Effects of Human Use of NCCP Reserves on Reptile and Mammal Species in San Diego

SARAH E. REED[1,2], COURTNEY L. LARSON[2] and KEVIN R. CROOKS[2]

[1]Americas Program, Wildlife Conservation Society
[2]Department of Fish, Wildlife & Conservation Biology, Colorado State University

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Executive Summary

Protected areas are commonly established with a dual mandate to provide public access for outdoor recreation while also protecting wildlife species and habitats. Recreation activity provides many human health and economic benefits; it also influences people's political and financial support for land and wildlife conservation. Outdoor recreation is often assumed to be compatible with species protection. However, a growing body of scientific research demonstrates that outdoor recreation can negatively impact plant and animal communities.

Many of the places where wildlife thrive in California are the same as those valued for recreation and other human activities, and demand by the public is increasing for recreational access to public lands, waterways, and ocean resources. To inform ongoing management of human activity and support future decisions regarding public access and designated use of reserve lands in California, we implemented a study of the possible effects of human recreation on wildlife populations in the San Diego County Natural Community Conservation Plan (NCCP) reserve system. The overall goal of our research was to assess the degree to which human use of NCCP reserves may be affecting Covered and sensitive species while also providing recreation opportunities and experiences for San Diego residents. Our specific objectives were to:

1) Validate a landscape-level spatial model of the intensity of human use among NCCP reserves;
2) Develop and test a citizen science approach for collection of fine-scale human use patterns within a reserve;
3) Implement an observational study in a gradient design to relate spatio-temporal variation in human activity to the occurrence and relative abundance of reptiles and mammals; and
4) Conduct a before-after control-impact (BACI) experiment to monitor the response of reptile and mammal species to changes in human activity patterns.

We monitored human activity at 92 sampling points within 14 NCCP reserves selected to represent a gradient of expected human visitation, as well as sites popular for different recreation activities (e.g., hiking, mountain biking, horseback riding). We used motion-triggered cameras and volunteered geographic datasets (e.g., Strava and Flickr) to monitor human activity in the study reserves. We also used motion-triggered cameras to sample mammal habitat use and relative activity, and we used artificial cover surveys and visual encounter surveys to sample reptile community composition and species occupancy. Monitoring of human activity, mammal and reptile communities was conducted between January 2017 and June 2018.

To validate a landscape-level spatial model of human use intensity among NCCP reserves, developed during a prior phase of the project (*Appendix B*), we compared visitation weights used in the sampling point selection process to empirical measures of visitation levels from the camera data. We found that the modeled visitation weights and actual visitation levels were strongly and positively correlated, especially when comparing the rank order of the sampling points, indicating that the landscape-level spatial model provides reliable estimates of relative human use intensity among NCCP reserves (*Chapter 1*).

We explored several alternative citizen science approaches for collecting fine-scale human use patterns within a reserve. We tested the effectiveness of volunteered geographic datasets by comparing data collected from Strava (i.e., cyclist activity for trail segments) and Flickr (i.e., photo-user days per 50 m pixel) to empirical measures of visitation levels from the camera data in the

largest and most heavily visited study reserve, Mission Trails Regional Park. Linear regression models and rank-order correlations indicated that actual visitations levels from the camera data were not significantly related to human use patterns from either Strava or Flickr data (*Chapter 2*). We suspect the lack of relationship may be attributable to spatial and temporal mismatches between the extents and resolutions of the citizen science and empirical datasets.

We investigated relationships between spatio-temporal variation in human activity to reptile and mammal communities in the 14 NCCP reserves. We hypothesized that reptile species richness, community composition and species occupancy are driven primarily by habitat characteristics, topography, and human activity. We observed a decline in reptile species richness in association with human activity, driven primarily by a decrease in lizard richness. The proportion of reptile 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 side-blotched lizard, a slight but uncertain decline in occupancy of the orange-throated whiptail, and no relationship with western fence lizard occupancy (*Chapter 3*).

We hypothesized that mammal habitat use and relative activity are driven primarily by habitat characteristics, urban development, and human activity. Human activity was associated with declines in habitat use of several mammal species, particularly bobcats and mule deer, though the strength of these relationships was relatively weak in comparison with the effects of habitat and development covariates. Although human activity may not often extirpate mammal species from urban habitat fragments, it can reduce habitat suitability. In particular, we found that bobcat, gray fox, mule deer, and raccoon were less active in areas with higher levels of human activity (*Chapter 3*).

We conducted the before-after control-impact (BACI) study at two study reserves: Black Mountain Open Space Preserve, where a trail was closed from January 2017-April 2018, and Hollenbeck Canyon Wildlife Area, where a hunting dog training area is opened from September-February each year. At Black Mountain, human activity was approximately twice as high at the impact points after trails were reopened. At Hollenbeck Canyon, human activity did not differ significantly between open and closed seasons. We did not record sufficient detections of reptiles to assess their response to changes in human activity patterns. At Black Mountain, bobcat and coyote detection probabilities were reduced at impact points after trail re-opening, suggesting that some mammal species may shift their activity patterns in response to changes in human activity patterns (*Chapter 4*).

With growing human populations at their borders, protected areas will 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 visitation rates to NCCP reserves by 46% by 2050. Our study showed that human recreation activity can reduce the ability of urban habitat fragments to conserve diverse reptile and mammal communities. 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 some areas trail-free and, where possible, to separate high-intensity recreation areas from quality habitats harboring populations of sensitive species. In addition, encouraging visitors to stay on trails, respect seasonal closures, minimize noise, and not approach wildlife can further help mitigate the impacts of recreationists on sensitive species and their habitats. Minimizing the effects of recreation within fragmented protected areas helps ensure that the fragments provide habitat for species whose sensitivity to disturbance and low dispersal ability through the urban matrix may limit their ability to seek alternative habitat elsewhere.

Background and Objectives

Background

Protected areas are commonly established with a dual mandate to provide public access for outdoor recreation, education, and other human activities while also protecting plant and animal species, their habitats, and the ecological processes upon which they depend. Outdoor recreation has many human health (Frumkin 2001) and economic benefits (Goodwin 1996); it also influences people's political and financial support for land and wildlife conservation (Zaradic et al. 2009). Although the negative effects of extractive and consumptive land uses within protected areas are well known (e.g., Liu et al. 2001), outdoor recreation is often assumed to be compatible with species protection (Reed & Merenlender 2008). However, a growing body of research demonstrates that outdoor recreation can negatively impact plant and animal communities (Liddle 1997). Recreation is the second-leading cause of endangerment to species occurring on U.S. federal lands (Losos et al. 1995), and of all U.S. states, California has the greatest number of listed species threatened by recreation (Czech et al. 2000). Recreation activity has been linked to declines in wildlife species occupancy, abundance and density (Banks & Bryant 2007, Reed & Merenlender 2008, Larson et al. 2016), changes in spatial or temporal habitat use (George & Crooks 2006, Cardoni et al. 2008), increased physiological stress (Arlettaz et al. 2007), reduced reproductive success (Finney et al. 2005), and behavioral effects such as increased vigilance and flight (Taylor & Knight 2003) (*Appendix B*).

Participation in outdoor recreation and rates of visitation to protected areas are increasing rapidly in the U.S. (Cordell 2008) and around the world (Balmford et al. 2008). Land and wildlife managers are seeking solutions to balance the benefits of outdoor recreation for human communities with its potentially negative effects on species and ecosystems (Hadwen et al. 2007). Despite growing evidence of recreation impacts, few studies have made comparisons between protected areas that do and do not permit recreation (Reed & Merenlender 2008), examined recreational impacts among multiple sites within a reserve network (Forrest & St. Clair 2006), or compared the responses of multiple species in a community (Blumstein et al. 2005). Landscape-level studies of the effects of recreation on wildlife communities are needed in order to understand which species are most likely to be sensitive to human recreation and in which locations those species are exposed to a level of human use that exceeds their threshold of disturbance, with potentially negative population- and community-level consequences.

Linkage to California State Wildlife Action Plan

Wildlife provide significant economic benefits to the State of California through recreation, tourism, and commercial harvest. Many of the places where wildlife thrive are the same as those valued for recreation and other human activities, and accompanying growth and development is an increasing demand by the public for recreational access to public lands, waterways, and ocean resources. In the 2005 California State Wildlife Action Plan (SWAP), recreational pressures were identified as major wildlife stressors identified for the South Coast, Central Coast, and Sierra Nevada regions, and intensity of human recreation use was included as a variable that could be used to monitor landscape-level issues that affect multiple natural community assemblages or otherwise cross-cutting issues. In the South Coast region in particular, with nearly 20 million people living within driving distance of the region's national forests and other public lands, recreational access and its subsequent effects are a major concern. Concentrated recreational use of streams and riparian areas

is particularly troublesome. Not only off-road vehicles, but hikers, picnickers, and equestrians in large numbers can damage these systems, reducing vegetative cover and disturbing sensitive species. Species identified as particularly vulnerable include herpetofauna such as the two-striped garter snake (*Thamnophis hammondii*), mountain yellow-legged frog (*Rana muscosa*), and arroyo toad (*Anaxyrus californicus*) (Stephenson & Calcarone 1999). To conserve habitat and species in the South Coast Region's rapidly urbanizing areas, the primary conservation action recommended by the SWAP is for wildlife agencies and local governments to work to improve the development and implementation of NCCPs.

Project history

In 2012, a Local Assistance Grant (#P1182112) was awarded by California Department of Fish and Wildlife (CDFW) for the first phase of a collaborative project among the Wildlife Conservation Society (WCS), Colorado State University (CSU), and University of California, Berkeley (UCB) to develop a research plan for assessing the possible effects of human recreation on wildlife populations in the San Diego County Natural Community Conservation Plan (NCCP) reserve system. Specific objectives of this applied research project were to: 1) Develop a research design in collaboration with local researchers and managers for studying the effects of recreation on wildlife species to inform adaptive management decisions; and 2) Test methods for monitoring levels of recreational disturbance and complete a pilot study, in order to revise and improve the research design and maximize our ability to detect the possible effects of recreation on multiple species.

During the first phase of this project, we implemented a systematic review of studies examining the impacts of recreation on wildlife; acquired and refined a geographic information system (GIS) database to facilitate field site selection and spatial analysis; created a database of official and unofficial trails digitized from aerial imagery; conducted an expert opinion survey to assess relative levels of visitation to 35 NCCP reserves; implemented a pilot field study to test methods for monitoring recreation visitation and provide a quantitative estimate of overall visitation levels at 18 reserves; completed a detailed survey of variation in visitation patterns within the interior of one reserve; built a random forest model to identify biophysical and socioeconomic factors that influenced patterns of human activity; estimated visitation at a larger network of 28 additional reserves; and compared predicted patterns of occurrence of 5 bird and 30 reptile species with estimates of visitation rates in order to identify species that are likely exposed to high levels of recreational use. This work resulted in two peer-reviewed scientific publications: one article reporting results of the global systematic review of recreation effects on wildlife (Larson et al. 2016; *Appendix B*) and another article summarizing results of the landscape-level model of recreation visitation and exposure of wildlife species (Larson et al. 2018; *Appendix C*).

This preliminary research yielded important information regarding gaps in our knowledge of species responses to recreation, estimates of the relative exposure of wildlife species to recreation activity across the NCCP reserves, and recommendations for survey techniques and designing sampling strategies for monitoring recreation activity. The pilot results provided the foundation for designing a second field study that integrated species monitoring with recreation monitoring to systematically assess recreation's direct and indirect effects on sensitive wildlife species, to improve our understanding of the trade-offs inherent in multiple-use management of reserves and ensure that NCCP reserves are providing the required levels of protection and achieving the goals of the NCCP program.

Multi-species benefit

The current study focused on two groups of species of local conservation concern: reptiles and mammals. Reptile communities in San Diego County include three species that are Covered Species in the San Diego MSCP and/or are listed as Species of Special Concern by CDFW: orange-throated whiptail (*Aspidoscelis hyperythrus beldingi*), San Diego horned lizard (*Phrynosoma coronatum*), and two-striped garter snake (*Thamnophis hammondii*). Herpetofauna are among the least well-studied groups of taxa in response to recreation. Fewer than 6% of published studies of recreation impacts on wildlife focus on reptiles or amphibians, but 63% of those studies found statistically significant effects (Larson et al. 2016). Reptiles are likely to be vulnerable to disturbance because their habitats are also desirable destinations for humans, they are targets of unsustainable collection (Buhlmann & Tuberville 1998, Gibbons et al. 2000), human activity is a source of direct mortality along roads and trails (Rochester et al. 2001), and because 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 impact the survival (Iverson et al. 2006), population size (Garber & Burger 1995), and physiological condition (Amo et al. 2006) of reptiles and amphibians. However, to date no study has been conducted of the effects of recreation on reptiles or amphibians at the community- or landscape-level.

The second group of focal taxa for this study was mid-sized to large mammals. The response of mid-sized to large mammal species to recreation has been examined in other California ecosystems, with species such as bobcats (*Felis rufus*) and coyotes (*Canis latrans*) exhibiting decreased activity or temporal displacement in response to human activity (George & Crooks 2006, Reed & Merenlender 2008). One prior study in San Diego County demonstrated that mountain lions (*Puma concolor*) were negatively associated with recreational biking, but did not include reserves without public access or measure relative levels of human visitation (Markovchick-Nicholls et al. 2008). 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). 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), and the resulting comparisons among categories make it difficult to assess the sensitivity of species responses to changes in the intensity of human use. Those studies that do quantify recreation 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). Our study aimed to address these knowledge gaps by assessing changes in mammal habitat use and relative activity over a broad range of visitation levels, allowing managers to assess when and where recreational use exceeds thresholds of human activity known to alter animal behavior.

Objectives

The overall goal of our research was to assess the degree to which human use of NCCP reserves may be affecting Covered and sensitive species while also providing recreation opportunities and experiences for San Diego residents. Our specific objectives were to:

1) Validate a landscape-level spatial model of the intensity of human use among NCCP reserves;

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By implementing our study along a gradient of human use intensity, we were able to evaluate alternative use-impact relationships between human activity and wildlife responses (Monz et al. 2013) and identify possible thresholds of the level, type, timing, and spatial extent of human activities that lead to wildlife impacts. Community-level surveys allowed us to determine which reptile and mammal species were most sensitive to disturbance by human use, and in which locations those species were exposed to a level of human activity that exceeds their threshold of disturbance. Pairing the observational study with a before-after control-impact (BACI) experiment provided an explicit test of management alternatives of restricting or closing NCCP reserves to public access. Results of this project are intended to inform ongoing management of human activity in NCCP reserves and support future decisions regarding public access and designated use of reserve lands statewide.

Chapter 1. Landscape Model Validation

Landscape model development

During the prior phase of this project (see *Project history*, above), we monitored human activity at 18 NCCP reserves along an expected gradient of recreation activity based on distance from densely-populated areas and anecdotal reports of use. We selected an additional 27 unsampled reserves dispersed over a larger spatial extent than the sampled reserves. All reserves were publicly owned, part of the MSCP, and least 100 ha in area. Seven reserves were closed to the public.

At each sampled reserve, we identified all official entrances and stratified them into three categories: staging areas (primary access points with parking lots), trailheads (entrances depicted on reserve maps and accessible by car, often with street parking), and connectors (entrances typically used to enter from an adjacent neighborhood or reserve). At closed reserves, we assumed that service roads that intersected the reserve boundary would be the most likely entry points for unauthorized use. We used remotely-triggered cameras (Bushnell TrophyCam) to document human activity at reserve entrances from July to October 2013. We installed cameras at all staging areas and trailheads and a random sample of at least 50% of connectors, except for one reserve with an unusually large number of entrances. In total, we installed cameras for at least 14 days at 83 entrances across the 18 reserves. Cameras captured a single photo at each trigger and took a maximum of one photo every ten seconds.

We randomly truncated the beginning or end of each sampling period to obtain 14-day periods for analysis. For cameras that recorded more than 2000 photos during the sampling period (*n*=22), we randomly subsampled the data to reduce time spent sorting photos. We viewed each photo and counted the number of hikers, bicyclists, and people riding or leading horses ("equestrians"). We also recorded the direction of travel to quantify visitors entering versus exiting the reserve. We combined detections of hikers, bicyclists, and equestrians to create reserve-level empirical estimates of the number of visits per day (henceforth: visitation rate) and visitation intensity (visits/hectare/day) by hikers, bicyclists, and equestrians for each reserve.
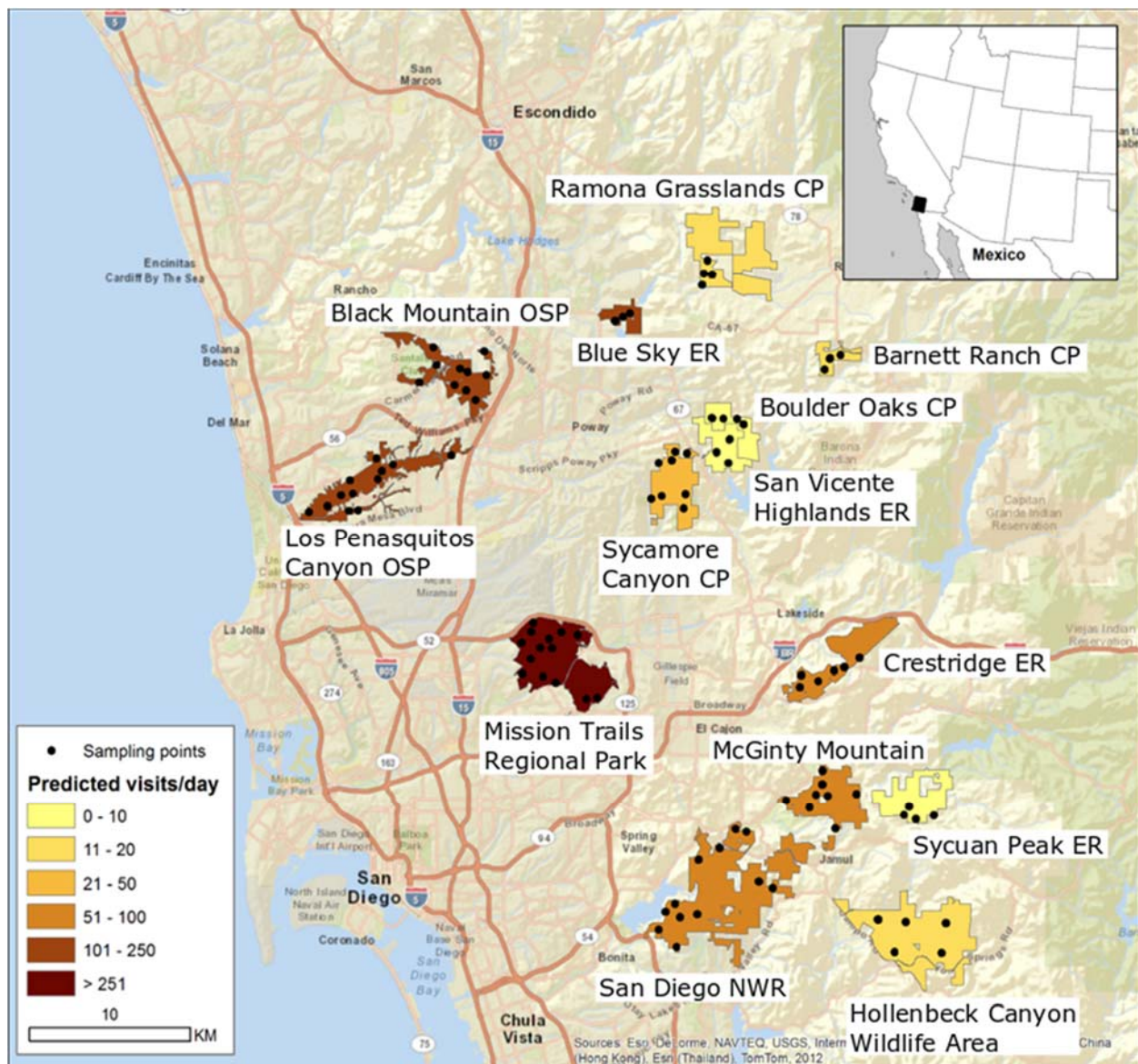
We modeled visitation rates using groups of explanatory variables that we expected to be influential based on previous research: accessibility variables (number of entrances, parking lots, and nearby housing units; open or closed to the public), landscape variables (distance from coast, number of nearby "substitute" reserves), and reserve characteristics (slope, elevation, area, vegetation, trail length and density). We used random forest models to model the visitation rates and intensity of hikers and bicyclists at the 18 sampled reserves. We did not model equestrian visitation due to low counts and limited variability. We log-transformed the response variables to limit the influence of outliers (Knudby et al. 2010). We then estimated visitation rates and intensity of hikers and bicyclists within sampled and unsampled reserves using the *predict* function in the randomForest package, and we refer to these as model "projections." We assessed model fit and performance using the percent of variation explained and Pearson correlations between the projected and empirically-estimated values for the 18 sampled reserves.

For more details on the development of the landscape model, please refer to Larson et al. (2018) (*Appendix B*).

Monitoring human activity

During the current phase of this project, we monitored human activity at 14 NCCP reserves (*Figure 1*). We used predictions from the landscape-level spatial model of human use intensity, described above, to choose reserves along a gradient of expected human visitation, as well as sites 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 size, and vegetation communities included chaparral, coastal sage scrub, native and nonnative grasslands, oak and sycamore woodlands, and riparian habitats.

Figure 1. Sampling design with predicted visitation levels to 14 NCCP reserves and locations of 92 monitoring points. Label abbreviations are as follows: CP: County Park, OSP: Open Space Preserve, ER: Ecological Reserve, and NWR: National Wildlife Refuge.

We located 92 sampling points along official and unofficial trails within the study reserves (*Figure 1*). 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 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 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). In closed reserves, we ensured that sampling points were located on service roads or animal trails similar in width to recreational trails.
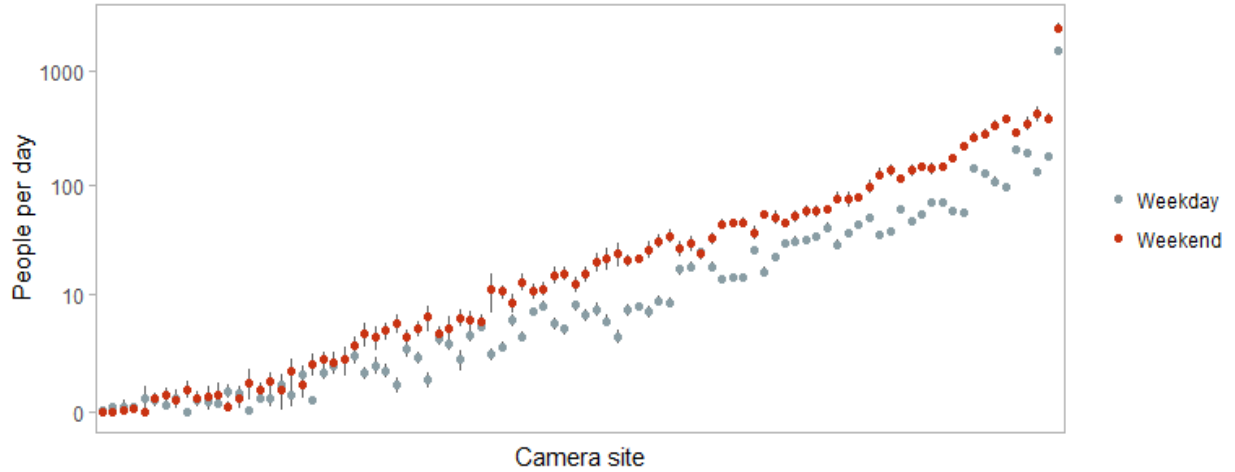
To monitor human activity, as well as mammal habitat use, we installed one motion-triggered camera (Bushnell TrophyCam HD Aggressor) at each sampling point. Cameras were housed in locked metal security boxes and affixed to metal poles pounded into the soil facing recreational trails. We did not bait the cameras to avoid influencing animal activity patterns and behavior (Kays & Slauson 2008; Wearn & 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). Domestic dogs were considered a human associate since daily counts of dogs and humans were highly correlated ($r = 0.87$).

Comparing model predictions to monitoring 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, including vehicles and dogs, was 41.8 $\pm$ 144.9 (range: 0 - 1797.2) per day. Recreation rates were higher on weekends than on weekdays (*Figure 2*), 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).
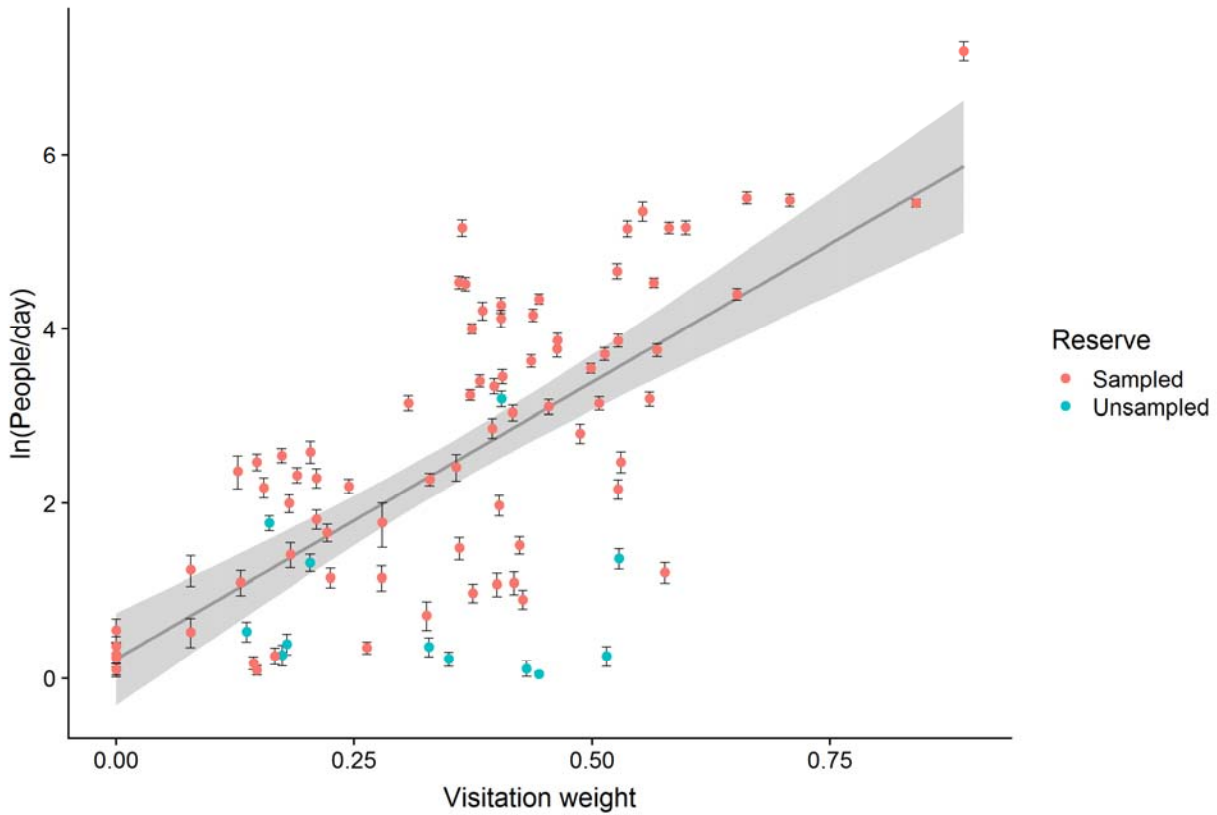
Figure 2. Total human activity at 92 sampling points on weekend days and weekdays (mean count per day). Error bars show 95% confidence intervals.

To assess the accuracy of the landscape model projections described above, we compared the visitation weights used in the sampling point selection process to the empirical estimates of visitation levels from the cameras (*Figure 3*). The visitation weights and empirical estimates were positively correlated ($r = 0.51$, $p < 0.001$), more strongly when comparing the rank orders (Spearman's rho = 0.65, $p < 0.001$).

A greater proportion of our sampling points had little to no use than predicted by the landscape model. This is likely because the data used to estimate visitation weights was collected from trailheads. We used distance from trailhead to model decay in visitation as distance from trailhead increased, but it appears the predictions would be more accurate with a steeper decay function. Additionally, several of the sampling points for which visitation weights were not a strong predictor of empirical estimates (i.e., those points with the largest residuals) were located in reserves not used to build the landscape visitation model. It is not surprising that the model predicted visitation more accurately within the reserves used to parameterize the model; conversely, visitation at some "unsampled" points was predicted quite accurately.

Figure 3. Relationship between visitation weights created from the landscape visitation model and empirical estimates of visitation (ln mean people per day). Sample points are located in reserves for which trailhead data were used in building the landscape visitation model, while unsampled points are located in reserves that were not used in building the model.

Chapter 2. Citizen Science Monitoring

Citizen science approaches

Visitation data are not always collected in protected areas, and the data that are collected can be too coarse or incomplete to be used to plan effective management strategies (Hadwen et al. 2007; Watson et al. 2000). Many commonly used monitoring methods have significant flaws. Visitor surveys are expensive to conduct and may not accurately reflect visitation patterns (Cole and Daniel 2003). Entrance counts obtained from entrance fees or motion-triggered monitoring devices, while simple to collect, give little information about the spatial dynamics of visitation (Watson et al. 2000), which are important to consider since visitation is not evenly distributed across trail segments (Meijles et al. 2014; Monz et al. 2010; Taczanowska et al. 2014; van der Zee 1990).

GPS tracking of visitors to obtain high-resolution spatial and temporal visitation data is an emerging approach and is often accomplished by distributing GPS tracking devices to visitors to use during their visit (Beeco et al. 2013; D'Antonio et al. 2010; Meijles et al. 2014). This approach is promising but can be limited by the number of GPS devices that can be distributed to and recovered from participants (Hallo et al. 2012; Meijles et al. 2014). Another recent development in research methodology is to use volunteered geographic data. Visitors often record geo-referenced information about their visits to protected areas, such as taking photos and tracking their route. Some visitors make this information publicly available using social media.

Recently, researchers have started to use volunteered geographic data to learn about trends in physical activity in urban areas (Hirsch et al. 2014) and visitation patterns to protected areas at global (Levin et al. 2015), regional (Orsi and Geneletti 2013), and local (Korpilo et al. 2017) scales. Commonly used volunteered georeferenced data include tweets from Twitter (Donahue et al. 2018; Hamstead et al. 2018; Tenkanen et al. 2017; Stelmach and Beddow 2016), photos from Flickr (Donahue et al. 2018; Fisher et al. 2018; Ghermandi 2016; Hamstead et al. 2018; Hausmann et al. 2018; Tenkanen et al. 2017; Levin et al. 2017; Mancini et al. 2018; Sessions et al. 2016; Sonter et al. 2016; Stelmach and Beddow 2016; Wood et al. 2013) or Instagram (Hausmann et al. 2018; Heikinheimo et al. 2017; Tenkanen et al. 2017), and running or cycling routes from Strava (Headwaters Economics 2018, Stelmach and Beddow 2016) or MapMyFitness (Hirsch et al. 2014; Norman and Pickering 2017).

About 64% of American adults, and 82% of Americans aged 18-49, own a "smart," app-enabled mobile phone (Pew Research Center 2015). Smartphones commonly contain GPS receivers and accelerometers capable of tracking a users' location to within 5-15m accuracy at a frequency of once per second (Doherty et al. 2014; Korpilo et al. 2017). Health and fitness-related apps are popular; an estimated 58% of mobile phone users have downloaded a health app (Krebs and Duncan 2015). We expected that apps that collect volunteered geographic data are commonly used within protected areas, especially in urbanized areas such as southern California, and have potential to be useful sources of high-resolution visitor use data.

Approaches explored but not used

We explored several approaches to gather volunteered geographic information from recreationists. First, we developed an outreach program in which we used signs at trailheads and visitor centers to encourage trail users to become "friends" or "followers" of project accounts on MapMyFitness and

Strava. Both these platforms allow route information, including spatial and temporal data, to be downloaded from friends or followers via a web interface. Signs were posted starting in February 2017 and by the end of the outreach program in February 2018 we had 88 Strava followers and 29 MapMyFitness friends. However, we found that it was prohibitively time-consuming to download and use activity data because it must be downloaded one route at a time, and it is difficult to tell which routes were within our project study reserves until they were downloaded. In addition, temporal data about the speed or total elapsed time on the route were not available. Ultimately, we could not easily download the quantity of high-quality data that we needed from either the Strava or MapMyFitness web interfaces.
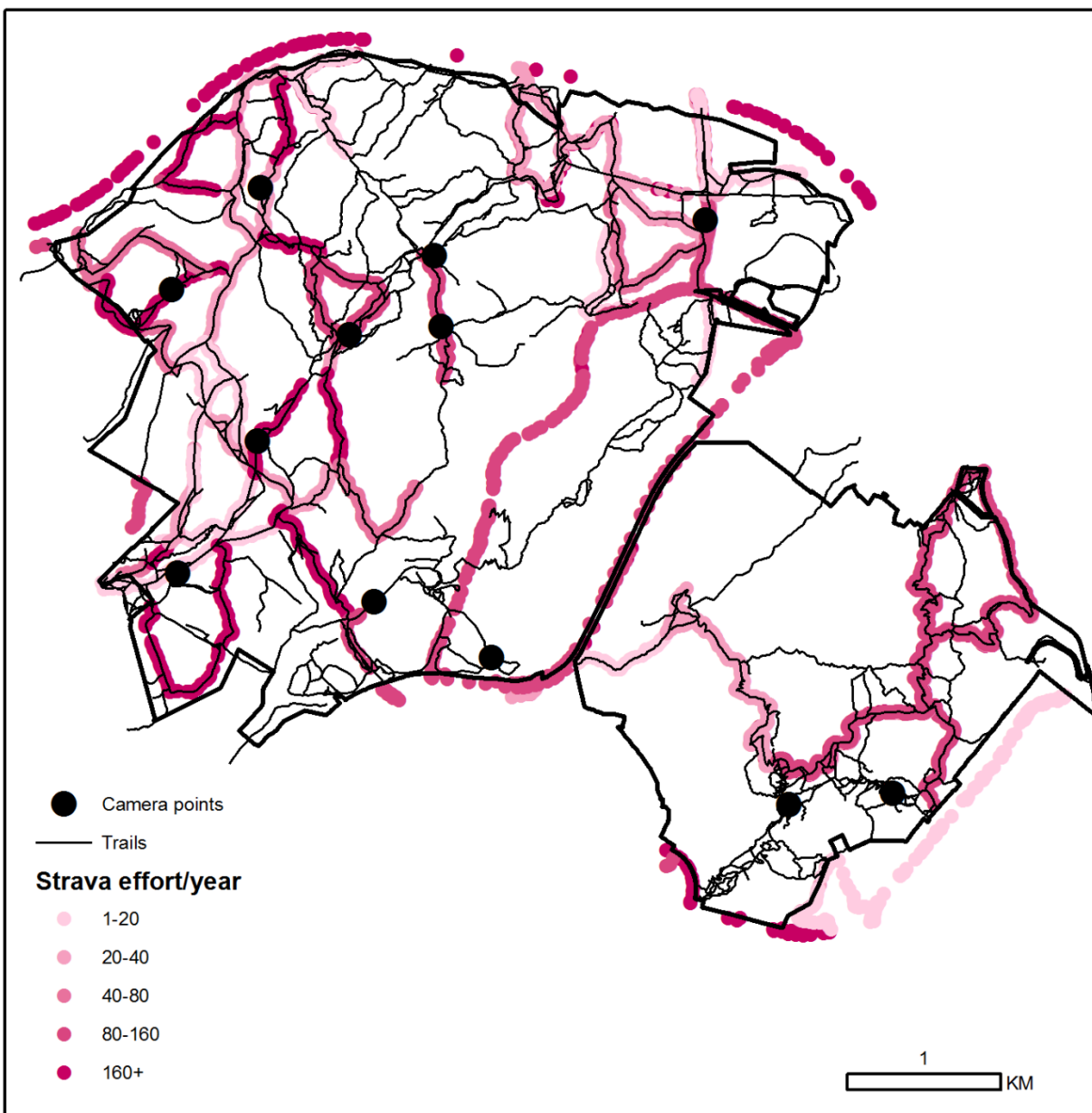
Second, we contacted Strava and MapMyFitness and requested data in August 2017. After repeated attempts we received no response from MapMyFitness. We had several conversations with a Strava data scientist who was potentially willing to provide us with the Strava Heatmap, which is a raster representation of GPS pulse point saturation (i.e., an image file depicting how often Strava users' GPS devices log a spatial location). However, our conversations about these data were halted because Strava was not willing to provide this dataset at a price that was reasonable within our project budget.

