Rapidly growing vegetation, high temperatures, and wind led to large numbers of "false triggers," mostly in the mid-morning to late afternoon. Therefore, we randomly subsampled 20% of photos between 11 am and 5 pm at all sampling points to reduce time spent sorting photos. Photos were organized in the Colorado Parks & Wildlife Photo Warehouse (Ivan & Newkirk 2016). Humans appearing in photos were categorized by activity (pedestrian, cyclist, equestrian, or vehicle) and animals were identified to species, with the exception of the brush rabbit (*Sybrilagus bachmant*) and desert cottontail (*S. audobonii*), which are difficult to distinguish in photos and were both labeled "rabbit." Domestic dogs were considered a human associate since daily counts of dogs and humans were highly correlated (r = 0.87).

Analytical methods

We used three response variables – habitat use, relative activity, and detection probability – to assess species' responses to recreation activity over different time periods. Habitat use and detection probability were derived from occupancy models. Because our sampling locations were smaller than the home range of an individual animal, we interpret occupancy estimates as the probability of habitat use rather than true probability of occupancy of the site (MacKenzie et al. 2017). Specifically, habitat use estimates the probability that a species used a given sampling point during each 4-week sampling period. Therefore, declines in habitat use can also be viewed as an increased likelihood of local extirpation. Detection probability estimated the probability of detecting

a species within each 5-day sampling occasion given that the species used the sampling point. We thus interpret detection probability as habitat use on a fine temporal scale. Relative activity, modeled using negative binomial regression models, measured the frequency of species detections over each 4-week period. Relative activity and detection probability measure similar properties of detection frequency, and prior researchers have used detection probability as a measure of relative activity (e.g., Lewis et al. 2015; Wang et al. 2015). Unlike detection probability, however, relative activity data are counts rather than binary (detection/non-detection), and relative activity measures detections over a longer time period. Since it reflects intensity of habitat use, we interpret relative activity as an indication of habitat quality (Manly et al. 2002; Lewis et al. 2015).

Occupancy models were single-species, single-season models with implicit dynamics (MacKenzie et al. 2017), built for the species with sufficient detections for models to converge using the R package *unmarked* (Fiske and Chandler 2011). We pooled detections into 5-day sampling occasions so that detection histories were not overly sparse (MacKenzie et al. 2002; Welsh et al. 2013). We used a parametric bootstrapping procedure to evaluate goodness-of-fit and overdispersion (MacKenzie and Bailey 2004). When the results of this procedure suggested overdispersion in the data, we adjusted the model selection results using the estimated overdispersion parameter (\hat{c}), resulting in a QAIC_c value.

We fit negative binomial regression models to evaluate the effects of habitat, topography, development, and human activity on the relative activity rates of mammal species for which there were sufficient detections for models to converge. Our measure of relative activity rate was the number of hours per day in which at least one individual of a given species was detected, summed over the same 4-week sampling period used in the occupancy models. This measure helps ensure that multiple photos of the same individual animal within a short period of time do not overestimate the overall relative level of use (Burton et al. 2015). Negative binomial regression models are suitable

for count data in which overdispersion prevents the use of a Poisson regression model (Lawless, 1987). We assessed model fit by visually inspecting rootograms (Kleiber & Zeileis 2016; Appendix 2.1).

We hypothesized that mammal habitat use and relative activity would be driven by habitat characteristics, topography, development, and human activity (Table 2.1). To describe habitat, we used the percent cover of chaparral and riparian vegetation types within a 500 m buffer, plant greenness as measured by the normalized difference vegetation index (NDVI), and years since the last recorded fire. We used elevation to represent changes in topography. Our measure of development was the number of housing units within 500 m of the sampling point. To represent human activity, we used mean daily counts of pedestrians, cyclists, and total human activity. Due to low variability in the equestrian and vehicle counts, we did not model relationships between these activities and mammal habitat use, but we did include them in the total human activity counts. Human activity levels varied by season in a complex way that covaried with landscape position and reserve. Accordingly, we treated each combination of sampling point and camera rotation as a separate data point, which allowed us to assess species responses to human activity levels at a finer temporal scale than using the mean across the duration of the study. However, since this approach artificially inflates sample size, we used the number of sampling units (n=92) in model comparison and selection. We used the same variables to model detection probability over the 5-day occasions except for elevation and with the addition of Julian date and trail width (Table 2.1). We tested all variables for collinearity and eliminated variables with a correlation coefficient greater than 0.7 (Burnham and Anderson 2002). All variables were scaled (by subtracting the mean and dividing by the standard deviation) to facilitate comparison among regression coefficients.

In the occupancy and negative binomial regression models for each species, we used a stepwise model building procedure (Lebreton et al. 1992) to first select the best additive

combinations of habitat, topography, and development variables and subsequently add human activity variables. For occupancy models, which allow covariates to be used to model both occupancy and detection probability, we first ran models to determine the variables that best explained detection probability (p) while holding occupancy (ψ) at a global structure that was constant across species and included housing units, chaparral and riparian cover, years since fire, NDVI, and elevation. We used Akaike's information criterion corrected for small sample size (AIC_c) to rank and compare occupancy models (Burnham and Anderson 2002). We used the combinations of variables for detection probability from up to three best-supported models ($\leq 2 \Delta$ AIC_c) in the next step, assessing how occupancy (ψ) varied in relationship to habitat, topography, and development variables. We limited occupancy structures to two habitat variables, topography, and development, and ran all possible combinations of additive models (43 models per detection structure). Finally, we added each of the human activity covariates (singly) to up to three bestsupported models ($\leq 2 \Delta$ AIC_c), as a covariate on detection probability, occupancy, and both, and again ranked and compared models. For the relative activity models, this process was simpler but similar: we first built a series of models using additive combinations of up to two habitat, topography, or development variables. To each model with $\leq 2 \Delta$ AIC_c, we added human activity variables and again compared Δ AIC_c values. We considered human activity to have an important effect if models containing human activity variables reduced AIC_c values. We also examined the effect size compared to other variables by comparing regression coefficients and their confidence intervals.

Results

The cameras ran for over 12,000 camera days, producing approximately 2.7 million photos. Trimming to 4-week periods reduced the number of photos to 1.8 million, and 737,486 photos remained after subsampling, which a team of assistants viewed and recorded the contents. Overall mean (\pm SD) human activity across all sites was 41.8 \pm 144.9 (range: 0 - 1797.2) people, vehicles, and dogs per day. Recreation rates were higher on weekends than on weekdays (Figure 2.1), and generally higher in winter and spring than in summer, though seasonal patterns varied based on location. Pedestrians were the most common human activity (33.3 \pm 134.5 per day, n=305,836 total detections), followed by dogs (4.1 \pm 10.2 per day, n=37,928), cyclists (3.2 \pm 11.6 per day, n=29,520), equestrians (0.6 \pm 2.9 per day, n=5,613), and motorized vehicles (0.5 \pm 2.4 per day, n=4,248). In addition to domestic dogs, we detected 13 mammal species squirrel-sized or larger: coyote (*Canis latrans*, n=8,854), brush rabbit and desert cottontail (*Sylvilagus bachmani* and *Sylvilagus audobonii*, n=8,178), black-tailed jackrabbit (*Lepus californicus*, n=2,379), mule deer (*Odocoileus hemionus*, n=844), bobcat (*Lynx rufus*, n=723), gray fox (*Urocyon cinereoargenteus*, n=614), California ground squirrel (*Otospermophilus beecheyi*, n=316), striped skunk (*Mephitis mephitis*, n=128), raccoon (*Procyon lotor*, n=122), mountain lion (*Puma concolor*, n=16), domestic cat (*Felis catus*, n=10), and Virginia opossum (*Didelphis virginiana*, n=8).

Habitat use and detection probability

Species modeled with single-species occupancy models were bobcat, gray fox, black-tailed jackrabbit, mule deer, raccoon, striped skunk, and California ground squirrel. Coyotes could not be modeled with occupancy models because they were present at nearly every sampling location (detected at 96.7% of sampling point-camera rotation combinations). The remaining mammal species were detected too infrequently for occupancy models to converge (mountain lion, Virginia opossum, domestic cat), or occupancy models did not fit adequately (rabbit; $\hat{c} > 4$), perhaps because the category included two species.

Models containing a human activity variable outcompeted those without a human activity variable for all species except for striped skunk (Table 2.2). We observed a negative relationship between habitat use and total human and pedestrian activity for five out of seven modeled species (bobcat, gray fox, mule deer, raccoon, and striped skunk; Figure 2.2). The bobcat, gray fox, mule deer, and striped skunk coefficients were the most strongly negative, though the confidence interval for striped skunk was wide (Figure 2.3). Jackrabbits had a fairly strong positive relationship between habitat use and cyclist activity, while ground squirrel habitat use was positively related to total human and pedestrian activity and negatively related to cyclist activity, though the estimates were imprecise. Relationships between detection probability and human activity were generally similar to patterns in habitat use (Figure 2.3). However, the coefficients for striped skunk habitat use and detection probability diverged strongly; detection probability was higher while habitat use was lower with higher levels of human activity.

The covariates that appeared in the best-supported habitat use models most frequently were NDVI, elevation, and development (Figure 2.4). In these models, percent cover of chaparral was positively associated with habitat use of gray fox, mule deer, and raccoon, and percent cover of riparian vegetation was positively associated with ground squirrel habitat use. Years since fire had a strong positive association with striped skunk habitat use and a negative association with ground squirrel and jackrabbit habitat use. NDVI had a positive relationship with habitat use of bobcat, gray fox, ground squirrel, mule deer, raccoon, and striped skunk, and a negative relationship with jackrabbit habitat use. Gray fox and ground squirrel habitat use increased and jackrabbit and mule deer habitat use decreased at higher elevations. Development was negatively related to jackrabbit and striped skunk habitat use and positively related to ground squirrel and raccoon habitat use. In general, many of the relationships between covariates and habitat use were stronger than those between human activity and habitat use.

Covariates affecting detection probability in the best-supported habitat use models included chaparral and riparian vegetation, years since fire, NDVI, development, trail width, and Julian date (Figure 2.5, Appendix 2.2). Chaparral cover had a negative relationship with ground squirrel detection probability and a positive relationship with gray fox detection probability. Riparian cover was negatively associated with raccoon and jackrabbit detection probability. Years since fire was positively associated with bobcat detection probability and negative relationship with detection probability of raccoon and striped skunk. NDVI had a positive relationship with raccoon detection probability and a negative relationship with jackrabbit detection probability. Development had a positive relationship with bobcat detection probability and a negative relationship with gray fox detection probability. Trail width had a negative association with bobcat and gray fox detection probability. Julian date was modeled as a quadratic relationship; detection probability was highest in late spring/early summer for ground squirrel, fall through early winter for mule deer, and late winter/early spring for striped skunk (Appendix 2.2).

Relative activity

In the relative activity analysis we modeled coyote and rabbit in addition to the seven previously modeled species. Coyote (mean hours per day detected \pm SD = 0.93 \pm 1.37) and rabbit (0.86 \pm 1.7) were the most frequently detected species, followed by jackrabbit (0.25 \pm 0.99), mule deer (0.09 \pm 0.35), bobcat (0.08 \pm 0.31), gray fox (0.06 \pm 0.31), ground squirrel (0.03 \pm 0.26), striped skunk (0.01 \pm 0.13), and raccoon (0.01 \pm 0.12).

Human activity was a well-supported predictor of relative activity for all nine species (Table 2.3). Relative activity of bobcat, gray fox, mule deer, and raccoon were negatively associated with total human and pedestrian activity (Figures 2.3, 2.6). Coyote, ground squirrel, jackrabbit, rabbit, and striped skunk relative activity was positively associated with total human and pedestrian activity, but

the confidence intervals were wide for all but coyote and rabbit. Relationships with cyclist activity were more variable. Gray fox, ground squirrel, and mule deer relative activity was negatively related to cyclist activity, whereas coyote, jackrabbit, rabbit, and striped skunk relative activity was positively related to cyclist activity, with a particularly strong relationship for jackrabbit relative activity.

Relative activity was related to other variables in addition to human activity, most commonly chaparral cover and NDVI (Figure 2.7). Chaparral cover was negatively associated with relative activity of coyote, ground squirrel, and rabbit, and positively associated with relative activity of mule deer. Years since fire was positively associated with bobcat and gray fox relative activity and negatively associated with ground squirrel activity. NDVI was positively associated with relative activity of bobcat, coyote, mule deer, raccoon, and striped skunk, and strongly negatively associated with jackrabbit activity. Gray fox, jackrabbit, and striped skunk were more active at higher elevations. Development was positively associated with raccoon relative activity and negatively associated with striped skunk activity.

Discussion

Human activity was associated with declines in habitat use of several mammal species, particularly bobcats and mule deer. The magnitude of these effects was often relatively small in comparison with the effects of covariates representing habitat, topography, and development. However, our results suggest that although human activity may not often extirpate species from urban habitat fragments (as measured by habitat use), it can reduce habitat quality (as measured by relative activity). In particular, four species, bobcat, gray fox, mule deer, and raccoon, were less active in areas with higher levels of human activity. Our study demonstrates the importance of examining a full gradient of human activity, including locations with no recreation and very high levels of recreation, to understand which species are sensitive to recreation, to what thresholds of

disturbance they respond, and whether their response results in reduced habitat quality or in local extirpation.