Third, we explored obtaining data from Twitter, which has an application programming interface (API) that provides access to publicly available spatial and temporal data for tweets. The API returns a random 1% of public tweets for a given search string. However, we abandoned this approach because we were not able to specify both the geography and time period when querying the database, and only about 30% of the tweets downloaded via the API had a GPS coordinate associated with them, of which very few were located in the study reserves.

Strava and Flickr data collection and analysis methods

In contrast to the Strava web interface approach described above, the Strava API allows easier access to larger quantities of data. However, rather than full routes, data available from the API are segments, or sections of routes on which users log their best times and compete with one another. Segment lengths vary widely and can overlap. We worked with Ryan Becwar, a graduate student in the Colorado State University Computer Science department to obtain segment data from the Strava API. We obtained cyclist activity data for Mission Trails Regional Park, a large reserve containing 148 cycling segments. Data included GPS coordinates, the date the segment was created, and the number of times the segment has been attempted by Strava users. We calculated the effort per year for each Strava segment in Mission Trails Regional Park as the total number of times a segment was attempted divided by the total number of years the segment has been active on Strava (*Figure 4*).

Figure 4. Mean effort per year for cycling segments located in Mission Trails Regional Park, collected from Strava.

We also obtained data from Flickr using the InVEST software program (Wood et al. 2013). The program calculates the photo-user days (PUD) within a specified geography, time period, and resolution. A PUD at a given location is one unique photographer who took at least one photo on a specific day. We calculated the total number of photos taken in each study reserve between 2005 and 2017 (*Table 1*) and there were two study reserves with adequate data: Mission Trails Regional Park (1122 photos between 2005 and 2017; *Figure 5*) and Los Peñasquitos Canyon (366 photos between 2005 and 2017). For these two reserves, we used the InVEST software to calculate the average annual PUD per 50 m pixel.

Table 1. Flickr photos available for each study reserve from 2005-2017

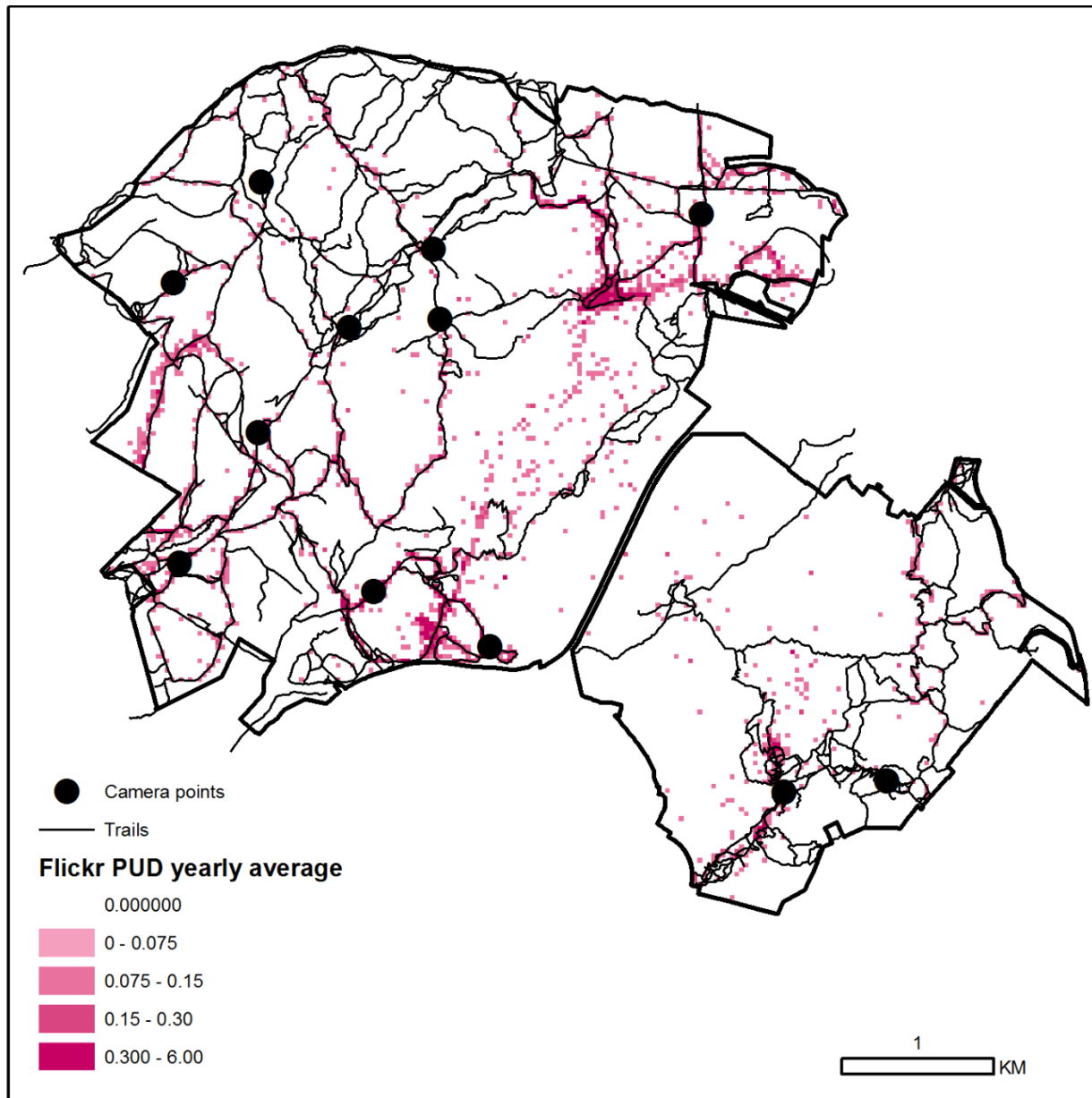| Reserve	Flickr photos 2005-2017
Barnett Ranch County Preserve	10
Black Mountain Open Space Preserve	115
Blue Sky Ecological Reserve	43
Boulder Oaks County Preserve	3
Crestridge Ecological Reserve	11
Hollenbeck Canyon Wildlife Area	34
Los Penasquitos Canyon Open Space Preserve	366
McGinty Mountain (section of San Diego National Wildlife Refuge)	7
Mission Trails Regional Park	1122
Ramona Grasslands County Preserve	51
San Diego National Wildlife Refuge (main section)	66
San Vicente Highlands Ecological Reserve	3
Sycamore Canyon/Goodan Ranch County Preserve	22
Sycuan Peak Ecological Reserve	4

Comparison with human activity monitoring data

We tested the effectiveness of volunteered geographic datasets by comparing the data collected from Strava and Flickr to empirical measures of visitation levels from motion-triggered cameras in Mission Trails Regional Park. The spatial overlap between the camera data collection points and the Strava and Flickr data was limited; 5 of 12 Mission Trails camera points overlapped with Strava segments, and 8 of 12 Mission Trails camera points overlapped with Flickr data. We used linear regression models and rank-order correlations to test the strength of the relationship between the mean number of people per year per camera point and visitation data from Strava and Flickr. For Strava, we compared the number of cyclists detected by cameras to cycling effort per year for each Strava segment. For Flickr, we compared the number of all visitors detected by cameras to the sum of all average annual Flickr PUD pixels within a 50 m buffer of a camera point.

Regressions and rank-order correlations indicated that camera data were not significantly related to either Strava (Spearman's rho = -0.1, $p = 0.95$, linear regression $R^2 = 0.14$, $p = 0.53$) or Flickr (Spearman's rho = 0.14, $p = 0.75$; linear regression $R^2 = 0.05$, $p = 0.57$) data. However, in the comparison between Strava and camera data, one location had the highest level of use in the camera data and the lowest level of use in the Strava data. Excluding this outlier, there was a strong positive rank-order correlation between camera point and Strava data (rho = 0.8, $p = 0.33$), though it was not statistically significant due to small sample size (n=4). At least one of the Strava segments overlapping the omitted camera point has not recorded any cycling attempts since 2014, so average yearly cycling effort from this segment is unlikely to reflect current cycling activity patterns recorded by the cameras.

We suspect that the lack of a relationship between Strava or Flickr data and counts from camera traps could have several explanations. First, the temporal scale of the datasets differ; we had to use longer time scales for Strava (9 years) and Flickr (13 years) in order to gather sufficient data, whereas the camera trap data were all collected within one year. Second, our sample sizes were small due to limited overlap of the camera points and the Strava and Flickr data. Finally, many of the previous

studies that have found strong relationships between volunteered geographic data and empirical visitor counts have taken place in national parks (e.g., Hausmann et al. 2018; Heikinheimo et al. 2017; Tenkanen et al. 2017; Mancini et al. 2018), where visitors may be likely to travel from further distances than visitors to San Diego-area reserves; this may affect the number and spatial distribution of photos that are taken in our study reserves and uploaded to platforms such as Flickr.

Figure 5. Average annual photo-user days (PUD) per 50 m pixel between 2005 and 2017 at Mission Trails Regional Park, collected from Flickr.

Chapter 3. Effects of Human Activity on Reptiles and Mammals

Reptile monitoring

We monitored reptile species at the same 14 NCCP reserves and 92 sampling points where we monitored human activity and mammal species (*Figure 1*). 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 a small 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.

We collected 1077 detections of 11 lizard and 11 snake species over 1305 survey occasions (*Table 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 (± SD) of 3.6 ± 1.5 species per sampling point (range: 1 - 8) over the course of the study.

Mammal monitoring

We monitored mammal species at the same 14 NCCP reserves and 92 sampling points where we monitored human activity and reptile species (*Figure 1*). We used motion-triggered cameras to monitor mammal habitat use and relative activity, as well as human activity, at each sampling point. Animals appearing in photos were identified to species, with the exception of the brush rabbit (*Sylvilagus bachmani*) and desert cottontail (*S. audubonii*), which are difficult to distinguish in photos and were both labeled "rabbit."

In addition to domestic dogs (*Canis lupus*), we detected 13 mammal species squirrel-sized or larger: coyote (*Canis latrans, n=8,854*), brush rabbit and desert cottontail (*Sylvilagus bachmani* and *S. audubonii*, 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).

Table 2. Characteristics and numbers of detections of each reptile species detected. SVL is body size as measured by snout-vent length.

Scientific name	Common name	Habitat specificity[a]	SVL (cm)[b]	Board detections	Transect detections	Total 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

[a] Franklin et al. (2009)
[b] Jones and Lovich (2009)

Vegetation surveys

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 10m 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 0.5m intervals, we held a measuring rod

Table 3. Variables used to model reptile occupancy (ψ), detection probability (p), species richness (SR), and community composition (CC).

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

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 10m 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 vegetation is generally 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%. Plant cover often summed to > 100% because multiple plants were often recorded at the

Table 4. Variables used to model mammal habitat use (ψ), detection probability (p), and relative activity (RA).

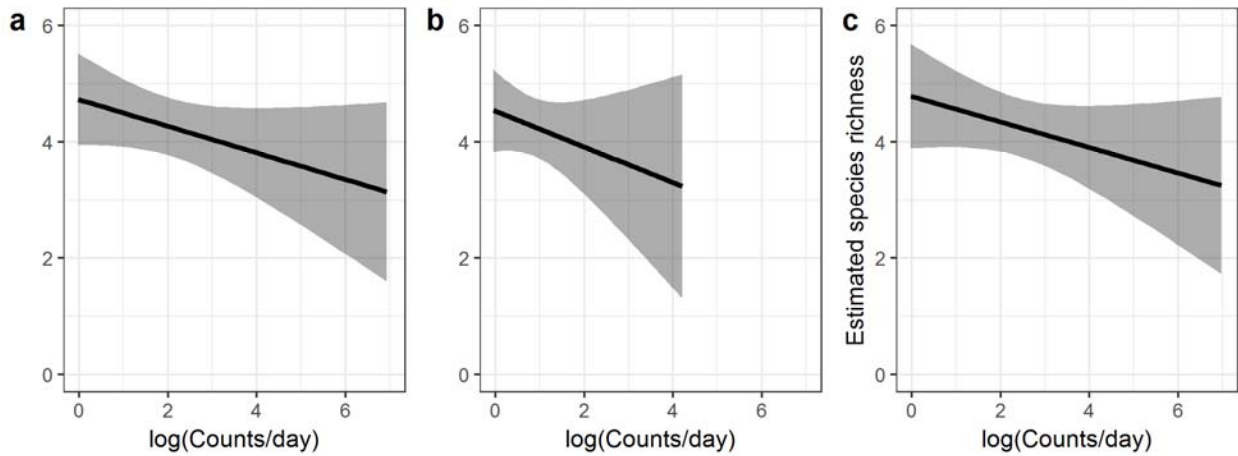| Covariate	Category	Description	Data source	Observed range	Parameter
Cyclists	human	mean per day	field	0 - 102	ψ, RA
Pedestrians	human	mean per day	field	0 - 2,826	ψ, RA
Total humans	human	mean per day	field	0 - 2944	ψ, p, RA
Development	human	housing units within 500m of point	GIS	0 - 375	ψ, p, RA
Elevation	topography	meters, mean value within 10m of point	GIS	5.3 – 203.2	ψ, RA
Slope	topography	degrees, mean value within 10m of point	GIS	0.6 - 20.4	ψ, RA
Chaparral	habitat	% cover within a 500m buffer of point	GIS	3 - 100	ψ, p, RA
Riparian	habitat	% cover within a 500m buffer of point	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 of point	GIS	0.2 - 0.62	ψ, p, RA
Julian date	temporal	day of the year on the first day sampling period	field	1 - 326	p, RA
Trail width	observation process	meters	field	1.0 - 8.3	P

same transect point. We removed plant species that we found at fewer than five sampling points. We 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.

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.

Model covariates

We hypothesized that reptile species richness, community composition, and occupancy is driven primarily by habitat characteristics, topography, and human activity (*Table 3*). We used plant
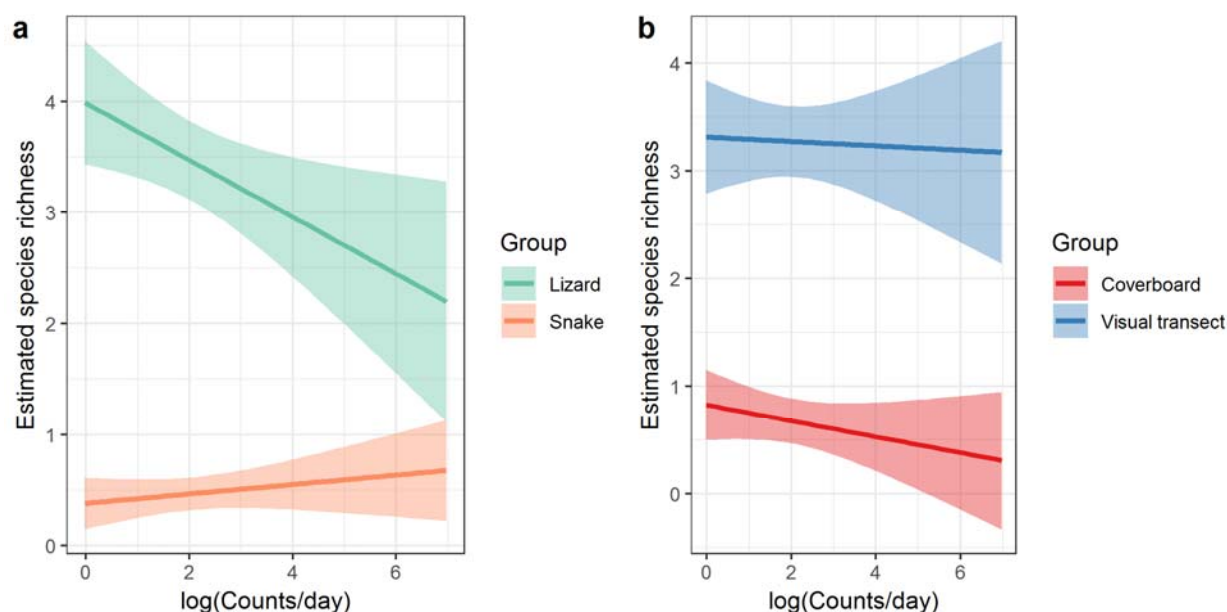
Figure 6. Estimated reptile species richness at the sampling-point level (Chao estimator) in relation to daily counts of a) pedestrian b) cyclist, and c) total human activity. The shaded areas show 95% confidence intervals.

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 as variables describing habitat. 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 and variability 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 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*). We also included total human activity as a covariate for detection probability because lizards may have responded to humans behaviorally in a way that affected their detectability (e.g., hiding or fleeing) but continued to occupy the area. We tested all variables for collinearity and eliminated variables with a correlation coefficient greater than 0.7 (Burnham & Anderson 2002).

We hypothesized that mammal habitat use and relative activity is driven by habitat characteristics, topography, development, and human activity (*Table 4*). To describe habitat, we used the percent cover of 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 and slope to model topography. Our measure of development was the number of housing units within 500 m of the sampling point. To model 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. To model detection probability, we used percent cover of vegetation types, housing units, total human activity (all recreation types plus vehicle counts), Julian date, and trail width. We tested all variables for collinearity and eliminated variables with a correlation coefficient greater than 0.7 (Burnham & Anderson 2002).

Figure 7. Estimated sampling-point level richness (Chao estimator) of a) lizards and snakes and b) reptile 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.
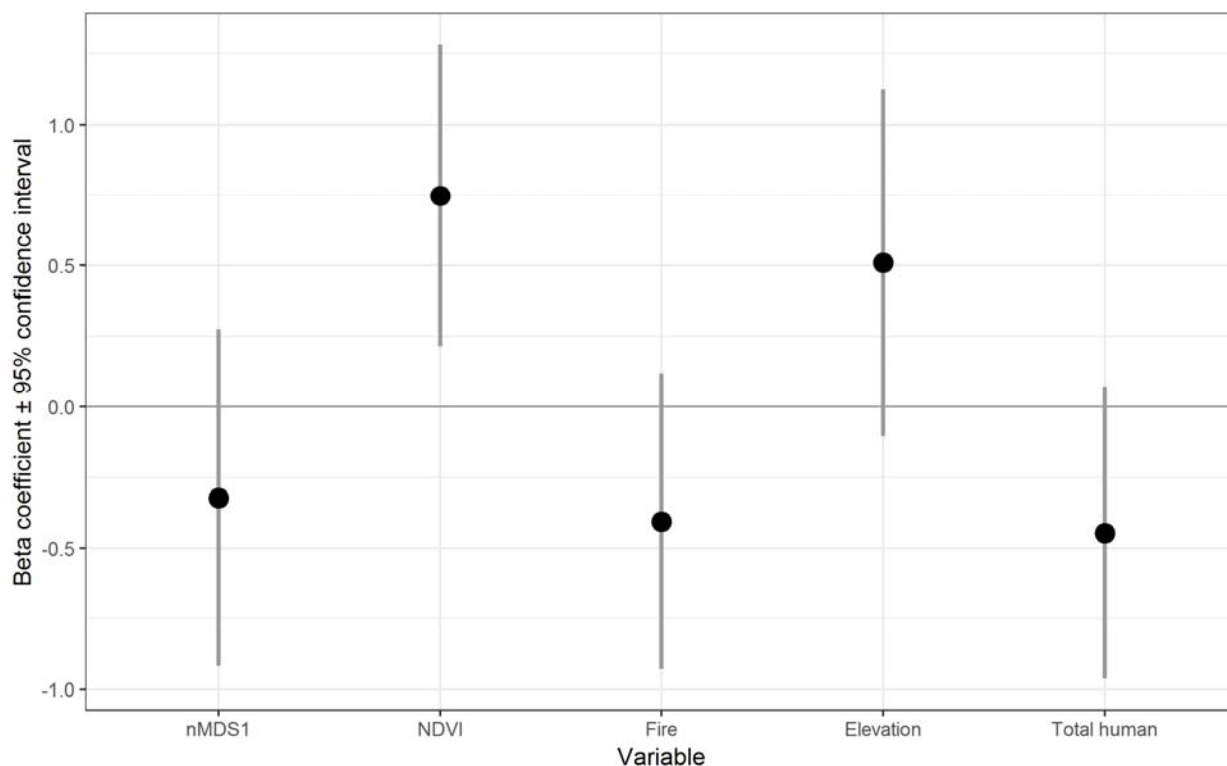

Reptile statistical analyses

We used species accumulation models to estimate the number of undetected reptile 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 relationship among 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 versus those primarily detected via visual transects.

To assess whether reptile 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 also recorded body size (median snout-vent length [SVL]; Lemm 2006; *Table 1*). We restricted the body size analysis to lizards since snakes were rarely detected but had widely varying body sizes. We then examined the effects of habitat, topography, and human activity on the relative dominance of specialists and the mean body size of lizard species and individuals at each sampling point. We used beta regression models to test how the proportion of specialist species observed and the proportion of detections of specialists varied in association with habitat, topography, and human activity variables (Hinners et al. 2012; Farr et al. 2017). We used linear regression models to evaluate how mean body size of lizard species and individuals varied in response to these variables.

For the reptile species richness linear regression models and the reptile community composition beta and linear regression models, we built a series of models with a maximum of two habitat variables

Figure 8. Beta coefficients and 95% confidence intervals for the relationship between habitat, topography, and human variables and estimated reptile species richness, from linear regression models selected as the best model containing the variable of interest. See Table 3 for explanation of the variables.
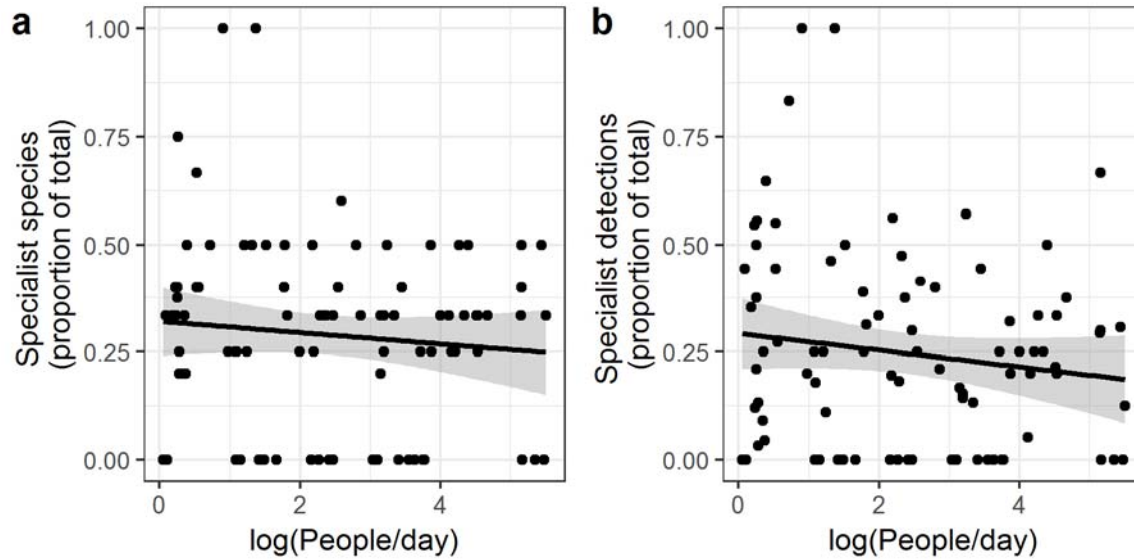

and one topography variable. We used Akaike's information criterion corrected for small sample size (AICc) to rank and compare models (Burnham & Anderson 2002) using the R package AICcmodavg (Mazerolle 2019), and then added each human activity covariate (singly) to each of the models with ≤2 Δ AICc. We considered human activity to have an important effect if models containing human activity variables reduced AICc values, and if the confidence intervals of the corresponding regression coefficient did not overlap zero (Olson et al. 2005).

We modeled the occupancy of lizard species for which we had sufficient detections 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.

We used a stepwise model building procedure (Lebreton et al. 1992), first running models to determine the variables that best explained detection probability while holding occupancy (ψ) at a global structure. We used combinations of variables for detection probability from all models with

Figure 9. Proportion of reptile a) specialist species and b) detections of specialist individuals in relation to daily counts of total human activity. The line shown is a univariate linear regression model and associated 95% confidence interval.
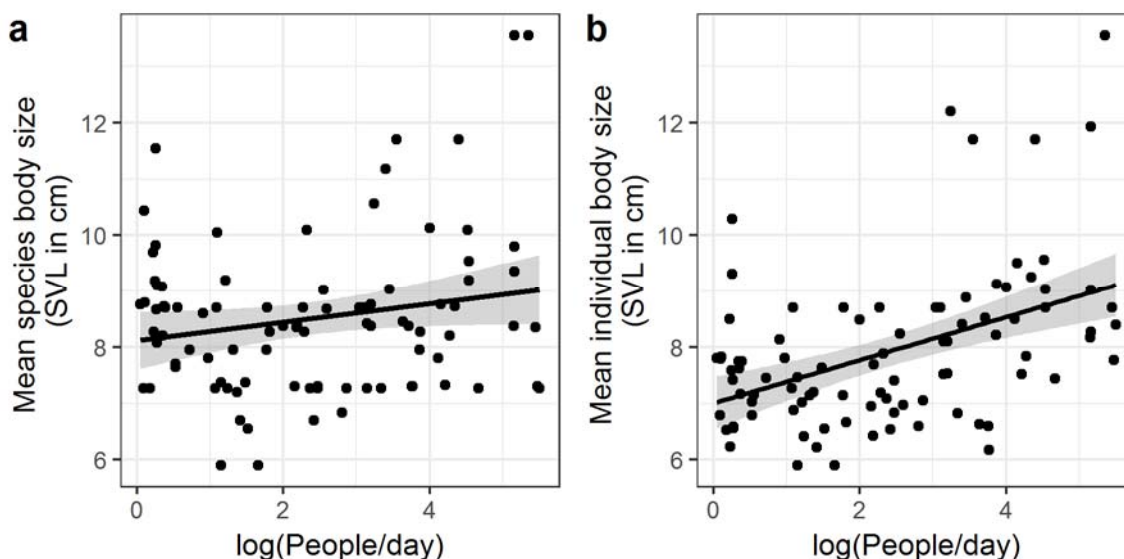

ΔAICc ≤ 2, assessing how occupancy varied in relationship to habitat and topography variables. We limited models to two habitat variables and one topography variable, and ran all possible combinations of additive models (30 models for each detection structure). Finally, we added each of the human activity covariates to each of the models with ≤2 Δ AICc. We used a parametric bootstrapping procedure to compare the observed χ^2 statistic for the most general model to the χ^2 statistic from 10,000 simulated datasets (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 (ĉ), resulting in a QAICc value. We considered human activity to be an important predictor if models containing human activity variables reduced QAICc values, and if the confidence intervals of the corresponding regression coefficients did not overlap zero.

Effects of human activity on reptiles

The total number of reptile species across all sampling points, including undetected species, was estimated to be 26 ± 5.2 using the Chao estimator. Human activity was associated with a decline in estimated species richness (*Figure 6*). Total human, pedestrian, or cyclist activity were included in six of eleven top models with ΔAICc ≤ 2 (*Table A1 in Appendix A*), and each of the four best-supported regression models contained either total human or pedestrian activity rates. Total human (β [95% CI] = -0.45 [-0.96, 0.07]) and pedestrian (-0.40 [-0.93, 0.12]) activity were negatively associated with species richness, though confidence intervals overlapped zero slightly. Cyclist activity (-0.29, [-0.80, 0.23]) had a negative but imprecise relationship with estimated species richness.

Lizard richness declined in association with human activity, while snake richness was not related to human activity (*Figure 7a*). Richness of species detected primarily with coverboards (n=9) and of species detected primarily with visual transects (n=13) both declined only slightly as human activity increased (*Figure 7b*).

Figure 10. Mean body size of lizard 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.
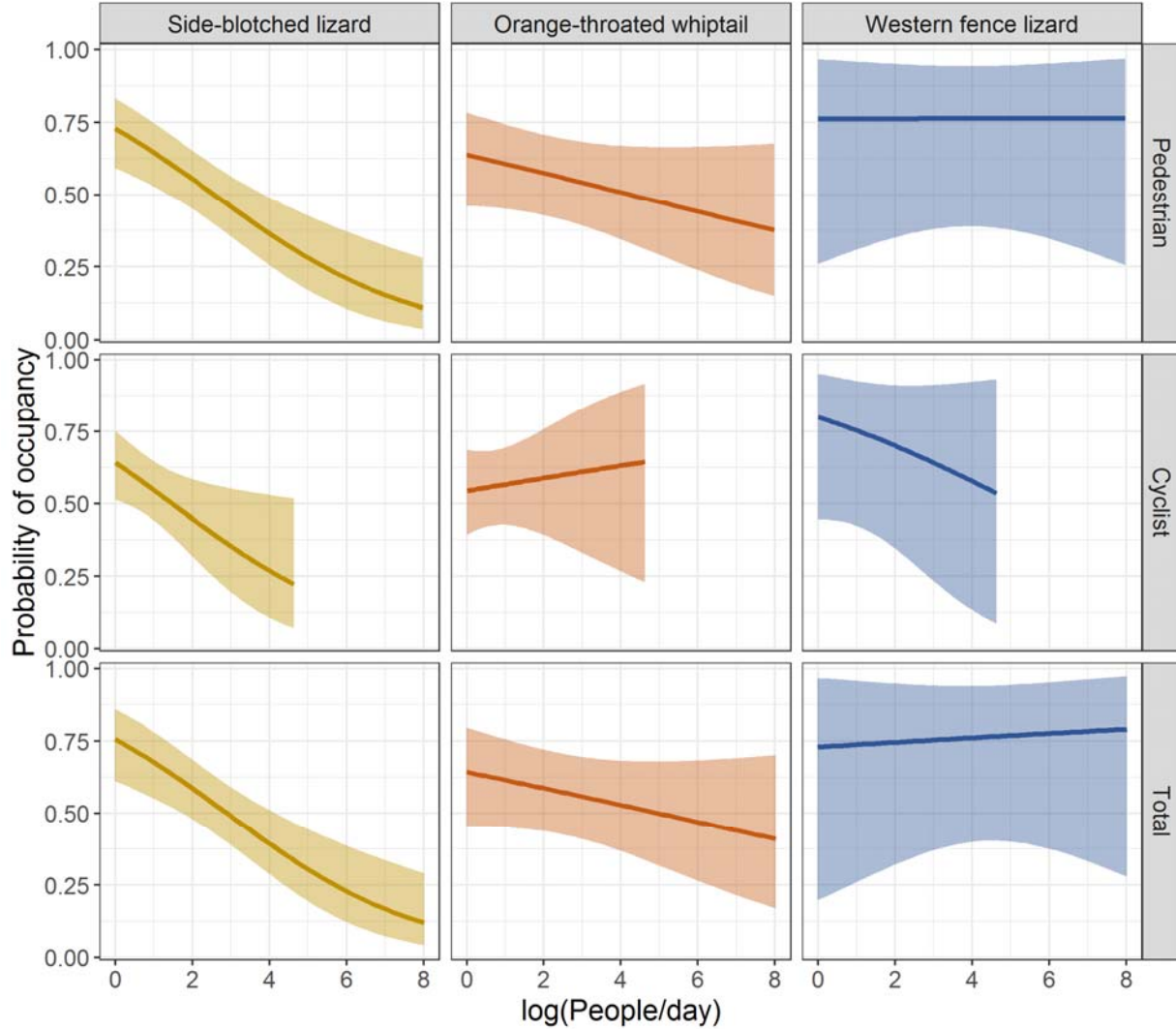

Reptile species richness was positively related to NDVI (β [95% CI] = 0.66 [0.13, 1.19]; *Figure 8*), which was included in each of the eleven best-supported models with $\Delta AICc \leq 2$ (*Table A1 in Appendix A*). Years since fire was included in six of eleven top models and had a negative association with species richness (-0.29 [-0.89, 0.30]). Elevation was included in four of eleven top models and had a positive association with species richness (0.34 [-0.23, 0.92]). nMDS1 was included in two of eleven models and had a negative association with species richness (-0.38 [-0.97, 0.21]). However, only the confidence interval for NDVI did not include zero.

The proportion of specialist species per sampling point averaged 0.29 ± 0.22, and the proportion of detections of specialist individuals averaged 0.25 ± 0.23. Neither the proportion of specialist species nor the proportion of specialist detections showed a clear trend in relation to human activity (*Figure 9*), and in general 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 species (*Table A2 in Appendix A*), but the confidence interval of the beta coefficient included zero (β [95% CI] = -0.14 [-0.42, 0.14]). The four best-supported models for proportion of specialist detections included two models with a human activity variable (cyclist and total human activity; *Table A2 in Appendix A*), though both of the confidence intervals for the beta coefficients included zero (cyclist: -0.15 [-0.43, 0.13]; total human: -0.03 [-0.18, 0.11]).
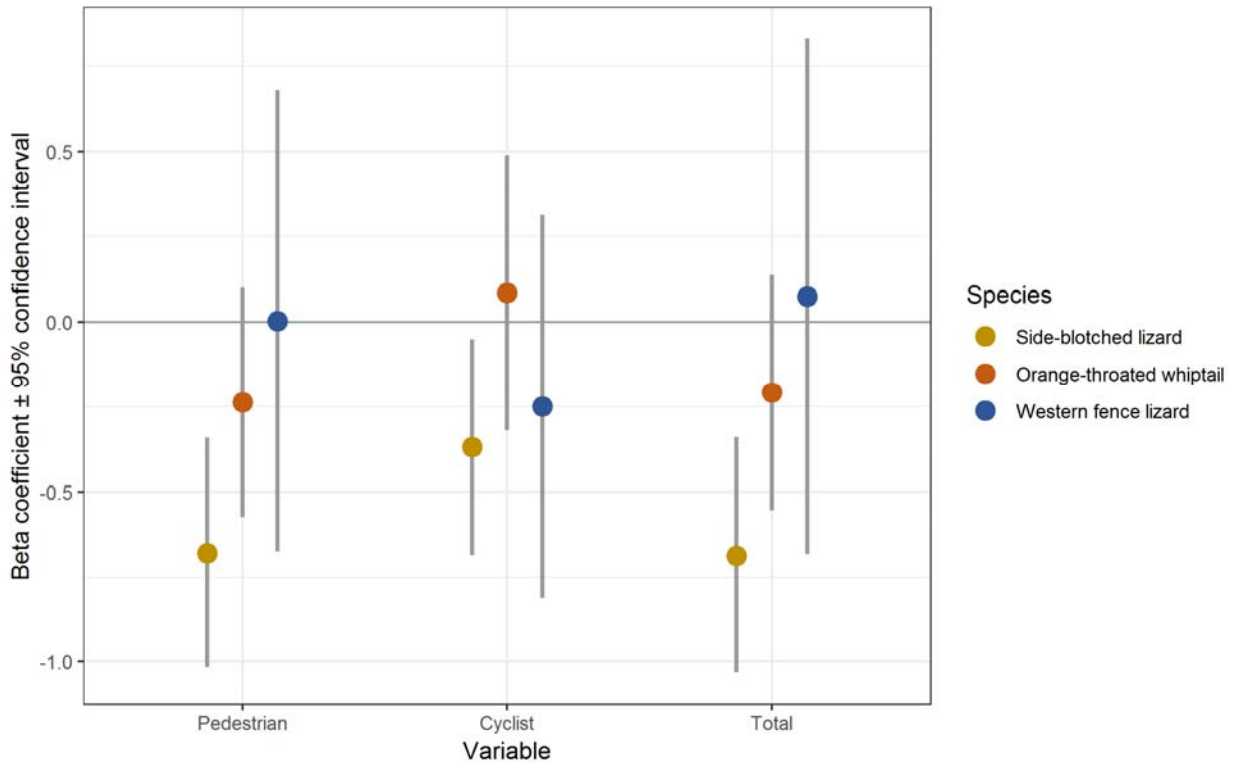
Mean body size of lizard species and mean body size of individuals detected per sampling point increased as human activity increased, more strongly for mean body size of individuals (*Figure 10*). Seven of nine best-supported linear regression models for body size of species included a human activity variable, whereas all eight best-supported models for mean body size of individuals included pedestrian or total human activity (*Table A3 in Appendix A*). The top linear regression models had an R^2 of 0.15 for body size of species and 0.28 for body size of individuals. Beta coefficients for total human activity included zero for body size of species (β [95% CI] = 0.09 [-0.08, 0.27]), but did not for body size of individuals (0.31 [0.16, 0.47]).

Figure 11. 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. Shaded areas show 95% confidence intervals.

We had sufficient detections of three lizard species to model occupancy: the orange-throated whiptail (*Aspidoscelis hyperythra*), western fence lizard (*Sceloporus occidentalis*), and common side-blotched lizard (*Uta stansburiana*). 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 A4 in Appendix A*). Common side-blotched lizard occupancy was negatively related to all three human activity variables, most strongly for total human (β [95% CI] = -0.69 [-1.03, -0.34]) and pedestrian (-0.68 [-1.02, -0.34]) activity (*Figures 11, 12*); these effect sizes were larger than any other covariate except years since fire (*Figure 13*). nMDS2 (-0.15 [-0.51, 0.2]) and years since fire (-0.85 [-1.2, -0.5]) had negative relationships with occupancy, while elevation (0.13 [-0.32, 0.59]) and solar radiation (0.25 [-0.07, 0.58]) had positive relationships with occupancy, although confidence intervals overlapped zero for all variables except years since fire

Figure 12. 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 variable of interest.
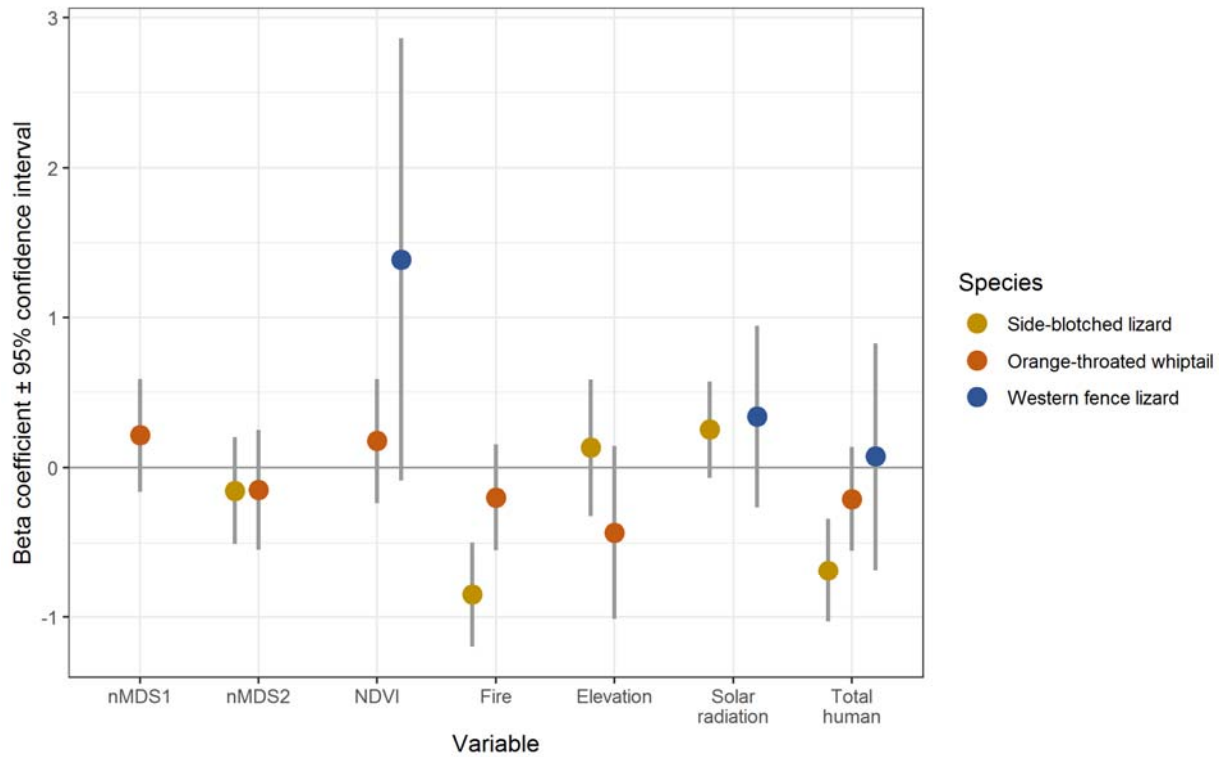

(*Figure 13*). Common side-blotched lizard detection probability was higher in sunny conditions and when CLL was the observer rather than a technician or volunteer (*Table A4 in Appendix A*).

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 A4 in Appendix A*). Total human (β [95% CI] = -0.21 [-0.55, 0.14]) and pedestrian (-0.24 [-0.57, 0.10]) activity were negatively related to occupancy and cyclist activity was slightly positively related to occupancy (0.08 [-0.32, 0.49]), but confidence intervals overlapped zero (*Figures 11, 12*). Orange-throated whiptail occupancy was negatively related to nMDS2 (-0.15 [-0.55, 0.25], years since fire (-0.20 [-0.55, 0.15]), and elevation (-0.43 [-0.92, 0.08]) and positively related to nMDS1 (0.22 [-0.16, 0.59]) and NDVI (0.18 [-0.24, 0.60]; *Figure 13*). Confidence intervals for all environmental variables overlapped zero. Orange-throated whiptail detection probability was higher in sunny conditions, in summer months (June-August), and with greater search effort (>1 observer; *Table A4 in Appendix A*).

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 A4 in Appendix A*), but coefficients for total human (0.07 [-0.68, 0.83]) and pedestrian (0.003 [-0.67, 0.68]) activity were approximately zero. There was a slight negative relationship between occupancy and cyclist activity (-0.25 [-0.81, 0.31]; *Figures 11, 12*). NDVI and solar radiation were the only two environmental variables selected in top models for the western fence lizard (*Table A4 in Appendix A*).

Figure 13. 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 the best single-species occupancy models containing the variable of interest.
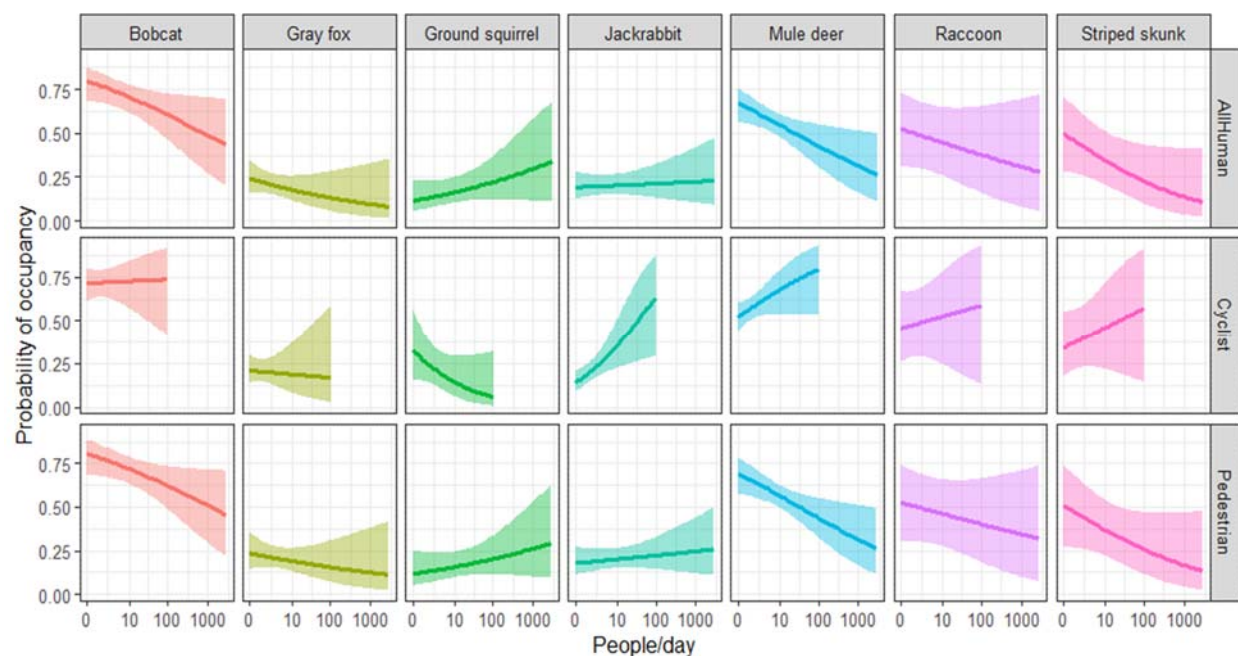

Occupancy was positively related to NDVI (β [95% CI] = 1.39 [-0.09, 2.86] and solar radiation (0.34 [-0.27, 0.95]), though confidence intervals for both variables overlapped zero, just slightly for NDVI (*Figure 13*). Human activity, included in the detection structure of three of the four top models, was a better predictor of western fence lizard detection probability than occupancy (*Table A4 in Appendix A*). 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; *Table A4 in Appendix A*).

Mammal statistical analyses

We modeled mammal habitat use using single-species, single-season occupancy models with implicit dynamics (MacKenzie et al. 2017) for the species with sufficient detections for models to converge, using the R package unmarked (Fiske & Chandler 2011). Human activity levels varied by season in a complex way that covaried with landscape position and individual site. Treating each combination of sampling point and camera rotation as a separate data point 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 assumed that our sampling points were closed to changes in occupancy status over the roughly one-year study duration because most of our focal species have lifespans of several years and maintain fairly stable home ranges, and most of our study reserves are bounded by urban development, limiting immigration and emigration. Sampling locations were smaller than the home range of an individual animal, so we interpret occupancy

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Figure 14. Probability of habitat use of seven mammal species in relation to daily counts of total human activity, cyclists, and pedestrians, from single-species occupancy models. Shaded areas show 95% confidence intervals.
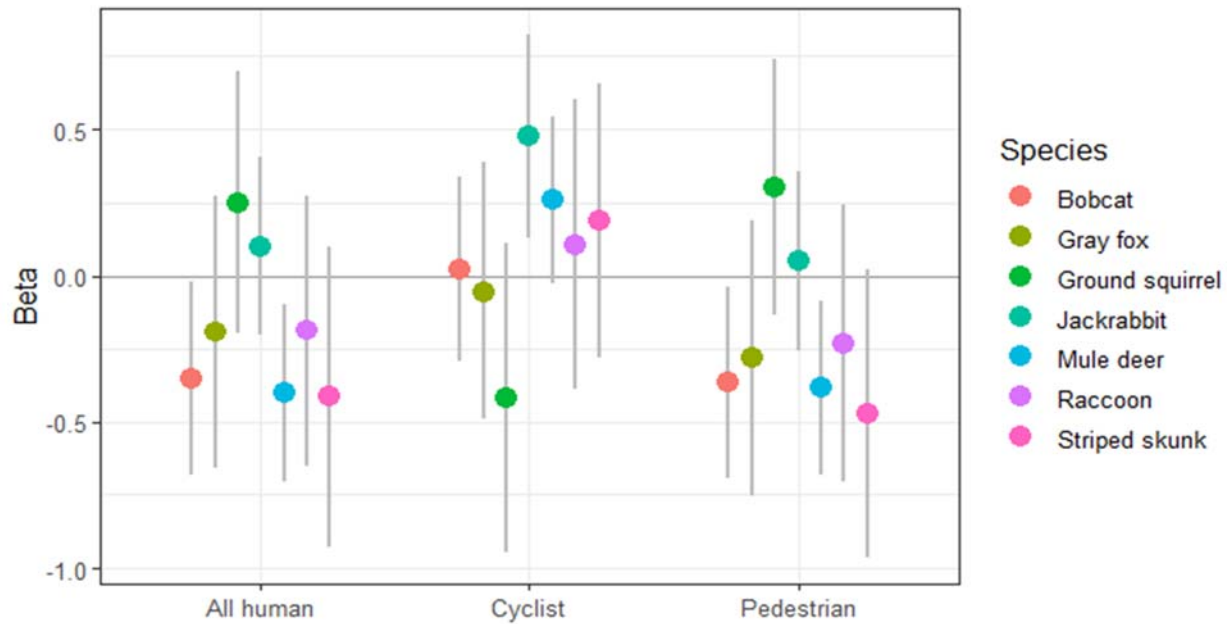

estimates as probability of habitat use rather than true probability of occupancy of the site (MacKenzie et al. 2017). We pooled detections into 5-day sampling occasions so that detection histories were not overly sparse (Welsh et al. 2013).

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. We used Akaike's information criterion corrected for small sample size (AICc) to rank and compare occupancy models (Burnham & Anderson 2002). We used the combinations of variables for detection probability from the best-supported models ($\leq 2\ \Delta$ AICc) in the next step, assessing how occupancy (ψ) varied in relationship to habitat, topography, and development variables. We limited models to two habitat variables, one topography variable, and development, and ran all possible combinations of additive models (60 models per detection structure). Finally, we added each of the human activity covariates (singly) to each of the best-supported models ($\leq 2\ \Delta$ AICc) and again ranked and compared models. We considered human activity to have an important effect if models containing human activity variables reduced AICc values, and if the confidence intervals of the corresponding regression coefficients did not overlap zero (Olson et al. 2005). We used a parametric bootstrapping procedure to compare the observed χ^2 statistic for the most general model to the χ^2 statistic from 10,000 simulated datasets (MacKenzie & 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 QAICc value.

In addition to modeling mammal habitat use, we also estimated relative activity rates for each species, given relative use of an area may reflect habitat quality (Manly et al. 2002; Lewis et al. 2015). Specifically, we hypothesized that lower frequency of use of a sampling point can be interpreted as selection against landscape characteristics (including human activity levels) at each point. Our

Figure 15. Beta coefficients and 95% confidence intervals for the relationship between daily counts of human activities (total human activity, cyclists, and pedestrians) and mammal habitat use, from best single-species occupancy models containing the variable of interest.
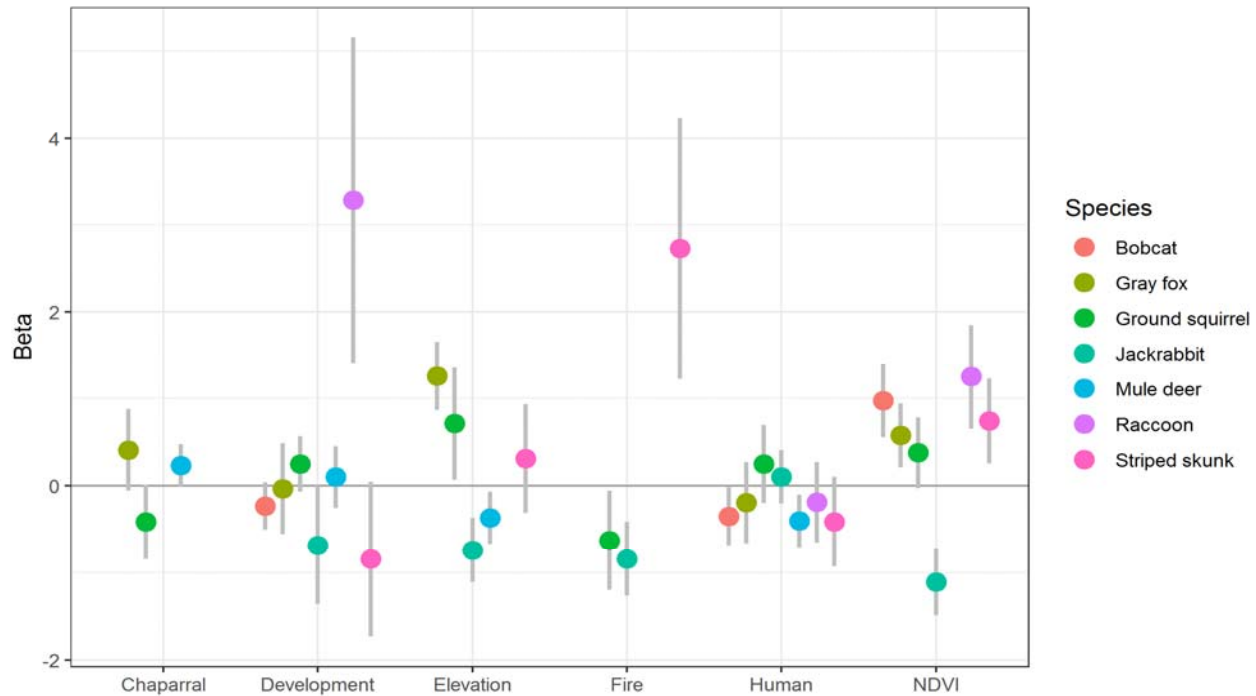

measure of relative activity rate was the number of hours per day in which at least one individual of a given species was detected. This measure helps ensure that multiple photos of the same individual animal within a short period of time do not overestimate the overall relative level of use (Burton et al. 2015).

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, using the same variables as in the occupancy models described above. Negative binomial regression models are suitable for count data in which overdispersion prevents the use of a Poisson regression model (Lawless 1987). We built a series of models using additive combinations of up to two habitat, topography, or development variables. To each model with ≤2 Δ AICc, we added human activity variables and again compared Δ AICc values. As above, we considered human activity to have an important effect if models containing human activity variables reduced AICc values, and if the confidence intervals of the corresponding regression coefficients did not overlap zero (Olson et al. 2005). We assessed model fit by visually inspecting rootograms (Kleiber & Zeileis 2016).

Effects of human activity on mammals

Mammal 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

Figure 16. Beta coefficients and 95% confidence intervals for the relationship between habitat, topography, and human covariates and mammal habitat use, from the best single-species occupancy models containing the variable of interest.
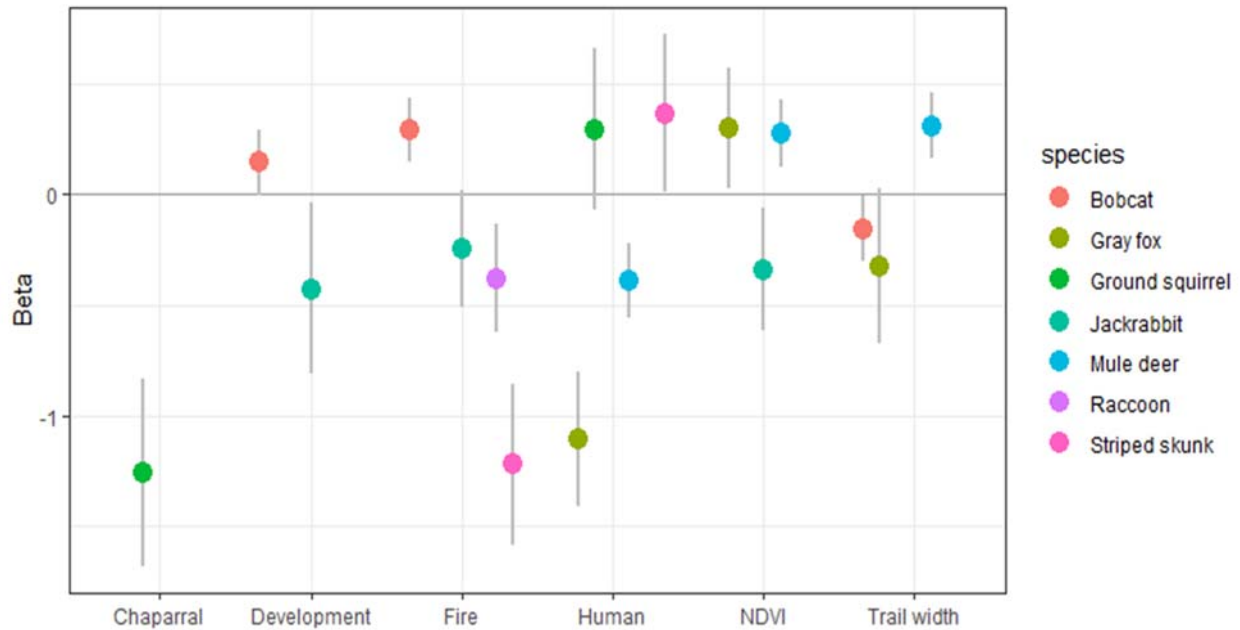

opossum, domestic cat), or occupancy models did not fit adequately (rabbit; ĉ > 4), perhaps because the category included two species.

Models containing a human activity variable outcompeted those without a human activity variable for bobcat, mule deer, jackrabbit, striped skunk, and ground squirrel (*Table A5 in Appendix A*). 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 14*), but the coefficients in only the bobcat and mule deer models had confidence intervals that did not include zero (confidence intervals for striped skunk overlapped zero only slightly; *Figure 15*). In contrast, jackrabbit habitat use was positively related to all three human activity types and ground squirrel habitat use was positively related to total human and pedestrian activity, though confidence intervals included zero in all but one case (cyclist counts in the jackrabbit model). We also observed a positive relationship between cyclist activity and habitat use for bobcat, mule deer, raccoon, and striped skunk, though each of these except mule deer had confidence intervals that extended far below zero.

The covariates that affected mammal habitat use most frequently were development, elevation, and NDVI (*Figure 16*). Development had a negative relationship with habitat use of jackrabbit and striped skunk and had a strong positive relationship with raccoon habitat use. Gray fox and ground squirrel habitat use increased and jackrabbit and mule deer habitat decreased at higher elevations. NDVI had a positive relationship with habitat use of bobcat, gray fox, raccoon, striped skunk, and ground squirrel, and a negative relationship with jackrabbit habitat use. Percent cover of chaparral was positively associated with habitat use of gray fox and mule deer and negatively associated with
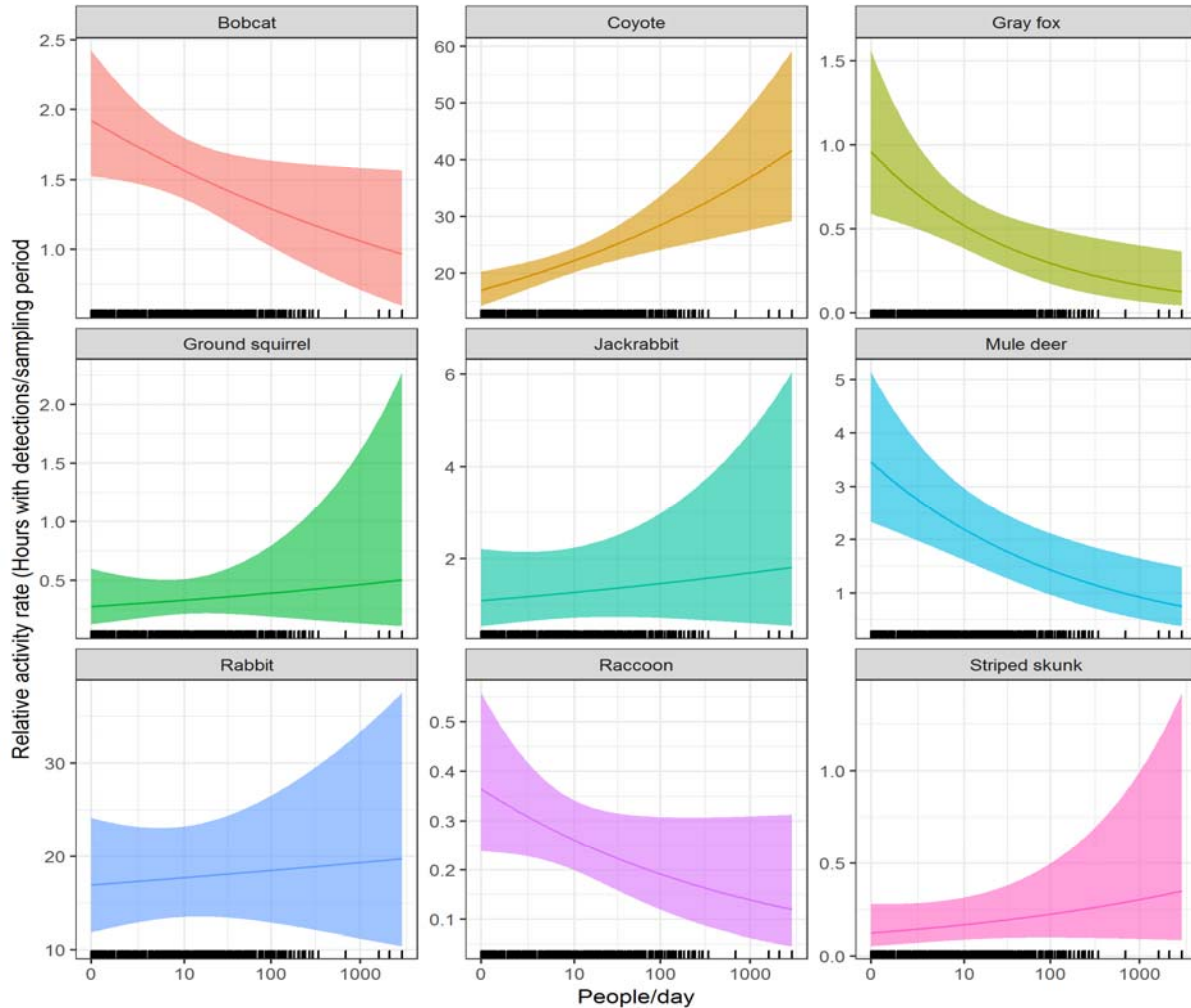
Figure 17. Beta coefficients and 95% confidence intervals for the relationship between habitat, topography, and human variables and mammal detection probability, from the best single-species occupancy models containing the variable of interest.

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. In general, many of the relationships between covariates and habitat use were stronger than those between human activity and habitat use.

Variables affecting mammal detection probability included chaparral cover, development, years since fire, human activity, NDVI, trail width, and Julian date (*Figure 17*). Chaparral cover had a negative relationship with ground squirrel detection probability. Development had a positive relationship with bobcat detection probability and a negative relationship with jackrabbit detection probability. Years since fire was positively associated with bobcat detection probability and negatively associated with detection probability of jackrabbit, mule deer, and striped skunk. Total human activity had a positive relationship with striped skunk detection probability and a negative relationship with gray fox and mule deer detection probability. NDVI had a positive relationship with gray fox and mule deer detection probability and a negative relationship with jackrabbit detection probability. Trail width had a positive association with mule deer detection probability and a negative association with bobcat and gray fox detection probability. Julian date was modeled as a quadratic relationship; detection probability was highest in winter for gray fox, late spring/early summer for ground squirrel, late winter through spring for jackrabbit, fall through early winter for mule deer, and late
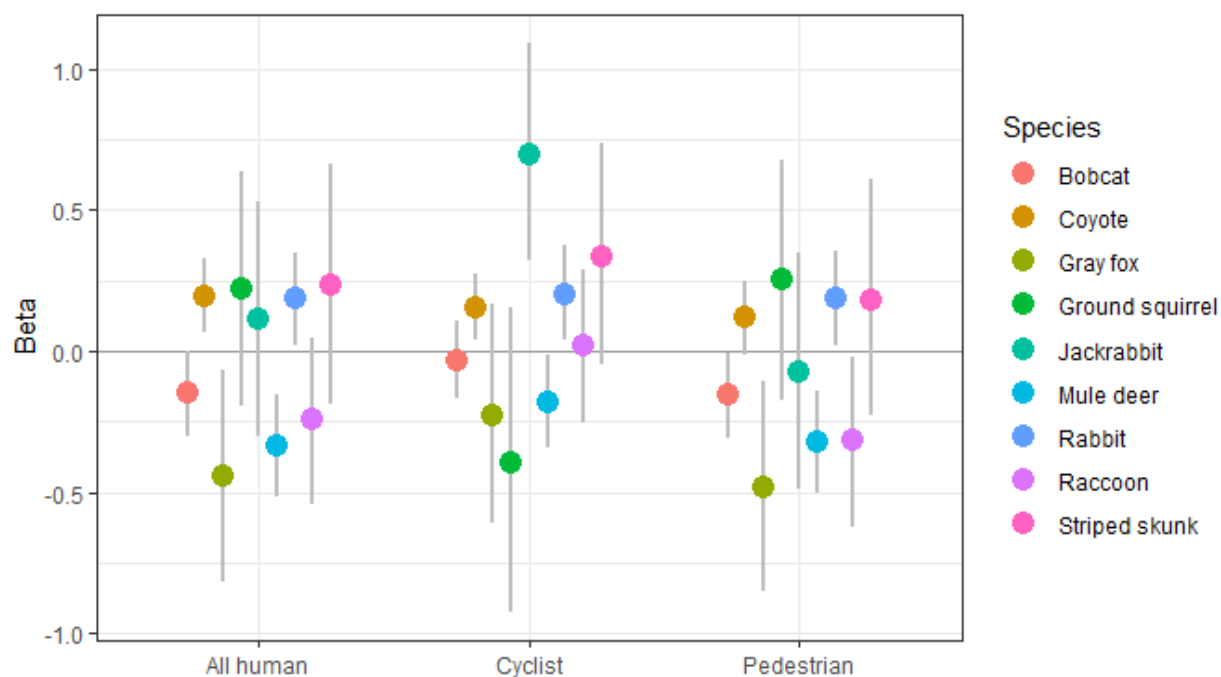
Figure 18. Relative activity rates (sum of hours detected over the four-week sampling period) of nine mammal species in relation to daily counts of total human activity, from negative binomial regression models. Shaded areas show 95% confidence intervals.

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

For eight of nine modeled species (all but ground squirrel), the best-supported models of relative activity included a human activity variable as a predictor (*Table A6 in Appendix A*). Relative activity of bobcat, gray fox, mule deer, and raccoon were negatively associated with total human and pedestrian activity (*Figure 18*), although the confidence interval slightly overlapped zero for the raccoon total human activity coefficient (*Figure 19*). Coyote and rabbit relative activity was positively associated with total human and pedestrian activity, but the confidence interval for the coyote pedestrian activity coefficient slightly overlapped zero. Relationships with cyclist activity were more variable. Gray fox, mule deer, and ground squirrel relative activity was negatively related to cyclist activity (though confidence intervals for gray fox and ground squirrel overlapped zero), whereas

Figure 19. Beta coefficients and 95% confidence intervals for the relationship between daily counts of total human activity and mammal relative activity rates, from the best negative binomial regression models containing the variable of interest.

coyote, jackrabbit, rabbit, and striped skunk relative activity was positively related to cyclist activity (though confidence intervals for raccoon and striped skunk overlapped zero).

Relative activity was related to other variables in addition to human activity, most commonly chaparral cover and NDVI (*Figure 20*). Chaparral cover was positively associated with relative activity of coyote, ground squirrel, and rabbit, and negatively associated with relative activity of mule deer. NDVI was positively associated with relative activity of bobcat, coyote, mule deer, raccoon, and striped skunk, and negatively associated with jackrabbit activity. Development was positively associated with raccoon relative activity and negatively associated with striped skunk activity. Gray fox, jackrabbit, and striped skunk were more active at higher elevations. Years since fire was positively associated with bobcat and gray fox relative activity and negatively associated with ground squirrel activity.

Figure 20. Beta coefficients and 95% confidence intervals for the relationship between habitat, topography, and human covariates and mammal relative activity rates, from the best negative binomial regression models containing the variable of interest.