Species-specific responses to human activity

Bobcats and gray foxes are known to be sensitive to urbanization (Riley 2006; Ordeñana et al. 2010), but responses to recreation have been mixed in previous studies, with reductions in detection frequency and activity rates in some studies (George & Crooks 2006; Reed & Merenlender 2008; Patten & Burger 2018) but no effects on occurrence in others (Markovchick-Nicholls et al. 2008; Reilly et al. 2017). We observed declines in bobcat and gray fox habitat use, detection probability, and relative activity as human activity increased. Habitat use of both species was more strongly related to human activity than to urban development, which was not a well-supported predictor of habitat use. Gray fox occurred sparsely in our study area and were estimated to use fewer than one-quarter of the sampling points. Their habitat use was more strongly related to vegetation characteristics and elevation than to human activity. Prior research has similarly found gray foxes to be sparsely distributed in coastal southern California, and rare or absent from some urban habitat fragments, potentially due to intraguild competition with dominant carnivores such as coyotes and bobcats (Crooks et al. 2010). Dietary overlap among bobcats, gray foxes, and coyotes increases with higher human activity (Smith et al. 2018), which may suggest that the negative impact of recreation on bobcats and gray foxes could be partially caused by increased competition with coyotes in areas with high human activity.

Coyotes were distributed widely across the study area, occupying nearly every sampling point. Their relative activity increased with human activity, but they were never detected at the highest-use sampling point, which averaged over 1700 people per day. Coyotes can thrive in urban areas due to their adaptable behavior and omnivorous diet (Riley et al. 2003; Ordeñana et al. 2010;

Bateman & Fleming 2012); however, they rarely inhabit very small or highly isolated urban habitat fragments (Crooks 2002), suggesting a threshold of tolerance to urbanization. We speculate that a similar threshold could exist for human activity within protected areas, but given our limited sample of very high visitation levels, we were not able to detect it.

Mule deer showed reductions in habitat use in association with total human and pedestrian activity, and the strength of these effects were similar to the effects of the other covariates we considered. Relative activity of mule deer also declined with human activity, as did detection probability. The reduced habitat use and activity of mule deer that we observed support previous studies, which have shown spatial avoidance (Lenth et al. 2008; Patten & Burger 2018) and reduced daytime activity (George & Crooks 2006) among mule deer in association with recreation, but our results further suggest that mule deer may stop using some areas altogether if human activity is too high.

Raccoons and striped skunks are urban-adapted mesopredators (Crooks 2002), however, their responses to human activity differed. Both species showed a trend toward reduced habitat use in association with human activity, but their habitat use was more strongly related to other covariates, specifically development and NDVI for raccoons and NDVI, years since fire, and development for striped skunks. However, raccoon relative activity rates decreased in association with human activity while relative activity rates of striped skunk increased slightly with human activity. Our detections of raccoons were very low across all sites, and they were among the most nocturnal species in our study. This may indicate that raccoons are not actually responding to human activity, but the relationship we observed might instead be primarily driven by detections at a few low-use sampling points. Striped skunks appear to prefer habitat along the edge of development or in small habitat fragments, where they can take advantage of human food resources while using natural habitat for den sites (Ordeñana et al. 2010). This preference for edge habitat may contribute

to the positive relationship between human and striped skunk activity given human activity is also more concentrated closer to the edge of protected areas.

The small herbivores (jackrabbit, rabbit, and ground squirrel) generally did not have strong relationships with human activity. Jackrabbits showed avoidance of development and positive associations with locations that were lower elevation, more recently burned, and had lower NDVI. Jackrabbits are adapted to desert and shrubland habitats, but in contrast to our results, a previous study found them to be relatively tolerant of urbanization (DaVanon et al. 2016). In our system, drier and more open shrubland habitats – which are preferred by jackrabbits – tend to be located further from dense human development, which may explain the observed avoidance of development. Rabbits (including brush rabbit and desert cottontail) had slightly higher activity rates with higher human activity and a negative association between activity rate and chaparral cover; these rabbit species are tolerant of urbanization and often found within the urban matrix and in riparian and brushy areas (DaVanon et al. 2016; Kelt et al. 2014). Finally, ground squirrels were predicted to occur more often in higher elevation, higher NDVI, and more recently burned habitats, and in habitat types other than chaparral, consistent with previous research that documented a preference for grassland and open woodland habitats where burrow locations have good visibility (Ordeñana et al. 2012).

The relative activity results can be used to assess the level of recreation that is associated with unacceptable declines in mammal activity rates. For example, if we consider a reduction in a species' relative activity to 50% of the maximum recorded activity rate as an indication of poor habitat suitability, then 13 people per day is enough to make an area poorly suitable for gray fox; this level of visitation occurred at 42% of our sampling points on an average day and 53% of sampling points on an average weekend day. A visitation rate of 39 people per day reduced mule deer activity below the 50% threshold, affecting 27% of sampling points on an average day and 35% on a

weekend day. Raccoon activity declined below 50% of maximum when human activity exceeded 156 people per day, making 10% of sampling points poorly suitable on an average day and 12% on a weekend day. Bobcat activity declined more gradually; activity rates were reduced to 50% of maximum at the highest observed levels of human use.

Types of human recreation activity

We found that habitat use of most mammal species declined in relationship with pedestrian activity but was neutral or increased in relationship with cyclist activity, despite a positive correlation (r = 0.5) between pedestrian and cyclist activity. For ungulates, a person in a vehicle may be perceived as less threatening than a person on foot (Stankowich 2008), and there could be a similar phenomenon associated with people on bicycles. The highest pedestrian counts were far greater than the highest cyclist counts, so if observed negative relationships between habitat use and pedestrian activity are driven by avoidance of areas with very high use, then we would not expect a similar pattern for cyclist activity. On the other hand, many species perceive humans approaching at greater speeds as more threatening (Samia et al. 2016; Stankowich 2008; Lethlean et al. 2017), and cyclists generally move much faster than pedestrians. It is not clear why animals would respond positively to cyclist activity. It is possible that positive relationships between habitat use or activity rate and cyclist activity are artefactual correlations with unmeasured covariate(s) rather than cyclists acting as an attractant. For instance, many of the sampling points with relatively low pedestrian counts and higher cyclist counts are in the interior of the reserve, so avoidance of edge habitats could be manifesting as a positive relationship with cyclist activity.

Implications for future research on recreation effects

In studies employing a gradient design, the gradient must be sufficiently broad to encompass the level at which the focal species responds. Avoidance of high human activity but tolerance of lower human use could explain some inconsistencies among prior studies of recreation effects on animals (Larson et al. 2016). Some studies may not include sufficiently high levels of human activity to detect responses of species that can tolerate lower levels of disturbance. For example, Kays et al. (2017), which did not observe decreases in occupancy or relative activity in relation to human activity, had a maximum daily count of 100 groups of people, much lower than the peak visitation levels recorded in our study (maximum count of 3,401 people/day). Additionally, studies lacking sites with no human activity (e.g., Morrison et al. 2011, Kays et al. 2017) are potentially limited in their ability to detect responses by species that are highly sensitive to human disturbance. Fine-scale temporal shifts in activity likely occur at low levels of human activity, with detectable shifts in daily activity patterns occurring at threshold levels as low as 2 people per day (Wang et al. 2015). Our gradient included two locations with essentially no human activity (mean of ≤ 0.1 person per day), whereas our highest-use site had on average 1797 people per day. Though an outlier, this location ensured that we included human disturbance high enough to trigger responses in less-sensitive species, and this appeared to be sufficiently disturbed for most species, as we observed only rabbits using this location during 7.5 weeks of camera monitoring.

Additionally, several studies that have used occupancy as a response variable (or occupancy interpreted as habitat use) have observed limited effects of recreation (e.g., Kays et al. 2017, Reilly et al. 2017). However, studies that measure abundance, relative abundance, or species richness generally observe stronger effects (Larson et al. 2019). For species with relatively large home ranges that can tolerate some level of human disturbance, or for generalist species, occupancy may not be a sufficiently sensitive response variable, which may have been the case for coyotes in our study.

Differences between occupancy and relative activity or detection probability results could also represent an extinction debt (Tilman et al. 1994) if species are declining but still widely distributed. While results from our habitat use, relative activity, and detection probability analyses were similar, we detected some additional negative relationships with human activity when relative activity or detection probability was the response variable. Collecting recreation data in conjunction with ongoing animal population monitoring efforts would be a valuable way to further our understanding of the effects of human disturbance on demographic trends, since it can be difficult to link occupancy, relative activity, or detection probability to abundance or density (Efford & Dawson 2012).

Our measure of recreation effect depends on the ability of animals to move away from habitat that is degraded because of human activity. However, behavioral responses, including shifts in habitat use, do not necessarily occur if there is no alternative habitat nearby or if movement costs are high (Gill et al. 2001). Accordingly, recreation could have other negative effects we cannot detect. The majority of studies that investigate physiological effects of recreation demonstrate negative effects, and these responses can translate more directly to animal fitness than behavioral responses (Bateman & Fleming 2017). Studies that combine behavioral responses with physiological or demographic metrics would help calibrate the relationships between behavioral responses and population-level effects.

Though we cannot predict the proportion of each protected area affected by recreation, we suspect it may be large in some areas. To avoid people, animals can move to sections of protected areas further from trails, yet the effect zone of recreationists has been estimated at 350-1000 m for carnivores and ungulates (Dertien et al. 2018). Given the dense trail network and small size of some of the protected areas included in this study (the smallest were \sim 300 ha), an effect distance of several hundred meters extending from either side of a trail would encompass a large proportion of

the total area. However, the effect zone likely varies depending on the magnitude of human activity as well as the species response, and therefore it may not be constant across the trail network. Our understanding of recreation effects would be advanced by further work that evaluates displacement of animals away from recreational trails, thus allowing estimation of effect zones and the proportion of protected areas that are suitable for various taxa. The effect zone, however, can be difficult to measure because detection rates of many mammals using cameras are dramatically reduced off-trail (Reilly et al. 2017, Dertien et al. 2017).

Implications for conservation and protected area management

Human populations are continuing to grow in the San Diego region (San Diego Association of Governments 2010), as well as in urban areas throughout the world (United Nations 2014). With increased human populations at their borders, protected areas receive increased rates of human activity and increased demand for recreational access to natural areas. For example, population growth in San Diego County is predicted to increase protected area visitation rates by 46% by 2050 (Larson et al. 2018). Consequently, thresholds of human activity that trigger animal responses will be exceeded more frequently, adding to the challenge of balancing recreation and conservation in protected areas.

Threats to ecological communities posed by recreation are often underestimated or ignored, perhaps because of the many benefits provided by recreation and ecotourism to conservation (Naughton-Treves et al. 2005). We recommend that managers improve public access plans and visitor management policies by implementing targeted temporal and/or spatial separation of recreation and conservation priorities. Seasonal closures during breeding periods or other times of heightened animal sensitivity are becoming more common (e.g., Richardson & Miller 1997). Spatial separation within individual protected areas may work particularly well when critical habitat features,

such as wildlife corridors, are impacted by recreation (e.g, Clevenger and Waltho 2000). Managers and planners can also consider spatial separation at a regional scale, allowing recreational access to some but not all protected areas. In addition, negative effects of recreation can be buffered by higher-quality habitat (Coppes et al. 2018), suggesting that habitat restoration could also help mitigate recreation effects. Ultimately, for animals that avoid human activity, it is unlikely that dualuse protected areas will provide sufficient high-quality habitat, and therefore limiting recreation in strategic locations and circumstances will be necessary to achieve conservation objectives.

			Data	Observed	
Covariate	Category	Description	source	range	Parameter
Cyclists	human activity	mean per day	field	0 - 102	ψ, p, RA
Pedestrians	human activity	mean per day	field	0 - 2,826	ψ, p, RA
Total humans	human activity	mean per day	field	0 - 2944	ψ, p, RA
Development	development	housing units within 500m	GIS	0 - 375	ψ, p, RA
Elevation	topography	meters, mean value within 10m	GIS	5.3 - 203.2	ψ, RA
Chaparral	habitat	% cover within 500m	GIS	3 - 100	ψ, p, RA
Riparian	habitat	% cover within 500m	GIS	0 - 41	ψ, p, RA
Fire	habitat	years since the last recorded fire	GIS	3 - 139	ψ, p, RA
NDVI	habitat	metric of plant greenness, mean value within 10m	GIS	0.2 - 0.62	ψ, p, RA
Julian date	temporal	day of the year at the start of the sampling occasion	field	1 - 326	р
Trail width	observation process	meters	field	1.0 - 8.3	р

Table 2.1. Variables used to model occupancy (ψ), detection probability (p), and relative activity (RA)

Table 2.2. Mammal habitat use models ranked by QAIC_c. Items in the Model column show variables used to model habitat use (ψ) and detection probability (p). K is the number of parameters, Δ QAIC_c is the difference between the QAIC_c of the model and the best-supported model, w is the Akaike weight, and -2/ is twice the negative log likelihood. Only models with Δ QAIC_c \leq 2 are shown. Estimates of the overdispersion parameter (\hat{c}) from the goodness-of-fit test are provided next to each species name.

Model	K	QAIC _c	ΔQAIC _c	w	-21
Bobcat ($\hat{c} = 1.92$)					
ψ (NDVI + pedestrian)					
p(fire)	6	923.52	0.00	0.07	910.53
$\psi(ext{NDVI} + ext{total human})$					
p(fire)	7	923.74	0.23	0.06	910.75
ψ (NDVI + pedestrian)					
p(development + fire)	7	923.79	0.27	0.06	908.46
$\psi(ext{NDVI})$					
p(fire)	5	923.80	0.28	0.06	913.10
$\psi(ext{NDVI})$					
p(fire + trail width)	6	923.91	0.39	0.06	910.92
$\psi(ext{NDVI} + ext{total human})$					
p(development + fire)	7	924.02	0.51	0.06	908.69
$\psi(\text{NDVI} + \text{pedestrian})$					
p(fire + trail width)	7	924.07	0.55	0.05	908.73
$\psi(\text{NDVI} + \text{total human})$					
p(fire + trail width)	7	924.28	0.76	0.05	908.94
$\psi(ext{NDVI})$					
p(fire + pedestrian)	6	924.35	0.83	0.05	911.36
$\psi(ext{NDVI})$					
p(development + fire)	6	924.43	0.92	0.05	911.44
$\psi(ext{NDVI})$					
p(fire + total human)	6	924.56	1.04	0.04	911.57
$\psi(ext{NDVI})$					
p(development + fire + pedestrian)	7	924.80	1.29	0.04	909.57
$\psi(ext{NDVI})$					
p(development + fire + total human)	7	924.96	1.45	0.04	909.63
$\psi(\text{NDVI} + \text{pedestrian})$					
p(fire + pedestrian)	7	925.38	1.87	0.03	910.05
ψ(.)p(.)	3	954.31	30.80	0.00	948.04
Gray fox ($\hat{c} = 1.35$)					
ψ (chaparral + NDVI + elevation)					
p(development + trail width + total human)	9	602.63	0.00	0.17	582.43
ψ (NDVI + elevation)					
p(chaparral + trail width + total human)	8	602.95	0.33	0.15	585.22
ψ (chaparral + NDVI + elevation)					
p(chaparral + trail width + total human)	9	603.41	0.79	0.12	583.22

ψ (NDVI + elevation + total human)					
p(chaparral + trail width + total human)	9	604.22	1.60	0.08	584.03
ψ (chaparral + NDVI + elevation + total human)					
p(development + trail width + total human)	10	604.45	1.82	0.07	581.73
ψ(.)p(.)	3	692.25	89.63	0.00	685.98
Ground squirrel ($\hat{c} = 1.11$)					
ψ (development + riparian + fire + elevation)					
p(chaparral + Julian ² + pedestrian)	10	526.31	0.00	0.08	503.60
ψ (development + riparian + fire + elevation)					
p(chaparral + Julian ² + total human)	10	526.55	0.24	0.07	503.84
ψ (development + riparian + fire + elevation +					
pedestrian)					
p(chaparral + Julian ²)	10	526.60	0.28	0.07	503.88
ψ (development + riparian + fire + elevation)					
p(chaparral + Julian ²)	9	527.04	0.73	0.06	506.85
ψ (development + riparian + fire + elevation + cyclist)					
$p(chaparral + Julian^2)$	10	527.10	0.79	0.06	504.39
ψ (development + riparian + fire + elevation + total					
human)					
p(chaparral + Julian ²)	10	527.24	0.92	0.05	504.52
ψ (development + chaparral + fire + elevation +					
pedestrian)					
p(chaparral + Julian ²)	10	527.45	1.13	0.05	504.73
ψ (NDVI + fire + elevation)					
p(chaparral + Julian ² + pedestrian)	9	527.78	1.47	0.04	507.60
ψ (NDVI + fire + elevation + pedestrian)					
p(chaparral + Julian ²)	9	527.79	1.48	0.04	510.19
ψ (NDVI + fire + elevation)					
p(chaparral + Julian ²)	8	527.92	1.61	0.04	502.74
ψ (development + riparian + fire + elevation +					
pedestrian)					
p(chaparral + Julian ² + pedestrian)	11	528.04	1.72	0.03	507.90
ψ (NDVI + fire + elevation)					
p(chaparral + Julian ² + total human)	9	528.09	1.78	0.03	507.97
ψ (development + chaparral + fire + elevation)					
p(chaparral + Julian ²)	9	528.16	1.85	0.03	508.01
ψ (NDVI + fire + elevation + cyclist)					
p(chaparral + Julian ²)	9	528.21	1.89	0.03	505.55
ψ (development + chaparral + fire + elevation + total					
human)					
p(chaparral + Julian ²)	10	528.27	1.95	0.03	505.62
$\psi(.)$ p(.)	2	583.42	57.11	0.00	579.29
Jackrabbit ($\hat{c} = 2.2$)					
ψ (development + fire + NDVI + elevation)					
p(riparian + NDVI + cyclist)	10	440.55	0.00	0.27	417.84

ψ (development + fire + NDVI + elevation + cyclist)					
p(riparian + NDVI + cyclist)	11	440.83	0.28	0.23	415.53
ψ (fire + NDVI + elevation + cyclist)					
p(riparian + NDVI + cyclist)	10	441.31	0.76	0.18	418.60
ψ (fire + NDVI + elevation)					
p(riparian + NDVI + cyclist)	9	441.32	0.76	0.18	421.12
ψ(.)p(.)	3	499.01	58.46	0	492.74
Mule deer ($\hat{c} = 1.74$)					
ψ (elevation + chaparral)					
$p(Julian^2 + trail width + total human)$	9	957.03	0.00	0.11	936.83
ψ (elevation + chaparral + total human)					
$p(Julian^2 + trail width + total human)$	10	957.07	0.05	0.10	934.36
ψ (elevation + chaparral + NDVI + total human)					
$p(Julian^2 + trail width + total human)$	11	957.36	0.34	0.09	932.06
ψ (elevation + chaparral + pedestrian)					
$p(Julian^2 + trail width + pedestrian)$	10	958.07	1.05	0.06	935.36
ψ (elevation + chaparral)					
$p(Julian^2 + trail width + pedestrian)$	9	958.11	1.08	0.06	937.91
ψ (elevation + chaparral + NDVI + pedestrian)					
$p(Julian^2 + trail width + pedestrian)$	11	958.16	1.13	0.06	932.86
ψ (elevation + chaparral + NDVI + total human)					
p(Julian ² + trail width)	10	958.17	1.15	0.06	935.46
ψ (elevation + chaparral + NDVI + total human)					
$p(Julian^2 + trail width)$	10	958.23	1.21	0.06	935.52
ψ (elevation + chaparral + total human)					
$p(Julian^2 + trail width)$	9	958.27	1.25	0.06	938.08
ψ (elevation + chaparral + NDVI)					
$p(Julian^2 + trail width + total human)$	10	958.28	1.25	0.06	935.56
ψ (elevation + chaparral + pedestrian)	0	0.50 / 0		~ ~ -	
$p(Julian^2 + trail width)$	9	958.43	1.41	0.05	938.24
ψ (chaparral)	0	0.50 / /		~ ~ -	o .o - .
$\frac{p(Julian^2 + trail width + total human)}{p(Julian^2 + trail width + total human)}$	8	958.44	1.42	0.05	940.71
$\psi(.)p(.)$	3	970.62	13.60	0.00	964.35
Raccoon ($\hat{c} = 0.75$)					
ψ (development + NDVI)	_				
p(riparian + fire + cyclist)	7	659.28	0.00	0.12	643.94
ψ (development + NDVI)	_	150 00	0.50		
p(riparian + NDVI + pedestrian)	1	659.80	0.52	0.09	644.47
ψ (development + NDVI)			0.07	0.00	
$\frac{p(riparian + NDVI)}{p(riparian + NDVI)}$	6	660.14	0.86	0.08	647.15
ψ (development + chaparral + NDVI)	_		0.00	0.00	< + + ^ =
$\frac{p(\text{tire} + \text{NDVI})}{p(1)}$	7	660.21	0.93	0.08	644.87
ψ (development + NDVI)	,		4 40	0.01	
p(riparian + tire)	6	660.75	1.48	0.06	64/./6

ψ (development + chaparral + NDVI)					
p(fire + NDVI + pedestrian)	8	660.80	1.52	0.06	643.06
ψ (development + NDVI)					
p(riparian + NDVI + total human)	7	660.80	1.52	0.06	645.47
$\psi(.)$ p(.)	2	697.87	38.59	0.00	693.74
Striped skunk ($\hat{c} = 1.02$)					
ψ (development + fire + NDVI)					
p(fire + Julian ²)	8	535.69	0.00	1	517.96
$\boldsymbol{\psi}(.)\mathbf{p}(.)$	2	578.20	42.51	0	574.09

Table 2.3. Mammal relative activity rate negative binomial regression models ranked by AIC_c. K is the number of parameters, Δ AIC_c is the difference between the AIC_c of the model and the best-supported model, w is the Akaike weight, and -2/is twice the negative log likelihood. Only models with Δ AIC_c \leq are shown.

Model	K	QAIC _c	$\Delta QAIC_c$	w	-21
Bobcat					
NDVI + fire + pedestrian	5	1272.40	0.00	0.40	1261.70
NDVI + fire + total human	5	1272.68	0.28	0.35	1261.98
NDVI + fire	4	1273.97	1.57	0.18	1265.51
Coyote					
chaparral + NDVI + total human	5	2998.11	0.0	0.75	2987.41
Gray fox					
fire + elevation + pedestrian	5	778.01	0.00	0.51	767.32
fire + elevation + total human	5	778.88	0.87	0.33	768.18
Ground squirrel					
chaparral + elevation	4	263.57	0.00	0.26	255.11
chaparral + elevation + pedestrian	5	264.59	1.01	0.16	253.89
chaparral + elevation + total human	5	264.78	1.21	0.14	254.08
chaparral + fire	4	265.11	1.54	0.12	256.65
chaparral + elevation + cyclist	5	265.16	1.58	0.12	254.46
Jackrabbit					
$NDVI + Julian^2 + cyclist$	6	1190.22	0.00	0.99	1177.24
Mule deer					
$NDVI + Julian^2 + total human$	6	1326.16	0.00	0.55	1313.17
$NDVI + Julian^2 + pedestrian$	6	1327.03	0.87	0.36	1314.04
Rabbit					
fire + Julian ² + cyclist	6	2719.16	0.00	0.29	2706.17
fire + Julian ² + total human	6	2720.11	0.95	0.18	2707.12
fire + Julian ² + pedestrian	6	2720.27	1.11	0.17	2707.28
chaparral + Julian ²	5	2720.67	1.51	0.14	2709.97
Raccoon					
development + NDVI + pedestrian	5	500.84	0.00	0.48	490.14
development + NDVI + total human	5	502.38	1.54	0.22	491.68
development + NDVI	4	502.38	1.54	0.22	493.92
Striped skunk					
elevation + Julian ²	5	448.71	0.00	0.14	438.01
NDVI + elevation	4	449.10	0.39	0.12	440.64
elevation + Julian ² + cyclist	6	449.26	0.55	0.11	436.27
NDVI + elevation + cyclist	5	449.50	0.79	0.10	438.80
NDVI + elevation + total human	5	450.31	1.60	0.06	439.61
elevation + Julian ² + total human	6	450.40	1.69	0.06	437.41



Figure 2.1. Total human activity at 92 sampling points on weekend days and weekdays (mean count per day). Error bars show one standard error.



Figure 2.2. Probability of habitat use of seven mammal species in relation to daily counts of total human activity, cyclists, and pedestrians, from the best-supported single-species occupancy models that included the specified covariate. Shaded areas show 95% confidence intervals.



Figure 2.3. Beta coefficients and 95% confidence intervals for the relationship between daily counts of human activities (total activity, cyclists, pedestrians) and mammal habitat use, detection probability, and relative activity. Each coefficient and corresponding confidence intervals is drawn from the best-supported occupancy or negative binomial regression models containing the specified human covariate.



Figure 2.4. Beta coefficients and 95% confidence intervals for the relationship between habitat, topography, and human covariates and mammal habitat use, from single-species occupancy models selected as the best model containing the specified covariate.



Figure 2.5. Beta coefficients and 95% confidence intervals for the relationship between habitat, topography, and human variables and mammal detection probability, from single-species occupancy models selected as the best model containing the specified covariate.



Figure 2.6. Relative activity rates (sum of hours detected over the four-week sampling period) of nine mammal species in relation to daily counts of total human activity, from the best-supported negative binomial regression models that included the specified covariate. Shaded areas show 95% confidence intervals.



Figure 2.7. Beta coefficients and 95% confidence intervals for the relationship between habitat, topography, and human covariates and mammal relative activity rates, from negative binomial regression models selected as the best model containing the specified covariate.

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CHAPTER 3 : REPTILE COMMUNITY RESPONSES TO RECREATION IN URBAN HABITAT FRAGMENTS³

Summary

The world is urbanizing rapidly, resulting in increasing rates of habitat loss and fragmentation. Protected areas are commonly established to restrict development and conserve native ecological communities, but urban protected areas often receive high levels of recreational activity, which can reduce their conservation effectiveness because of disturbance to animals. Recreation has negative consequences for many animal species, but its effects on reptiles are largely unknown. We evaluated the effects of non-consumptive recreation on reptiles within urban protected areas in a fragmented landscape in coastal southern California, USA. We surveyed for lizards and snakes, quantified human activity, and modeled species richness, community composition, and occupancy in relation to human activity along with other variables known to affect reptile distributions. We observed a decline in reptile species richness in association with human activity, which was primarily driven by a decrease in lizard richness. The proportion of specialist species was not related to recreation, but smaller-bodied lizards were less common at sites with high human activity. Human activity was associated with a decline in occupancy of the common sideblotched lizard (Uta stansburiana), a slight but uncertain decline in occupancy of the orange-throated whiptail (Aspidoscelis hyperythra) and no relationship with western fence lizard (Sceloporus occidentalis) occupancy. Our study demonstrates that increasing rates of recreation activity can reduce the ability of urban protected areas to conserve diverse reptile communities.

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Introduction

Half of the world's human population currently lives in urban areas, and this figure is expected to grow to two-thirds by 2050 (United Nations 2014). The rate of land conversion to urban development exceeds the urban population growth rate (Seto et al. 2011), leading to rapid habitat loss and fragmentation. Urbanization also affects ecological communities through the removal and introduction of plant and animal species (McKinney 2002; Martin et al. 2004), exposure to pollutants and pesticides (Paul & Meyer 2008), changes to resource availability and biogeochemical processes (McDonnell et al. 2008), among other effects (Reed et al. 2012). By 2030 it is expected that urbanization will encroach upon or destroy the habitat of 205 species listed as critically endangered or endangered by the IUCN (Seto et al. 2012), and in the United States, urbanization is linked to the decline of over half the species listed as threatened or endangered under the U.S. Endangered Species Act (Czech et al. 2000).