Chapter 4. Before-After Control-Impact Experiment

BACI experimental design

We conducted the before-after control-impact (BACI) study at Black Mountain Open Space Preserve, where the Miner's Ridge loop trail was closed in January 2017 for remediation of high arsenic levels in the soil and re-opened in April 2018. For the impact points, we installed camera posts and coverboards at two sampling points along the Miner's Ridge loop trail at the beginning of the closure (*Table 5*). For the control points, we selected five of the other sampling points in Black Mountain OSP located on trails not affected by the closure. In the "before" period, we began monitoring human activity and mammal and reptile communities at the impact points in late October 2017, leaving the cameras running continually and completing four reptile surveys. We used camera and reptile survey data collected at the control points between November 2017 and February 2018. During the "after" period, cameras operated at all seven sampling points for at least four weeks after the trail was opened, ending in June 2018, and we completed another 3-5 reptile surveys at each sampling point. Motion-triggered camera and reptile survey protocols were the same as those described in *Chapter 3*.

We identified another opportunity to conduct a BACI comparison at Hollenbeck Canyon Wildlife Area. The wildlife area contains a hunting dog training area that is open each year from September to February and is accessed via a gate that is locked during the closed season. We had one sampling point located on an unofficial trail/old road beginning at the dog training area parking lot, where we expected that trail use would be higher during the dog training season. We made comparisons between this point ("impact" point) and the four other sampling points at Hollenbeck Canyon that were not affected by seasonal closures ("control" points) using data collected during the 2017 open season, 2017 closed season, and 2018 open season (*Table 5*).

BACI analysis

To assess changes in mammal habitat use before and after changes in trail status at Black Mountain and Hollenbeck Canyon, we used single-species occupancy models for the species with sufficient detections. When species were ubiquitous across the sampling points, we assessed changes in detection probability rather than occupancy as a measure of relative activity or frequency of habitat use (Lewis et al. 2015, Wang et al. 2015). Detection data were pooled into 5-day sampling occasions, with five survey occasions before and after the trail re-opening at Black Mountain. We did not include habitat covariates because sample sizes were low, minimal changes in habitat occurred between the sampling periods, and our primary interest was in investigating the interaction of treatment (control or impact sampling point) and time period (before or after the change in trail status). Therefore, treatment and time period were the only variables included in the models. We compared models with an interaction against models without an interaction and against a null model.

Table 5. Dates of "before" and "after" data collection at control and impact sampling points at Black Mountain Open Space Preserve and Hollenbeck Canyon Wildlife Area.

Sampling point	"Before" camera days	# reptile surveys	"After" dates camera days	# reptile surveys
Black Mountain OSP				
Impact 1	11/01/2017 – 04/17/2018	4	04/19/2018 – 05/31/2018	4
Impact 2	11/01/2017 – 04/17/2018	4	04/19/2018 – 04/28/2018	4
Control 1	12/17/2017 – 02/01/2018	3	05/18/2018 – 05/30/2018	3
Control 2	12/17/2017 – 02/01/2018	3	05/04/2018 – 05/31/2018	3
Control 3	11/18/2017 – 12/13/2017	4	05/04/2018 – 05/11/2018	4
Control 4	11/18/2017 – 12/22/2017	4	05/04/2018 – 05/30/2018	4
Control 5	11/19/2017 – 12/22/2017	5	05/04/2018 – 05/31/2018	4
Hollenbeck Canyon Wildlife Area				
Impact	02/01/2017 – 02/28/2017	2	03/01/2017 – 03/05/2017	1
	09/06/2017 – 09/28/2017	2	04/25/2017 – 05/09/2017	1
	11/03/2017 – 11/19/2017	1	06/02/2017 – 06/12/2017	2
	12/07/2017 – 12/15/2017	2		
Control 1	01/29/2017 – 02/28/2017	2	03/01/2017 – 03/05/2017	1
	09/06/2017 – 09/18/2017	2	04/25/2017 – 05/03/2017	1
	11/03/2017 – 11/19/2017	1	06/02/2017 – 06/13/2017	2
	12/07/2017 – 12/15/2017	2	08/04/2017 – 08/16/2017	1
Control 2	09/30/2017 – 10/26/2017	3	03/08/2017 – 03/22/2017	1
	12/18/2017 – 01/05/2018	1	04/12/2017 – 04/22/2017	2
	02/08/2018 – 02/14/2018	2	06/15/2017 – 06/27/2017	1
			07/06/2017 – 07/18/2017	1
Control 3	09/30/2017 – 10/26/2017	3	03/08/2017 – 03/21/2017	1
	12/18/2017 – 01/05/2018	1	04/12/2017 – 04/23/2017	2
	02/08/2018 – 02/14/2018	2	06/15/2017 – 06/27/2017	1
			07/06/2017 – 07/28/2017	2
Control 4	09/30/2017 – 10/26/2017	3	03/08/2017 – 03/21/2017	1
	12/18/2017 – 01/05/2018	1	04/12/2017 – 04/23/2017	2
	02/08/2018 – 02/14/2018	2	06/15/2017 – 06/27/2017	1
			07/06/2017 – 07/18/2017	2

Figure 21. Human activity (mean people per day) before and after trails were reopened at Black Mountain OSP, at impact and control sampling points. Error bars show standard error. Differences between time periods were significant ($p < 0.05$ using a t-test) at Impact 1, Impact 2, and Control 5.

Human activity

At Black Mountain OSP, human activity at each of the impact points was approximately twice as high after trails were reopened ($t < -4.3$, $p < 0.001$), whereas human activity was significantly different at just one of five control points (*Figure 21*). However, human activity was not absent during the closed period at the impact points, averaging 18 and 20 people per day at the two points.

At Hollenbeck Canyon, human activity did not differ significantly between open and closed seasons at the impact point ($t = 0.16$, $p = 0.87$; *Figure 22*). Human activity was similar between periods at the control points, with the difference approaching significance for one sampling point, where use was higher in the open season ($t = 1.84$, $p = 0.07$).

Figure 22. Human activity (mean people per day) while the hunting dog training area was closed and open at Hollenbeck Canyon Wildlife Area, at impact and control sampling points. Error bars show standard error. Differences between time periods were not significant ($p < 0.05$ using a t-test) at any of the sampling points.
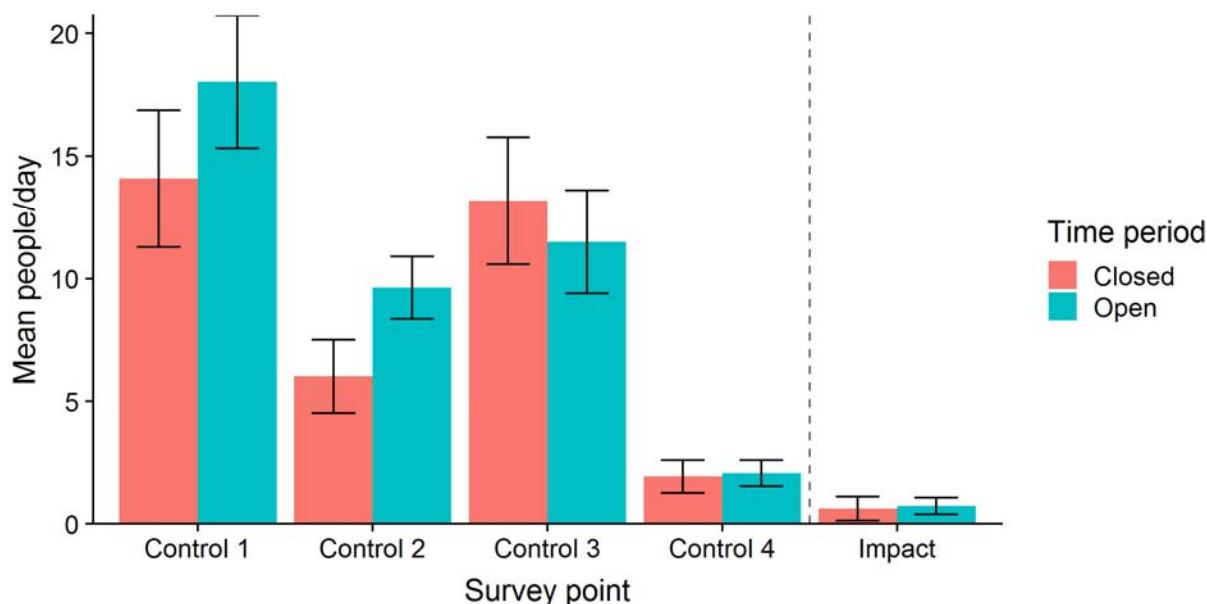

Mammal habitat use

Bobcats were detected at six out of seven Black Mountain OSP sampling points, while coyote and rabbits were detected at all seven points. At sampling points where they were detected, each species was detected at least once both before and after the trail re-opening. Accordingly, occupancy was not an informative parameter since nearly all locations were occupied during both time periods, and we instead used detection probability to assess the relative frequency of habitat use. Other species were not detected frequently enough for occupancy models to converge.

The null occupancy model was the best-supported model for all three species. However, models with an interaction term between time period and treatment showed that detection probability was reduced at impact points after the trail re-opening for bobcats and coyotes, especially bobcats (*Figure 23*).

Since there was no meaningful difference in human activity between closed and open seasons at the impact point, we did not analyze changes in mammal habitat use at Hollenbeck Canyon.

Figure 23. Mammal detection probabilities for bobcats, coyotes, and rabbits before and after trails were re-opened at Black Mountain OSP at impact and control points.

Reptile occurrence

Reptile detections at Black Mountain OSP were low, with just 17 detections in 53 visits to the seven sampling points. At four of the sampling points, including both the impact points, we had just one detection (of western fence lizard). The timing of the "before" data was not ideal for reptiles, with surveys done from November 2017 to February 2018, when most species are relatively inactive. Due to low detections, we did not analyze differences before and after the trail re-opening.

Since there was no meaningful difference in human activity between closed and open seasons at the impact point, we did not analyze changes in reptile occurrence at Hollenbeck Canyon.

Discussion

Human recreation activity was associated with declines in reptile species richness and the occupancy, habitat use, and relative activity of several reptile and mammal species in NCCP reserves in San Diego County, California. Our project demonstrates the importance of examining the effects of recreation across a full 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, or 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. 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 species conservation.

Effects of human recreation activity on reptiles

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 no 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 reptile richness associated with human activity parallels observed declines in bird and mammal richness in connection to human activity (e.g., Bötsch et al. 2017, Reed & Merenlender 2011, Banks & Bryant 2007). In our recent meta-analysis, we found that in 70% of comparisons, vertebrate richness or abundance was reduced in association with higher recreation activity (*Appendix D*). 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 minor differences in habitat use (e.g., use of heavily modified areas) influence species' tolerance of recreation. Instead, we found evidence that small-bodied 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 (*Figure 10*), probably because of frequent detections of the common side-blotched lizard and orange-throated whiptail. Nevertheless, the 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 (i.e., the distance from a stimulus at which an animal initiates an escape response) generally increases with body size. However, smaller bird species do not adjust their escape response to human disturbance as much as

larger birds, meaning that they likely incur higher energetic costs of human disturbance, rendering them more vulnerable to disturbance by human activity (Samia et al. 2016). We suspect a similar pattern could occur in lizards.

Most reptile species had insufficient detections to model a relationship with recreation activity. However, two of three lizards, the common side-blotched lizard and orange-throated whiptail, exhibited negative relationships between occupancy and human activity, though the relationship was stronger and more certain for the common side-blotched lizard (*Figure 11*). The common side-blotched lizard is the smallest lizard in the region, and it occurs in arid and semi-arid habitats including coastal scrub, chaparral, woodland, and grassland habitats (Jones & Lovich 2009). Though it is locally abundant (Franklin et al. 2009), the common side-blotched lizard had lower survival rates in urban areas where they had higher levels of physiological stress compared to rural areas (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 would be more sensitive to human activity than the other lizard species because 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 not found in degraded or developed areas (Jones & Lovich 2009). It is a species of conservation concern listed under the San Diego County Multiple Species Conservation Plan (MSCP Policy Committee & MSCP Working Group 1998). We observed a negative trend between occupancy and human activity, but with considerable uncertainty. A lack of flexibility in habitat use may also 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 (Suarez et al. 1998). Human activity also increases near residential development (Larson et al. 2018), 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 very tolerant of humans, inhabiting many types of natural habitat as well as backyards and highly modified city parks and (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 studies on this species show mixed results, with some finding no differences in

escape behavior between areas with high and low human activity, potentially indicating a lack of habituation (Putman et al. 2017), and others documenting longer flight initiation distances in areas with low human activity compared to high, suggesting that western fence lizards do habituate to human presence (Grolle et al. 2014).

Although we detected 22 species of reptiles, 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 (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). For example, 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.

Effects of human recreation activity on mammals

Human activity was associated with declines in habitat use of several mammal species, particularly bobcats and mule deer (*Figure 14*). 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, it can reduce habitat suitability. In particular, four species, bobcat, gray fox, mule deer, and raccoon, were less active in areas with higher levels of human activity (*Figure 18*).

Bobcats are known to be sensitive to urbanization (Riley 2006; Ordeñana et al. 2010), but responses to recreation have been mixed in previous studies in California, 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). In our study, bobcat habitat use and relative activity declined similarly as human activity increased. Bobcat habitat use was more strongly negatively related to human activity than to urban development, which also decreased the probability of habitat use.

Mule deer showed reductions in habitat use in association with total human and pedestrian activity, and human activity had a stronger relationship with mule deer habitat use than any other variable we considered. Relative activity of mule deer also declined with human activity, as did detection probability. Relative activity and detection probability measure similar properties of detection frequency (and some researchers use detection probability as a measure of relative activity; e.g., Lewis et al. 2015, Wang et al. 2015), so it is unsurprising that they show similar relationships with human activity. 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.

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; habitat use increased with NDVI and at higher elevations. However, gray fox relative activity and detection probability both declined in association with pedestrian and total human activity. Prior studies have similarly found gray foxes to be sparsely

distributed in coastal southern California, and rare or absent from some urban habitat fragments (Crooks 2002), potentially due to intraguild competition with dominant carnivores such as coyotes and bobcats (Crooks et al. 2010).

Raccoons are considered to be an urban-adapted mesopredator (Crooks 2002). They showed a trend toward reduced habitat use in association with human activity, but their habitat use was more strongly related to other covariates, specifically a positive relationship with development and NDVI. However, raccoon relative activity rates decreased in association with pedestrian activity. Our detections of raccoons were very low across all sites, so the relationship may be primarily driven by detections at a few relatively low-use sampling points.
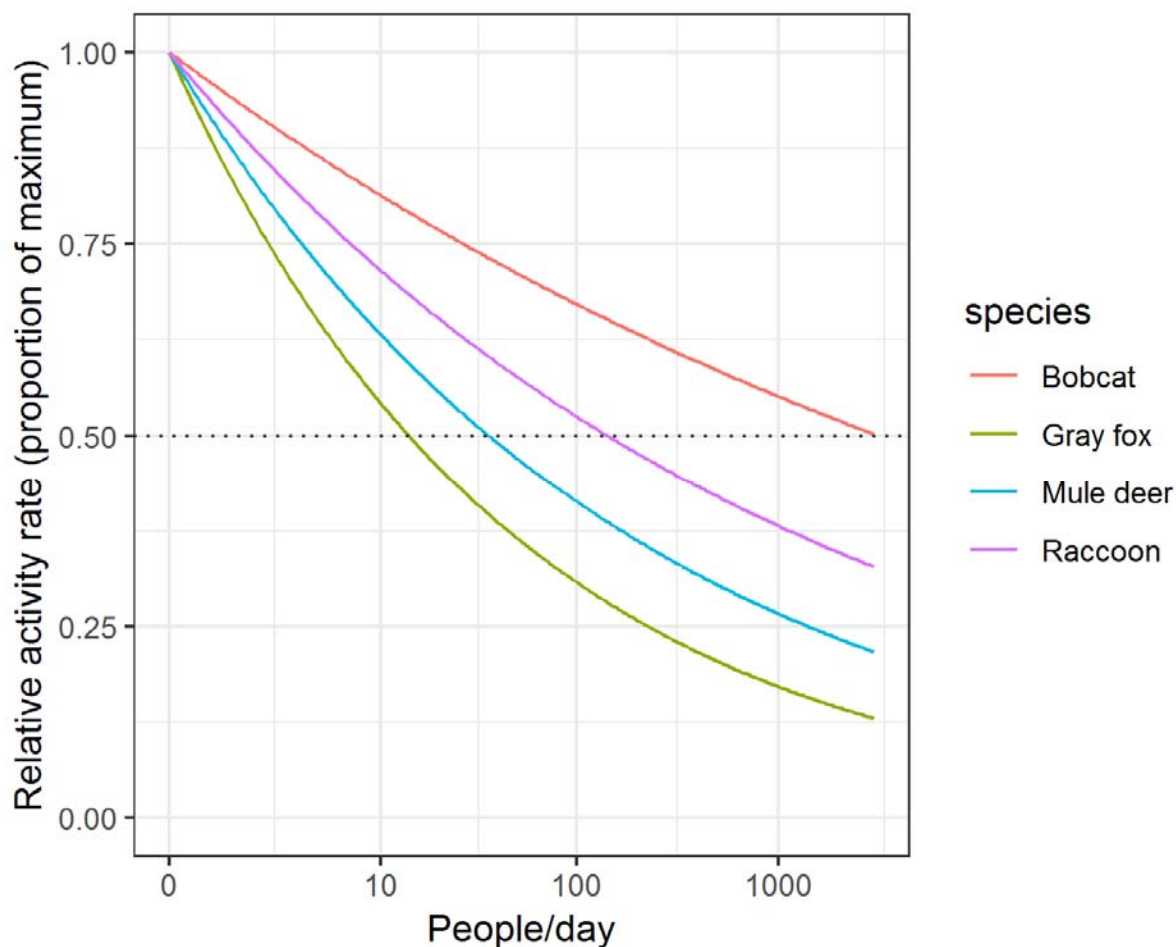
We did not detect negative relationships between human activity and the habitat use or relative activity of the remaining five species: coyote, striped skunk, ground squirrel, jackrabbit, and rabbit. Coyotes were distributed widely across the study area, occupying nearly every sampling point. Their relative 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 persist 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 tolerance threshold 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.

Striped skunks are also urban-adapted (Crooks 2002). They showed a trend toward reduced habitat use in association with human activity, but their habitat use was more strongly related to other covariates, particularly years since fire (positive relationship), NDVI (positive), and development (negative). Their relative activity increased slightly in association with human activity. 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 (Crooks 2002; Ordeñana et al. 2010). Thus, our relative activity results may reflect an increase in activity in areas closer to the edge of protected areas where human activity is more concentrated.

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 habitat at lower elevation, more recently burned, and with 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). 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 detected 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 (*Figure 24*). 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

Figure 24. Predicted relative activity rates as a proportion of maximum observed activity rate in relation to daily counts of total human activity, from negative binomial regression models. Only species that had a negative relationship between relative activity rates and human activity are shown. The dotted line shows a 50% reduction in relative activity rate.

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.

We found that habitat use of some mammal species (mule deer, striped skunk) declined in relationship with pedestrian activity, but was neutral or increased in relationship with 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, which could explain a dampened response to cyclists compared to pedestrians. Additionally, 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 covariates 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 appear as a positive relationship with cyclist activity.

Recommendations for future research

In studies of recreation and wildlife that employ 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, *Appendix B*). 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) had a maximum daily count of 100 groups of people, much lower than the peak visitation levels recorded in our study, and they did not observe decreases in occupancy or relative activity in relation to human activity. 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 two 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 anecdotally this appeared to be sufficiently disturbed for most species, as we observed only rabbits, and no other mid- to large-bodied wildlife species, using this location during 7.5 weeks of camera monitoring.

Additionally, several studies that have documented limited effects of recreation (e.g., Kays et al. 2017, Reilly et al. 2017) have used occupancy as a response variable (or occupancy interpreted as habitat use, as we do here). However, studies that use abundance, relative abundance, or species richness generally observe stronger effects of recreation (Larson et al. in review; *Appendix D*). 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. Differences between occupancy and relative activity 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 and relative activity analyses were similar, we detected some additional negative relationships with human activity when relative activity was the response variable. However, in most situations neither occupancy nor relative activity can provide reliable information about the abundance or density of a population (Efford & Dawson 2012). 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.

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.

Our sampling points were all located on recreational trails. As a result, we were not able to quantify the effect zone of recreational disturbance extending away from the trail or the proportion of each reserve affected by recreation. Animals may move to areas of reserves further from trails. However, the effect zone of recreation activity has been estimated at 350-1000 m for larger mammal species (e.g., carnivores and ungulates; Dertien et al. 2018). Given the dense trail network and small size of some reserves included in this study (~300 ha), an effect distance of several hundred meters on either side of a trail would encompass a large proportion of these reserves. For reptiles, 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). 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. Additionally, the effect zone likely varies depending on the magnitude of human activity and therefore may not be consistent 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.

Recommendations for recreation planning and 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). The distance between cities and protected areas is shrinking (McDonald et al. 2008) and residential development near protected areas is growing rapidly (Radeloff et al. 2010). 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; *Appendix C*). 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. Our previous work in the region highlighted the importance of reserve accessibility (including the presence of parking lots) in predicting levels of recreational use (Larson et al. 2018). Consequently, one approach to manage recreation impact is via the placement of access points and parking lots to influence the spread of visitors across the area of a reserve. Avoiding access points near sensitive habitat areas would help to mitigate potential impacts of recreation on vulnerable species.

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. Temporally, seasonal closures during breeding periods or other times of heightened animal sensitivity are becoming more common (e.g., Richardson & Miller 1997). Our BACI experiment showed that wildlife can respond rapidly after a change in human activity, with

significantly decreased bobcat detection probability observed in the four-week period following the trail re-opening at Black Mountain OSP. Accordingly, temporal closures have the potential to reduce disturbance during critical periods for some species.

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 & Waltho 2000). In fragmented landscapes such as the San Diego area, critical connectivity linkages for wildlife may also contain recreational trails and serve as links between reserve trail networks. 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 dual-use protected areas will be entirely sufficient, and limiting recreation in strategic locations and circumstances will be necessary to achieve conservation objectives.

This study shows that human recreation activity can reduce the ability of urban habitat fragments to conserve diverse reptile and mammal communities. 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 some areas trail-free and, at least to some extent, to separate high-intensity recreation areas from quality habitats harboring populations of sensitive species. In addition, encouraging visitors to stay on trails, respect seasonal closures, minimize noise, and not approach wildlife can further help mitigate the impacts of recreationists on sensitive species and their habitats (Larson et al. 2016, *Appendix B*). Minimizing the effects of recreation within fragmented protected areas helps ensure that the fragments provide habitat for species whose sensitivity to disturbance and low dispersal ability through the urban matrix may limit their ability to seek alternative habitat elsewhere.

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Appendix A

Supplementary tables (*Tables A1-A6*)

Table A1. Reptile species richness linear regression models ranked by AICc. K is the number of parameters, ΔAICc is the difference between the AICc of a given model and the best-supported model, and w is the Akaike weight. Only models with ≤ 2 ΔAICc are shown. Human activity variable names are in bold.

Model name	K	AIC_c	ΔAIC_c	w
fire + NDVI + **total human**	5	428.15	0.00	0.11
NDVI + **total human**	4	428.34	0.19	0.10
fire + NDVI + **pedestrian**	5	428.76	0.61	0.08
NDVI + **pedestrian**	4	428.84	0.68	0.08
fire + NDVI	4	428.94	0.78	0.07
nMDS1 + NDVI + elevation	5	429.04	0.89	0.07
fire + NDVI + elevation	5	429.69	1.54	0.05
NDVI	3	429.75	1.60	0.05
fire + NDVI + **cyclist**	5	429.92	1.77	0.05
nMDS1 + NDVI + elevation + **total human**	6	429.95	1.79	0.05
fire + NDVI + elevation + **total human**	6	429.96	1.80	0.04

Table A2. Proportion of reptile specialist species and specialist detections beta regression models ranked by AICc. K is the number of parameters, ΔAICc is the difference between the AICc of a given model and the best-supported model, and w is the Akaike weight. Only models with ≤ 2 ΔAICc are shown. Human activity variable names are in bold.

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

Table A3. Lizard body size linear regression models ranked by AICc. Models of mean body size (snout-vent length) of all species per sampling point are shown first, followed by models of mean body size of all individuals per sampling point. K is the number of parameters, ΔAICc is the difference between the AICc of the model and the best-supported model, and w is the Akaike weight. Only models with ≤ 2 ΔAICc are shown. Human activity variable names are in bold.

Model name	K	AIC_c	ΔAIC_c	w
Mean body size of species				
NDVI + **cyclist**	4	309.87	0.00	0.14
nMDS1 + NDVI + elevation + **cyclist**	6	310.13	0.25	0.12
NDVI	3	310.43	0.56	0.10
nMDS1 + NDVI	4	311.09	1.21	0.07
NDVI + **pedestrian**	4	311.36	1.49	0.06
nMDS1 + NDVI + **cyclist**	5	311.42	1.55	0.06
NDVI + **total human**	4	311.48	1.60	0.06
nMDS1 + NDVI + elevation + **pedestrian**	6	311.55	1.67	0.06
nMDS1 + NDVI + elevation + **total human**	6	311.74	1.86	0.05
Mean body size of individuals				
NDVI + **total human**	4	294.59	0.00	0.14
NDVI + **pedestrian**	4	294.63	0.04	0.13
fire + NDVI + **total human**	5	295.47	0.88	0.09
fire + NDVI + **pedestrian**	5	296.76	1.17	0.08
nMDS1 + NDVI + **pedestrian**	5	296.20	1.61	0.06
nMDS1 + NDVI + **total human**	5	296.27	1.67	0.06
nMDS2 + NDVI + **total human**	5	296.32	1.73	0.06
nMDS2 + NDVI + **pedestrian**	5	296.42	1.82	0.06

Table A4. Common side-blotched lizard (*Uta stansburiana*), orange-throated whiptail (*Aspidoscelis hyperythra*) and western fence lizard (*Sceloporus occidentalis*) occupancy models ranked by QAICc. Models for each species share a common detection structure, noted in the species header, plus any additional detection variables are labeled p(variable name) in the model column. K is the number of parameters, ΔQAICc is the difference between the QAICc of a given model and the best-supported model, and w is the Akaike weight. Only models with ≤ 2 ΔAICc are shown. Human activity variable names are in bold.

Model	K	QAIC$_c$	ΔQAIC$_c$	w
Common side-blotched lizard, detection structure p(cloud cover + observer)				
ψ(fire + **total human**)	7	541.09	0.00	0.17
ψ(fire + **pedestrian**)	7	541.10	0.01	0.17
ψ(fire + solar radiation + **pedestrian**)	8	541.96	0.87	0.11
ψ(fire + solar radiation + **total human**)	8	542.14	1.05	0.10
ψ(nMDS2 + fire + **total human**)	8	543.07	1.98	0.06
Orange-throated whiptail, detection structure p(cloud cover + Julian date^2)				
ψ(fire)	7	428.62	0.00	0.06
ψ(nMDS1)	7	428.80	0.18	0.06
ψ(nMDS2)	7	429.08	0.46	0.05
ψ(NDVI)	7	429.45	0.83	0.04
ψ(fire) p(search effort)	8	429.47	0.84	0.04
ψ(nMDS1) p(search effort)	8	429.75	1.13	0.03
ψ(nMDS2) p(search effort)	8	430.01	1.39	0.03
ψ(fire + elevation)	8	430.14	1.52	0.03
ψ(nMDS1 + **pedestrian**)	8	430.15	1.53	0.03
ψ(nMDS2 + fire)	8	430.26	1.64	0.03
ψ(fire + **pedestrian**)	8	430.31	1.69	0.03
ψ(nMDS1 + nMDS2)	8	430.35	1.73	0.03
ψ(nMDS1 + **total human**)	8	430.42	1.80	0.03
ψ(NDVI + **pedestrian**)	8	430.43	1.80	0.02
ψ(nMDS1 + fire + elevation)	9	430.46	1.84	0.02
ψ(NDVI) p(search effort)	8	430.50	1.88	0.02
ψ(fire + **total human**)	8	430.51	1.88	0.02
Western fence lizard, detection structure p(temperature^2 + Julian date^2)				
ψ(NDVI) p(**total human**)	9	378.40	0.00	0.26
ψ(NDVI)	8	379.83	1.43	0.13
ψ(NDVI + solar radiation) p(**total human**)	10	380.33	1.92	0.10
ψ(NDVI + **total human**)	9	380.35	1.94	0.10

Table A5. Mammal habitat use models ranked by QAICc. Items in the Model column show variables used to model habitat use (ψ) and detection probability (p). K is the number of parameters, ΔQAICc is the difference between the QAICc of the model and the best-supported model, and w is the Akaike weight. Only models with ΔQAICc ≤ 2 are shown.

Model	K	QAIC$_c$	ΔQAIC$_c$	w
Bobcat				
ψ(NDVI + **pedestrian**) p(development + fire + trail width)	8	1367.17	0.00	0.12
ψ(NDVI + **pedestrian**) p(development + fire)	7	1367.45	0.29	0.10
ψ(NDVI + **total human**) p(development + fire + trail width)	8	1367.50	0.33	0.10
ψ(NDVI + **total human**) p(development + fire)	7	1367.80	0.63	0.09
ψ(NDVI + **pedestrian**) p(fire)	6	1368.19	1.03	0.07
ψ(development + NDVI + **pedestrian**) p(development + fire + trail width)	9	1368.42	1.25	0.06
ψ(NDVI + **total human**) p(fire)	6	1368.53	1.36	0.06
ψ(NDVI) p(development + fire + trail width)	7	1368.56	1.39	0.06
ψ(development + NDVI + **total human**) p(development + fire + trail width)	9	1368.72	1.55	0.05
ψ(development + NDVI + **pedestrian**) p(development + fire)	8	1368.90	1.73	0.05
ψ(development + NDVI) p(development + fire + trail width)	8	1368.93	1.77	0.05
Gray fox				
ψ(development + NDVI + elevation) p(**total human** + NDVI + Julian^2)	10	598.35	0.00	0.13
ψ(development + chaparral + NDVI + elevation) p(**total human** + NDVI + Julian^2)	11	598.71	0.36	0.11
ψ(development + chaparral + NDVI + elevation) p(**total human** + NDVI)	9	599.83	1.49	0.06
ψ(development + NDVI + elevation) p(**total human** + NDVI)	8	599.91	1.56	0.06
ψ(development + chaparral + NDVI + elevation) p(**total human** + NDVI + trail width)	10	599.93	1.59	0.06
ψ(development + NDVI + elevation + **pedestrian**) p(**total human** + NDVI + Julian^2)	11	600.00	1.65	0.06
ψ(development + NDVI + elevation) p(**total human** + NDVI + trail width)	9	600.28	1.93	0.05
Ground squirrel				

ψ(development + fire + NDVI + elevation + **cyclist**) p(**total human** + chaparral + Julian^2)	11	527.98	0.00	0.16
ψ(development + fire + NDVI + elevation) p(**total human** + chaparral + Julian^2)	10	528.33	0.35	0.13
ψ(development + chaparral + fire + elevation) p(**total human** + chaparral + Julian^2)	10	528.55	0.57	0.12
ψ(development + chaparral + fire + elevation + **cyclist**) p(**total human** + chaparral + Julian^2)	11	528.98	1.00	0.09
ψ(development + fire + elevation) p(**total human** + chaparral + Julian^2)	9	529.14	1.16	0.09
ψ(development + chaparral + fire + elevation + **pedestrian**) p(**total human** + chaparral + Julian^2)	11	529.30	1.32	0.08
ψ(development + fire + elevation + **pedestrian**) p(**total human** + chaparral + Julian^2)	10	529.64	1.66	0.07
ψ(development + fire + elevation + **cyclist**) p(**total human** + chaparral + Julian^2)	10	529.83	1.85	0.06
ψ(development + chaparral + fire + elevation + **total human**) p(**total human** + chaparral + Julian^2)	11	529.97	1.99	0.05
Jackrabbit				
ψ(development + fire + NDVI + elevation + **cyclist**) p(NDVI)	9	453.92	0.00	0.14
ψ(development + fire + NDVI + elevation + **cyclist**) p(development)	9	454.11	0.19	0.13
ψ(development + fire + NDVI + elevation + **cyclist**) p(fire)	9	454.91	0.99	0.09
ψ(development + fire + NDVI + elevation) p(NDVI)	8	454.91	1.00	0.08
ψ(development + fire + NDVI + elevation + **cyclist**) p(Julian^2)	10	454.93	1.02	0.08
ψ(development + fire + NDVI + elevation + **cyclist**) p(development + NDVI)	10	455.14	1.22	0.08
ψ(development + fire + NDVI + elevation) p(development)	8	455.23	1.31	0.07
Mule deer				
ψ(elevation + total human) p(total human + NDVI + trail width)	8	958.96	0.00	0.10
ψ(elevation + pedestrian) p(total human + NDVI + trail width)	8	959.21	0.26	0.08
ψ(chaparral) p(total human + NDVI + trail width)	7	959.30	0.35	0.08
ψ(development + chaparral + elevation) p(total human + NDVI + trail width)	9	959.63	0.67	0.07
ψ(chaparral) p(total human + NDVI + Julian^2)	8	959.73	0.78	0.06
ψ(development + chaparral + elevation + total human)	10	960.11	1.16	0.05

p(total human + NDVI + trail width)				
ψ(chaparral + cyclist) p(total human + NDVI + Julian^2)	9	960.24	1.28	0.05
ψ(development + chaparral + elevation + pedestrian) p(total human + NDVI + trail width)	10	960.26	1.31	0.05
ψ(development + chaparral + elevation) p(total human + NDVI + Julian^2)	10	960.39	1.43	0.05
ψ(chaparral + cyclist) p(total human + NDVI + trail width)	8	960.49	1.53	0.04
ψ(elevation) p(total human + NDVI + trail width)	7	960.53	1.58	0.04
ψ(development + chaparral) p(total human + NDVI + trail width)	8	960.56	1.60	0.04
Raccoon				
ψ(development + NDVI) p(fire)	5	660.17	0.0	0.44
ψ(development + NDVI + **pedestrian**) p(fire)	6	661.53	1.4	0.22
ψ(development + NDVI + **total human**) p(fire)	6	661.81	1.6	0.19
Striped skunk				
ψ(development + fire + NDVI + elevation + **pedestrian**) p(**total human** + fire + Julian^2)	11	536.03	0.00	0.39
ψ(development + fire + NDVI + elevation) p(**total human** + fire + Julian^2)	10	536.80	0.77	0.27
ψ(development + fire + NDVI + elevation + **total human**) p(**total human** + fire + Julian^2)	11	536.99	0.96	0.10

Table A6. Mammal relative activity rate negative binomial regression models ranked by AICc. K is the number of parameters, ΔAICc is the difference between the AICc of the model and the best-supported model, and w is the Akaike weight. Only models with ΔAICc ≤ 2 are shown.