Typically, animal responses to urbanization vary with life history traits. Those able to persist or even thrive in urban landscapes tend to be generalists that can exploit anthropogenic resources in the built environment (e.g., cultivated landscape plants or garbage; McKinney 2002). While responses of birds and mammals to urbanization are increasingly understood (Aronson et al. 2014), reptile responses to urbanization are rarely studied (Magle et al. 2012), and their distribution patterns are poorly represented by those of other vertebrates (Powney et al. 2010). Grant et al. (2011) hypothesized that "urbanophile" reptiles and amphibians are habitat and dietary generalists with high mobility and reproductive output and small body size, "urbanophobes" are habitat and dietary specialists with low mobility and low reproductive output, and "urbanoblivious" are species that can persist in isolated refugia with a mix of traits from the other categories. For example, urbanoblivious species include small-bodied specialists with limited dispersal abilities and home ranges that persist in urban landscapes when relatively small habitat fragments, such as open space preserves or riparian

corridors, can meet their habitat requirements. Thus, understanding the effects of human disturbance on small, low-mobility habitat specialists in urban areas is critical for their conservation since they depend on remaining intact habitat and have limited ability to move to other suitable habitat.

Protected areas are commonly established to restrict development and conserve native ecological communities threatened by urbanization (Watson et al. 2014). In urban areas, protected areas face increased pressures, such as fragmentation and edge effects (Woodroffe & Ginsberg 1998), loss of connectivity (Braaker et al. 2014), invasive species (Riley et al. 2005) and pollution (Grimm et al. 2008). These threats are growing as residential development intensifies around protected areas (Mcdonald et al. 2008; Radeloff et al. 2010). With more people living nearby, protected areas have increased rates of human activity, including recreation, within their boundaries (Chung et al. 2018; Larson et al. 2018). In this way, parks and preserves with high levels of human activity could be ecological traps (Schlaepfer et al. 2002) if populations decline but animals are not able to move to alternate habitat because of the impermeability of the urban matrix (Delaney et al. 2010).

Recreation has negative effects on many animal species (Martínez-Abraín et al. 2010; Sato et al. 2013; Larson et al. 2016; Larson et al. 2019), and thus protected areas with high human use may not effectively conserve sensitive species. Reptile responses to recreation are not well understood; fewer than 6% of published studies of recreation impacts on animals focus on reptiles, but they are the taxa most frequently impacted, with 63% of studies observing significant effects (Larson et al. 2016). Reptiles are likely to be vulnerable because they are targets of unsustainable collection (Gibbons et al. 2000), they may be drawn to trails for thermoregulation (Mccardle & Fontenot 2016), human activity is a source of direct mortality along roads and trails (Rochester et al. 2001), and they are sensitive to displacement by competitor and predator species adapted to human activity

(Spinks et al. 2003). Prior studies have shown that recreation can affect the survival (Iverson et al. 2006), population size (Garber & Burger 1995), and physiological condition (Amo et al. 2006) of reptiles. However, most studies focus on individual reptile species; we are not aware of prior studies on the effects of recreation on reptiles at the community level.

We evaluated the effects of non-consumptive recreation on the species richness, community composition, and occurrence of reptiles within habitat fragments in an urbanized landscape. We hypothesized that in areas with higher recreational activity, sensitive species would disappear, thereby reducing species richness and shifting community composition toward greater representation of urbanophile species. We also examined how traits associated with urbanoblivious species (e.g., habitat specialization and small body size) are related to human activity; if these traits are associated with negative responses, recreation may reduce the suitability of habitat fragments that would otherwise support populations of such species. To test our hypotheses, we measured recreational activity and reptile occurrence along trails in parks and open space preserves across the urban-wildland interface in San Diego, California, USA. We modeled reptile species richness, community composition, and occupancy as a factor of human activity as well as other variables known to affect reptile distributions, such as habitat characteristics and topography. Our findings help establish that recreation is a significant concern for the conservation of reptiles in urbanized landscapes. Our conclusions about the traits that influence reptile responses to recreation can also help researchers and managers identify the species that are the most likely to be affected in other systems.

Methods

Study sites

We conducted our study in 14 publicly-owned parks and preserves ("reserves") in coastal San Diego County, California, all of which are part of the San Diego County Multiple Species Conservation Program. Previous recreation monitoring in the region showed variation in recreation activity ranging from zero to over 1,800 people per day at the reserve level (Larson et al. 2018). Based on this work, we selected reserves from a pool of potential study areas to span a gradient in expected human activity, including two reserves closed to the public. Reserves were at least 100 ha in size. The vegetation communities were variable and included chaparral, coastal sage scrub, native and nonnative grasslands, oak and sycamore woodlands, and riparian habitats.

We located 92 sampling points along official and unofficial trails within the study reserves. Points were allocated to reserves proportionally based on length of the total trail network and reserve area, such that a minimum of three and a maximum of 12 points were located within each reserve. The point locations were selected using a spatially balanced random design using the RRQRR algorithm on the rasterized trail network (Theobald et al. 2007). Visitation rates can be highly variable within a single reserve (Taczanowska et al. 2014), and even reserves with high total visitation rates likely have low-use areas within them. Therefore, to ensure that our study included sampling points with high levels of human use, we allocated greater weight to trail cells expected to receive higher use, based on a) distance from the nearest trailhead and b) estimates of daily human use at trailheads from Larson et al. (2018). We removed trail cells within 100 m of a road or residential parcel to avoid confounding the effects of recreation with those of roads and development. We generated 296 points and screened potential points using aerial imagery and initial field visits, removing point locations that were not located on human trails (e.g., ridgelines, streambeds) and points with excessively steep slopes or thick vegetation such that coverboards could not be placed and visual surveys could not be conducted. In closed reserves, we ensured that sampling points were located on service roads or wildlife trails similar in structure (e.g., width) to recreational trails.

Sampling methods

We sampled the reptile community with a combination of artificial cover surveys and visual encounter surveys. Artificial cover objects (e.g., plywood, carpet, or tin sheets) mimic natural cover such as rocks and logs, create microhabitats sought out by reptiles for thermoregulation and refugia, can be easily surveyed without damaging natural habitat, and can detect both surface-dwelling and fossorial reptile species (Ryan et al. 2002; Willson 2016). Each sampling point had an array of four coverboards varying in size and material to maximize detections of different species (Grant et al. 1992) and consisted of one 61 x 122 cm plywood board, two 61 x 61 cm plywood boards, and one 61 x 61 cm piece of carpet. Coverboards were allowed to age in place for a minimum of five weeks, and then were checked 14-17 times between January 2017 and June 2018. In combination with coverboard checks, we conducted visual transect surveys in which an observer slowly walked a 400m transect along the trail, centered at the sampling point, scanning for animals and recording the number and species of all individuals sighted. We rotated the order in which points were sampled and recorded air temperature, cloud cover, and wind speed at the start of each survey. Detections from the coverboards and the visual encounter survey were pooled for each survey visit.

To monitor human activity, we installed a motion-triggered camera (Bushnell TrophyCam HD Aggressor) at each sampling point. Cameras were housed in locked metal security boxes and affixed to metal poles pounded into the soil facing recreational trails. Cameras were programmed to take two pictures per trigger with a five second delay between triggers. Sampling periods were four weeks, with a check after approximately two weeks, and sampling periods were repeated four times

between January 2017 and February 2018 to capture seasonal variability in human use. High temperatures, rapidly growing vegetation, and wind led to large numbers of "false triggers" at many camera locations, mostly in the mid-morning to late afternoon. Therefore, we randomly selected 20% of photos between 11 am and 5 pm for viewing and identification to reduce time spent sorting photos. Photos and metadata were stored and organized in the Colorado Parks & Wildlife Photo Warehouse (Ivan & Newkirk 2016). Humans appearing in photos were categorized by activity (pedestrian, cyclist, equestrian, vehicle). Domestic dogs were considered human-associated, since daily counts were highly correlated with human counts (r = 0.85). Pairs of photos taken from the same trigger were labeled identically (using the higher count of people from the two) and then total counts were divided by two to correct for duplicate photos. We summed counts of all human activities (including dogs) as a measure of total overall human activity, and used the mean daily counts as our primary human activity variable. For dates in April-June 2018, when we conducted reptile surveys but the camera traps were not operational, we used human activity data from similar dates in 2017 in our analyses.

We surveyed vegetation using a point-intercept transect technique modified from Fisher et al. (2008). We established two transects originating at the edge of the trail and extending 10 m into the vegetation on the side of the trail where the coverboards were located. If boards were on both sides of the trail, one transect was established on each side. At 0.5 m intervals, we held a measuring rod vertically to the ground and recorded each plant species that touched the rod and their heights, using general categories for grasses and forbs. After completing the transects, we recorded any incidental plant species in the general area of the sampling point (roughly within 10 m on either side of transects) that were not recorded at any point on the transects. All vegetation surveys were conducted between mid-May and mid-June when most vegetation was at its maximum height and greenness.

Vegetation data were summarized into percent cover by species at each sampling point. Plants incidentally recorded at the site but not the sampling transects were assigned a percent cover value of 1% (Fisher et al. 2008). Plant cover often summed to > 100% because multiple plants could be recorded at the same transect point. We removed plant species that we found at fewer than five sampling points, then used non-metric multidimensional scaling (nMDS) to reduce the number of dimensions of the data while preserving as much information as possible (Beals 2006), using the *vegan* package for R (Oksanen et al. 2018). We used the Bray-Curtis distance measure and reduced to two dimensions based on preliminary analysis in which we varied the number of dimensions and examined reduction in the stress metric. To interpret the resulting nMDS dimensions, we examined the highest and lowest scores of individual plant species on each nMDS dimension and qualitatively described the associations of these species.

Model covariates

We hypothesized that reptile species richness, community composition, and occupancy were primarily driven by habitat characteristics, topography, and human activity. Specifically, to describe habitat we used plant community composition as represented by the two dimensions from the nMDS analysis, plant greenness as measured by the normalized difference vegetation index (NDVI), and years since the last recorded fire (Table 3.1). For topography, we included solar radiation and elevation, and we eliminated slope and aspect after preliminary analysis showed that they had little relationship reptile species richness, community composition, or occupancy. For human activity, we used mean daily counts of pedestrians, cyclists, and total human activity. Due to low counts of equestrians and vehicles, we did not model relationships between these activities and our response variables, but did include them in counts of total human activity. We tested all variables for collinearity and eliminated variables with a correlation coefficient greater than 0.7 (Burnham &

Anderson 2002). All variables were scaled (by subtracting the mean and dividing by the standard deviation) to allow for comparisons among regression coefficients.

Species richness and community composition analysis

We used species accumulation models to estimate the number of undetected species at each sampling point. These models use counts of individuals and assume that the number of undetected species is related to the number of species detected only once or twice (Chiu et al. 2014). We used the Chao estimator with the small-sample correction term, implemented with the *vegan* package for R (Oksanen et al. 2018). We then used linear regression models to assess the relationships between estimated species richness and habitat, topography, and human activity variables. To further investigate patterns in species richness, we also separately examined the richness of snakes and lizards, and the richness of species primarily detected via coverboards (mostly nocturnal and/or fossorial species) versus those primarily detected via visual transects (mostly diurnal and/or surface-active species).

To assess whether species traits influence their response to human activity rates, we assigned each species to categories describing their habitat specificity (specialist or generalist, Franklin et al. 2009) and gathered body size data from the literature (median adult snout-vent length [SVL]; Lemm 2006; Table 3.2). We restricted the body size analysis to lizards since we rarely detected snakes but they can vary widely in body size. For each sampling point, we calculated the relative dominance of specialists (the proportion of specialist species and the proportion of detections of specialist species) and the mean lizard body size (the mean body size of all species detected at the point and the mean body size of all individuals detected at the point). We used beta regression models to test how the relative dominance of specialists varied in association with habitat, topography, and human activity variables (Hinners et al. 2012; Farr et al. 2017), and linear regression models to evaluate how mean lizard body size varied in response to these variables.

For the species richness linear regression models and the community composition beta and linear regression models, we built a series of models with a maximum of two habitat variables and one topography variable. We used Akaike's information criterion corrected for small sample size (AIC_c) to rank and compare models (Burnham & Anderson 2002) using the R package *AICcmodavg* (Mazerolle 2019), and then added each human activity covariate (singly) to each of the models with $\leq 2 \Delta$ AIC_c. We considered human activity to have an important effect if models containing human activity variables reduced AIC_c values. We also examined the effect size of human activity compared to other variables by comparing regression coefficients and their confidence intervals.

Single-species occupancy analysis

We had sufficient detections to model occupancy of three lizard species: the orange-throated whiptail (*Aspidoscelis hyperythra*), western fence lizard (*Sceloporus occidentalis*), and common sideblotched lizard (*Uta stansburiana*). Though selected for modeling because of greater numbers of detections, these species vary in their degree of habitat specialization and body size; side-blotched lizards are the smallest (median 5.1 cm SVL) and are intermediate in terms of specialization, orange-throated whiptails are small (median 6.0 cm SVL) and the most specialized, and western fence lizards are a medium-sized (median 7.6 cm SVL) and highly generalist species (Lemm 2006). We modeled the occurrence of these three lizards using single-species, single-season occupancy models with implicit dynamics (MacKenzie et al. 2017) using the R package *unmarked* (Fiske & Chandler 2011). Each combination of sampling point and sampling period was treated as an independent data point (O'Connell et al. 2006). This allowed us to use mean human activity during the camera rotation as a predictor of occupancy rather than mean human activity across the duration of the study, which was important because of seasonal increases in human activity at many of our sampling locations that coincided with the breeding season of most reptile species. To avoid inflating our sample size as a consequence of this approach, we used the number of sampling points (n=92) as the effective sample size in model comparison and selection. We removed survey data from late October to mid-February when the focal species are relatively inactive and difficult to detect, so each sampling point had data from 10-12 repeat surveys in total (2-3 per camera rotation).

We hypothesized that lizard occupancy was related to habitat characteristics, topography, and human activity, and we used the same list of variables from the species richness and community composition analyses (Table 3.1). We expected that lizard detection probability was a function of weather (i.e., cloud cover, wind speed, and temperature), temporal variability (i.e., Julian date and time of day), and the observation process (i.e., observer, survey effort, and trail width; Table 3.1). We also included total human activity as a covariate for detection probability because lizards may respond to humans behaviorally in a way that affects their detectability (e.g., hiding or fleeing), or use the habitat less frequently. Human activity could also influence local abundance at occupied sampling points, which would affect detection probability (Royle and Nichols 2003).

We used a stepwise model building procedure (Lebreton et al. 1992), first running models to determine the variables that best explained detection probability (p) while holding occupancy (ψ) at a global structure, constant across all species, that included plant community composition, elevation, years since fire, NDVI, and solar radiation. We used Akaike's information criterion corrected for small sample size (AIC_c) to rank and compare occupancy models (Burnham and Anderson, 2002). We used combinations of variables for detection probability from all models with $\leq 2 \Delta \text{ AIC}_c$ in the next step, assessing how occupancy varied in relationship to habitat and topography variables. We limited occupancy structures to two habitat variables and one topography variable, and ran all possible combinations of additive models (30 models for each detection structure). Finally, we added

each of the human activity covariates (singly) to each of the models with $\leq 2 \Delta$ AIC_c as a covariate on detection probability, occupancy, and both, and again ranked and compared models. We considered human activity to be an important predictor if models containing human activity variables reduced AIC_c values. We also examined the direction and magnitude of the human activity effect by comparing the regression coefficient point estimates and their confidence intervals to those of other variables. In text and figures, we report results for the best-supported models containing the specified covariate(s). We used a parametric bootstrapping procedure evaluate goodness-of-fit and overdispersion (MacKenzie & Bailey 2004). When the results of this procedure showed that there was overdispersion in the data, we adjusted the model selection results using the estimated overdispersion parameter (\hat{c}), resulting in a QAIC_c value.

Results

We collected 1077 detections of 11 lizard and 11 snake species over 1305 survey occasions (Table 3.2). Visual transect surveys accounted for 85.1% of total detections, and coverboard and transect methods detected 17 species each, with 12 species detected using both survey methods. The distribution of species detections was skewed; we detected the three most commonly observed species more than 200 times (common side-blotched lizard [431 detections], western fence lizard [247], orange-throated whiptail [205]), a middle group of six species between 10 and 53 times, and 13 species less than 10 times. We detected a mean (\pm SD) of 3.6 \pm 1.5 species per sampling point (range: 0 - 8) over the course of the study.

Overall mean (\pm SD) human activity across all sites was 41.8 \pm 144.9 (range: 0 - 3401) people, vehicles, and dogs per day. Pedestrians were the most common human activity with a mean daily count of 33.3 \pm 134.5 (range: 0 - 3249) and were present at 97.8% of sites, followed by dogs, which averaged 4.1 \pm 10.2 per day (range: 0 - 173) and were present at 89.1% of sites. Cyclists

averaged 3.2 ± 11.6 per day (range: 0 - 303) and were present at 83.7% of sites, equestrians averaged 0.6 ± 2.9 per day (range: 0 - 67) and were present at 50.0% of sites, and motorized vehicles averaged 0.5 ± 2.4 per day (range: 0 - 46) and were present at 63.0% of sites.

Twenty-six plant species, genera, and general categories (e.g., grass, forb) were observed at more than five of the sampling points and were used in our vegetation analysis. The plants with the highest scores on nMDS dimension 1 were black sage (*Salvia mellifera*), chaparral yucca (*Hesperoyucca whipplei*), manzanita (*Arctostaphylos spp.*), and chamise (*Adenostoma fasciculatum*), all plants associated with chaparral communities. The lowest scores were assigned to thistles, grasses, and oaks (*Quercus spp.*). Plants with high scores on nMDS dimension 2 were black sage, lemonade berry (*Rhus integrifolia*), *Ceanothus spp.*, and manzanita, all coastal sage scrub/chaparral plants. Plants with the lowest scores on nMDS dimension 2 were San Diego sunflower (*Viguiera laciniata*), buckwheat (*Erigonum fasciculatum*), invasive mustard (*Brassica spp.*), and singlewhorl burrobrush (*Ambrosia monogyra*), the last two of which are common in disturbed areas. Therefore, we interpret nMDS1 as a continuum between chaparral and grassland/oak woodlands, and nMDS2 as separating coastal sage scrub and chaparral communities from more disturbed coastal sage scrub.

Species richness and community composition

The total number of species across all sampling points, including undetected species, was estimated to be 26 \pm 5.2 using the Chao estimator. Human activity was associated with a decline in estimated species richness (Figures 3.1, 3.3). Total human, pedestrian, or cyclist activity were included in seven of eleven top models with $\Delta AIC_c \leq 2$ (Table 3.3), and each of the four best-supported regression models contained either total human or pedestrian activity rates. Cyclist activity had a negative but less precise relationship with estimated species richness than pedestrian and total human activity. Lizard richness declined in association with human activity, while snake richness was

not strongly related to human activity (Figure 3.2a). Richness of species detected primarily with coverboards (n=9) and of species detected primarily with visual transects (n=13) declined slightly as human activity increased (Figure 3.2b). Species richness was positively related to NDVI (Figure 3.3), which was included in all eleven best-supported models (Table 3.3). Years since fire was included in six of eleven top models and had a negative association with species richness. Elevation was included in four of eleven top models and had a positive association with species richness. The magnitude of the human activity effect size was similar to or greater than all other covariate effect sizes except for the effect size of NDVI (Figure 3.3).

The proportion of specialist species per sampling point averaged 0.29 \pm 0.22, and the proportion of specialist detections averaged 0.25 \pm 0.23. Neither the proportion of specialist species nor the proportion of specialist detections showed a clear trend in relation to human activity (Figure 3.4), and the beta regression models performed poorly with a pseudo-R² of 0.03 for each of the top models. Cyclist activity was selected in one of the three best-supported models for proportion of specialist detections included two models with a human activity variable (cyclist and total human activity; Table 3.4), though effects were weak.

Mean lizard body size increased as human activity increased, more strongly when it was calculated as a mean of all individuals detected (Figure 3.5). Seven of nine best-supported linear regression models for body size of species included a human activity variable and all eight best-supported models for body size of individuals included pedestrian or total human activity (Table 3.5). The top linear regression models had an R² of 0.15 for body size of species and 0.28 for body size of individuals. Other covariates affecting mean body size included NDVI (positive effect), elevation (positive), nMDS1 (negative), and years since fire (positive).

Single-species occupancy

Human activity was an important predictor of common side-blotched lizard occupancy. Each of the five best-supported occupancy models contained either total human or pedestrian activity rates (Table 3.6). Common side-blotched lizard occupancy was negatively related to all three human activity variables, most strongly for total human and pedestrian activity (Figures 3.6, 3.7); these effect sizes were larger than any other covariate except years since fire (Figure 3.8). nMDS2 and years since fire had negative relationships with occupancy, while elevation and solar radiation had positive but imprecise relationships with occupancy (Figure 3.8). Common side-blotched lizard detection probability was higher in sunny conditions and varied among observers.

Orange-throated whiptail occupancy models that included human activity did not outperform those built with environmental variables only, appearing in only five of the seventeen best-supported models and none of the top eight (Table 3.6). Total human and pedestrian activity were negatively related to occupancy and cyclist activity was slightly positively related to occupancy (Figures 3.6, 3.7). However, the effect sizes of most environmental variables were similar to or smaller than the effect of human activity except for elevation. Orange-throated whiptail occupancy was negatively related to nMDS2, years since fire, and elevation, and positively related to nMDS1 and NDVI (Figure 3.8). Orange-throated whiptail detection probability was higher in sunny conditions, in summer months (June-August), and with greater search effort (> 1 observer).

Western fence lizard occupancy had little relationship to human activity. One of the four best-supported models included total human activity as a predictor of occupancy (Table 3.6), but coefficients for total human and pedestrian activity were approximately zero (Figure 3.7). There was a slight negative relationship between occupancy and cyclist activity (Figures 3.6, 3.7). NDVI and solar radiation were the only two environmental variables selected in top models for the western fence lizard (Table 3.6). Occupancy was positively related to NDVI and solar radiation; these effects

sizes were both considerably larger than the effect size of total human activity (Figure 3.8). Human activity, included in the detection structure of three of the four top models, was a better predictor of western fence lizard detection probability than occupancy (Table 3.6). Detection probability was positively related to human activity and was higher in late spring and early summer, with moderately warm temperatures (70-80 degrees F).

Discussion

Human recreation activity had a negative relationship with reptile species richness in habitat fragments in an urbanized landscape. The decline in overall richness was driven primarily by reduced lizard richness; snake richness showed little relationship to human activity. Specifically, small-bodied lizards, but not specialist species, were less common in sites with more recreation. Human activity, including both pedestrian and cyclist activity, was also associated with declines in occupancy of the common side-blotched lizard. The orange-throated whiptail showed a slight decline in occupancy in relationship to human activity, but there was considerable uncertainty. Western fence lizard occupancy declined slightly in association with cyclist activity but was unrelated to pedestrian or total human activity.

The decline in lizard richness associated with human activity parallels observed declines in bird and mammal richness in connection to human activity (e.g., Bötsch et al. 2018, Reed & Merenlender 2011, Banks & Bryant 2007). A recent meta-analysis found that vertebrate richness or abundance was reduced in association with higher recreation activity in 70% of comparisons (Larson et al. 2019). In addition, our results are consistent with the findings of Ficetola et al. (2007) who observed a decrease in reptile species richness in association with the presence of people in an urban park in northern Italy, though the community comprised only four species of lizards and snakes.

We hypothesized that reptile richness would decline because sensitive species would disappear from sampling locations with higher human activity. However, we did not find evidence for differential responses of specialists and generalists. It is possible that our binary categorization of specialists and generalists was not sensitive enough to detect how smaller differences in habitat use (e.g., use of human-modified areas) influenced tolerance of recreation. Instead, we found evidence that smallbodied lizards may be more sensitive to human disturbance, since they were less likely to be found in areas with high levels of human activity. This relationship was more pronounced when we examined mean body size of individuals, probably because of frequent detections of the common sideblotched lizard and orange-throated whiptail. Nevertheless, the similar but weaker relationship between mean body size of lizard species and human activity suggests a more general pattern of differential responses to human activity based on body size.

Lizard flight initiation distance (the distance from a stimulus at which an animal initiates an escape response) generally increases with body size, meaning that smaller lizards permit closer approaches by humans before fleeing (Samia et al. 2016), possibly because smaller-bodied species are more sensitive to reduced foraging success than larger species (Møller 2009). However, in birds, smaller species have been shown to be less tolerant of human disturbance than larger birds, meaning that they likely incur higher energetic costs from fleeing more frequently (Samia et al. 2015); if this is true for lizards it could explain our finding that small-bodied lizards are more vulnerable to recreation. Another possibility may be that diurnal, small-bodied lizards tend to bask on or near trails during times of high human activity (e.g., early to mid-morning) to achieve body temperatures suitable for activity. For example, body temperatures of the common side-blotched lizard have been shown to increase over the morning hours and then stabilize throughout the rest of the day (Goller et al. 2014), meaning that they bask to raise their body temperature during the morning, which was the most popular time of day for recreation in our study.

Most reptile species had insufficient detections to model the relationship between occupancy and recreation activity. However, of the three lizards for which we modeled occupancy, two (common side-blotched lizard and orange-throated whiptail) exhibited negative relationships with human activity, though the relationship was stronger and more certain for the common sideblotched lizard. The common side-blotched lizard is the smallest lizard in the region and occurs in arid and semi-arid habitats including coastal scrub, chaparral, woodland, and grassland habitats (Jones & Lovich 2009). Though it can be locally abundant (Franklin et al. 2009), the common sideblotched lizard had lower survival rates in urban areas where physiological stress levels were higher compared to rural areas where stress was lower (Lucas & French 2012). Therefore, the reduced occupancy we observed could result from a pattern of diminished survival in areas with high levels of human disturbance. Although it is a generalist, the common side-blotched lizard is rarely found in more altered landscapes such as yards and landscaped urban parks and has limited dispersal ability (Doughty & Sinervo 1994). Its inability to move between isolated habitat fragments can result in substantial genetic isolation among populations (Delaney et al. 2010).

We expected that the orange-throated whiptail, a species of conservation concern listed under the San Diego County Multiple Species Conservation Plan (MSCP Policy Committee & MSCP Working Group 1998), would be more sensitive to human activity than the other lizard species. It has the most specialized habitat requirements of the three, occurring only in coastal sage scrub and chaparral, often in association with buckwheat, black sage, white sage, and chamise, and is rarely found in degraded or developed areas (Jones & Lovich 2009). However, we found that the species is more likely to occur in chaparral communities but within those areas, showed a preference for somewhat disturbed vegetation communities. We observed a negative trend between occupancy and human activity, but with considerable uncertainty. A lack of flexibility in habitat use may prevent the orange-throated whiptail from moving away from human activity if there is little suitable habitat

nearby (Gill et al. 2001), as it is small and has limited dispersal ability (Delaney et al. 2010). Previous studies have shown that prey abundance, specifically abundance of *Crematogaster* ants, is an important predictor of orange-throated whiptail abundance (Ver Hoef et al. 2001). We did not quantify prey abundance, but native ant communities are known to decline in the presence of the exotic Argentine ant (*Linepithema humile*), which is more abundant near development and in areas with non-native vegetation (Suarez et al. 1998). Human activity also increases near residential development (Larson et al. 2018) and is associated with introduction of exotic plants (Anderson et al. 2015), and so disturbance from recreation could work synergistically with prey declines to decrease habitat suitability for the orange-throated whiptail.