Model	K	QAIC$_c$	ΔQAIC$_c$	w
Bobcat				
NDVI + fire + **pedestrian**	5	1291.33	0.00	0.43
NDVI + fire + **total human**	5	1291.67	0.34	0.36
Coyote				
chaparral + NDVI + **total human**	5	3043.65	0.0	0.67
chaparral + NDVI + **cyclist**	5	3045.55	1.9	0.26
Gray fox				
fire + elevation + **pedestrian**	5	788.08	0.00	0.52
fire + elevation + **total human**	5	789.96	0.88	0.34
Ground squirrel				
chaparral + fire	4	494.74	0.00	0.20
chaparral + fire + **cyclist**	5	494.97	0.23	0.18
chaparral + elevation	4	494.97	0.23	0.18
chaparral + elevation + **pedestrian**	5	495.85	1.11	0.11
chaparral + elevation + **total human**	5	496.10	1.36	0.10
chaparral + fire + **pedestrian**	5	496.60	1.85	0.08
chaparral + fire + **total human**	5	496.70	1.96	0.07
chaparral + elevation + **cyclist**	5	496.72	1.98	0.07
Jackrabbit				
NDVI + Julian^2 + **cyclist**	6	1200.43	0.00	0.99
Mule deer				
NDVI + Julian^2 + **total human**	6	1347.43	0.00	0.58
NDVI + Julian^2 + **pedestrian**	6	1348.42	0.98	0.35
Rabbit				
fire + Julian^2 + **cyclist**	6	2752.95	0.00	0.30
fire + Julian^2 + **total human**	6	2753.93	0.99	0.18
fire + Julian^2 + **pedestrian**	6	2754.09	1.14	0.17
chaparral + Julian^2	5	2754.53	1.59	0.13
Raccoon				
development + NDVI + **pedestrian**	5	503.35	0.00	0.53
development + NDVI + **total human**	5	505.02	1.70	0.23
Striped skunk				
elevation + Julian^2 + **cyclist**	6	456.47	0.00	0.14
NDVI + elevation + **cyclist**	5	456.65	0.18	0.12
elevation + Julian^2	5	457.05	0.58	0.10
NDVI + elevation	4	457.45	0.98	0.08
NDVI + elevation + **total human**	5	457.96	1.49	0.06
elevation + Julian^2 + **total human**	6	458.19	1.71	0.06
development + NDVI	4	458.32	1.85	0.05

Appendix B

Larson, C.L., S.E. Reed, A.M. Merenlender and K.R. Crooks. 2016. Effects of recreation on animals revealed as widespread through a global systematic review. *PLoS ONE* 11: e0167259.

Effects of Recreation on Animals Revealed as Widespread through a Global Systematic Review

Courtney L. Larson[1]*, **Sarah E. Reed**[1,2], **Adina M. Merenlender**[3], **Kevin R. Crooks**[1]

1 Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado, United States of America, **2** North America Program, Wildlife Conservation Society, Bozeman, Montana, United States of America, **3** Department of Environmental Science, Policy, and Management, University of California-Berkeley, Berkeley, California, United States of America

* courtney.larson@colostate.edu

Abstract

Outdoor recreation is typically assumed to be compatible with biodiversity conservation and is permitted in most protected areas worldwide. However, increasing numbers of studies are discovering negative effects of recreation on animals. We conducted a systematic review of the scientific literature and analyzed 274 articles on the effects of non-consumptive recreation on animals, across all geographic areas, taxonomic groups, and recreation activities. We quantified trends in publication rates and outlets, identified knowledge gaps, and assessed evidence for effects of recreation. Although publication rates are low and knowledge gaps remain, the evidence was clear with over 93% of reviewed articles documenting at least one effect of recreation on animals, the majority of which (59%) were classified as negative effects. Most articles focused on mammals (42% of articles) or birds (37%), locations in North America (37.7%) or Europe (26.6%), and individual-level responses (49%). Meanwhile, studies of amphibians, reptiles, and fish, locations in South America, Asia, and Africa, and responses at the population and community levels are lacking. Although responses are likely to be species-specific in many cases, some taxonomic groups (e.g., raptors, shorebirds, ungulates, and corals) had greater evidence for an effect of recreation. Counter to public perception, non-motorized activities had more evidence for a negative effect of recreation than motorized activities, with effects observed 1.2 times more frequently. Snow-based activities had more evidence for an effect than other types of recreation, with effects observed 1.3 times more frequently. Protecting biodiversity from potentially harmful effects of recreation is a primary concern for conservation planners and land managers who face increases in park visitation rates; accordingly, there is demand for science-based information to help solve these dilemmas.

Introduction

Visitation to protected areas, ranging in scope from international ecotourism to local park visits, was recently estimated at 8 billion visits per year [1]. In the United States, the number of participants in outdoor recreation increased by 7.5% and total visitor days increased by 32.5% between 2000 and 2009 [2]. Driven in part by rapid growth in international tourism [3], recreation and ecotourism are also expanding in the developing world [4]; visits to protected areas in Africa, Asia, and Latin America increased by 2.5 to 5% between 1992 and 2006 [5].

Recreation is commonly assumed to be compatible with biodiversity conservation, in contrast to more well-known threats such as population growth and development at protected area edges [6,7] or subsistence use within reserves to help sustain local livelihoods [8]. Most protected areas have a dual mandate to conserve biodiversity and improve human welfare through resource use or outdoor recreation [8,9]. Accordingly, recreation is permitted in over 94% of International Union for Conservation of Nature (IUCN) protected areas globally (categories Ib-VI; [10,11]). In the United States and other developed nations, providing opportunities for outdoor recreation has historically been an important reason for the designation of protected areas [12], whereas in the developing world, ecotourism has been embraced as a potential win-win solution for poverty alleviation and conservation [8]. Furthermore, there are numerous benefits of outdoor recreation for human health and communities. People with access to natural areas have lower mortality rates [13], and outdoor play promotes mental and physical health in children [14]. Recreation and ecotourism can also be a source of economic revenue for protected areas and the communities around them [15,16], and can help garner support for conservation [17].

Despite these benefits, there is growing recognition that outdoor recreation can have negative impacts on biological communities. Recreation is a leading factor in endangerment of plant and animal species on United States federal lands [18], and is listed as a threat to 188 at-risk bird species globally [19]. Effects of recreation on animals include behavioral responses such as increased flight and vigilance [20,21]; changes in spatial or temporal habitat use [22,23]; declines in abundance, occupancy, or density [9,24,25]; physiological stress [26,27]; reduced reproductive success [28,29]; and altered species richness and community composition [30,31]. Many species respond similarly to human disturbance and predation risk, meaning that disturbance caused by recreation can force a trade-off between risk avoidance and fitness-enhancing activities such as foraging or caring for young [32].

Although there is a growing body of empirical studies of the effects of recreation on animals, a recent global review of the scientific literature does not exist. Early reviews [33–36] provide valuable definitions and conceptual frameworks, but were not systematic and need updating to reflect studies published in recent decades. In addition, contemporary reviews have restricted their scope by location or habitat type [37–39], taxonomic group [40–45], or recreation activity [46–48].

We conducted a global review of the published scientific literature to synthesize effects of non-consumptive recreation across all animal taxa. Such a review adds to the evidence base necessary to help bridge the gap between conservation science and practice [49]. To aid decision-makers faced with dilemmas about managing the demand for recreation while trying to fulfill mandates to protect species, it is critical to understand the degree to which biodiversity conservation and recreation are compatible, and under what circumstances. First, we examined trends in recreation research, including publication rates over time, geographic distribution, and study design. Second, we investigated which taxonomic groups were most commonly studied, and which had more or less evidence for effects of recreation. Similarly, we investigated which recreation activities and types of responses (e.g., behavioral, abundance, or

survival) were most frequently measured, and what effects were observed. Finally, we examined management strategies proposed by the authors to avoid or mitigate these effects.

Methods

Search strategy

Because our objective was to locate studies of all animal species and all types of recreation, our search protocol was designed to produce a broad list of articles. We did not include taxonomic keywords since titles and abstracts often refer only to the study's focal species. Instead, we limited the search to journals within four categories within the Institute for Scientific Information Web of Science database (Thompson Reuters, New York, NY, USA) that were the most relevant to our goals: biodiversity conservation, ecology, zoology, and behavioral sciences. From this list, we removed journals that were not published in English, or could not be reasonably expected to publish articles on recreation and animals (n = 166 journals included in the final list). We then searched the database with the Boolean search string: *(ts = (touris* OR recreat*) AND so = (journal list))*, where *ts* indicates topic keywords and *so* restricts the search to the list of 166 journals described above. This search strategy has high sensitivity (the proportion of all relevant information that the search locates) and low specificity (the proportion of search results that are relevant), which helps reduce bias and increase repeatability [50]. To reduce the effect of dissemination bias in our analysis, we included articles published in regional and lesser-known journals as well as the most widely-read publications [51]. Since our search strategy made use of the journal category feature within Web of Science, we were not able to replicate the search in other databases. However, our strategy produced a more thorough and comprehensive list of articles than if we had restricted our search with taxonomic keywords.

Screening and data extraction

Our keyword search (performed 30 January 2013 and again on 21 March 2016) resulted in a comprehensive list of 2,306 articles. We first reviewed titles and abstracts and eliminated obviously irrelevant records (e.g., tourism management papers with no wildlife component; Fig 1). We then reviewed the full text of the remaining 403 articles and assessed them against our inclusion criteria, recording the reason for rejection if necessary [50]. We excluded consumptive activities, which we define following Duffus and Dearden [34] as activities that "purposefully remove or permanently affect wildlife" (e.g., hunting, fishing). We focused on non-consumptive forms of recreation (e.g., hiking, skiing) because these activities are permitted more widely throughout protected areas. However, studies examining consumptive activities as a source of disturbance for non-target species (e.g., effects of fishing on waterbirds; [52]) were retained. We also rejected articles if they did not study one or more animal species (*n* = 2), did not test effects of non-consumptive recreation via a statistical test (*n* = 70), did not collect empirical field data (e.g., were review or simulation articles; *n* = 23), studied the effects of recreation infrastructure independently of human activity (e.g., presence of ski lifts; *n* = 20), or examined recreation as a vector for invasive species dispersal (*n* = 14). Experimental treatments designed to mimic recreational activities were included. The final list included 274 articles (S1 Appendix) with 2,048 distinct results.

Data collected from each article included publication information, geographic location (country and continent), study design, taxonomic group(s), recreation activities, response types and effects found, and management recommendations (Table 1). For articles that studied multiple species, recreation activities, or response types, we treated each combination of variables as a separate "result," rather than attempting to determine an overall effect for each article, which would ignore valuable findings from within each article. For example, Banks and
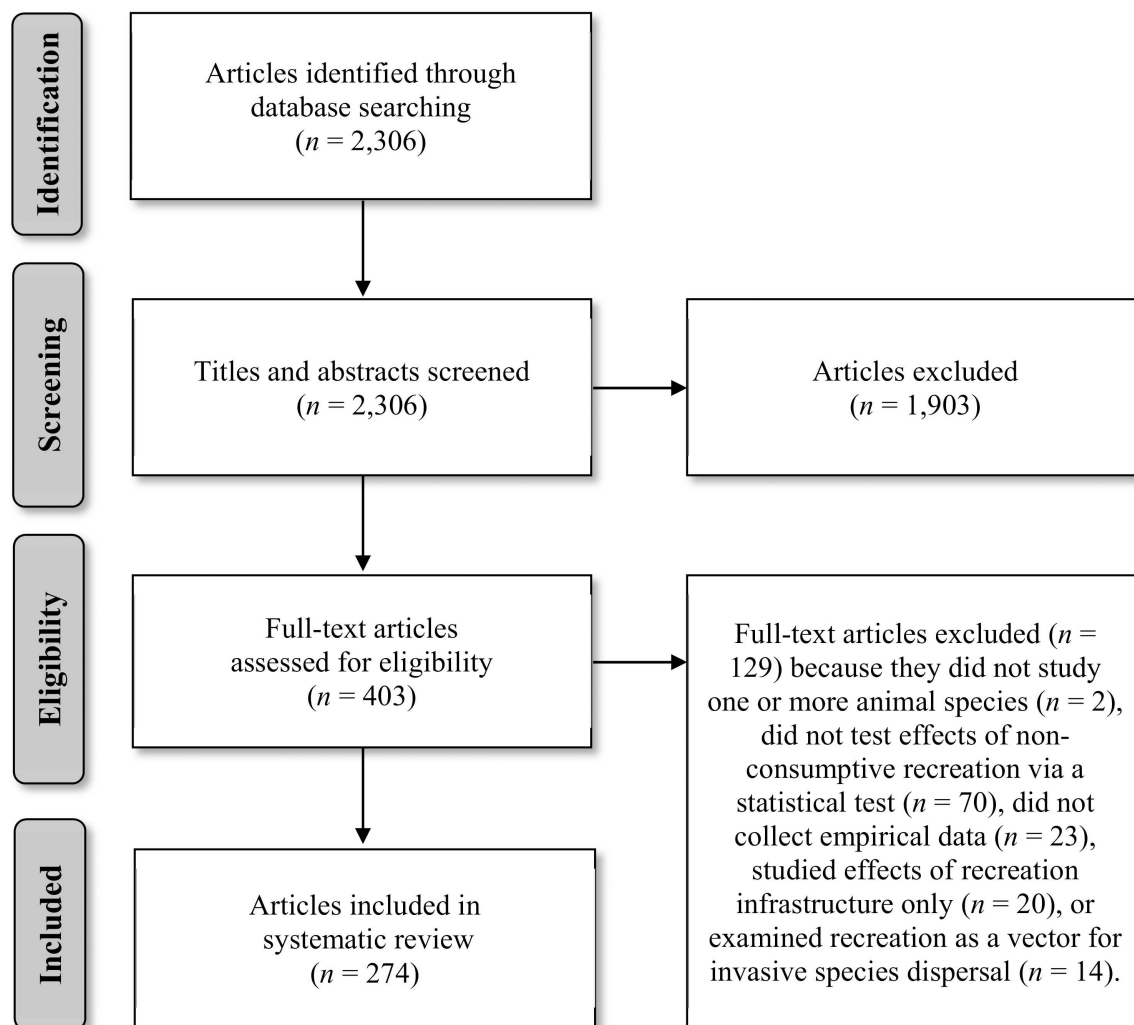
Fig 1. PRISMA literature search flow diagram. The number of studies that were located, retained, and discarded are shown at each stage of the literature review process.

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Bryant [24] examined the effects of hiking and dog-walking on bird abundance and richness, so we recorded four combinations of "results" in our database. While results from the same study often rely on the same animal populations, locations, and data collection efforts, we examined each result separately since effects often differed. Because each article could be considered an experimental unit, we added a random effect for article in the analysis to control for this potentially confounding factor (see "Statistical analysis").

The "effect" variable (Table 1), which was the response variable for several of our research questions, was a binary variable indicating whether the recreation effect documented by the authors was statistically significant (as defined by the authors). We categorized all significant effects as negative, positive, or unclear. Negative responses were consistent with the following effects of recreational disturbance at the community, population, or individual (behavioral or physiological) levels: decreased species richness or diversity; decreased survival, reproduction, occurrence, or abundance; behaviors typically assumed to reflect negative responses to anthropogenic disturbance (e.g., decreased foraging or increased vigilance); and physiological condition typically assumed to reflect disturbance effects (e.g., decreased weight or increased stress).

Table 1. List of variables collected from articles included in the review of the effects of non-consumptive recreation on animals.

Category	Variable	Description or list of categories	Data type
Publication	Author(s)		text
	Title		text
	Journal		text
	Journal type	Behavior, conservation, ecology, ecosystem/region-specific, general biology, taxa-specific, zoology/wildlife, other	categorical
	Publication year		numeric
Geographic	Continent		categorical
	Country		text
	Habitat type	Agricultural, beach, desert, forest, freshwater, grassland, marine, polar, shoreline, urban, scrub/shrub, tundra, wetland, other	categorical
Study design	Measure of recreation*	Direct observation, experimental treatment, expert opinion, remote monitoring, permitted use, proxy	categorical
	Experiment	Was it an experimental study?	yes/no
	Control	Did the study include a control treatment? (e.g. a "no-recreation" site)	yes/no
	Replication	Did the study replicate treatments, study sites, observation periods, etc?	yes/no
Effect	Effect*	Did the authors find a significant recreation impact?	yes/no
	Effect direction*	Positive, negative, unclear	categorical
Taxonomic	Multiple species	Were multiple species studied?	yes/no
	Taxa group	Amphibian, bird, fish, invertebrate, mammal, reptile	categorical
	Scientific name*		text
	Common name*		text
Recreation	Activity*	Alpine skiing, beach use, biking, boating (non-motorized), camping, nordic ski/snowshoeing, dog-walking, equestrian, hiking/running, motorized (boat), motorized (land), motorized (snow), swimming/diving, wildlife feeding, wildlife viewing (boat), wildlife viewing (land), other (aquatic), other (terrestrial)	categorical
Response	Type*	Abundance, behavioral, community (species richness, diversity, or composition), occurrence, physiological, reproductive, survival, other	categorical
Management	Recommendations	Cap visitation, improve infrastructure, rule change, staff training, spatial restrictions, temporal restrictions, visitor education, none, other	categorical

* For articles that studied multiple species, recreation activities, or response variables, we treated each combination of variables as a separate "result," and recorded the information marked with an asterisk (*) for each result individually.

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Conversely, positive responses were in the opposite direction. We were unable to classify some responses as positive or negative and labeled them "unclear." Examples of unclear effects were behavioral responses that did not have obvious fitness consequences (e.g., decreased vocalizing) and results with non-linear responses (e.g., highest reproductive success at an intermediate level of recreation). We note that positive responses do not necessarily imply beneficial outcomes for biodiversity conservation; for example, an increase in species richness could be attributable to an increase in non-native species.

We caution that a statistically significant effect of recreation does not necessarily provide insight into the effect's magnitude or biological significance. Authors may also include statistically significant results while omitting non-significant findings due to publication bias [53]. A formal meta-analysis framework can help researchers summarize effect sizes and detect and adjust for publication bias [54], but the study design must be similar across all studies included, with comparable predictor and response variables [55]. This was not feasible given the broad scope of our review, and accordingly, we do not make statistical comparisons among groups. Ultimately, we believe our approach provides a meaningful representation of the weight of evidence that currently exists.

Publication trends and geographic distribution

We summarized the number of articles by publication year, journal type, country, continent, and habitat type. Journals were classified into eight broad types using the journal title and online aims and scope statement to identify the appropriate primary category. Articles were also assigned to one or more habitat classes on the basis of authors' descriptions (Table 1).

Study design

To examine how recreation studies have been designed and conducted, we recorded the proportion of articles that used an experimental design and included controls and replication. For our purposes, any kind of an experimental treatment (e.g., experimental boat passes near a raptor nest; [56]) counted as an experimental design, and any treatment or site without recreation counted as a control. We also examined the method used to measure recreation: direct observation (with human observers), experimental treatment (e.g., researchers simulating recreation activities), expert opinion, remote monitoring (e.g., automatic counters), permitted use (e.g., whether a site was open to a specific recreational activity), or proxy variables (e.g., car counts).

Taxonomic groups

We examined differences in research focus and evidence for recreation effects among six broad taxonomic groups: amphibians, birds, fish, invertebrates, mammals, and reptiles. We divided groups with sufficient sample size ($\geq$ 15 results on $\geq$ 3 different species) into narrower taxonomic classifications (Classes for invertebrates and fish; Orders for birds, mammals, and reptiles; amphibians were omitted due to small sample size). We then subdivided Classes or Orders with sufficient sample sizes ($\geq$ 15 results on $\geq$ 3 different species) once again into Orders or Families. We also grouped species by their IUCN status [57].

Recreation activities

We grouped recreation activities into 18 types (Table 1) and created broader categories for more general comparisons: winter terrestrial (snow and ice-based activities such as skiing and snowmobiling), summer terrestrial (land activities not requiring snow or ice), and aquatic activities. We also compared motorized and non-motorized activities.

Response types

We categorized animal responses into eight types: community (species richness, diversity, or composition metrics), survival, reproduction, abundance, occurrence, behavior, and physiological measures, as well as "other" responses (e.g., sex ratio). For more general comparisons, we also grouped the response types hierarchically into community-, population- (survival, reproduction, abundance, and occurrence), and individual-level (behavior and physiological) responses.

Management recommendations

To qualify the management recommendations noted in the articles and provide a useful synthesis for land managers, we categorized recommended management actions as follows: spatial restrictions, capping visitation, increasing visitor education, temporal restrictions, improving infrastructure, adding or changing rules, enforcement of existing rules, staff training, or "other" (Table 2). Calls for additional research, although common in the literature, were not considered to be management recommendations.

Table 2. General management recommendations suggested by authors of articles included in the review.

Recommendation	Examples	Frequency (%)*
Spatial restrictions	Designate a trail-free area within protected area; establish minimum approach distances to animals	32.1
Visitor education	Educate SCUBA divers about the impacts of human contact on coral; instruct visitors about effects of noise on sensitive species	15.0
Cap visitation	Limit the number of visitors that can enter the area per day	14.2
Temporal restrictions	Limit recreational access during the breeding season	13.1
Rule change	Restrict boat speed in sensitive areas; prohibit wildlife feeding	9.9
Physical improvements	Restore habitat; install fencing around sensitive areas	9.5
Other	Species translocations; increased use of private land for conservation	8.8
Enforcement	Enforce leash laws; keep people on trails	6.9
Staff training	Train staff to recognize signs of animal disturbance	2.2
No recommendations		40.5

* Percentages do not sum to 100 because some articles made more than one management recommendation.

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Statistical analysis

We used linear regression to assess trends in the total number of articles over time as well as the proportion of included articles out of the total publication volume in the selected journals. To assess gaps in the literature, we used chi-square goodness of fit tests to determine if the distribution of articles differed significantly from an expected distribution. For journal type, the expected distribution was the proportion of journals in the journal set that belonged to each type. For geographic distribution, we compared the distribution of articles by continent to the total land area and human population density of each continent. For IUCN status and taxonomic groups, the expected distribution was the number of known species in each group, starting with the broadest groups and progressing down to Family when possible [57]. We did not use chi-square tests if articles were counted under more than one category (e.g., articles examining multiple types of recreation, such as hiking, biking, and equestrian) since this violates the assumption of independence.

We estimated the amount of evidence for a recreation impact as the overall percentage of results that found a statistically significant effect of recreation. These percentages were estimated for results summarized by taxonomic groups, recreation activities, and response types. Because most articles included multiple results, the percentages (± SE) we report are least-squares means and standard errors obtained from models that included article as a random effect. We used generalized linear mixed models (GLMMs) with a logit link function to estimate the frequency of overall effects among taxonomic groups, recreation activities, and response types, and we used proportional odds models [58] to estimate the proportion of overall effects that were negative, positive, or unclear. All statistical analyses were conducted in R using packages lme4, ordinal, and lsmeans [59–62].

Results

Publication trends and geographic distribution

The earliest articles discovered by our search were published in 1981, and the peak year was 2008 with 23 articles. The number of articles published per year that met our criteria increased 23.5% on average per year from 1981 to 2015 (β = 0.66, 95% CI = (0.53, 0.80), $p < 0.0001$). This increase was not solely a result of increasing publication volume; the proportion of
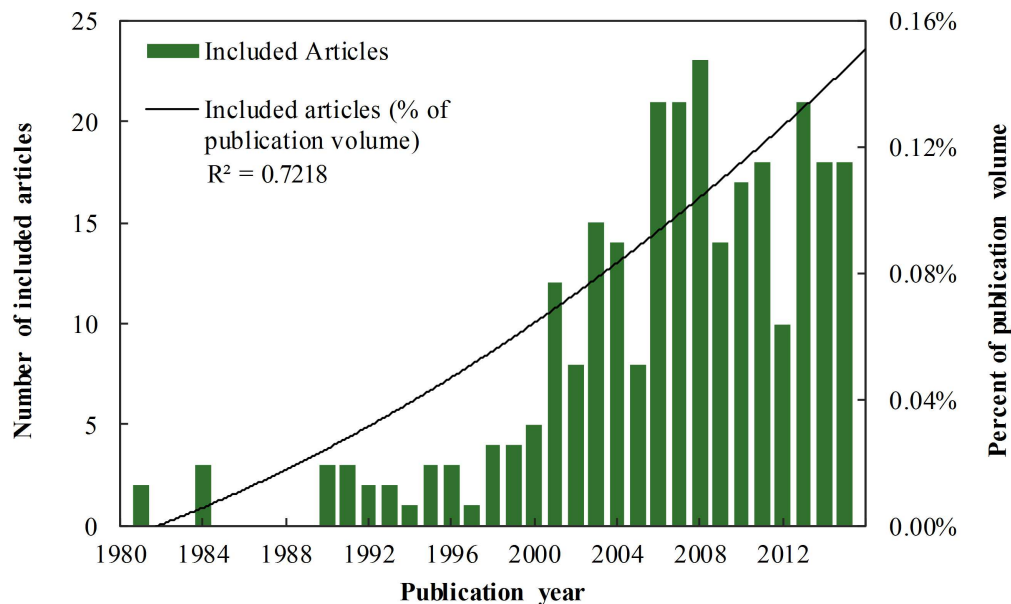
Fig 2. Published articles on the effects of non-consumptive recreation on animals by publication year. The numbers of articles are shown as raw numbers (shaded bars) and as percentages of the overall publication volume in the journal set used in this review (trendline; a second order polynomial function).

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included articles out of the total articles published in the journal set increased by 8.8% on average per year (β = 0.000043, 95% CI = (0.000033, 0.000053), p < 0.0001; Fig 2). The distributions of the journal set into journal types (e.g., conservation, wildlife) and individual articles into journal types were significantly different (χ^2 = 632.4, df = 7, p < 0.0001). Most of the included articles were published in conservation (38.7%) and wildlife (19.7%) journals, followed by ecology (13.5%), taxa-specific (13.1%), ecosystem or region-specific (9.9%), and behavior journals (3.3%); very few articles were published in general biology (0.7%) or other (0.7%) journal categories.

Geographically, studies of recreation on animals were conducted mostly in North America (37.7%), Europe (26.6%), and Oceania (13.1%), and relatively few in South America (9.1%), Asia (5.5%), Africa (5.1%), and Antarctica (2.9%; Fig 3A). This distribution among continents was not proportional to the land area (χ^2 = 366.3, df = 6, p < 0.0001) nor human population density (χ^2 > 500, df = 6, p < 0.0001) of the continents. The United States accounted for 27.0% of the articles, followed by Australia (7.7%), Spain (5.8%), New Zealand (5.5%), the United Kingdom (4.7%), Argentina (4.4%), and Canada (4.4%). Most studies were conducted in forest (35.4%), marine (23.4%), grassland (15.7%), and shoreline (13.9%) habitats (Fig 3B). The least well-studied habitat types were polar (2.9%), and desert (1.5%), as well as human-modified habitats (agricultural and urban, representing 10.2% of articles combined).

Study design

Less than one-third (30.3%) of the articles contained an experimental component, and 60.9% of articles contained controls. Most (85.4%) articles had replication of study sites, treatments, or groups. Direct observation was the most common method for measuring recreation (38.1% of results), followed by proxy variables (19.9%), expert opinion (19.6%), and experimental treatment (18.0%). Permitted use as a measure of recreation was less common (12.5%), as was remote monitoring (6.7%).

Fig 3. Distribution of published articles on the effects of non-consumptive recreation on animal species. Panel (a) shows the countries where studies were conducted, and panel b) shows the distribution of studies into major habitat type (s). Since some studies involved multiple habitat types, the sum (424) is greater than the total number of articles (274). Numbers at the end of bars represent the total number of articles in each category.

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Taxonomic groups

Research effort in our sample of articles was not proportional to the number of species within all taxonomic groups at the broadest level ($\chi^2 = 377.3$, df = 5, $p < 0.0001$), nor to the number of species in bird ($\chi^2 = 988.7$, df = 5, $p < 0.0001$) and mammal ($\chi^2 = 290.3$, df = 3, $p < 0.0001$)

Orders or invertebrate Classes (χ^2 = 98.1, df = 2, p < 0.0001; [Fig 4]). Mammals (41.6%) and birds (36.9% of articles) were the focus of the majority of recreation studies, followed by invertebrates (12.4%), reptiles (5.5%), fish (5.1%), and amphibians (0.7%). Studies of a single species were more common (69.0%) than those that examined at least two species. Research on mammals focused mainly on ungulates (28.9%), carnivores (26.3% of articles), cetaceans (21.9%), and primates (12.3%). Among birds, the most commonly researched Orders were Passeriformes (passerine birds; 24.8% of articles), Charadriiformes (wading birds and gulls; 23.8%), Sphenisciformes (penguins; 13.9%), and Accipitriformes (hawks, eagles, vultures; 9.9%). Many of the invertebrate studies (35.2%) focused on the effects of snorkeling or SCUBA diving on corals, followed by studies on arachnids, bivalves, and insects (each 14.7%). The most commonly studied fish Class was Actinopterygii (ray-finned fish; 57.1%), followed by Chondrichthyes (sharks, stingrays; 42.9%). Research on reptiles focused on Orders Squamata (lizards, snakes; 78.6%) and Testudines (turtles; 21.4%).

We identified the IUCN status of the species for 68.7% of results, representing 305 unique species; the remaining results examined multiple species or species not evaluated by the IUCN. The distribution of these results into IUCN status categories was not proportional to the distribution of all animal species into these categories (χ^2 = 108.3, df = 5, p < 0.0001), with many more species than expected in the least concern category (80.7%), slightly more than expected in the near threatened (6.9%), and fewer than expected in the data deficient (1.6%), vulnerable (6.5%), endangered (3.6%), and critically endangered (0.1%) categories. Endangered species that were studied included three mammals (black howler monkey *Alouatta pigra*, Hector's dolphin *Cephalorhynchus hectori*, and the Barbary macaque *Macaca sylvanus*), three fish (dusky grouper *Epinephelus marginatus*, Nassau grouper *Epinephelus striatus*, and the brownstriped gaunt *Anisotremus moricandi*), two birds (Egyptian vulture *Neophron percnopterus* and the yellow-eyed penguin *Megatypes antipodes*), two reptiles (wood turtle *Glyptemys insculpta* and Lilford's wall lizard *Podarcis lilfordi*), and the boulder star coral *Montastraea annularis*. The only critically endangered animals were the Western lowland gorilla *Gorilla gorilla gorilla* and the Mexican howler monkey *Alouatta palliata mexicana*.

Of the 274 articles analyzed, 93.1% documented at least one effect of recreation on animal populations, individuals, or communities. Negative effects of recreation were the most frequent (59.4%), followed by unclear (25.9%) and positive (14.7%) effects. Most (83.6%) of the unclear effects were behavioral responses.