The limited response of the western fence lizard to human activity was not surprising. It is a medium-sized habitat generalist that is tolerant of humans, inhabiting many types of natural habitat as well as backyards and highly modified city parks (Jones & Lovich 2009). However, it did show a slight decline in occupancy in response to cyclist activity. Anecdotally, we observed several dead western fence lizards on trails frequented by cyclists, as did Rochester et al. (2001). The western fence lizard had a higher probability of detection associated with higher levels of human activity. One possible explanation is that western fence lizards, true to their name, are commonly found basking and foraging on fences (Jones & Lovich 2009), and fences may be more common in areas with higher human activity to prevent people from straying from authorized trails, or near the boundaries of reserves and private developments where human use is also higher. Another potential explanation is that lizards inhabiting areas with high human activity may habituate to human disturbance (Rodríguez-Prieto et al. 2010) and are therefore more detectable in higher-use areas. However, prior behavioral studies on this species show mixed results. Putman et al. (2017) found no differences in escape behavior between areas with high and low human activity, potentially indicating a lack of habituation. In contrast, Grolle et al. (2014) documented longer flight initiation distances in

areas with low human activity compared to high, suggesting that western fence lizards do habituate to human presence.

Although we detected 22 reptile species, the numbers of detections were skewed, with many detections of a just few species, allowing us to model only the three most commonly-detected species in species-specific models. While threats to threatened and declining species with small population sizes are perhaps a more pressing conservation problem, it is also important to consider ecological effects of declines in abundant species (Adams et al. 2013; Baker et al. 2018). More than a quarter of species become functionally extinct before losing just 30% of the individuals in a population (Säterberg et al. 2013). In our system, the side-blotched lizard is an important prey species for a wide variety of species including other lizards, snakes, birds, and mammals (Jones & Lovich 2009), so its strong negative response to recreation could potentially affect species at higher trophic levels.

Our sampling points were all located on recreational trails, and we were not able to quantify the effect zone of recreational disturbance extending away from the trail. However, behavioral metrics such as alert distance (the distance from a stimulus at which an animal initiates vigilance behavior) and flight initiation distance may provide insight into recreation effect zones (Guay et al. 2016). For example, we might expect cyclists to have a stronger effect on reptile communities since approach speed influences lizard escape behaviors, with faster approaches triggering flight at a greater distance (Samia et al. 2016). Yet we found that cyclist activity was linked to similar or lesser effects than pedestrian activity in most cases. Lizard habitat selection can also affect escape behavior, with greater flight distances when lizards are further from refugia, on low perches, or in open habitats (Samia et al. 2016). Thus, in habitats that have become more open (e.g., from proliferation of unauthorized trails), restoration may help mitigate the effects of recreation (Coppes et al. 2018) by reducing the probability of flight. On the other hand, fire frequency, which tends to

open habitat, was an important positive predictor of occurrence for the orange-throated whiptail and side-blotched lizard, suggesting that open habitat may also have benefits for these species.

This study shows that human recreation activity can reduce the ability of urban habitat fragments to conserve a diverse reptile community, and it may especially affect small-bodied lizard species. The negative effects of recreation compound the numerous conservation challenges in fragmented landscapes, such as lack of connectivity and the resulting loss of genetic diversity in isolated populations. Accordingly, we recommend that managers carefully plan public access to keep a diversity of areas trail-free and, at least to some extent, to separate high-intensity recreation areas from quality habitat harboring populations of sensitive species. Minimizing the effects of recreation within fragmented protected areas helps ensure that the fragments provide habitat for species whose habitat requirements would otherwise be met, and whose small size and low dispersal ability through the urban matrix limit their ability to seek alternative habitat elsewhere.

				Observed	
	Covariate		Data	range/count	
Covariate	category	Description	source	by category	Parameter
Pedestrians	human	Mean per day	field	0 - 2,826	ψ, SR, CC
Cyclists	human	Mean per day	field	0 - 101.6	ψ, SR, CC
		Mean per day of combined cyclists, pedestrians, dogs,			
Total human	human	equestrians, and vehicles	field	0 -2,949	ψ, p, SR, CC
		nMDS axis from vegetation community data; low values			
		interpreted as grassland/oak woodland, high values			
nMDS1	habitat	interpreted as chaparral	field	-0.1 - 1.5	ψ, SR, CC
		nMDS axis from plant composition data; low values			
		interpreted as disturbed coastal sage scrub, high values			
nMDS2	habitat	interpreted as intact coastal sage scrub/chaparral	field	-1.2 - 1.0	ψ, SR, CC
NDVI	habitat	Index (0-1), within 10m of point	GIS	0.2 - 0.62	ψ, SR, CC
Fire	habitat	Years since fire	GIS	3 - 139	ψ, SR, CC
Elevation	topography	Meters, mean value within 10m of point	GIS	17.3 - 666.5	ψ, SR, CC
		Index (0-255; very cool to very warm), mean value within			
Solar radiation	topography	10m of point	GIS	163.9 - 241.4	ψ, SR, CC
Temperature	weather	°C, measured at start of survey	field	4.4 - 41.1	р
Wind speed	weather	Km/hr, measured at start of survey	field	0 - 16.7	р
		Categorical: sunny 0-50% cloud cover, cloudy 50-100% cloud		sunny: 1081	
Cloud cover	weather	cover	field	cloudy: 224	р
Julian date	temporal	Day of year	field	5 - 358	р
Time of day	temporal	Decimal hours, recorded at start of survey	field	8.0 - 20.1	р
	observation			CL: 654	
Observer	process	Categorical: CL or other (field assistant or volunteer)	field	other: 662	р
	observation				
Search effort	process	Number of observers	field	1 - 3	р
	observation				
Trail width	process	Meters	field	1 - 8.3	р

Table 3.1. Variables used to model occupancy (ψ), detection probability (p), species richness (SR), and community composition (CC)

		Habitat	SVL	Board	Transect	Total
Scientific name	Common name	specificity ^a	(cm) ^b	detections	detections	detections
Lizards						
Uta stansburiana	Common side-blotched lizard	generalist	5.1	50	381	431
Sceloporus occidentalis	Western fence lizard	generalist	7.6	30	217	247
Aspidoscelis hyperythra beldingi	Orange-throated whiptail	specialist	6.0	2	203	205
Aspidoscelis tigris	San Diegan tiger whiptail	generalist	9.4	3	50	53
Plestiodon skiltonianus	Western skink	generalist	7.0	34	1	35
Phrynosoma blainvillii	Blainville's horned lizard	specialist	8.9	0	23	23
Sceloporus orcutti	Granite spiny lizard	specialist	10.0	2	16	18
Plestiodon gilberti	Gilbert's skink	specialist	8.9	9	1	10
Anniella stebbinsi	California legless lizard	specialist	14.4	8	0	8
Elgaria multicarinata	Southern alligator lizard	generalist	12.5	6	1	7
Coleonyx variegatus	San Diego banded gecko	specialist	6.3	1	0	1
Snakes						
Crotalus oreganus helleri	Southern Pacific rattlesnake	generalist	94.0	4	7	11
Pituophis catenifer	Gopher snake	generalist	144.8	3	3	6
Coluber lateralis	California striped racer	generalist	99.1	2	3	5
Lampropeltis californiae	California kingsnake	generalist	91.4	2	3	5
Hypsiglena ochrorhyncha	Coast night snake	generalist	25.4	3	0	3
Thamnophis hammondii	Two-striped garter snake	specialist	61.0	0	3	3
Crotalus ruber	Red diamond rattlesnake	specialist	120.7	0	2	2
Coluber flagellum	Red racer	specialist	129.5	0	1	1
Diadophis punctatus	Ring-necked snake	generalist	34.3	1	0	1
Rhinocheilus lecontei	Long-nosed snake	generalist	58.4	1	0	1
Salvadora hexalepis	Patch-nosed snake	specialist	78.7	0	1	1

Table 3.2. Characteristics of the reptile species detected. SVL is body size as measured by median adult snout-vent length.

^a Franklin et al. (2009) ^b Lemm (2006)

Table 3.3. Species richness linear regression models ranked by AIC_c. K is the number of parameters, Δ AIC_c is the difference between the AIC_c of a given model and the best-supported model, w is the Akaike model weight, and -2/ is twice the negative log likelihood, a measure of fit. Only models with $\leq 2 \Delta$ AIC_c are shown. Human activity variable names are in bold.

Model name	K	AIC _c	ΔAIC_{c}	w	-21
fire + NDVI + total human	5	428.15	0.00	0.11	417.46
NDVI + total human	4	428.34	0.19	0.10	419.88
fire + NDVI + pedestrian	5	428.76	0.61	0.08	418.07
NDVI + pedestrian	4	428.84	0.68	0.08	420.38
fire + NDVI	4	428.94	0.78	0.07	420.48
nMDS1 + NDVI + elevation	5	429.04	0.89	0.07	418.34
fire + NDVI + elevation	5	429.69	1.54	0.05	418.99
NDVI	3	429.75	1.60	0.05	423.48
fire + NDVI + cyclist	5	429.92	1.77	0.05	419.23
nMDS1 + NDVI + elevation + total human	6	429.95	1.79	0.05	416.97
fire + NDVI + elevation + total human	6	429.96	1.80	0.04	417.41

Table 3.4. Proportion of specialist species and specialist detections beta regression models ranked by AIC_c. K is the number of parameters, ΔAIC_c is the difference between the AIC_c of a given model and the best-supported model, w is the Akaike model weight, and -2/ is twice the negative log likelihood, a measure of fit. Only models with $\leq 2 \Delta AIC_c$ are shown. Human activity variable names are in bold.

Model name	K	AIC _c	Δ AIC _c	w	-21
Proportion of specialist species					
nMDS1	3	-174.75	0.00	0.30	-181.03
nMDS1 + cyclist	4	-173.66	1.10	0.17	-182.13
nMDS1 + nMDS2		-173.28	1.47	0.15	-181.75
Proportion of specialist detections					
nMDS2	3	-199.89	0.00	0.28	-206.17
nMDS2 + cyclist	4	-198.92	0.97	0.17	-207.39
nMDS1 + nMDS2	4	-198.77	1.12	0.16	-207.24
nMDS2 + total human	4	-197.90	1.99	0.10	-206.37

Table 3.5. Body size linear regression models ranked by AIC_c. Models of mean lizard body size (snout-vent length) of all species detected per sampling point are shown first, followed by models of mean lizard body size of all individual detected per sampling point. K is the number of parameters, Δ AIC_c is the difference between the AIC_c of the model and the best-supported model, w is the Akaike model weight, and -2/ is twice the negative log likelihood, a measure of fit. Only models with $\leq 2 \Delta$ AIC_c are shown. Human activity variable names are in bold.

Model name	K	AIC _c	ΔAIC_{c}	W	-21
Mean body size of species					
NDVI + cyclist	4	309.87	0.00	0.14	301.40
nMDS1 + NDVI + elevation + cyclist	6	310.13	0.25	0.12	297.12
NDVI	3	310.43	0.56	0.10	304.15
nMDS1 + NDVI	4	311.09	1.21	0.07	302.62
NDVI + pedestrian	4	311.36	1.49	0.06	302.89
nMDS1 + NDVI + cyclist	5	311.42	1.55	0.06	300.71
NDVI + total human	4	311.48	1.60	0.06	303.00
nMDS1 + NDVI + elevation + pedestrian	6	311.55	1.67	0.06	298.53
nMDS1 + NDVI + elevation + total human	6	311.74	1.86	0.05	298.72
Mean body size of individuals					
NDVI + total human	4	294.59	0.00	0.14	286.12
NDVI + pedestrian	4	294.63	0.04	0.13	286.16
fire + NDVI + total human	5	295.47	0.88	0.09	284.76
fire + NDVI + pedestrian	5	296.76	1.17	0.08	285.04
nMDS1 + NDVI + pedestrian	5	296.20	1.61	0.06	285.49
nMDS1 + NDVI + total human	5	296.27	1.67	0.06	285.55
nMDS2 + NDVI + total human	5	296.32	1.73	0.06	285.60
nMDS2 + NDVI + pedestrian	5	296.42	1.82	0.06	285.70

Table 3.6. Common side-blotched lizard (*Uta stansburiana*), orange-throated whiptail (*Aspidoscelis hyperythra*) and western fence lizard (*Sceloporus occidentalis*) occupancy models ranked by QAIC_c. Model names includes variables used to model occupancy (ψ) and detection probability (p). K is the number of parameters, Δ QAIC_c is the difference between the QAIC_c of a given model and the best-supported model, w is the Akaike model weight, and -2/ is twice the negative quasi-log likelihood, a measure of fit. All models with $\leq 2 \Delta$ QAIC_c are shown, as well as a "null" model: ψ (.)p(.). Human activity variable names are in bold.

Model	K	QAIC _c	$\Delta QAIC_{c}$	w	-21
Common side-blotched lizard					
ψ (fire + total human)					
p(cloud cover + observer)	7	541.09	0.00	0.17	525.76
ψ (fire + pedestrian)					
p(cloud cover + observer)	7	541.10	0.01	0.17	525.77
ψ (fire + solar radiation + pedestrian)					
p(cloud cover + observer)	8	541.96	0.87	0.11	524.23
ψ (fire + solar radiation + total human)					
p(cloud cover + observer)	8	542.14	1.05	0.10	524.41
ψ (nMDS2 + fire + total human)					
p(cloud cover + observer)	8	543.07	1.98	0.06	525.33
$\psi(.)$ p(.)	3	584.17	43.07	0.00	525.43
Orange-throated whiptail					
$\psi(ext{fire})$					
p(cloud cover + Julian date ²)	7	428.62	0.00	0.06	413.29
ψ (nMDS1)					
p(cloud cover + Julian date ²)	7	428.80	0.18	0.06	413.47
ψ (nMDS2)					
p(cloud cover + Julian date ²)	7	429.08	0.46	0.05	413.75
$\psi(ext{NDVI})$					
p(cloud cover + Julian date ²)	7	429.45	0.83	0.04	414.12
$\psi(ext{fire})$					
p(cloud cover + Julian date ² + observer no.)	8	429.47	0.84	0.04	411.73
ψ (nMDS1)					
p(cloud cover + Julian date ² + observer no.)	8	429.75	1.13	0.03	412.02
ψ (nMDS2)					
p(cloud cover + Julian date ² + observer no.)	8	430.01	1.39	0.03	412.28
ψ (fire + elevation)					
p(cloud cover + Julian date ²)	8	430.14	1.52	0.03	412.41
ψ (nMDS1 + pedestrian)					
p(cloud cover + Julian date ²)	8	430.15	1.53	0.03	412.42
ψ (nMDS2 + fire)					
p(cloud cover + Julian date ²)	8	430.26	1.64	0.03	412.52
ψ (fire + pedestrian)					
p(cloud cover + Julian date ²)	8	430.31	1.69	0.03	412.58
ψ (nMDS1 + nMDS2)					
p(cloud cover + Julian date ²)	8	430.35	1.73	0.03	412.62

ψ (nMDS1 + total human)					
p(cloud cover + Julian date ²)	8	430.42	1.80	0.03	412.68
ψ (NDVI + pedestrian)					
p(cloud cover + Julian date ²)	8	430.43	1.80	0.02	412.69
ψ (nMDS1 + fire + elevation)					
p(cloud cover + Julian date ²)	9	430.46	1.84	0.02	410.27
ψ (NDVI)					
p(cloud cover + Julian date ² + observer no.)	8	430.50	1.88	0.02	412.77
ψ (fire + total human)					
p(cloud cover + Julian date ²)	8	430.51	1.88	0.02	412.77
ψ(.)p(.)	3	455.46	26.84	0.00	412.92
Western fence lizard					
$\psi(ext{NDVI})$					
p(temperature ² + Julian date ² + total human)	9	378.40	0.00	0.26	358.21
ψ (NDVI)					
p(temperature ² + Julian date ²)	8	379.83	1.43	0.13	362.10
ψ (NDVI + solar radiation)					
p(temperature ² + Julian date ² + total human)	10	380.33	1.92	0.10	357.61
ψ (NDVI + total human)					
p(temperature ² + Julian date ²)	9	380.35	1.94	0.10	360.15
ψ(.)p(.)	3	406.48	28.07	0.00	357.83



Figure 3.1. Estimated sampling-point level species richness (Chao estimator) in relation to daily counts of a) pedestrian b) cyclist, and c) total human activity. The shaded areas show 95% confidence intervals.



Figure 3.2. Estimated sampling-point level richness (Chao estimator) of a) lizards and snakes and b) species grouped by their primary detection method (coverboards or visual transects) in relation to daily counts of total human activity. The shaded areas show 95% confidence intervals.



Figure 3.3. Beta coefficients and 95% confidence intervals for the relationship between habitat, topography, and human covariates and estimated reptile species richness, from linear regression models selected as the best model containing the specified covariate.



Figure 3.4. Proportion of reptile specialist a) species and b) detections in relation to daily counts of total human activity. The line shown is a univariate linear regression model and associated 95% confidence interval.



Figure 3.5. Mean lizard body size of a) species and b) individuals detected at each sampling point in relation to daily counts of total human activity. The line shown is a univariate linear regression model and associated 95% confidence interval.



Figure 3.6. Probability of occupancy of common side-blotched lizard (*Uta stansburiana*), orange-throated whiptail (*Aspidoscelis hyperythra*), and western fence lizard (*Sceloporus occidentalis*) in relation to daily counts of pedestrian, cyclist, and total human activity, from the best-supported single-species occupancy models that included the specified covariate. Shaded areas show 95% confidence intervals.



Figure 3.7. Beta coefficients and 95% confidence intervals for the relationship between daily counts of human activities (number of pedestrians, cyclists, and total human activity) and occupancy of three lizard species (common side-blotched lizard, orange-throated whiptail, and western fence lizard), from single-species occupancy models selected as the best model containing the specified covariate.


Figure 3.8. Beta coefficients and 95% confidence intervals for the relationship between habitat, topography, and human variables and occupancy of three lizard species (common side-blotched lizard, orange-throated whiptail, and western fence lizard), from single-species occupancy models selected as the best model containing the specified covariate.

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APPENDICES

Chapter 1 Appendices

Appendix 1.1. Journals included in the literature search.

Acta Chiropterologica Acta Ethologica Acta Herpetologica Acta Ichthyologica Et Piscatoria Acta Oecologica Acta Ornithologica Acta Theriologica Acta Zoologica Acta Zoologica Bulgarica Advances in Ecological Restoration Advances in Microbial Ecology Advances in The Study of Behavior African Invertebrates African Journal of Ecology African Journal of Herpetology African Journal of Range & Forage Science African Natural History African Zoology American Journal of Primatology American Midland Naturalist American Naturalist Amphibia-Reptilia Animal Behaviour Animal Biology Animal Conservation Annual Review of Ecology Evolution and **Systematics** Applied Animal Behavior Science Applied Ecology and Environmental Research Applied Herpetology Aquatic Ecology Ardea Ardeola Asian Herpetological Research Auk Austral Ecology Australian Journal of Zoology Avian Conservation and Ecology Avian Conservation Ecology **Basic Applied Ecology**

Behavioral Ecology Behavioral Ecology and Sociobiology Behaviour **Behavioural Processes** Belgian Journal of Zoology Bioacoustics - The International Journal of Animal Sound and Its Recording Biodiversity and Conservation **Biological Conservation Biological Invasions Biology** Letters Biotropica Bird Conservation International Bird Study Bulletin of The Peabody Museum of Natural History California Fish and Game Canadian Field-Naturalist Canadian Journal of Zoology-Revue Canadienne De Zoologie Caribbean Journal of Science Chelonian Conservation and Biology Community Ecology Condor Conservation Biology **Conservation Letters** Contemporary Problems of Ecology Contributions to Zoology Copeia Cybium Diversity and Distributions Ecography **Ecological** Applications Ecological Complexity Ecological Modelling Ecological Monographs Ecological Research Ecology Ecology and Society Ecology Letters

Ecoscience Ecosystems Ecotropica Ekoloji Emu Environmental Biology of Fishes Ethology Ethology Ecology & Evolution European Journal of Wildlife Research Folia Primatologica Folia Zoologica Forktail Frontiers in Ecology and the Environment Frontiers in Zoology Gayana Herpetologica Herpetological Conservation and Biology Herpetological Journal Herpetological Monographs Herpetozoa Hystrix-Italian Journal of Mammology Ibis Ichthyological Exploration of Freshwaters Ichthyological Research Integrative Zoology International Journal of Primatology International Journal of Sustainable Development and World Ecology Israel Journal of Ecology and Evolution Italian Journal of Zoology Journal for Nature Conservation Journal of Animal Ecology Journal of Applied Ecology Journal of Arid Environments Journal of Avian Biology Journal of Biogeography Journal of Ecology Journal of Ethology Journal of Experimental Marine Biology and Ecology Journal of Experimental Psychology-Animal Behavior Processes Journal of Field Ornithology Journal of Freshwater Ecology Journal of Herpetology Journal of Mammalogy Journal of Natural History Journal of Ornithology

Journal of Raptor Research Journal of The Experimental Analysis of Behavior Journal of Tropical Ecology Journal of Wildlife Management Journal of Zoology Landscape and Urban Planning Landscape Ecology Mammal Review Mammal Study Mammalia Mammalian Biology Marine Biology Research Marine Ecology-Progress Series Marine Mammal Science Methods in Ecology and Evolution Natural Areas Journal Natural History Nature Neotropical Ichthyology New Zealand Journal of Ecology New Zealand Journal of Zoology Northeastern Naturalist Northwest Science North-Western Journal of Zoology Oecologia Oikos Ornis Fennica Ornithological Science Ornitologia Neotropical Oryx Ostrich Pachyderm Pacific Science Pakistan Journal of Zoology Polar Biology Polar Record Polar Research Polish Journal of Ecology Polish Polar Research Population Ecology Primates Proceedings of the National Academy of Sciences of the United States of America Proceedings of The Royal Society B-Biological Sciences Raffles Bulletin of Zoology Rangeland Ecology & Management

Rangeland Journal Restoration Ecology Russian Journal of Ecology Science South African Journal of Wildlife Research Southwestern Naturalist Spixiana Studies on Neotropical Fauna and Environment Theoretical Ecology Theoretical Population Biology Trends in Ecology & Evolution **Tropical Conservation Science** Tropical Ecology Tropical Zoology Turkish Journal of Zoology Ursus Waterbirds Western North American Naturalist Wetlands Wildlife Biology Wildlife Monographs Wildlife Research Wilson Journal of Ornithology Zoologica Zoologica Scripta Zoological Journal of The Linnean Society Zoological Science Zoological Studies Zoology Zoology in The Middle East

Appendix 1.2. Species richness comparisons

Species	Publication ¹	Recreation substrate	Recreation motorized	Comparison type	Disturbance type	Effect size	Effect size variance
Bird community	9	terrestrial	non-motorized	spatial	ongoing	0.277	0.135
Bird community	9	terrestrial	non-motorized	spatial	ongoing	-0.964	0.149
Bird community	9	terrestrial	non-motorized	spatial	novel	-1.312	0.162
Bird community	10	terrestrial	non-motorized	spatial	novel	-2.084	0.309
Bird community	10	terrestrial	non-motorized	spatial	ongoing	-1.237	0.238
Bird community	12	terrestrial	non-motorized	spatial	ongoing	-1.167	0.197
Bird community	34	terrestrial	non-motorized	spatial	ongoing	-0.373	0.093
Waterbirds	13	terrestrial	non-motorized	temporal	ongoing	-1.687	0.116
Cavity-nesting birds	14	terrestrial	non-motorized	spatial	novel	-0.089	0.047
Ground-nesting birds	14	terrestrial	non-motorized	spatial	novel	0.070	0.048
Open cup-nesting birds	14	terrestrial	non-motorized	spatial	novel	-0.632	0.045
Fish community	16	aquatic	non-motorized	spatial	ongoing	-0.141	0.376
Fish community	17	aquatic	non-motorized	temporal	ongoing	-0.645	0.058
Fish community	20	aquatic	non-motorized	spatial	ongoing	-0.205	0.056
Fish community	18	aquatic	non-motorized	temporal	ongoing	-0.855	0.546
Fish community	19	aquatic	non-motorized	spatial	ongoing	1.740	0.100
Fish community	15	aquatic	non-motorized	spatial	ongoing	-0.490	0.390
Carnivore community	23	terrestrial	non-motorized	spatial	ongoing	-1.438	0.227
Carnivore community	22	terrestrial	non-motorized	spatial	ongoing	-1.046	0.162
Bat community	33	terrestrial	non-motorized	spatial	ongoing	-0.360	0.020

¹ See Appendix 1.4 for full citations

Appendix 1.3. Abundance comparisons.

Species	Publication ¹	Recreation substrate	Recreation motorized	Comparison type	Disturbance type	Body mass (g)	Diet	Nesting behavior	Effect size	Effect size variance
Birds										
Eurasian teal (Anas crecca)	1	terrestrial	non-motorized	temporal	ongoing	320.0	herbivore	ground	-0.309	0.100
European nightjar (<i>Caprimulgus europaeus</i>)	2	terrestrial	non-motorized	spatial	ongoing	71.0	carnivore	ground	-2.107	0.311
Kentish plover (<i>Charadrius alexandrinus</i>)	3	terrestrial	non-motorized	temporal	novel	46.0	carnivore	ground	-2.170	0.250
Western snowy plover (Charadrius nivosus)	4	terrestrial	non-motorized	temporal	ongoing	46.0	carnivore	ground	-0.733	0.014
Roadrunner (Geococcyx californianus)	5	terrestrial	non-motorized	spatial	ongoing	379.5	omnivore	tree	0.840	0.188
Gray jay (Perisoreus canadensis)	6	terrestrial	non-motorized	spatial	novel	71.0	omnivore	tree	0.585	0.031
Grasshopper sparrow (Ammodramus savannarum)	7	terrestrial	non-motorized	spatial	ongoing	17.0	carnivore	ground	-0.984	0.128
Vesper sparrow (Pooecetes gramineus)	7	terrestrial	non-motorized	spatial	ongoing	24.0	carnivore	ground	-0.855	0.125
Chipping sparrow (Spizella passerina)	7	terrestrial	non-motorized	spatial	ongoing	13.5	herbivore	tree	-1.763	0.157
Western meadowlark (<i>Sturnella neglecta</i>)	7	terrestrial	non-motorized	spatial	ongoing	102.0	carnivore	ground	-1.469	0.144
Boreal chickadee (Poecile hudsonicus)	8	terrestrial	non-motorized	spatial	ongoing	9.5	carnivore	tree	-0.017	0.055
Blackpoll warbler (Setophaga striata)	8	terrestrial	non-motorized	spatial	ongoing	12.5	carnivore	tree	-0.013	0.055
Pygmy nuthatch (<i>Sitta pygmaea</i>)	7	terrestrial	non-motorized	spatial	ongoing	10.0	carnivore	tree	-1.455	0.144
Bicknell's thrush (<i>Catharus bicknelli</i>)	8	terrestrial	non-motorized	spatial	ongoing	28.0	carnivore	shrub	-0.214	0.056