Taxonomic groups with the most negative effects were amphibians (68.4 ± 20.2% of results), reptiles (56.3 ± 9.2%), and invertebrates (51.0 ± 5.1%), while mammals (5.3 ± 1.9%) and birds (4.3 ± 2.0%) had the most positive effects ([Fig 4]). Among bird Orders, evidence for overall and negative effects was greatest in Accipitriformes (e.g., eagles, hawks; 70.7 ± 10.7 and 47.7 ± 24.4%; [Fig 4]). Positive effects were greatest in Anseriformes (e.g., ducks, swans; 10.4 ± 22.6%) and Passeriformes (passerine birds; 6.9 ± 7.7%). Evidence of negative effects among Charadriiformes Families was greatest in Charadriidae (e.g., plovers, lapwings; 58.2 ± 18.6%). Among Passeriformes Families, Corvidae (e.g., crows, choughs) had the most positive effects (56.0 ± 4.9%). Among mammal Orders, Artiodactyla (even-toed ungulates) had the most negative effects (48.5 ± 8.0%) and Rodentia (rodents) had the most positive effects (14.4 ± 12.3%). At the family level, Bovidae (e.g., bison, bighorn sheep) had by far the most overall effects (93.8 ± 19.3%) and Delphinidae (dolphins) was also high (70.8 ± 6.8%). Several invertebrate Classes had considerable negative effects, including Anthozoa (corals; 56.6 ± 4.2%), Gastropoda (e.g., snails, slugs; 55.5 ± 6.7%), and "other" (e.g., insects, crabs; 51.4 ± 6.0%). Finally, the "other" grouping of fish Classes (e.g., sharks, stingrays) had more evidence for an overall and positive effect (64.9 ± 8.7% overall and 25.8 ± 15.7% positive) than Actinopterygii (ray-finned fish; 34.8 ± 8.5% overall and 5.4 ± 9.2% positive). Of the reptile

Birds — 729, 101, 135

- Order Accipitriformes (eagles, hawks) — 63, 10, 7
- Order Anseriformes (ducks, swans) — 40, 8, 7
- Order Charadriiformes — 120, 24, 50
  - Family Charadriidae (plovers, lapwings) — 33, 11, 13
  - Family Scolopacidae (sandpipers) — 55, 10, 18
  - Other families (stilts, terns) — 32, 11, 19
- Order Passeriformes — 159, 25, 73
  - Family Corvidae (choughs, crows) — 32, 6, 9
  - Family Turdidae (thrushes, robins) — 25, 9, 9
  - Other families (sparrows, warblers) — 102, 19, 55
- Order Pelecaniformes (herons, egrets) — 15, 6, 8
- Order Sphenisciformes (penguins) — 95, 14, 7
- Other bird orders (grouse, coots) — 237, 44, 33

Mammals — 757, 114, 88

- Order Artiodactyla — 129, 33, 24
  - Family Bovidae (bison, bighorn sheep) — 26, 11, 10
  - Family Cervidae (deer, moose) — 80, 23, 10
  - Other families (pronghorn, wild boar) — 24, 4, 3
- Order Carnivora — 247, 30, 27
  - Family Canidae (coyotes, foxes) — 35, 6, 3
  - Family Felidae (lions, bobcats) — 49, 10, 6
  - Family Ursidae (bears) — 99, 13, 4
  - Other families (sea lions, martens) — 54, 13, 16
- Order Cetacea — 203, 25, 10
  - Family Balaenopteridae (whales) — 80, 6, 3
  - Family Delphinidae (dolphins) — 123, 19, 7
- Order Primates (macaques, gorillas) — 76, 14, 9
- Order Rodentia (squirrels, marmots) — 44, 10, 9
- Other mammal orders (bats, wallabies) — 58, 17, 9

Invertebrates — 324, 34, 91

- Class Anthozoa (corals) — 117, 12, 5
- Class Arachnida (spiders) — 31, 5, 16
- Class Gastropoda (snails, slugs) — 41, 1, 38
- Other invertebrate classes (insects, crabs) — 135, 23, 32

Fish — 173, 14, 55

- Class Actinopterygii (snappers, mullets) — 109, 8, 51
- Other fish classes (sharks, stingrays) — 64, 11, 4

Reptiles — 56, 15, 13

- Order Squamata (lizards, iguanas) — 44, 10, 9
- Other reptile orders (turtles) — 12, 5, 4

Amphibians — 9, 2, 2

Legend: ■ Negative, □ Positive, □ Unclear

x-axis: 0.0%, 25.0%, 50.0%, 75.0%, 100.0%

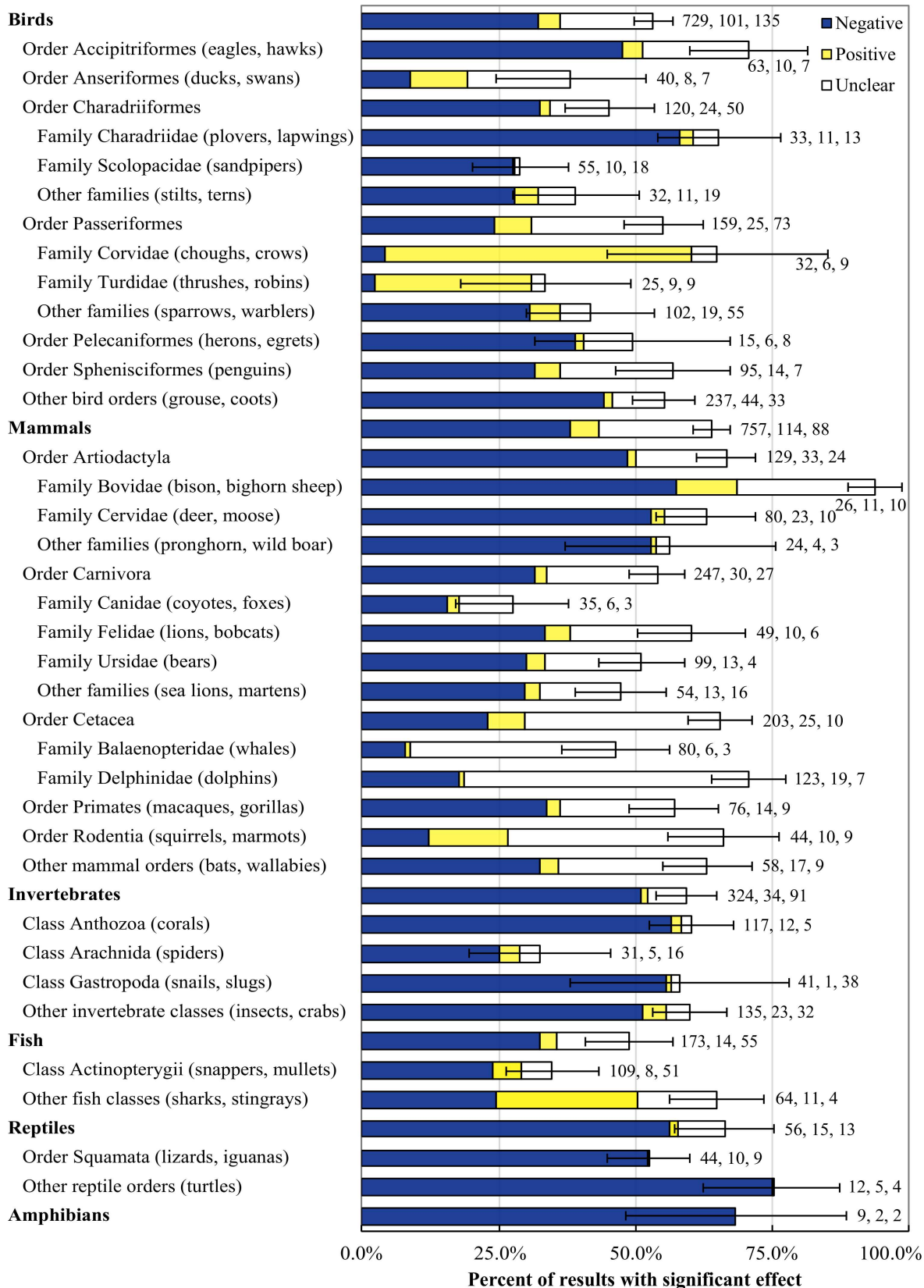**Percent of results with significant effect**

Fig 4. Evidence for an effect of recreation by taxonomic group. Evidence is measured as the proportion of results that were statistically significant. For articles that studied multiple recreation activities, species, or response variables, each combination of variables was treated as a separate result. Common names are examples of species occurring in the included articles. We present taxonomic groups that have at least 15 results and 5 species represented; the remaining taxa are included in "other" categories for comparative purposes. Numbers following bars show the number of results, number of articles, and count of unique species. Articles that studied functional groups or communities rather than individual species (e.g., insectivorous birds) were added to the relevant "other" category and were not counted as species. Error bars show standard error for the sum of all effects.

orders, Order Testudines (turtles) had more overall effects (75.0 ± 12.5%) effects than Order Squamata (lizards, iguanas; 52.3 ± 7.5). For both Orders, all of the effects were negative. Low sample sizes precluded comparisons among amphibian taxa.

Recreation activities

The articles in our sample examined a wide variety of recreation activities (Fig 5A). Summer terrestrial activities were the most common, studied by 66.7% of articles, followed by aquatic (27.8%) and winter terrestrial (5.6%). Motorized forms of recreation, including off-highway vehicles, snowmobiles, and motorized boats, were examined in 26.3% of articles. Hiking was studied much more often than any other recreation activity (27.5% of articles). Wildlife viewing was also relatively frequently studied, with 10.3% of articles studying land-based and 6.6% studying boat-based wildlife viewing.

Winter terrestrial activities had the most evidence of overall (77.3 ± 7.8% of results; Fig 5B) and negative (64.4 ± 10.1%) effects, compared to 58.5 ± 2.7% (overall) and 39.6 ± 4.6% (negative) for other terrestrial and 57.0 ± 3.8% (overall) and 33.4 ± 7.1% (negative) for aquatic activities. Although motorized and non-motorized activities had similar evidence for overall effects (57.0 ± 5.1% and 58.4 ± 2.5%), non-motorized had greater negative effects (40.3 ± 4.0% versus 34.0 ± 8.6%). Activities with the most evidence of overall effects included each of the snow activities (cross-country ski/snowshoeing: 81.0 ± 8.6%, motorized–snow: 77.8 ± 13.9%, alpine skiing: 71.0 ± 8.2%), as well as boat-based wildlife viewing (65.4 ± 5.4%) and beach use (64.8 ± 8.2%; Fig 5B).

Response types

Response types were not studied evenly; behavioral (45.5% of articles) and abundance (24.1%) responses to recreation were the most common (Fig 6A). Only 9.3% of articles measured community metrics (species richness, diversity, or composition) and 1.9% measured survival. Omitting survival responses due to small sample size, community responses had the most overall effects (64.6 ± 6.6% of results), followed by behavioral (63.5 ± 2.8%) and physiological (62.5 ± 4.9%) responses; reproductive responses (36.7 ± 6.3%) had the fewest overall effects (Fig 6B). Physiological (52.7 ± 4.8%) and occurrence (51.3 ± 4.6%) responses had the most negative effects, while behavioral responses had the most positive effects (9.8 ± 2.5%).

Management recommendations

More than one-third (40.5%) of the included articles did not provide management recommendations (Table 2). Of those that did include recommendations, the most common types were spatial restrictions (32.1%), visitor education (15.0%), and limiting visitation (14.2%), Enforcement of existing rules (6.9%) and staff training (2.2%) were the least frequently suggested management categories.
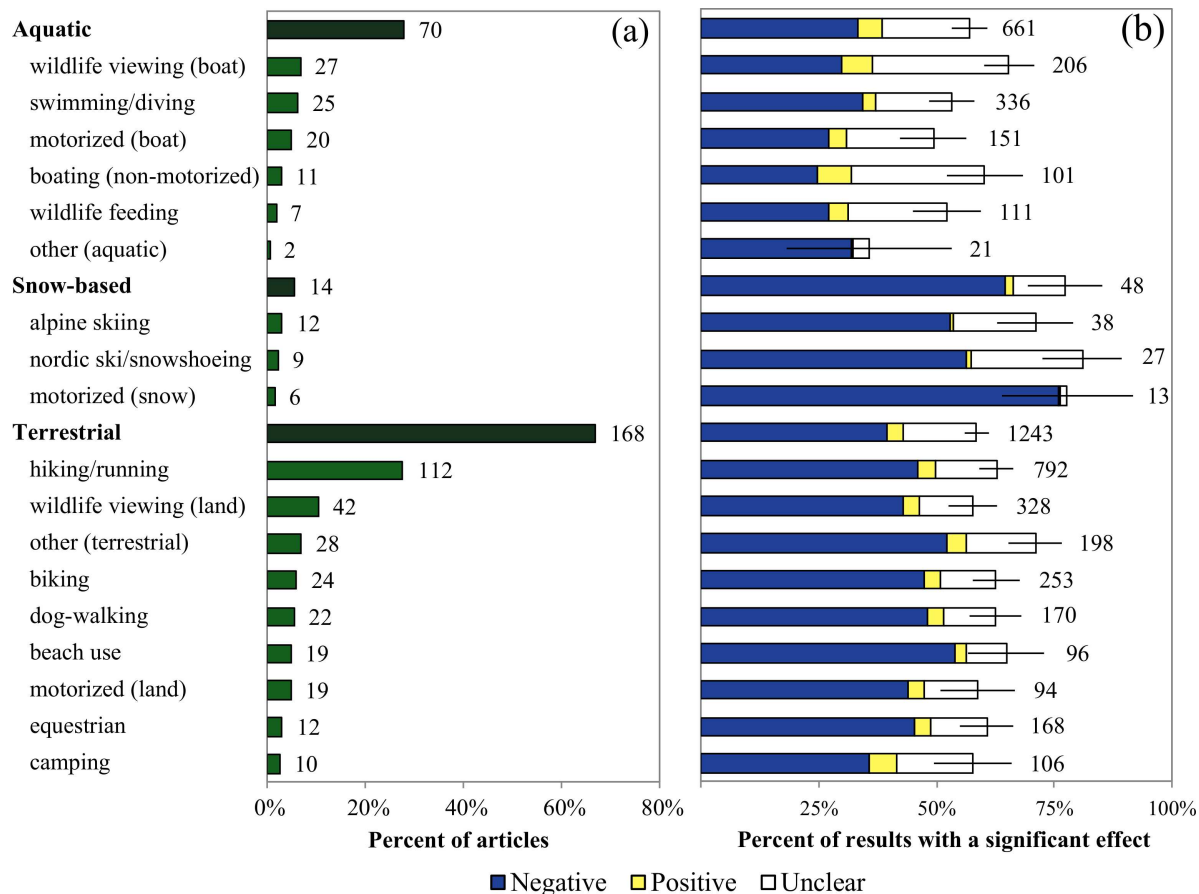
Fig 5. Recreation activities in the articles included in this review. Panel (a) shows the percent of articles that included each recreation activity (numbers of articles follow the bars), and panel (b) shows the percent of results in which a statistically significant effect of recreation on an animal species was observed (number of results follow the bars). Total percentages are divided into negative, positive, and unclear effects of recreation. Error bars show standard error for the sum of all effects.

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Discussion

Although published research on recreation effects on animals increased by an order of magnitude from 1981 to 2015, the percentage of the literature devoted to the subject remains small (0.16% of publication volume of the target journals in the peak year), and many gaps in knowledge remain. The literature is geographically biased in favor of North America and Europe, and taxonomically biased toward birds and mammals. Over 93% of reviewed articles documented at least one effect of recreation, and as expected, the majority of these effects were negative. Non-motorized and winter terrestrial activities had notable evidence for negative effects. Additionally, some of the least studied taxonomic groups (reptiles, amphibians, and invertebrates) had the greatest evidence for negative effects of recreation.

Though the amount of literature on this topic has increased in recent decades, it may not be reaching a broad audience even among conservation scientists and wildlife ecologists. Over 20% of articles were published in journals specific to a taxonomic group, geographic region, or ecosystem, whereas few were published in the broadest journals. Since the broadest journals are also among the highest-impact publications (e.g., *Science*, *Nature*), this could also indicate that the topic of recreation impacts on animals is not viewed as important within the peer-reviewed literature.
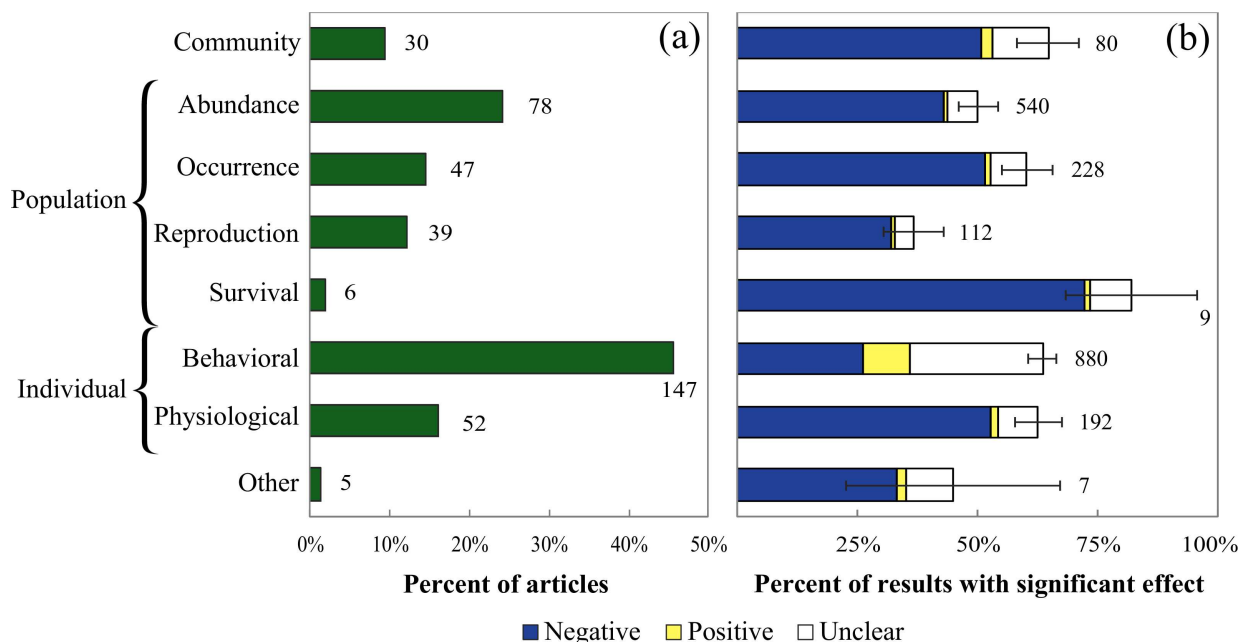
Fig 6. Types of animal responses to recreation in the articles included in this review. Response types have been categorized into community-, population-, and individual-level responses. Panel a) shows the percent of articles in which each response type is tested (numbers of articles follow the bars). Panel b) shows the percent of results in which a statistically significant effect of recreation on an animal species was observed (number of results follow the bars). Total percentages are divided into negative, positive, and unclear effects of recreation. Error bars show standard error for the sum of all effects.

The articles had a strong geographic bias toward North America and Europe. This reflects global patterns in visitation to protected areas since over 80% of visits occur in these two continents [1]. A surprising number of studies were conducted in Antarctica, as a result of a growing ecotourism industry that often includes visits to penguin colonies [63]. As South America, Africa, and Asia contain most of the world's biodiversity hotspots [64] as well as popular ecotourism destinations including Brazil, South Africa, Thailand, and Indonesia [65], we see an immediate need for studies of recreation effects in these areas. The few studies conducted in tundra, polar, and desert habitat types is likely a result of low rates of recreation and tourism occurring in these areas. However, our findings and those of Sato et al. [39] about the impacts of alpine activities indicate that it is an important area for future study.

Further, the distribution of articles among broad taxonomic groups was skewed in favor of mammals and birds, a trend consistent with conservation science as a whole [66]. However, these are large, diverse groups that still warrant more research; for example, passerine birds were the most frequently studied avian Order in our set of articles, but the 73 species examined therein comprise ~1% of the 5,000+ species in the Order. There is also an urgent need to understand more about the potential effects of recreation on invertebrates, fish, reptiles, and amphibians. We found only two articles on amphibians, but their known sensitivity to human disturbance [67] highlights the need to understand whether and how recreation affects them. Current research on recreation effects on animals does not include many species of urgent conservation concern; only about 10% of species studied are globally threatened (IUCN status of critically endangered, endangered, or vulnerable). Recreation may not be the primary reason for their endangerment, but it is a threat worth understanding because the disturbance may take place in the very protected areas designated to conserve these species. Finally, relatively few articles (31.0%) examined more than one species, and studies of species from

multiple trophic levels were especially rare (3.6%). More research is needed on community-level effects of recreation, including potential cascading effects [68].

Examination of the study designs of the included articles revealed some notable trends. A fairly high percentage (30%) of articles included an experimental component; most of these were recreation treatments applied in order to compare behavioral responses. Over 80% of results examined recreation as a categorical variable, typically with three or fewer levels (e.g., low vs. high recreation activity). Though a categorical approach is simpler to implement and analyze, it limits the ability of researchers to evaluate how responses may change with different recreation intensities. It has proven difficult to develop hypothesized response curves representing how animals respond to increasing levels of recreational use due to the diversity of responses [69]. Future research should measure recreation across intensity gradients to help verify the existence of thresholds and the shape of these relationships.

Most (59%) of the effects of recreation on animals documented in the reviewed articles were negative effects. This was particularly true for reptiles, amphibians, and invertebrates, although sample sizes were low. Among invertebrate Classes, Anthozoa (corals) frequently had physical damage or reduced abundance in areas frequented by recreational divers [70,71]. Though the rate of negative effects was generally lower for birds, mammals, and fish, some lower taxonomic groups had more evidence for negative effects of recreation. For example, Order Accipitriformes (e.g., eagles, hawks) had more evidence for negative effects compared to other bird Orders, consistent with a prior meta-analysis of human disturbance on nesting birds of prey [41]. Family Charadriidae (e.g., plovers, lapwings) also had considerable evidence for negative effects of recreation, which parallels a recent study that found that species from this Order (Charadriiformes) were more frequently threatened by tourism than other bird Orders [19]. Of the mammals, Order Artiodactyla (e.g., deer, bison) had substantial evidence for negative effects, mostly consisting of behavioral responses to recreation activity. Many researchers have investigated factors that influence ungulate flight responses, including speed of approach, animal and human group size, and habitat type [43,45]. For fish, several studies found negative physiological effects of wildlife viewing on Class Chondrichthyes (e.g., sharks, stingrays; [72,73]), and negative effects of diving on fish communities [70].

Evidence for positive effects of recreational activity was much less common. Birds, particularly corvids, had more evidence for positive effects compared to most other broad taxonomic groups. Many corvids are urban adaptors [74], and several studies found that they quickly habituate to human disturbance, allowing them to tolerate or even thrive in the presence of recreationists [75,76], sometimes at the expense of other species [77]. Mammals also had a relatively high rate of positive effects. Of the mammal Orders, rodents had the most evidence for positive effects; all but one of these effects were behavioral and most resulted from habituation (e.g., reduced flight responses in areas with higher levels of recreation; [78,79]. Habituation to recreation was discussed in many (39.4%) of the included articles and typically resulted in positive responses in our coding system (e.g., reduced flight initiation distances in habituated animals), but whether habituation is a beneficial outcome for animals (e.g., by reducing costly behavioral responses to humans) is unclear and warrants further study [80,81].

We found that non-motorized activities had more evidence for negative effects than motorized activities. Motorized activities are often expected to be more harmful to animals because of vehicle speed and noise [43], but our results suggest the opposite across a wide range of study locations and taxa. A few articles directly compared motorized and non-motorized activities; four mammals (guanaco *Lama guanicoe*, wolverine *Gulo gulo*, coyote *Canis latrans*, and bobcat *Lynx rufus*) showed behavioral or occurrence responses to non-motorized but not to motorized recreation [22,82,83], whereas the reverse was found for Hector's dolphin (*Cephalorhynchus hectori*) behavior [84] and ghost crab (*Ocypode quadrata*) abundance [85].

However, motorized activities often cover larger spatial extents than non-motorized activities, and since most studies did not compare effects across multiple spatial scales, it is possible that their impact has been underestimated. Additionally, motorized vehicles can also cause other types of harm not explored here, such as soil loss and vegetation disturbance [86]. A meta-analysis designed to explicitly compare the magnitude of effects of motorized and non-motorized recreation would be a valuable contribution to the literature.

Our results also suggest that winter terrestrial activities have greater evidence for effects on animals than summer terrestrial or aquatic activities, though the number of articles was small. A recent review of winter recreation effects on animals [39] supports this conclusion, finding that over half of the reviewed articles reported overall detrimental effects, particularly on birds and on species richness and diversity. There are several possible explanations for this result. Movement away from recreationists may be more energetically costly in snowy conditions [87]. For many species, food availability and quality is lower during winter [82,88], limiting their ability to relocate to avoid areas with human activity. There could also be habitat effects since vegetation in alpine and sub-alpine environments regenerates slowly, so habitat degradation caused by winter recreation could be more severe than that caused by other recreational activities in more temperate climates [39,89].

Overall, authors observed individual-level (behavioral and physiological) and community-level effects more frequently than most population-level (occurrence, abundance, and reproduction) effects. Though rarely measured, negative effects of recreation on survival–a particularly important response to understand for conservation purposes–were observed 1.4 times more frequently than the next highest response types (physiology and occurrence). Behavioral metrics, which were studied far more often than other types of responses, may be popular because they can be simpler to measure and have been proposed as a proxy for demographic parameters [90]. Nonetheless, behavioral metrics may not reflect the true population consequences of anthropogenic disturbance [91]. Study duration can also influence conclusions; one long-term study found that low-level recreation had an effect on dolphin habitat use that was not observed in a short-term behavioral study [81,92], while another found that short-term behavioral responses did not result in changes in the distribution or relative abundance of waterbirds [93].

Though most articles documented recreation effects, few presented specific, practical steps to minimize impacts. About 40% of the articles did not describe any management or mitigation actions, and many more contained only vague suggestions. We see a strong need for empirical tests of the effectiveness of management actions, which were rare. Encouraging examples of successful mitigation actions do exist, such as educating divers about avoiding damage to coral reefs [94], using volunteers to deter harassment of fur seals [95], and installing fences to establish disturbance-free areas [96,97]. This type of practical evaluation of management strategies is critical in assessing the ability of protected areas to meet demands for both recreational opportunities and the conservation of biodiversity. Interviewing practitioners would be a useful direction for future research in order to assess the type and extent of management strategies currently being employed. Even where management recommendations are provided in the scientific literature, it is unclear to what extent they are received by protected area managers [98]; a search of unpublished reports and other communications on the subject would help inform how well conservation scientists are reaching decision-makers.

The effects of recreation on animals is still a relatively unknown and low-profile topic in the conservation science literature, despite growing evidence that detrimental impacts can occur from a wide variety of recreational activities. Further, biophysical disturbances associated with recreation and tourism–including habitat conversion for roads and resorts, pollution from vehicles, and the spread of invasive species–are likely to have additional effects [19], increasing

the overall impact of the recreation and tourism industry. Recreation effects may also act synergistically with other threats to biodiversity such as urbanization and land-use change [18], which may result in increased access for recreation. This is a troubling problem for managers and conservation practitioners, since recreation is an integral part of protected areas worldwide [12]. Finding an appropriate balance between biodiversity conservation and outdoor recreation is complicated, especially since impacts vary among species and recreation activities. We must start by simply acknowledging that these uses are not necessarily compatible for all species, in all locations. This will make it easier to justify additional research on this topic, establish restrictions on recreation, and encourage changes in the behavior of recreationists, leading to improved conservation outcomes.

Supporting Information

S1 Appendix. Articles about recreation effects on animals included in the literature review.

(DOCX)

S1 File. Access database containing information extracted from reviewed papers.
(ACCDB)

S1 Table. PRISMA checklist.
(DOC)

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Author Contributions

Conceptualization: CLL SER AMM KRC.

Data curation: CLL.

Formal analysis: CLL.

Funding acquisition: SER KRC.

Investigation: CLL.

Methodology: CLL SER AMM KRC.

Project administration: SER KRC.

Supervision: SER KRC.

Visualization: CLL.

Writing – original draft: CLL.

Writing – review & editing: CLL SER AMM KRC.

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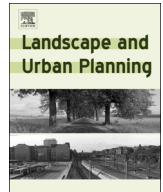
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Appendix C

Larson, C.L., S.E. Reed, A.M. Merenlender and K.R. Crooks. 2018. Accessibility drives species exposure to recreation in a fragmented urban reserve network. *Landscape and Urban Planning* 175: 62-71.

Research Paper

Accessibility drives species exposure to recreation in a fragmented urban reserve network

Courtney L. Larson[a,*], Sarah E. Reed[a,b], Adina M. Merenlender[c], Kevin R. Crooks[a]

[a] Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO 80523, USA
[b] North America Program, Wildlife Conservation Society, Bozeman, MT USA
[c] Department of Environmental Science, Policy, and Management, University of California, Berkeley, CA, USA

ABSTRACT

Outdoor recreation is a valuable ecosystem service permitted in most protected areas globally. Land-use planners and managers are often responsible for providing access to natural areas for recreation while avoiding environmental impacts such as declines of threatened species. Since recreation can have harmful effects on biodiversity, reliable information about protected-area visitation patterns is vital for managers. Our goal was to quantify recreational use in a fragmented urban reserve network and identify factors that influenced visitation. We empirically measured visitation rates at 18 reserves in San Diego County, California. Using random forest models, we identified biophysical and socioeconomic factors that influenced spatial variation in visitation rates and made projections to 27 additional reserves, validating with an expert opinion survey. Visitation rates varied widely across the reserve network. Accessibility variables, such as numbers of housing units and parking lots, were key explanatory variables that had positive relationships with visitation rates. To illustrate the applications of our models, we assessed the exposure of 7 species and subspecies of conservation concern to recreation by comparing predicted occurrence to projected visitation intensities. We found that several species and subspecies, including the orange-throated whiptail (*Aspidoscelis hyperythra*), western spadefoot (*Spea hammondii*), and the federally-threatened coastal California gnatcatcher (*Polioptila californica californica*), are likely exposed to high levels of recreational activity. Our results can be used to identify species for further research, highlight areas with potential conflict between recreation and conservation objectives, and forecast future changes in visitation.

1. Introduction

Outdoor recreation is a valuable cultural ecosystem service (Bergstrom & Cordell, 1991; Chan et al., 2012), providing important benefits for human health and well-being, local economies, and human livelihoods (Cisneros-Montemayor & Sumaila, 2010; Ekkel & de Vries, 2017). Globally, protected areas receive an estimated 8 billion visits per year (Balmford et al., 2015). In the United States, total visitor days increased by 32.5% from 2000 to 2009, and growth is expected to continue until at least 2060 (Cordell, 2012). Publicly-owned protected lands designated for conservation are open to recreation in most cases, including 94% of IUCN protected areas (Eagles, McCool, & Haynes, 2002; IUCN & UNEP, 2014). Land-use planners and managers are often responsible for providing access to natural areas for a wide variety of outdoor recreation activities while avoiding environmental impacts such as further declines of threatened species.

However, a growing body of research demonstrates that recreation can have various damaging effects on animals (Barros, Monz, &

Pickering, 2014; Larson, Reed, Merenlender, & Crooks, 2016; Monz, Pickering, & Hadwen, 2013; Sato, Wood, & Lindenmayer, 2013), including increased physiological stress (Arlettaz et al., 2007), reduced reproductive success (Beale & Monaghan, 2005), declines in abundance and occurrence (Reed & Merenlender, 2008), modified habitat use (George & Crooks, 2006), and altered species richness and community composition (Kangas, Luoto, Ihantola, Tomppo, & Siikamäki, 2010). These effects are widespread, as recreation activity is listed as a threat to birds in 65% of the world's biodiversity hotspots (Steven & Castley, 2013), and a recent review found that 93% of published studies documented at least one effect of recreation on animal species (Larson et al., 2016). The dual missions of protected lands create a dilemma for land-use planners and managers who must balance the growing demand for outdoor recreation with the protection of natural resources.

To best accommodate increased demand for outdoor recreation and manage potential effects on species, managers need reliable information about protected-area visitation patterns (McClaran & Cole, 1993). Measures such as the total number and the spatial and temporal

distribution of visitors participating in different recreation activities can help managers understand and mitigate potential impacts on ecological communities by identifying areas of particularly high use, re-orienting trail networks, allocating staff, and monitoring compliance with regulations (Cessford & Muhar, 2003; Hadwen, Hill, & Pickering, 2007). In addition, understanding the drivers of reserve visitation can help predict human activity at other reserves, make projections about the effects of future changes in the reserve network (e.g., addition of new reserves, construction of trails or parking lots), and inform reserve design and land management. However, visitation data is often sparse or non-existent despite the importance of understanding how, where, and when impacts of recreation on animals are occurring (Becken & Job, 2014), especially at the landscape level where monitoring efforts are rare (Braunisch, Patthey, & Arlettaz, 2011; Monz, Cole, Leung, & Marion, 2010; Rösner, Mussard-Forster, Lorenc, & Müller, 2014).

Here, we quantify spatial and temporal variability in recreation across a fragmented urban reserve network in San Diego County, California, where protections have been established for threatened species under a Multiple Species Conservation Program (MSCP) developed under Section 10 of the United States Endangered Species Act (U.S. Fish and Wildlife Service & National Marine Fisheries Service, 1996). We measured visitation using counts from remotely-triggered cameras and tested how visitation rates (visits/day) and intensity (visits/hectare/day) varied with reserve characteristics (e.g., reserve area, range in slope), accessibility (e.g., number of parking lots), and substitution factors (e.g., number of similar reserves within a 10 minute travel time). We then applied the models to estimate visitation at 27 additional reserves. We also surveyed reserve managers and staff, who are knowledgeable about how these areas are used, and used their answers to validate the model projections. As an illustration of how these models could be applied to help balance recreation and conservation goals in protected areas, we then examined the exposure to recreation of 7 species and subspecies of conservation concern. Since little is known about the effects of recreation on these species, developing landscape-scale recreation intensity models and comparing where recreational use overlaps with likely species occurrences can help set priorities for further study on those that are currently exposed to high levels of recreation and identify locations for potential management actions.

2. Methods

2.1. Study site

San Diego County, California has a large human population and high levels of biodiversity and endangerment. It is the fifth most populous county in the United States with over 3.2 million residents (U.S. Census Bureau, 2016). Coastal southern California is a hotspot of global biodiversity that is home to over 500 vertebrate species (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000) and contains large numbers of rare or threatened plants and animals (Crain & White, 2013; Dobson, Rodriguez, Roberts, & Wilcove, 1997). San Diego's MSCP, designed to protect 85 plant and animal species, was one of the first multiple species Habitat Conservation Plans developed under the United States Endangered Species Act (CA Department of Fish and Game, 2012). The MSCP establishes a comprehensive habitat conservation framework and allows the issuance of permits for incidental take of threatened and endangered species. San Diego County's MSCP reserves are managed by a variety of city, county, and state agencies, most of which have a mission statement that encompasses both human use and natural resource protection. Notably, the MSCP itself includes "access to natural preserves for passive recreation" as one of its objectives (MSCP Policy Committee and MSCP Working Group, 1998). MSCP reserves vary in size, distance from urbanized areas, and the expected intensity of recreational use. This gradient in recreational use presents a natural experiment over which recreational activity and

exposure of wildlife can be measured and compared.

2.2. Reserve selection

Local biologists and reserve managers aided our selection of 18 reserves for field study ("sampled reserves") along an expected gradient of recreation activity based on distance from densely-populated areas and anecdotal reports of use. We selected an additional 27 unsampled reserves dispersed over a larger spatial extent than the sampled reserves; however, we did not include reserves that were 2 or more standard deviations away from the mean value from the sampled reserves for 4 or more of the explanatory variables (Table 1; Appendix A). All reserves were publicly owned, part of the MSCP, and least 100 ha in area. This size threshold has been used as a minimum size designation for core conservation areas (Wade & Theobald, 2010), and many of the smaller reserves in San Diego County are heavily landscaped neighborhood parks unlikely to support populations of sensitive species. Seven reserves were closed to the public (two sampled and five unsampled reserves).

2.3. Field data collection

At each sampled reserve, we identified all official entrances and stratified them into three categories: staging areas (primary access points with parking lots), trailheads (entrances depicted on reserve maps and accessible by car, often with street parking), and connectors (entrances typically used to enter from an adjacent neighborhood or reserve). At closed reserves, we assumed that service roads that intersected the reserve boundary would be the most likely entry points for unauthorized use. Unofficial (typically user-created) entrances were common but difficult to locate systematically and were not included in the sampling design; however, based on our trail digitization effort we estimate that unofficial trails comprise up to 45% of the total trail network.

We used remotely-triggered cameras (Bushnell TrophyCam) to document human activity at reserve entrances from July to October 2013. We installed cameras at all staging areas and trailheads and a random sample of at least 50% of connectors, except for one reserve (Mission Trails) with an unusually large number of entrances. In total, we installed cameras for at least 14 days at 83 entrances across the 18 reserves. Cameras captured a single photo at each trigger and took a maximum of one photo every ten seconds.

2.4. Visitation estimates

We randomly truncated the beginning or end of each sampling period to obtain 14-day periods for analysis. For cameras that recorded more than 2000 photos during the sampling period ($n = 22$), we randomly subsampled the data to reduce time spent sorting photos. We viewed each photo and counted the number of hikers, bicyclists, and people riding or leading horses ("equestrians"). We also recorded the direction of travel to quantify visitors entering versus exiting the reserve. Imbalance in counts by direction was likely attributable to camera trigger speed (e.g., failing to capture bicyclists going downhill due to their speed), or to visitors entering and exiting through different entrances. For each reserve, we combined detections of hikers, bicyclists, and equestrians and the directional imbalance to create reserve-level empirical estimates of the number of visits per day (henceforth: visitation rate) and visitation intensity (visits/hectare/day). We calculated separate estimates of visitation rates and intensity by hikers, bicyclists, and equestrians for each reserve. For details of these calculations, see Appendix B.

We also conducted an online survey (SurveyGizmo, Widgix, LLC) of rangers and reserve staff to systematically collect expert opinion data on visitation patterns to use as a validation dataset for the 27 reserves at which we did not collect field data. The survey was open from May to

Table 1
Explanatory variables used to model visitation rates (visits/day) and intensity (visits/ha/day) at 18 sampled and 27 unsampled reserves in San Diego County, California. Bold numbers indicate differences that are statistically significant at the $p \leq 0.05$ level.