Swainson's thrush										
(Catharus ustulatus)	8	terrestrial	non-motorized	spatial	ongoing	34.0	carnivore	shrub	0.076	0.055
Townsend's solitaire										
(Myadestes townsendi)	7	terrestrial	non-motorized	spatial	ongoing	32.5	carnivore	ground	-0.442	0.118
American robin										
(Turdus migratorius)	7	terrestrial	non-motorized	spatial	ongoing	81.0	carnivore	tree	0.760	0.123
Western wood-pewee										
(Contopus sordidulus)	7	terrestrial	non-motorized	spatial	ongoing	12.5	carnivore	tree	-1.311	0.138
Yellow-bellied flycatcher										
(Empidonax flaviventris)	8	terrestrial	non-motorized	spatial	ongoing	12.5	carnivore	ground	0.001	0.055
Blue-headed vireo										
(Vireo solitarius)	7	terrestrial	non-motorized	spatial	ongoing	16.0	carnivore	tree	-1.035	0.129
Bird community	9	terrestrial	non-motorized	spatial	ongoing	n/a	n/a	n/a	0.068	0.133
Bird community	9	terrestrial	non-motorized	spatial	ongoing	n/a	n/a	n/a	-0.970	0.149
Bird community	9	terrestrial	non-motorized	spatial	novel	n/a	n/a	n/a	-1.719	0.183
Bird community	10	terrestrial	non-motorized	spatial	novel	n/a	n/a	n/a	0.964	0.223
Bird community	10	terrestrial	non-motorized	spatial	ongoing	n/a	n/a	n/a	-1.236	0.238
Bird community	11	terrestrial	non-motorized	spatial	ongoing	n/a	n/a	n/a	-1.240	0.082
Carnivores	12	terrestrial	non-motorized	spatial	ongoing	n/a	carnivore	n/a	-0.733	0.111
Granivores	12	terrestrial	non-motorized	spatial	ongoing	n/a	herbivore	n/a	0.024	0.095
Insectivores	12	terrestrial	non-motorized	spatial	ongoing	n/a	carnivore	n/a	-1.032	0.117
Omnivores	12	terrestrial	non-motorized	spatial	ongoing	n/a	omnivore	n/a	0.182	0.096
Waterbirds	13	terrestrial	non-motorized	temporal	ongoing	n/a	n/a	n/a	-1.780	0.242
Cavity-nesters	14	terrestrial	non-motorized	spatial	novel	n/a	n/a	tree	-0.192	0.044
Ground-nesters	14	terrestrial	non-motorized	spatial	novel	n/a	n/a	ground	0.056	0.043
Open cup-nesters	14	terrestrial	non-motorized	spatial	novel	n/a	n/a	tree	-0.795	0.046
Fish										
Giant moray										
(Gymnothorax javanicus)	15	aquatic	non-motorized	spatial	ongoing	n/a	carnivore	n/a	0.000	0.500
Blacktail reef shark		•		•	<u> </u>					
(Carcharhinus										
amblyrhynchos)	15	aquatic	non-motorized	spatial	ongoing	n/a	carnivore	n/a	0.248	0.504
Blacktip reef shark		•			~ ~					
(Carcharhinus melanopterus)	15	aquatic	non-motorized	spatial	ongoing	n/a	carnivore	n/a	-0.903	0.551
Whitetip reef shark		•								
(Triaenodon obesus)	15	aquatic	non-motorized	spatial	ongoing	n/a	carnivore	n/a	0.204	0.503

Island trevally										
(Carangoides orthogrammus)	15	aquatic	non-motorized	spatial	ongoing	n/a	carnivore	n/a	1.125	0.579
Giant trevally										
(Caranx ignobilis)	15	aquatic	non-motorized	spatial	ongoing	n/a	carnivore	n/a	-0.695	0.530
Bluefin trevally										
(Caranx melampygus)	15	aquatic	non-motorized	spatial	ongoing	n/a	carnivore	n/a	-0.096	0.501
Rainbow runner										
(Elegatis bipinnulata)	15	aquatic	non-motorized	spatial	ongoing	n/a	carnivore	n/a	-0.751	0.535
Doublespotted queenfish										
(Scomberoides lysan)	15	aquatic	non-motorized	spatial	ongoing	n/a	carnivore	n/a	0.786	0.539
Striped large-eye bream										
(Gnathodentex aureolineatus)	15	aquatic	non-motorized	spatial	ongoing	n/a	carnivore	n/a	-0.614	0.524
Longface emperor										
(Lethrinus olivaceus)	15	aquatic	non-motorized	spatial	ongoing	n/a	carnivore	n/a	-0.192	0.502
Yellowlip emperor										
(Lethrinus xanthochilus)	15	aquatic	non-motorized	spatial	ongoing	n/a	carnivore	n/a	0.309	0.506
Humpnose big-eye										
bream (Monotaxis										
grandoculis)	15	aquatic	non-motorized	spatial	ongoing	n/a	carnivore	n/a	0.980	0.560
Small toothed jobfish										
(Aphareus furca)	15	aquatic	non-motorized	spatial	ongoing	n/a	carnivore	n/a	0.684	0.529
Green jobfish										
(Aprion virescens)	15	aquatic	non-motorized	spatial	ongoing	n/a	omnivore	n/a	-1.243	0.597
Blacktail snapper										
(Lutjanus fulvus)	15	aquatic	non-motorized	spatial	ongoing	n/a	carnivore	n/a	-0.012	0.500
Humpback red snapper										
(Lutjanus gibbus)	15	aquatic	non-motorized	spatial	ongoing	n/a	carnivore	n/a	-1.192	0.589
Peacock hind										
(Cephalopholis argus)	15	aquatic	non-motorized	spatial	ongoing	n/a	carnivore	n/a	-0.055	0.500
Leopard hind										
(Cephalopholis leopardus)	15	aquatic	non-motorized	spatial	ongoing	n/a	omnivore	n/a	-0.751	0.535
Coral hind										
(Cephalopholis miniata)	15	aquatic	non-motorized	spatial	ongoing	n/a	carnivore	n/a	1.024	0.565
Darkfin hind										
(Cephalopholis urodeta)	15	aquatic	non-motorized	spatial	ongoing	n/a	carnivore	n/a	-1.901	0.726
Blacksaddle grouper										
(Epinephelus howlandi)	15	aquatic	non-motorized	spatial	ongoing	n/a	carnivore	n/a	-0.751	0.535

One-blotch grouper										
(Epinephelus melanostigma)	15	aquatic	non-motorized	spatial	ongoing	n/a	n/a	n/a	0.614	0.524
Camouflage grouper										
(Epinephelus polyphekadion)	15	aquatic	non-motorized	spatial	ongoing	n/a	carnivore	n/a	-0.971	0.559
(Epinephelus spiloceps)	15	aquatic	non-motorized	spatial	ongoing	n/a	n/a	n/a	0.751	0.535
Greasy grouper										
(Epinephelus tauvina)	15	aquatic	non-motorized	spatial	ongoing	n/a	carnivore	n/a	-0.201	0.503
Masked grouper										
(Gracila albomarginata)	15	aquatic	non-motorized	spatial	ongoing	n/a	carnivore	n/a	-0.302	0.506
Yellow-edged lyretail										
(Variola louti)	15	aquatic	non-motorized	spatial	ongoing	n/a	carnivore	n/a	0.000	0.500
Carnivores	17	aquatic	non-motorized	temporal	ongoing	n/a	carnivore	n/a	0.000	0.056
Fish community	16	aquatic	non-motorized	spatial	ongoing	n/a	n/a	n/a	0.000	0.375
Fish community	18	aquatic	non-motorized	temporal	ongoing	n/a	n/a	n/a	0.184	0.502
Fish community	19	aquatic	non-motorized	spatial	ongoing	n/a	n/a	n/a	1.300	0.090
Herbivores	20	aquatic	non-motorized	spatial	ongoing	n/a	herbivore	n/a	-0.379	0.399
Predators	17	aquatic	non-motorized	spatial	ongoing	n/a	carnivore	n/a	-0.290	0.202
Mobile invertivores	17	aquatic	non-motorized	temporal	ongoing	n/a	carnivore	n/a	-0.672	0.059
Omnivores	17	aquatic	non-motorized	temporal	ongoing	n/a	omnivore	n/a	2.190	0.089
Piscivores	17	aquatic	non-motorized	temporal	ongoing	n/a	carnivore	n/a	0.000	0.056
Planktivores	20	aquatic	non-motorized	temporal	ongoing	n/a	herbivore	n/a	0.000	0.056
Roving herbivores	17	aquatic	non-motorized	temporal	ongoing	n/a	herbivore	n/a	-0.389	0.057
Sessile invertivores	17	aquatic	non-motorized	temporal	ongoing	n/a	carnivore	n/a	0.000	0.056
Territorial herbivores	17	aquatic	non-motorized	temporal	ongoing	n/a	herbivore	n/a	-0.832	0.060
Mammals				•						
Mule deer										
(Odocoileus hemionus)	5	terrestrial	non-motorized	spatial	ongoing	83,800.0	herbivore	n/a	0.355	0.165
Woodland caribou		snow-		•						
(Rangifer tarandus caribou)	21	based	motorized	spatial	ongoing	108,000.0	herbivore	n/a	-2.049	0.467
Coyote (Canis latrans)	23	terrestrial	non-motorized	spatial	ongoing	12,000.0	carnivore	n/a	-2.289	0.236
Coyote (Canis latrans)	22	terrestrial	non-motorized	spatial	ongoing	12,000.0	carnivore	n/a	-3.336	0.389
Coyote (Canis latrans)	5	terrestrial	non-motorized	spatial	ongoing	12,000.0	carnivore	n/a	-0.403	0.162
Gray fox				1	0 0					
(Urocyon cinereoargenteus)	22	terrestrial	non-motorized	spatial	ongoing	3,830.0	omnivore	n/a	-0.203	0.054
Gray fox					0	-				
(Urocyon cinereoargenteus)	5	terrestrial	non-motorized	spatial	ongoing	3,830.0	omnivore	n/a	-0.319	0.169

Red for (Vultas vultas)	22	torrestrial	non motorized	spatial	ongoing	4 840 0	corpinore	n/a	0.589	0.056
Bobcat (Lynx rufus)	22	terrestrial	non-motorized	spatial	ongoing	6 390 0	carnivore	n/a	-0.307	0.050
Bobcat (Lynx rufus)	23	terrestrial	non-motorized	spatial	ongoing	6 390.0	carnivore	n/a	_1 578	0.105
Bobcat (Lynx rufus)	5	terrestrial	non motorized	spatial	ongoing	6 390.0	carnivore	n/a	0.222	0.255
Leopard (Panthera pardus)	24	terrestrial	non-motorized	temporal	ongoing	52 400 0	carnivore	n/a	-0.031	0.130
Courser (Puma concolor)	5	terrestrial	non-motorized	spatial	ongoing	53,900,0	carnivore	n/a	-0.878	0.333
American marten	5	terrestriai	non-motorized	spatiai	oligoling	55,700.0	carmone	11/ a	-0.070	0.217
(Martes americana)	25	multiple	motorized	spatial	oncoing	882.0	carnivore	n/a	0.440	0 1 9 4
Pacific marten	25	spow-	motonzed	spatiai	ongoing	002.0	carmone	11/ a	0.110	0.174
(Martes cauring)	26	based	non-motorized	spatial	ongoing	882.0	carnivore	n/a	-0.496	0.350
Pacific marten	20	snow-	non motorized	spatiai	ongoing	002.0	carmvore	11/ a	0.190	0.550
(Martes caurina)	26	based	non-motorized	spatial	ongoing	882.0	carnivore	n/a	0.108	0 1 9 0
Baccoon (Provan later)	5	terrestrial	non-motorized	spatial	ongoing	6 370.0	omnivore	n/a	-0.324	0.165
Brown bear (Ursus arctas)	27	terrestrial	non-motorized	temporal	novel	196,000,0	omnivore	n/a	-0.447	0.105
Brown bear (Ursus arctas)	27	terrestrial	non-motorized	temporal	novel	196,000.0	omnivore	n/a	-0.150	0.376
Opossum		terrestria	non motorized	temporta	nover	170,000.0	ommvore	11/ u	0.120	0.570
(Didelphis virginiana)	5	terrestrial	non-motorized	spatial	ongoing	2,470.0	omnivore	n/a	-0.709	0.184
Black-tailed jackrabbit				•	0 0	-				
(Lepus californicus)	5	terrestrial	non-motorized	spatial	ongoing	2,420.0	herbivore	n/a	-0.183	0.155
Woodrat (Neotoma spp.)	5	terrestrial	non-motorized	spatial	ongoing	224.0	herbivore	n/a	-0.439	0.194
Red squirrel				<u> </u>	~ ~ ~					
(Tamiasciurus hudsonicus)	28	terrestrial	non-motorized	spatial	novel	200.0	omnivore	n/a	-0.201	0.158
Prey community	24	terrestrial	non-motorized	temporal	ongoing	n/a	n/a	n/a	-0.100	0.029
Reptiles										
Allen Cays rock iguana										
(Cyclura cychlura inornata)	29	terrestrial	non-motorized	spatial	ongoing	n/a	omnivore	n/a	1.011	0.072
Flat-tailed horned lizard										
(Phrynosoma mcallii)	30	terrestrial	motorized	spatial	ongoing	37.8	carnivore	n/a	-0.571	1.080
Western fence lizard										
(Sceloporus occidentalis)	31	terrestrial	motorized	spatial	ongoing	23.2	carnivore	n/a	0.410	0.440
North American wood										
turtle (Glyptemys insculpta)	32	terrestrial	non-motorized	temporal	novel	n/a	omnivore	n/a	-1.772	0.156
turtle (<i>Glyptemys insculpta</i>)	32	terrestrial	non-motorized	temporal	novel	n/a	omnivore	n/a	-1.772	0.156

¹ See Appendix 1.4 for full citations

Appendix 1.4. Articles used in the meta-analysis. Numbers correspond to those appearing in Appendices 1.2 and 1.3.

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Chapter 2 Appendices

Appendix 2.1. Rootograms showing the fit of negative binomial regressions used to model a) bobcat, b) coyote, c) gray fox, d) ground squirrel, e) jackrabbit, f) mule deer, g) raccoon, h) rabbit, and i) striped skunk relative activity rates. The frequency of each count is shown 'hanging' from the fitted regression line; lack of fit is indicated when bars hang substantially above or below the x-axis or when there are clear patterns in the departures of the bars from the x-axis.



Appendix 2.2. Predicted relationships between Julian date and detection probability for the five mammal species for which it was a well-supported predictor. Shaded areas are 95% confidence intervals.