Variable	Mean ± SD, sampled reserves	Mean ± SD, unsampled reserves	Data source(s)
Accessibility			
Housing units within:	69,704 ± 83,669	46,484 ± 51,132	SanGIS parcel data, Orange County parcel data, Riverside County parcel data,
10 min. travel time			US Census TIGER/Line shapefiles 2014, SanGIS road data
20 min. travel time	285,467 ± 258,018	237,725 ± 214,734	
30 min. travel time	631,707 ± 370,953	537,171 ± 361,707	
40 min. travel time	997,535 ± 329,120	796,067 ± 413,663	
Parking lots	1.78 ± 1.99	1.29 ± 1.72	Field visits, reserve maps and websites, NAIP 2012 aerial imagery
Entrances	**6.33 ± 4.64**	**2.86 ± 2.56**	Field visits, reserve maps and websites, NAIP 2012 aerial imagery
Open to the public (%)	89 ± 32	82 ± 39	Reserve websites, reserve managers
Reserve attributes			
Area (ha)	982.8 ± 897.6	659.5 ± 638.6	Calculated in ArcGIS 10.1 using SDMMP conserved lands data
Official trail length[a] (km)	20.7 ± 21.1		Digitized trails from NAIP 2012 aerial imagery and imagery from ArcGIS online servers
Official trail density[a] (km/ha)	0.027 ± 0.019		Digitized trails from NAIP 2012 aerial imagery and imagery from ArcGIS online servers, reserve area
Unofficial trail length[a] (km)	16.1 ± 16.3		Digitized trails from NAIP 2012 aerial imagery and imagery from ArcGIS online servers
Unofficial trail density[a] (km/ha)	0.017 ± 0.011		Digitized trails from NAIP 2012 aerial imagery and imagery from ArcGIS online servers, reserve area
Total connected area (ha)	1780 ± 1465.1	1267.8 ± 1667.8	Calculated in ArcGIS 10.1 using SDMMP conserved lands data
Elevation range (m)	330.6 ± 173.3	289.9 ± 255.1	US Geological Survey National Elevation Dataset
Slope range (degrees)	48.88 ± 7.63	45.11 ± 14.35	Derived from elevation
Vegetation (% cover):			US Forest Service Calveg
herbaceous	0.107 ± 0.132	0.199 ± 0.239	
shrub	**0.838 ± 0.158**	**0.615 ± 0.351**	
hardwood	0.035 ± 0.049	0.073 ± 0.130	
Landscape context			
Distance from coast (km)	61.56 ± 38.42	57.45 ± 54.53	Calculated in ArcGIS 10.1
Substitute reserves within:			US Census TIGER/Line shapefiles 2014, SanGIS road data, SDMMP conserved lands data
10 min. travel time	4.17 ± 2.92	3.18 ± 2.61	
20 min. travel time	**14.94 ± 3.89**	**9.18 ± 5.46**	
30 min. travel time	**28.56 ± 7.67**	**18.64 ± 8.74**	
40 min. travel time	**43.11 ± 7.83**	**31.21 ± 12.81**	

[a] Trail variables were collected for sampled reserves but not unsampled reserves. A preliminary modeling exercise showed that these variables explained minimal additional variance, and they were not used in the final model building.

November 2013. All responses were anonymous, although respondents identified their employer. The survey asked respondents to: 1) choose the reserves (maximum 5) with which they were the most familiar from a list of 51, 2) estimate the visitation rates to those reserves on an average weekday and weekend day, 3) respond to other questions including seasonality of recreational activity and unauthorized use (see Appendix E for the full survey). Respondents selected from five categorical ranges in visitation: 0–9, 10–49, 50–199, 200–499, and 500 + visitors/day. We compared the midpoint of these categories with estimates from the field data and modeling approaches; for reserves with greater than one response, we used the median of the midpoints. We used the survey data as an independent source of information to validate the projections from the recreation model.

2.5. Recreation modeling

We modeled visitation rates using groups of explanatory variables that we expected would be influential based on previous research. We expected more accessible reserves to have higher levels of use (Degenhardt, Frick, Buchecker, & Gutscher, 2011; Ekkel & de Vries, 2017; Hill & Courtney, 2006; Shanahan, Lin, Gaston, Bush, & Fuller, 2015; Termansen, McClean, & Jensen, 2013), and reserves located close to other reserves to have lower levels of use, since the neighboring reserves could act as substitutes (De Valck et al., 2016; Termansen, Zandersen, & McClean, 2008). We also expected reserves with greater area and topographic relief to receive higher use (Hill & Courtney, 2006; Neuvonen, Pouta, Puustinen, & Sievänen, 2010; Shanahan et al., 2015; Siderelis, Moore, & Lee, 2011; Termansen, McClean, & Skov-Petersen, 2004; Termansen et al., 2013). This led to the following list of

variables (Table 1): accessibility variables (number of entrances, parking lots, and nearby housing units; open or closed to the public), landscape variables (distance from coast, number of nearby "substitute" reserves), and reserve characteristics (slope, elevation, area, vegetation, trail length and density). We derived these variables from spatial datasets using ArcGIS 10.1 and from field visits to the reserves.

We digitized trails in the sampled reserves, but not the unsampled reserves. Trail networks often connect reserves to one another, so we also considered a total connected area variable, which measured the area of a reserve plus the area of its neighbors (other reserves within 1 km). However, differences in explanatory power of models built with and without the trail and total connected area variables were minimal, so these variables were omitted from the final models. Similarly, the Julian start date of the sampling period was tested as a possible nuisance variable, but had low explanatory power in initial univariate regressions and was omitted.

We included a series of housing unit and substitute reserve variables calculated at increasing travel time distances (Wade & Theobald, 2010) since we suspected that these effects were scale-dependent but did not know the appropriate scale (Wilmers et al., 2013). We created raster datasets representing travel time distances using road data from San Diego, Orange, and Riverside counties (SanGIS and SANDAG, 2016; U.S. Census Bureau, 2014). We applied an average driving speed attribute from the San Diego county data to calculate the time to cross each 20 m pixel, assigning a speed of 5 km/hour to roadless pixels (Theobald, Norman, & Newman, 2010). We calculated the cost distance from every pixel to the nearest entrance of each reserve and inverted it to obtain travel time. We then summed the number of housing units and substitute reserves (publicly owned reserves greater than 100 ha)

within several travel time intervals (10, 20, 30, and 40 minutes).

We used random forest models to model the visitation rates and intensity of hikers and bicyclists at the 18 sampled reserves. We did not model equestrian visitation due to low counts and limited variability. Since prior knowledge of recreation in this system was minimal, exploratory analyses were more appropriate than confirmatory hypothesis-testing techniques. Random forest modeling is well-suited to exploratory analysis since it can handle a large number of predictors, is robust to correlated explanatory variables, and allows for varying functional relationships between predictor and response variables (Cutler et al., 2007; Hochachka et al., 2007).

We used the randomForest package in R (Breiman, 2001; Liaw & Wiener, 2002; R Core Team, 2015), using 1000 trees and node splitting (the *mtry* setting) set at 16 variables for the hiker model and 8 for the bicyclist model. These were the optimal *mtry* settings identified by the *tuneRF* function, which compares error rates among models built with different *mtry* values. We log-transformed the response variables to limit the influence of outliers (Knudby, Brenning, & LeDrew, 2010). We then identified variables with strong influence on visitation rates in the 18 sampled reserves using the *importance* function in the randomForest package. This function randomly permutes the values of a predictor variable over the dataset, making new predictions and calculating the mean square error (MSE), then calculating the difference in MSE when the true values of the variable are used to make predictions (Breiman, 2001). Important variables will have a larger increase in MSE when their values are permuted. We examined partial dependence plots for each variable (Appendix C) to assess the general direction of the relationship (i.e., overall positive, neutral, or negative relationships with visitation). We then estimated visitation rates and intensity of hikers and bicyclists within sampled and unsampled reserves using the *predict* function, and refer to these as "projections." Reported results are means and standard deviations of 1000 model runs. We assessed model fit and performance using the percent of variation explained and Pearson correlations between the projected and empirically-estimated values for the 18 sampled reserves.

2.6. Species exposure to recreation

We conducted an analysis of species exposure to recreation as a proof of concept for how recreation models can be used in conjunction with previously collected species distribution data to examine patterns and prioritize further study. To do this, we used existing species distribution models for reptiles and amphibians (Fisher et al., 2008; Franklin, Wejnert, Hathaway, Rochester, & Fisher, 2009) and ecological niche models for birds (Preston, Rotenberry, Redak, & Allen, 2008; Rotenberry, Preston, & Knick, 2006) to compare their exposure to recreation across all 45 reserves (see Table 2 for the full list of species and subspecies, hereafter jointly referred to as "species"). We focused our analyses on 7 species (4 reptile, 1 amphibian, and 2 bird) that are of conservation concern in the region and are covered by the MSCP, one of which is the federally-threatened coastal California gnatcatcher (*Polioptila californica californica*). To further explore exposure to recreation across a wider range of species, and to provide a resource for future research and management, we conducted additional analyses for species not identified as priorities by the MSCP (21 reptile, 4 amphibians, and 3 bird); we present results of these analyses in Appendix D.

To assess species exposure, we used linear regression to model projected visitation intensity using the median predicted probability of presence (for reptile or amphibian species) or median habitat similarity index (for bird species) as the sole predictor. This allows us to identify species that are likely to occupy areas with high levels of recreation, and where the overlaps between species occurrence and high human use occur spatially. We report the beta coefficients and standard errors as back-transformed values that represent the expected change in median probability of presence or habitat suitability that would result from a 68% increase in visitation intensity. An approximate 68%

Table 2

Results of the species exposure linear regression models for 4 reptile, 1 amphibian and 2 bird species and subspecies that are listed under the Multiple Species Conservation Plan (MSCP). These models use projected visitation intensity at 45 reserves in San Diego County, California to predict median probability of presence (for reptiles and amphibians) or median habitat suitability (for birds). Beta coefficients and standard errors have been back-transformed to represent the expected change in median probability of presence or habitat suitability produced by a 68% increase in visitation intensity. This increase is the mean model prediction of visitation intensity when housing units are increased by 165% from current levels to coarsely approximate the change that occurred from 1970 to 2015 in San Diego County (U.S. Census Bureau 1970, 2015). Statistically significant results ($p < 0.05$) are shown in bold text.

Species[a]	Effect of visitation intensity		
	$\beta \pm$ SE	p	R^2
More exposed species and subspecies (positive relationships)			
Western spadefoot	**0.026 ± 0.009**	**0.008**	**0.132**
Spea hammondii			
Orange-throated whiptail	**0.133 ± 0.032**	**< 0.001**	**0.275**
Aspidoscelis hyperythra			
Red diamond rattlesnake	0.007 ± 0.007	0.301	0.002
Crotalus ruber			
Two-striped gartersnake	0.011 ± 0.007	0.145	0.027
Thamnophis hammondii			
Coastal California gnatcatcher	**0.091 ± 0.031**	**0.005**	**0.147**
Polioptila californica californica			
Less exposed species and subspecies (negative relationships)			
Blainville's horned lizard	− 0.023 ± 0.021	0.286	0.004
Phrynosoma blainvillii			
Bell's sage sparrow	**−0.076 ± 0.030**	**0.015**	**0.109**
Amphispiza belli belli			

[a] English and scientific names of reptiles and amphibians follow SSAR (2015).

change is the mean model prediction of increased visitation intensity when housing units are increased by 165% from current levels to coarsely approximate the change that occurred from 1970 to 2015 in San Diego County (U.S. Census Bureau 1970, 2015). We also plotted the number of "more exposed" and "less exposed" species likely to occur at each reserve (i.e., have a predicted probability of presence at or above the median value) on maps that also display recreation intensity to visually assess spatial patterns in species exposure to recreation.

3. Results

3.1. Field and expert opinion data

The cameras captured 142,456 photos over 1379 camera-days, of which 78,551 were categorized (the remaining photos were excluded by the subsampling procedure). These included 41,336 photos of humans and 1944 wildlife photos. Mean (± SD) visitation for the 18 sampled reserves was 190.4 ± 420.7 (range: 0–1888) visits/day (Fig. 1a). The busiest reserve (1,888.0 ± 1356.1 visits/day) was an outlier with a visitation rate 5.9 times greater than the next highest reserve (318.0 ± 235.0 visits/day). Mean (± SD) visitation intensity was 0.23 ± 0.26 (range: 0–0.91) visits/hectare/day (Fig. 1b). Most recreationists were hikers (89.7%) with fewer bicyclists (9.0%) and equestrians (1.3%). Across all reserves, estimated visitation was 1.87 times higher on weekend days (285.4 ± 606.5) than on weekdays (152.9 ± 346.5; paired $t = −2.09$, $p = 0.05$).

We received 33 completed expert opinion surveys, with a total of 69 individual responses covering 36 reserves. Respondents had worked a mean of 7.7 (± 5.9) years and 113 (± 117) days per year in the reserves. Their estimates of recreational use had a high degree of agreement with one another; for reserves with multiple responses, respondents chose the same visitation rate category 74% of the time. Fourteen of the 18 sampled reserves were included in the survey responses. For these reserves, survey estimates and empirical estimates of recreation were strongly and positively correlated ($r = 0.650$,
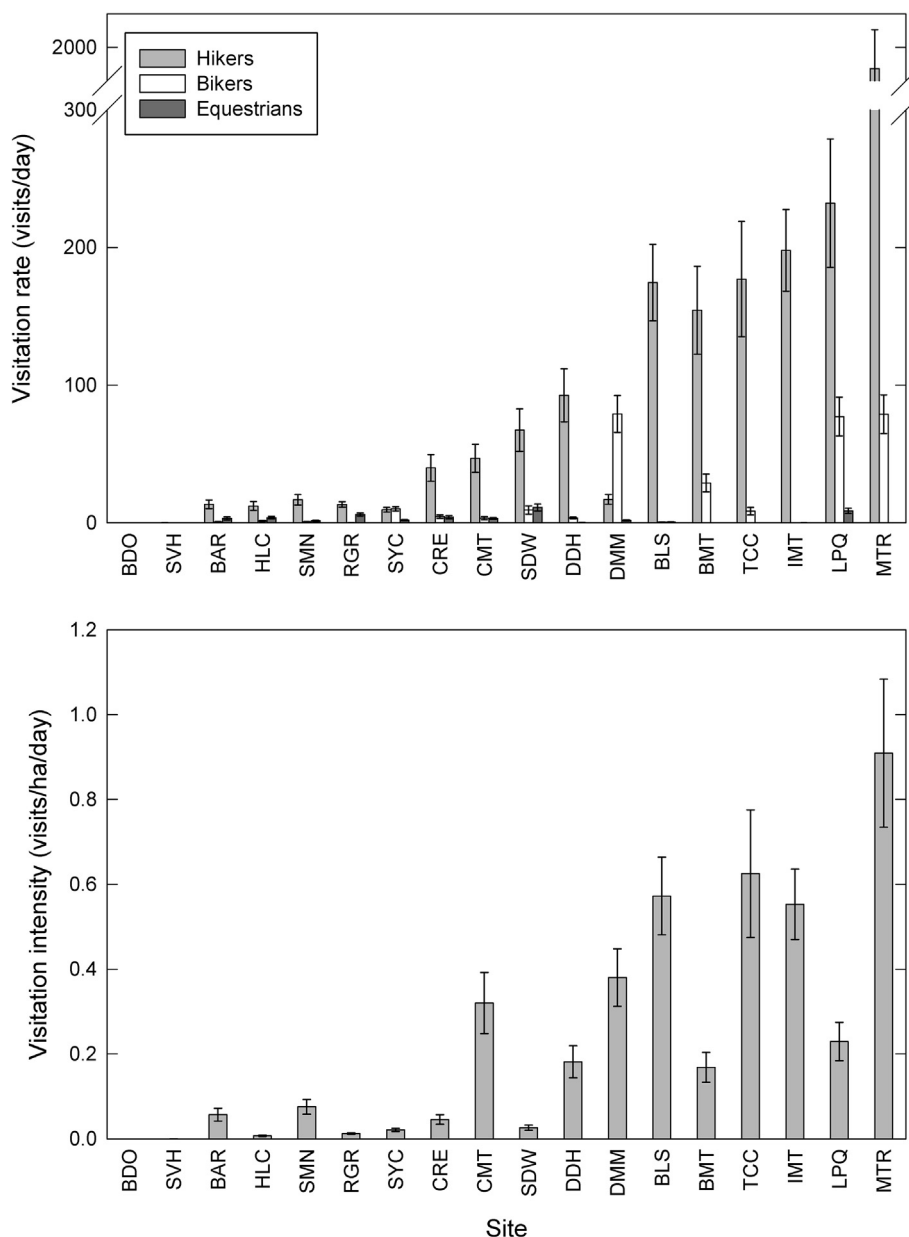
Fig. 1. Estimates of the level of recreational activity derived from empirical field data at the 18 sampled reserves. Panel a) shows estimated visitation rates (visits/day) for hikers, bicyclists, and equestrians, and b) shows estimated visitation intensity (visits/ha/day) for all recreational activities. Error bars show standard error. See Appendix A for the full names of reserves.

$p = 0.012$). Further, the ranked order of reserves did not differ significantly between the two estimation methods (Wilcoxon signed rank test; $V = 71$, $p = 0.268$).

3.2. Recreation modeling

The recreation models performed well, particularly the hiker model; the correlation between empirical and projected visitation rates ($r = 0.978$, $p < 0.0001$; $n = 18$ sampled reserves) and the percentage of variation explained ($46.6 \pm 2.1\%$) were both high. The bicyclist model also performed relatively well with a strong correlation ($r = 0.952$, $p < 0.0001$; $n = 18$) and moderate explanatory power ($29.2 \pm 1.8\%$). Thirty-three out of 45 sampled and unsampled reserves received survey responses; for these reserves, projected visitation rates and expert opinion survey responses were moderately correlated ($r = 0.499$, $p = 0.003$). However, the ranked order of the reserves differed between the survey responses and model projections (Wilcoxon

signed rank test; $V = 426$, $p = 0.008$).

Accessibility variables were the most important across both models (Fig. 2). Housing units within 10 minutes was the most important variable in the hiking model (% increase in MSE $\pm$ SD: $11.6 \pm 0.6\%$); other housing variables had slightly lesser importance (Fig. 2a). Whether a reserve was open to the public and the number of parking lots were also important ($4.5 \pm 0.7\%$) in the hiker model, while the number of entrances had little importance ($0.2 \pm 1.0\%$). In the bicyclist model, housing units within 30 minutes had the highest importance ($10.0 \pm 0.6\%$), and the other housing variables also had high values (Fig. 2b). In contrast to the hiking model, the number of entrances was highly important ($9.5 \pm 0.7\%$), whereas the number of parking lots was not ($0.8 \pm 1.0\%$). All accessibility variables had a positive relationship with visitation projections across both models (Appendix C).

Landscape context variables, specifically the number of substitute reserves within 20–40 minutes, were also important in both models
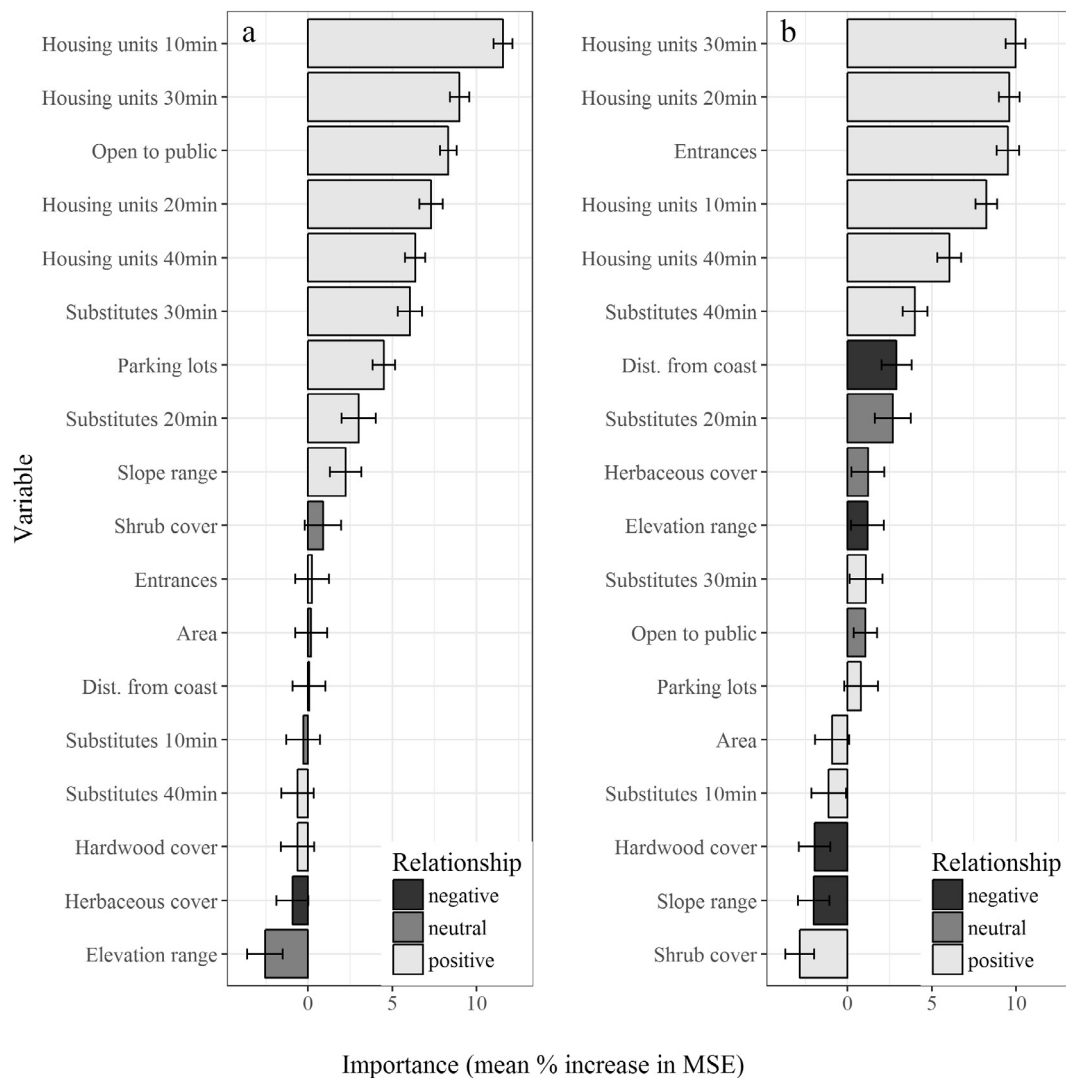
Fig. 2. Mean variable importance for a) hikers and b) bicyclists. A high value indicates that a variable is important to the random forest regression model because when this variable is randomly permuted, there is a relatively large change in the mean squared error (MSE) across all trees. A negative value means that the error decreased when the variable was randomly permuted and indicates very low importance. Accessibility variables have white bars, reserve characteristics have medium gray bars, and landscape context variables have dark gray bars. Error bars show the standard deviation for 1000 model runs.

(Fig. 2). The number of substitute reserves was positively related to visitation, more strongly for travel times of 20 minutes or greater (Appendix C). Substitute reserves within 20 and 30 minutes were the most important (3.0 ± 1.0 and 6.0 ± 0.7%) for the hiker model, while the number of substitute reserves within 20 and 40 minutes were most important in the bicyclist model (2.7 ± 1.1% and 4.0 ± 0.7%). Distance from the coast was also moderately important in the bicyclist model (2.9 ± 0.9%) and had a negative relationship with visitation. Finally, reserve characteristics, such as elevation and vegetation types, had low importance apart from range in slope, which was somewhat important (2.2 ± 0.9%) for the hiker model and had a positive relationship with visitation rate (Appendix C).

3.3. Species exposure to recreation

Three species had significant positive linear relationships between projected visitation intensity and median probability of presence or habitat suitability (Table 2): western spadefoot (*Spea hammondii*; β ± SE = 0.026 ± 0.009, p = 0.008, R^2 = 0.132), orange-throated whiptail (*Aspidoscelis hyperythra*; β ± SE = 0.133 ± 0.032, p < 0.001, R^2 = 0.275), and coastal California gnatcatcher (β ± SE = 0.091 ± 0.031, p = 0.005, R^2 = 0.147). We interpret

positive relationships between visitation intensity and probability of presence or habitat suitability as an indication that a species is exposed to relatively high levels of recreational activity ("more exposed" species). Species with positive relationships between predicted probability of presence and visitation intensity were more likely to occur in reserves closer to the coast, especially the west-central region where visitation intensity is high (Fig. 3).

One species, Bell's sage sparrow (*Amphispiza belli belli*), had a significant negative linear relationship between projected visitation intensity and median probability of presence (β ± SE = −0.076 ± 0.030, p = 0.015, R^2 = 0.109; Table 2). This suggests that it is exposed to comparatively lower levels of activity ("less exposed"); however, it does not mean this species is unaffected by current activity levels. The Bell's sage sparrow was likely to occur at locations dispersed throughout the study area (Fig. 3).

4. Discussion

We found that recreational activity varied widely in this diverse and spatially-expansive network of reserves within the San Diego MSCP. The key factors influencing this variation were accessibility variables – including the number of housing units and entrances, and whether the
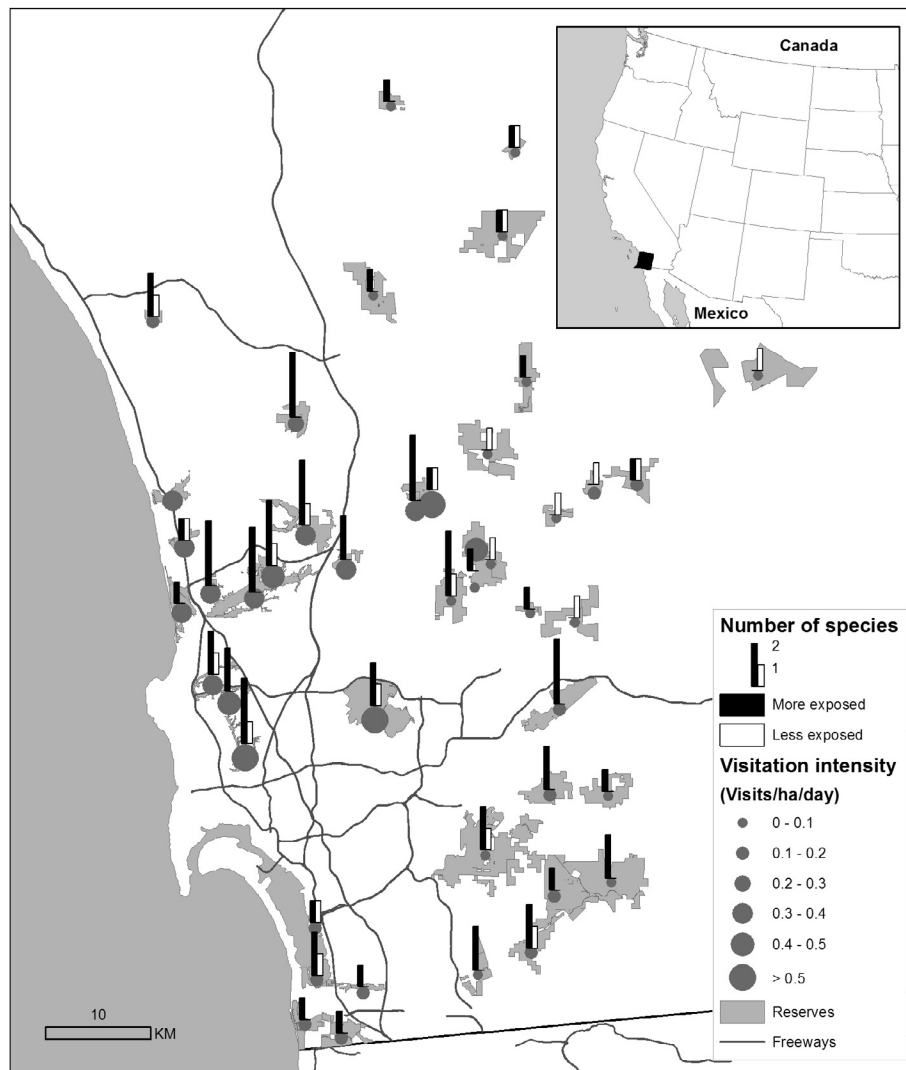
Fig. 3. Number of MSCP-listed species and subspecies that are likely to occur (i.e., have a predicted probability of presence at or above the median value for the reserve network) at each reserve. Only species with a statistically significant ($p \leq 0.05$) linear relationship between predicted probability of presence and projected visitation intensity are shown. Black bars represent species more exposed to recreation (i.e., relationships are positive; $n = 3$) and white bars represent species less exposed to recreation (i.e., relationships are negative; $n = 1$, Bell's sage sparrow). Projected visitation intensity at each reserve is represented by proportional gray circles.

reserve was open to the public – and the number of nearby reserves. Our models predict that several reptile, amphibian, and bird species are exposed to high levels of recreation, indicating a need to understand the species-specific responses to recreation disturbance.

4.1. Recreation modeling

The most important drivers of visitation rates were related to reserve accessibility, particularly the number of housing units, parking lots, and entrances, echoing the findings of other researchers who found that accessibility (or travel cost) was an important factor in explaining visitation rates (Degenhardt et al., 2011; Hill & Courtney, 2006; Ode & Fry, 2006; Shanahan et al., 2015; Termansen et al., 2013). In our analysis, it appears that bicyclists are willing to travel further to recreate than hikers, since importance values were highest for the variables counting the number of housing units within 20 and 30 minutes in the bicyclist model, whereas for hikers importance declined for housing unit variables beyond a 10 minute travel time. The importance of the "open" variable suggests that opening land to public access increases recreational pressure by hikers. This is hardly surprising, but it means that public agencies that use open space acquisition as a primary conservation strategy may be substituting one threat (habitat loss from

development) for another (habitat loss or degradation due to recreation). This variable had little importance in the bicyclist model, yet no bicyclists were observed using closed reserves based on the camera data.

We expected that the number of nearby reserves that could act as substitutes would be negatively related to visitation since they could compete for visitors (Termansen et al., 2008), yet our models show positive relationships, especially in moderate travel times. We suspect clusters of reserves may have acted as an attractant because of trail networks spanning multiple reserves, or due to visitors' greater awareness of the vicinity as a destination for recreation (Boll, von Haaren, & von Ruschkowski, 2014; Degenhardt et al., 2011). As a group, the reserve characteristics were relatively unimportant, contrasting with several studies that found that reserve area (Hill & Courtney, 2006; Termansen et al., 2013), topography (Termansen et al., 2013), or "naturalness" (Boll et al., 2014) were important predictors. Though we did not include trail variables in our models, several prior studies found that trail length was not an important predictor of visitation because most visitors remain close to parking lots (Beeco, Hallo, & Brownlee, 2014; Hill & Courtney, 2006; Meijles, de Bakker, Groote, & Barske, 2014; Taczanowska et al., 2014).

Our results also demonstrate that modeling visitation rates for these

reserves was possible using publicly available GIS data (e.g., parcels, elevation). However, our estimates do have limitations. Since we monitored recreation from July to October, our estimates do not reflect seasonal variation, which the expert opinion survey indicated could be substantial. Additionally, although we attempted to correct for observational error by incorporating a term for the net imbalance in visitor entrances and exits to a reserve (Appendix B), this correction is complicated by visitors entering and exiting through unsampled entrances. Instead, visual observations could be used to estimate the error rate of each camera and calibrate them accordingly (Pettebone, Newman, & Lawson, 2010). Nonetheless, the strong correlations between the expert opinion survey and the empirical estimates suggest that the relative magnitude and ordering of reserve visitation rates is accurate.

The strength of these correlations is an intriguing result considering that expert opinion data is rarely considered an option for visitor monitoring (Arnberger, Haider, & Brandenburg, 2005; Cessford & Muhar, 2003) or used to create visitation estimates (but see Rösner et al., 2014). Our experts may have been particularly successful at estimating visitation rates because the respondents had considerable experience working in the reserves and largely agreed with each other. However, our survey results should be interpreted with caution due to the small sample size and because we were unable to assess non-response bias. In reserve networks with experienced staff, a systematic survey may be a relatively simple approach to develop coarse estimates of visitation. Rangers and other staff are also aware of unauthorized human activity, such as off-trail or unauthorized use, which other visitor count methods may have difficulty detecting (Rösner et al., 2014).

4.2. Species exposure to recreation

We identified three species with significant positive relationships between visitation intensity and probability of presence/habitat suitability, which indicates greater exposure to recreation. One species (Bell's sage sparrow) had a significant negative relationship between visitation intensity and probability of presence/habitat suitability, meaning it is likely less exposed to recreation. "More exposed" species were more likely to occur closer to the coast; this is logical since visitation rates tended to be higher along the more urbanized coast. These results could help managers concerned about human impacts on native species to focus on the most exposed species, and narrow the area of primary focus to the reserves where the overlap is most likely to occur.

Though we believe these relationships are valuable for assessing the likely exposure of species to recreation, we note that we cannot determine the mechanism underlying these patterns due to the simplicity of our overlay approach. That is, negative relationships with projected visitation intensity may imply that humans and wildlife are selecting for different attributes, or that negative effects of human disturbance on animal species have already occurred and degraded habitat quality. Avoidance of habitat areas with high recreational use has been documented in various species, including reptiles and passerine birds (Ficetola et al., 2007; Finney, Pearce-Higgins, & Yalden, 2005; Kangas et al., 2010; Mallord, Dolman, Brown, & Sutherland, 2007).

Though we interpret positive relationships as an indication that recreation could be affecting a species, it could alternatively mean that humans and wildlife are selecting for similar attributes, or even that recreation is benefiting certain species, which has been documented in corvids (Gutzwiller, Riffell, & Anderson, 2002; Storch & Leidenberger, 2003). Ultimately, we believe it is most appropriate to examine potential recreation effects where high levels of recreation overlap with areas occupied by species of conservation concern (Braunisch et al., 2011). In our study, this means the orange-throated whiptail, western spadefoot, and coastal California gnatcatcher should be prioritized for future research. Understanding their response to recreation and how to mitigate any potentially harmful effects could be critical in

conservation efforts for these species. Though recreation can have direct mortality effects, the majority of impacts are indirect (Larson et al., 2016), which are difficult to quantify and may not be considered "take" under the MSCP or other legal frameworks. This means that land conserved for species protection may not be adequately protecting listed species if recreational disturbance has considerable detrimental effects.

Our species exposure analysis is a first step toward identifying species that may be exposed to high levels of recreational activity, illustrating how our modeling approach could be used to compare exposure among species. However, the visitation rate and intensity measures are averaged across the sampling period, masking temporal peaks. Further, we were unable to examine spatial activity patterns within reserves. Recreationists are known to concentrate near entrances, facilities, and attractions (Monz et al., 2010; van der Zee, 1990), and spatially or temporally concentrated activity can have diverse effects on animals (Kerbiriou et al., 2009; Malo, Acebes, & Traba, 2011). Accordingly, future research should examine how temporal and spatial peaks in visitation may influence animals differently than overall rates. Identifying threshold levels of recreation at which animal responses increase or asymptote (Monz et al., 2013) would be particularly useful for wildlife and land managers.

4.3. Management implications

Our models can help future reserve management by forecasting the amount of use in newly acquired land or by projecting changes in recreation with alterations in surrounding land use. The population of the San Diego region is expected to grow by 40% and housing is expected to increase by 34% between 2008 and 2050 (San Diego Association of Governments, 2010), meaning that reserves that are currently at the urban edge may experience rapid housing growth along their borders. For example, if housing within 30 minutes of each reserve increased by 34% as predicted, projected visitation rates would increase by up to 46%. Further, variables that can be manipulated by land-use planners and managers, such as the number of parking lots, could be used to concentrate visitor use into certain areas or to influence the overall level of visitation to a reserve.

Our approach to modeling recreation and evaluating species exposure can be used to guide future research and inform land-use policy. For example, similar methods could be applied in other areas to estimate visitation rates and examine which factors drive recreational use in different contexts. Further, existing studies of the effects of recreation on animals rarely suggest practical management actions that could reduce impacts or test the effectiveness of such interventions (Larson et al., 2016; but see Ikuta & Blumstein, 2003; Thiel, Menoni, Brenot, & Jenni, 2007; Thompson, 2015). Our approach helps address this gap by improving our understanding of the drivers and spatial patterns of recreation. With such models, we can project visitation rates, forecast changes in visitation in response to population growth or altered reserve management, identify focal species for management action, and prioritize locations within the reserve network with potential conflict between recreation and biodiversity conservation.

Addressing the trade-offs between recreation and biodiversity conservation is a difficult challenge. The biodiversity value of protected areas is important to visitors (Siikamäki, Kangas, Paasivaara, & Schroderus, 2015), especially those seeking to observe wildlife, who are a rapidly-growing segment of outdoor recreation participants (Cordell 2012). Funding for acquiring and protecting land is often tied to mandates that require public access for recreation, which can constrain managers' ability to prevent or limit access to sensitive areas. Since most protected areas will continue to be open to recreation, it is critical that we improve our understanding of the various effects of recreation on wildlife in order to efficiently manage protected areas and ensure minimal conflicts among uses.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.landurbplan.2018.03.009.

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Appendix D

Larson, C.L., S.E. Reed, A.M. Merenlender and K.R. Crooks. (*In review.*) A meta-analysis of recreation effects on vertebrate species richness and abundance. *Conservation Science and Practice.*

A meta-analysis of recreation effects on vertebrate species richness and abundance

Courtney L. Larson (corresponding author)
Department of Fish, Wildlife, and Conservation Biology, Colorado State University
1474 Campus Delivery, Fort Collins CO 80523-1474 USA
+1 (612) 599-9912
courtney.larson@colostate.edu

Sarah E. Reed
Americas Program, Wildlife Conservation Society
Department of Fish, Wildlife, and Conservation Biology, Colorado State University
sreed@wcs.org

Adina M. Merenlender
Department of Environmental Science, Policy, and Management, University of California-
Berkeley
adinam@berkeley.edu

Kevin R. Crooks
Department of Fish, Wildlife, and Conservation Biology, Colorado State University
kevin.crooks@colostate.edu

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1   **Abstract**

2   Most protected areas globally have a dual mission to conserve natural resources and

3   provide access for outdoor recreation or ecotourism, yet questions remain about the

4   ecological effects of recreation. We conducted a global meta-analysis of the effects of

5   recreation on vertebrate richness and abundance. We estimated that vertebrate richness

6   (n=15 articles) and abundance (n=32) are lower in association with higher levels of

7   recreation in over two-thirds (70%) of cases. We observed a moderate negative group-level

8   effect of recreation on bird and mammal abundance, but the group-level effect on fish and

9   reptiles was not significant. Effects were stronger for carnivores and herbivores than for

10   omnivores, and stronger for small-bodied birds and ground-nesting birds than larger and

11   tree- and shrub-nesting birds. Terrestrial activities were associated with reduced

12   vertebrate abundance, whereas aquatic activities were not. Both motorized and non-

13   motorized activities were associated with reduced vertebrate abundance, but the effect for

14   motorized activities was uncertain due to small sample size. These results pose a challenge

15   to natural resource management agencies who must balance recreation access with natural

16   resource protection, and to conservation organizations that rely on outdoor recreation for

17   public support and funding. We recommend that managers plan recreational access at a

18   regional scale and include some areas that are closed to recreation to minimize trade-offs

19   between recreation and animal conservation.

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).

49   Meta-analysis is increasingly popular in ecology and conservation as a tool to

50 synthesize evidence across studies and explore large-scale patterns. Meta-analyses can

51 combine data from similar studies to estimate overall effect sizes while considering sources

52 of heterogeneity such as differences in methods or study taxa (Haddaway 2015). Previous

53 meta-analyses on recreation effects on wildlife have focused on winter recreation (Sato et

54 al. 2013) and behavioral and physiological measures (Bateman & Fleming 2017). Our

55 analysis complements and builds upon these prior studies by encompassing many types of

56 recreation and focusing on responses at the population and community levels, where

57 decisions about animal conservation and management are typically made. More

58 specifically, we examine differences in vertebrate richness and abundance in response to

59 outdoor recreation. We ask if there are differences among classes of vertebrates, species

60 characteristics, types of recreation, and temporal and spatial patterns of recreational use.

61 Managers of protected areas are increasingly aware of the potential for recreation to

62 impact biodiversity, but little information is available to help them evaluate management

63 options. Examining the findings of individual studies in a synthetic fashion, we provide

64 broader conclusions about recreation effects that can help inform management decisions to

65 reduce impacts from recreational use of protected areas.

66

67 **Methods**

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69 *Article selection*

70   Our search protocol, fully described in Larson et al. (2016), was designed for a high-

71 sensitivity, low-specificity search (Pullin & Stewart 2006). We used the keywords "tourism"

72 and "recreation" to systematically search for articles published through March 2018 within

73 a list of 196 journals drawn from five Web of Science categories (biodiversity conservation,

74 ecology, zoology, ornithology, and behavioral sciences; Table S1). Since we relied on the

75 journal category feature within Web of Science to narrow the scope of our search, we did

76 not replicate the search in additional databases or gray literature. We screened titles and

77 abstracts to remove clearly irrelevant articles, then reviewed full-text articles and selected

78 those that met the following inclusion criteria: 1) articles estimated species richness

79 and/or abundance of at least one animal species; 2) articles reported species richness

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80 and/or abundance estimates at two or more categorical levels of non-consumptive

81 recreation while other site characteristics were similar; 3) articles included sufficient data

82 (in results, figures, or supplemental materials) to calculate effect sizes (Fig. 1). We define

83 "abundance" to include indices of relative abundance or activity levels, such as detection

84 frequencies of animals or sign. The second criterion ensured that studies had similar

85 designs that compared recreation effects between categorical levels of use (e.g., sites with

86 relatively low and high levels of recreation), while other site characteristics (e.g., habitat,

87 geographic location) did not differ substantially (as assumed or measured by the study

88 authors). While studies measuring recreation as a continuous variable are useful for

89 understanding effects of recreation, they were difficult to include in meta-analyses because

90 authors frequently analyzed such data with multivariate models (i.e., recreation variables

91 along with covariates), meaning that the reported effect of recreation was conditional on

92 the effects of covariates. We therefore excluded these studies from our analysis. The second

93 criterion also filtered out studies examining consumptive forms of recreation such as

94 hunting, fishing, and collecting.

95

96 *Data extraction*

97   We extracted pairs of estimates ("comparisons") of vertebrate richness or

98 abundance at low and high levels of recreation from each included article. Many articles

99 contained data for multiple species or temporal and spatial scales, which we retained as

100 separate comparisons in the database. For each comparison, we recorded the focal taxa,

101 type of recreation activity (aquatic, winter, or terrestrial; motorized or non-motorized),

102 and type of response variable (species richness or abundance; Table 1). We recorded

103 whether the recreation disturbance was a temporal difference, defined as a comparison

104 between recreation levels at the same site(s) at different times, or a spatial difference,

105 defined as a comparison between recreation levels at different sites at the same time. We

106 categorized the recreation disturbance as "novel" to the study system if it differed from the

107 baseline recreation level based on the authors' descriptions (e.g., an experimental hiking

108 treatment in a forest closed to recreation); otherwise, the disturbance was labeled

109 "ongoing." From external databases, we collected the average body mass, diet category, and

110 nesting behavior (for birds) of each species (Jones et al. 2009; Parr et al. 2014; Cornell Lab

111   of Ornithology 2018; Myers et al. 2018). We then extracted the means, standard deviations,

112   and sample sizes of species richness or abundance estimates at low and high recreation

113   levels from the text, supplemental materials, or figures using an online digitization tool

114   (Rohatgi 2017). We used data from the lowest taxonomic grouping available.

115   We pooled data to increase consistency among articles, including species richness

116   and abundance estimates from individual study sites or sampling seasons within each

117   article. When measurements were taken multiple times before or after a recreation

118   'treatment' (n=1 article), we used only the time points closest to the treatment to increase

119   similarity among comparisons. Likewise, when articles (n=2) tested three or more levels of

120   recreation (e.g., no, low, and high recreation sites), we used data from the lowest and

121   highest impact sites. Finally, we pooled estimates from population segments such as age

122   class or sex.

123

124   *Statistical methods*

125   For each comparison, we calculated hedges' g and its variance, a standardized

126   difference of means commonly used as an effect size in meta-analysis (Koricheva et al.

127   2013). We used means and standard deviations when available; otherwise we converted

128   test statistics such as chi-square or F-statistics to hedges' g. The units of g are standard

129   deviations separating the means of the low and high recreation groups. Negative values of g

130   indicate that vertebrate richness or abundance was greater with lower levels of recreation,

131   and positive values mean that richness or abundance was greater with higher levels of

132   recreation. We consider absolute values of $g \geq 0.8$ a large effect, 0.5 a moderate effect, and

133   0.2 a small effect (Cohen 1988). A hypothetical example in which a mean of 12 (SD=3)

134   species were observed at 10 sites with recreation and 14 (SD=3) species were observed at

135   10 sites without recreation would result in g=-0.64, a moderate negative effect. Confidence

136   intervals (95%) accompany all hedges' g values; if these do not include zero, we conclude

137   that the means of low and high recreation estimates are significantly different.

138   We built multi-level mixed-effects models (Nakagawa & Santos 2012) for richness

139   and abundance to calculate the pooled effect size across all included studies, using the R

140   package metafor (Viechtbauer 2010). In each model we included a random effect for article,

141   because some articles contributed multiple data points from the same location and

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142   investigator team, and for species since we expected effects of recreation to differ among

143   species. Effect sizes were weighted by inverse variances in all models (Koricheva et al.

144   2013). We did not separately model relative abundance measures (detections of animals or

145   sign; n=88) from estimates derived from mark-recapture analyses (n=6) or from complete

146   censuses of territories (n=4) because preliminary analysis showed little difference in

147   pooled effect sizes among these measures. We then built models to explore how effect size

148   varied with the following covariates: broad taxonomic group, recreation activity categories,

149   novel or ongoing disturbance, recreation disturbance type (spatial or temporal), body

150   mass, diet, and nesting location. We present hedges' g estimates for each level of

151   categorical covariates and regression coefficients ($\beta \pm SE$) for continuous covariates. To

152   assess publication bias, which occurs when studies with statistically significant results are

153   more likely to be published than those without (Nakagawa & Santos 2012), we visually

154   inspected funnel plots and used Egger's regression to examine correlations between effect

155   size and sampling variance (Egger et al. 1997). To assess our ability to detect effects of

156   varying magnitudes, we conducted a retrospective power analysis using the mean sample

157   sizes, effect sizes, and effect size variances from the included studies (Valentine et al. 2010).

158

159   **Results**

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161   Our inclusion criteria filtered the initial list of 2612 articles down to 34, yielding 20

162   species richness comparisons and 103 abundance comparisons (Tables S2, S3). Birds were

163   well-represented, with 45 comparisons (37% of 123 total) on 20 species from 15 articles

164   (44% of 34 total). There were a similar number of comparisons for fish (47, or 38% of

165   total) on more species (28), but from fewer articles (6, or 18% of total). Mammals had 27

166   comparisons (22% of total) on 16 species from 10 articles (29% of total). Reptiles were

167   poorly represented, with 4 comparisons (3% of total) on 3 species from 4 articles (12% of

168   total). There were no articles on amphibians included in the dataset. Across all

169   comparisons for which diet type could be specified, 70% measured responses of carnivores

170   or insectivores, 17% omnivores, and 13% herbivores. For bird comparisons for which

171   nesting behavior could be specified, 50% measured responses of tree-nesters, 42%

172   ground-nesters, and 8% shrub-nesters. Most comparisons assessed responses to terrestrial

173   (59%) or aquatic (38%) recreation activities, with few (2%) assessing responses to winter

174   recreation. Nearly all comparisons focused on non-motorized (97%) rather than motorized

175   (3%) recreation. Most comparisons were spatial (83%) rather than temporal (17%) and

176   investigated recreation disturbance that was not novel to the system (87%) rather than

177   novel (13%).

178   We found a moderate negative effect of recreation on vertebrate richness (hedges' g

179   [95% CI]=-0.58 [-1.01, -0.15]; Fig. 2a) and a small to moderate negative effect on

180   abundance (-0.45 [-0.72, -0.18]; Fig 2b). Retrospective power analysis showed that we

181   could detect a moderate effect on richness with power of 0.64 and on abundance with

182   power of 0.77. Egger's regressions were non-significant, suggesting little evidence of

183   publication bias (richness: z=-1.62, p=0.1; abundance: z=-0.73, p=0.47).

184

185   *Taxonomic differences and species traits*

186   Effect sizes were large and negative for bird (-0.89 [-1.5, -0.28]; Fig. 2a) and

187   mammal (-0.88 [-1.78, 0.01]) richness. Fish richness was similar at low and high recreation

188   levels (-0.02 [-0.69, 0.66]). Insufficient data precluded separate analyses of differences in

189   reptile richness. We observed a moderate negative effect of recreation on bird (-0.58 [-0.97,

190   -0.19]; Fig. 2b) and mammal (-0.74 [-1.22, -0.27]) abundance, but no differences in fish (0.1

191   [-0.48, 0.68]) or reptile (-0.18 [-1.11, 0.75]) abundance between recreation levels.

192   Bird body mass was positively related to hedges' g for abundance, meaning that small bird

193   abundance was more strongly reduced in association with high recreation than the

194   abundance of larger birds ($\beta \pm SE = 0.36 \pm 0.17, p$=0.04). There was no relationship

195   between mammal body mass and hedges' g for abundance ($\beta \pm SE = -0.08 \pm 0.09$,

196   p=0.41). We observed a moderate negative effect of recreation on carnivore (-0.67 [-1.01, -

197   0.33]) and herbivore (-0.72 [-1.21, -0.23]) abundance, while omnivore abundance (-0.07 [-

198   0.52, 0.38]; Fig. 3a) did not differ between high and low levels of recreation. The difference

199   in abundance was especially pronounced for carnivorous birds (-0.79 [-1.32, -0.26]) and

200   mammals (-0.84 [-1.39, -0.28]), whereas the confidence interval of every other combination

201   of diet and taxonomic group included zero. The abundance of ground-nesting birds was

202   lower when recreation was higher (moderate effect size of -0.64 [-1.21, -0.07]), whereas

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203 tree-nesting (-0.36 [-0.94, 0.21]) and shrub-nesting (-0.36 [-1.47, 0.75]) bird abundance

204 was reduced, but not significantly (Fig. 3b).

205

206 *Recreation types and timing*

207 We observed a large negative effect of terrestrial recreation on vertebrate richness

208 (-0.88 [-1.37, -0.4]) and a moderate negative effect on abundance (-0.61 [-0.91, -0.31]; Fig.

209 3c), but no effect of aquatic recreation (richness: -0.01 [-0.66, 0.64]; abundance: 0.1 [-0.46,

210 0.66]). We detected a small to moderate negative effect of non-motorized recreation on

211 vertebrate abundance (-0.46 [-0.75, -0.18]) whereas the effect of motorized recreation was

212 not significantly different from zero (-0.35 [-1.38, 0.67]; Fig. 3d). Studies of temporal

213 differences in recreation levels (richness: -1.08 [-2.06, -0.09]; abundance: -0.67 [-1.21, -

214 0.12]) reported larger negative effect sizes than did studies of spatial differences (richness:

215 -0.46 [-0.94, 0.01]; abundance: -0.38 [-0.71, -0.06]; Fig. 3e). Both vertebrate richness and

216 abundance were lower in association with novel disturbances (richness: -1.23 [-1.99, -

217 0.47]; abundance: -0.55 [-1.06, -0.04]) than with ongoing disturbances (richness: -0.48 [-

218 0.94, -0.01]; abundance: -0.43 [-0.73, -0.14]; Fig. 3f).

219

220

221 **Discussion**

222 Across many vertebrate species, species richness and abundance were lower in

223 association with higher levels of recreation. Differences in vertebrate richness and

224 abundance were approximately half a standard deviation between high and low recreation

225 levels. This means that in approximately 7 out of 10 comparisons, vertebrate richness or

226 abundance is expected to be lower with higher levels of recreation.

227 Despite substantial knowledge gaps and high variability in wildlife responses to

228 recreation, we identified some traits that may indicate sensitivity to recreation. Bird and

229 mammal richness and abundance were reduced in association with higher levels of

230 recreation whereas fish richness and abundance and reptile abundance were not. However,

231 the near-zero effect sizes for fish and reptiles may be due in part to differential responses

232 to ecotourism operations that involve supplemental feeding versus those that do not.

233 When analyzed separately, recreation involving feeding had a slight positive effect size for

234   fish abundance (0.09 [-0.31, 0.48]) and richness (0.19 [-0.78, 1.16]) whereas recreation

235   without feeding had a slight negative effect size for abundance (-0.11 [-0.46, 0.23]) and a

236   moderately strong negative effect size for richness (-0.67 [-2.25, 0.93]), though all the

237   estimates were imprecise. Just one study involved supplemental feeding of reptiles

238   (Iverson et al. 2006), but when abundance models were run excluding this study, the effect

239   size for reptile abundance was large and negative (-0.81 [-1.92, 0.30]). The change in effect

240   size when this comparison was removed also highlights how limited literature in certain

241   subgroups, such as reptiles, limits inference regarding recreation impacts.

242   Carnivore and herbivore abundances were reduced in high recreation areas more

243   often than omnivore abundance; this effect was even stronger for avian and mammalian

244   carnivores. Dietary and habitat generalists are known to be more human-tolerant than

245   specialists (Devictor et al. 2008) so it is logical that omnivores would be less sensitive;

246   however, we were not able to examine differences among species with narrow or broad

247   diets within these general categories. For birds, the abundance of small-bodied and

248   ground-nesting species was more frequently reduced with high recreation levels than the

249   abundance of larger-bodied and tree- and shrub-nesting species. This finding is consistent

250   with Samia et al. (2015), who found that smaller birds had reduced tolerance of people

251   compared to larger birds, perhaps because larger animals are more likely to become

252   tolerant to reduce costs associated with regular disturbance. However, our dataset did not

253   include studies on the abundance of raptors, some of which respond strongly to human

254   disturbance (Spaul & Heath 2016).

255   Impacts of recreation differed among types of recreational activities. Terrestrial

256   recreation had stronger effects on vertebrate richness and abundance than aquatic

257   recreation. Though just two studies in our analysis examined winter recreation, the authors

258   observed dramatically lower animal densities in areas with recreation (Seip et al. 2007;

259   Slauson et al. 2017). Further, our results imply that non-motorized activities can affect

260   vertebrate abundance just as strongly as motorized recreation, though the small sample

261   size for motorized activities (n=4 articles) suggests that this finding should be considered

262   preliminary. Previous research shows that non-motorized recreation may have more

263   frequent impacts on wildlife (Larson et al. 2016) and it can interact with motorized

264   recreation to facilitate increased disturbance by pedestrians (Spaul & Heath 2016).

265   Reductions in vertebrate abundance were greater for temporal than for spatial

266 comparisons. Long-term temporal comparisons (multiple years at each level of recreation,

267 n=3) had the greatest effect sizes, perhaps suggesting that repeated human disturbance can

268 have cumulative effects. However, novel disturbances had a stronger effect than ongoing

269 disturbances, suggesting that in some contexts, habituation to recreation may occur.

270 Findings from studies focused on habituation to recreation have been mixed, with some

271 finding evidence for habituation (e.g., Ellenberg et al. 2009; Baudains & Lloyd 2007) and

272 others finding little (e.g., Neumann et al. 2010; Constantine et al. 2004). The apparent

273 contradiction in our results echoes the variability of wildlife responses to recreation

274 documented in the literature; it is not yet clear under which circumstances (e.g., species,

275 landscape factors, intensity of recreational use) recreation effects accumulate or attenuate

276 over time and space, but there is some evidence that habituation potential depends on

277 body size, sex, and temperament of individual animals (e.g., boldness; Ellenberg et al. 2009;

278 Samia et al. 2015). Furthermore, very short temporary disturbances (≤ 1 day) are rarely

279 studied (n=2) despite the increasing popularity of adventure racing and other high-

280 intensity, short-term events inside protected areas (Newsome 2014).

281   The shape of the wildlife response curve as recreational use increases remains an

282 open question (Monz et al. 2013). Our low and high recreation categories spanned a wide

283 range of intensities and were relative within studies rather than absolute measures. The

284 large variation in how recreation levels were measured and reported meant we were

285 unable to reclassify and standardize levels across articles or satisfactorily categorize the

286 spatial scale of the recreation comparison. Future studies should provide clear empirical

287 estimates of recreation levels at all study locations to aid comparisons across studies and

288 allow identification of thresholds of recreational use at which effects become more severe.

289 Further, we encourage the publication of full results for all species and population

290 segments measured in the study, including those with non-significant results, to help assess

291 sensitivity within and among animal taxa.

292   Our findings show that recreation has an overall negative effect on vertebrate

293 species richness and abundance. Despite variability in animal responses to recreation and

294 remaining knowledge gaps, we believe our findings underline the importance of managing

295 recreation on conservation lands. The trade-offs between recreation and conservation pose

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296   a problem for conservation organizations and natural resource managers, given

297   participation in outdoor recreation has been linked to interest in conservation easements

298   (Farmer et al. 2016), financial contributions to conservation organizations (Zaradic et al.

299   2009), and pro-conservation behaviors (Cooper et al. 2015). Funding sources for land

300   acquisition (e.g., the U.S. Land and Water Conservation Fund) often mandate public access,

301   limiting managers' ability to restrict recreation for conservation objectives. While publicly-

302   owned protected areas are the cornerstone of global conservation efforts, an estimated

303   94% of them are open to recreation (Eagles et al. 2002; IUCN & UNEP 2014). This includes

304   the strictest IUCN categories (1a and 1b), which allow "non-intrusive" recreation (Dudley

305   2008), although the types and intensities of recreation considered to be non-intrusive is

306   not specified.

307   Despite the need to manage recreation, management agencies rarely have enough

308   resources to adequately monitor recreational use given considerable spatial and temporal

309   variability in visitation (Cessford & Muhar 2003; Larson et al. 2018). Thus, even if

310   researchers had a clear understanding of threshold levels of recreational use that result in

311   negative outcomes for wildlife, managers may struggle to ascertain where or when

312   recreational limits are exceeded. Public opposition to trail closures, caps on daily visitation,

313   or reservation systems can be strong and could damage the support for conservation

314   agencies and organizations. Therefore, we believe that the best option to minimize trade-

315   offs between recreation and species conservation is to maintain some areas that are closed

316   to recreation. If planning for recreational access is done at the regional level, managers

317   could ensure that protected area networks include some areas that are closed to

318   recreation, balancing the dual land uses of conservation and recreation at the scale of the

319   protected area network instead of each individual protected area.

320

321   **Acknowledgements and Data**

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Figure legends

Table 1. Covariates extracted from the included studies

Figure 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.
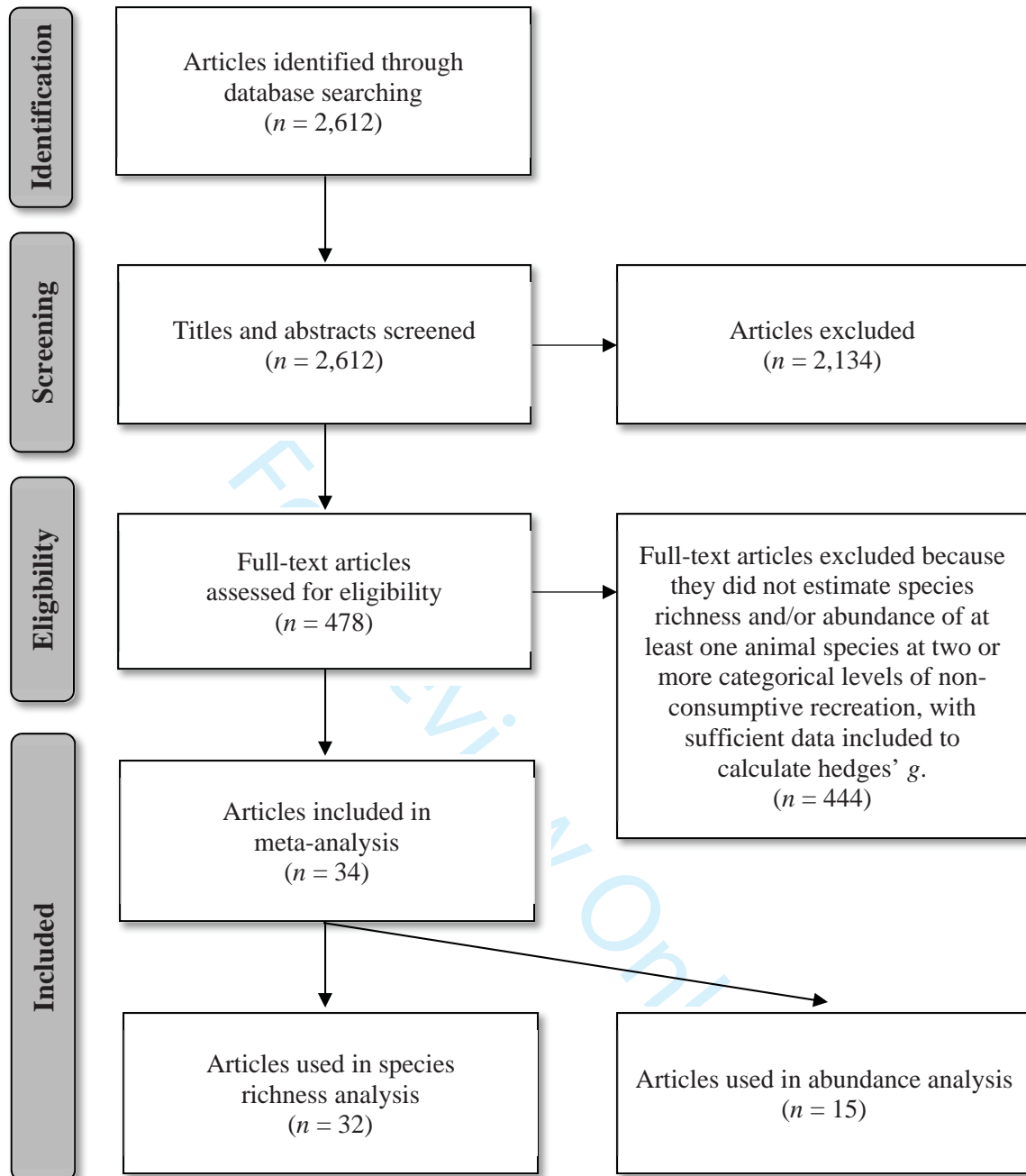
Figure 2. Effect sizes comparing differences in a) species richness and b) abundance between low-recreation and high-recreation groups, broken down into broad taxonomic groups. The dot size is proportional to the sample size in each sub-group (the size of the diamond is not meaningful for the 'all vertebrates' group). Error bars show 95% confidence intervals.
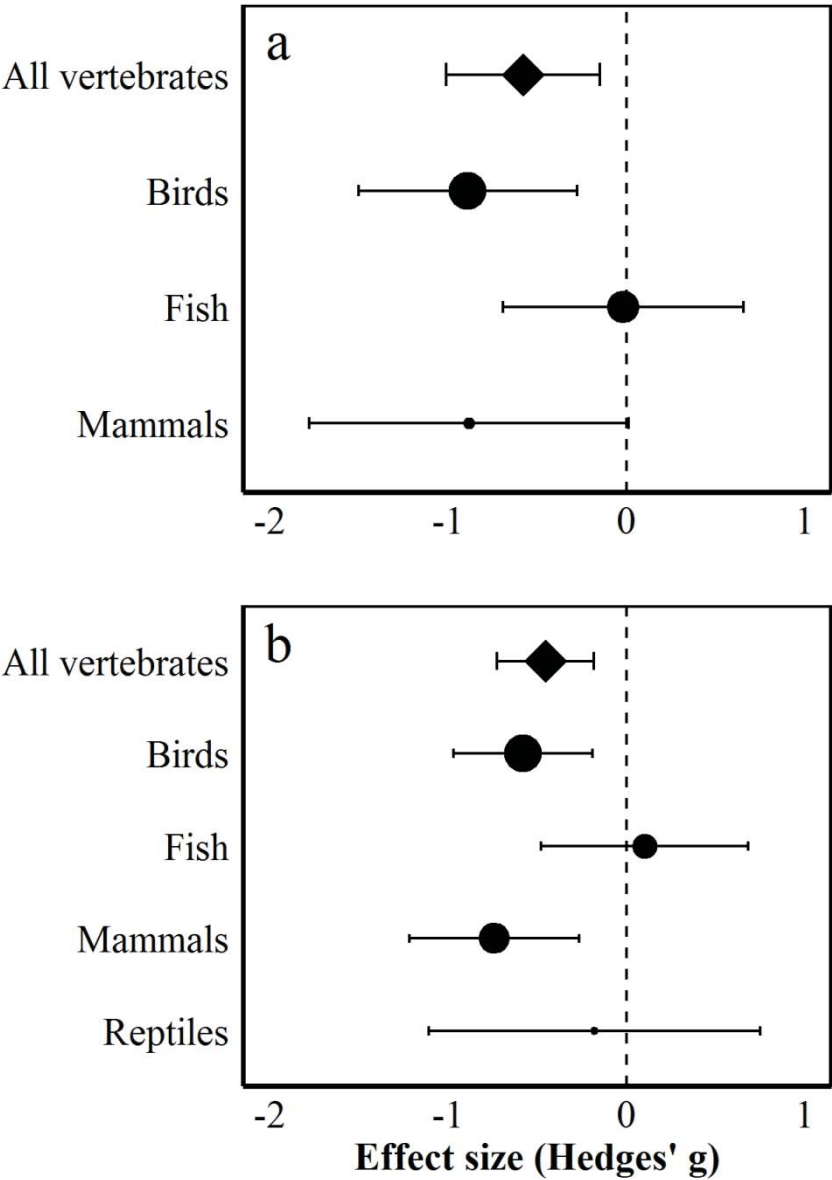
Figure 3. Effect sizes comparing differences in abundance between low-recreation and high-recreation groups, broken down by a) diet type, b) nesting behavior (bird data only), c) aquatic or terrestrial recreation activities, d) motorized or non-motorized activities, e) spatial or temporal comparison 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.

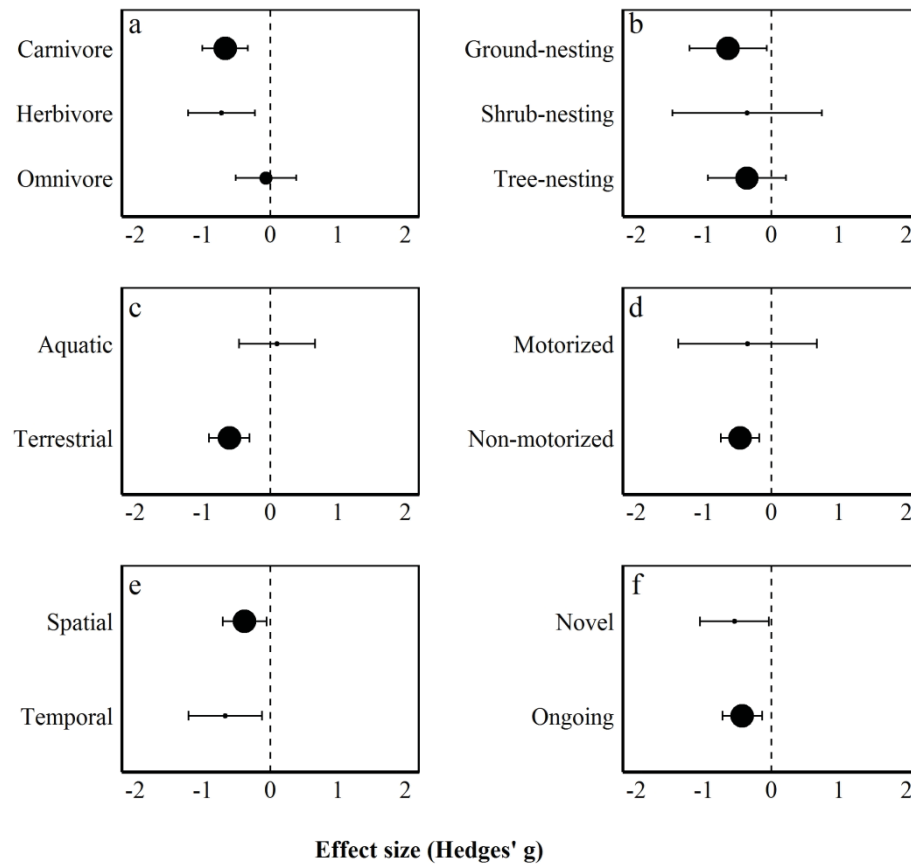Table 1. Covariates extracted from the included studies

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)
Diet[a]	Carnivore, omnivore, herbivore
Nesting behavior[a]	Ground-nesting, shrub-nesting, tree-nesting

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

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.

114x152mm (300 x 300 DPI)

Effect sizes comparing differences in abundance between low-recreation and high-recreation 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.

203x177mm (300 x 300 DPI)