Landscape and Urban Planning 175 (2018) 62–71

Contents lists available at ScienceDirect

Landscape and Urban Planning

journal homepage: www.elsevier.com/locate/landurbplan

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

ARTICLE INFO

Keywords:
Recreation
Protected areas
Visitation
Disturbance
Species exposure

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

* Corresponding author.
E-mail addresses: courtney.larson@colostate.edu (C.L. Larson), sreed@wcs.org (S.E. Reed), adinam@berkeley.edu (A.M. Merenlender), kevin.crooks@colostate.edu (K.R. Crooks).

https://doi.org/10.1016/j.landurbplan.2018.03.009
Received 10 May 2017; Received in revised form 9 March 2018; Accepted 12 March 2018
Available online 26 March 2018
0169-2046/

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: 10 min. travel time	69,704 ± 83,669	46,484 ± 51,132	SanGIS parcel data, Orange County parcel data, Riverside County parcel data, 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% 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.

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 *Spea hammondii*	**0.026 ± 0.009**	**0.008**	**0.132**
Orange-throated whiptail *Aspidoscelis hyperythra*	**0.133 ± 0.032**	**< 0.001**	**0.275**
Red diamond rattlesnake *Crotalus ruber*	0.007 ± 0.007	0.301	0.002
Two-striped gartersnake *Thamnophis hammondii*	0.011 ± 0.007	0.145	0.027
Coastal California gnatcatcher *Polioptila californica californica*	**0.091 ± 0.031**	**0.005**	**0.147**
Less exposed species and subspecies (negative relationships)			
Blainville's horned lizard *Phrynosoma blainvillii*	−0.023 ± 0.021	0.286	0.004
Bell's sage sparrow *Amphispiza belli belli*	**−0.076 ± 0.030**	**0.015**	**0.109**

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

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 ($r = 0.650$,

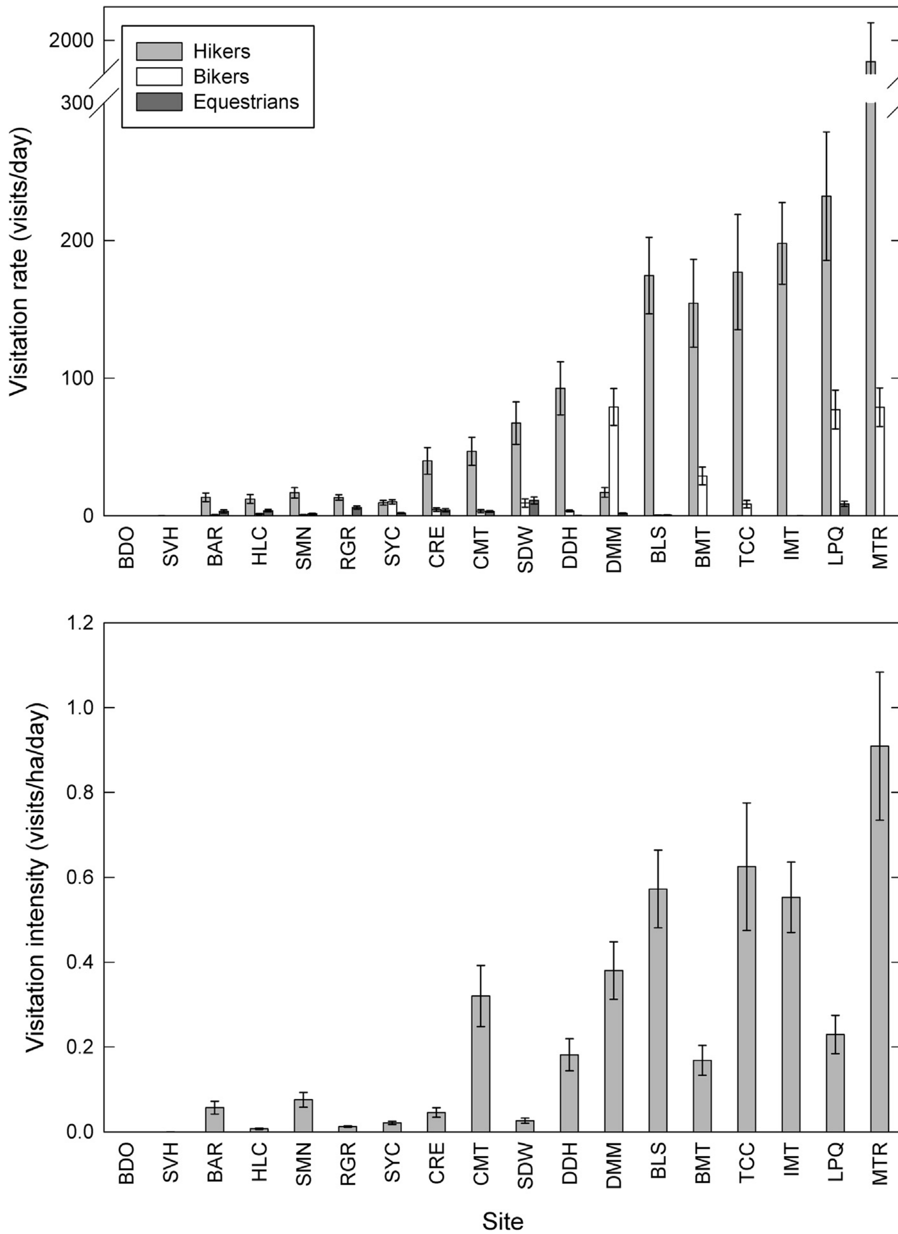

Fig. 1. Estimates of the level of recreational activity derived from empirical field data at the 18 sampled reserves. Panel a) shows estimated visitation rates (visits/day) for hikers, bicyclists, and equestrians, and b) shows estimated visitation intensity (visits/ha/day) for all recreational activities. 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 ± 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 ± 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 ± SD: 11.6 ± 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 ± 0.7%) in the hiker model, while the number of entrances had little importance (0.2 ± 1.0%). In the bicyclist model, housing units within 30 minutes had the highest importance (10.0 ± 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 ± 0.7%), whereas the number of parking lots was not (0.8 ± 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

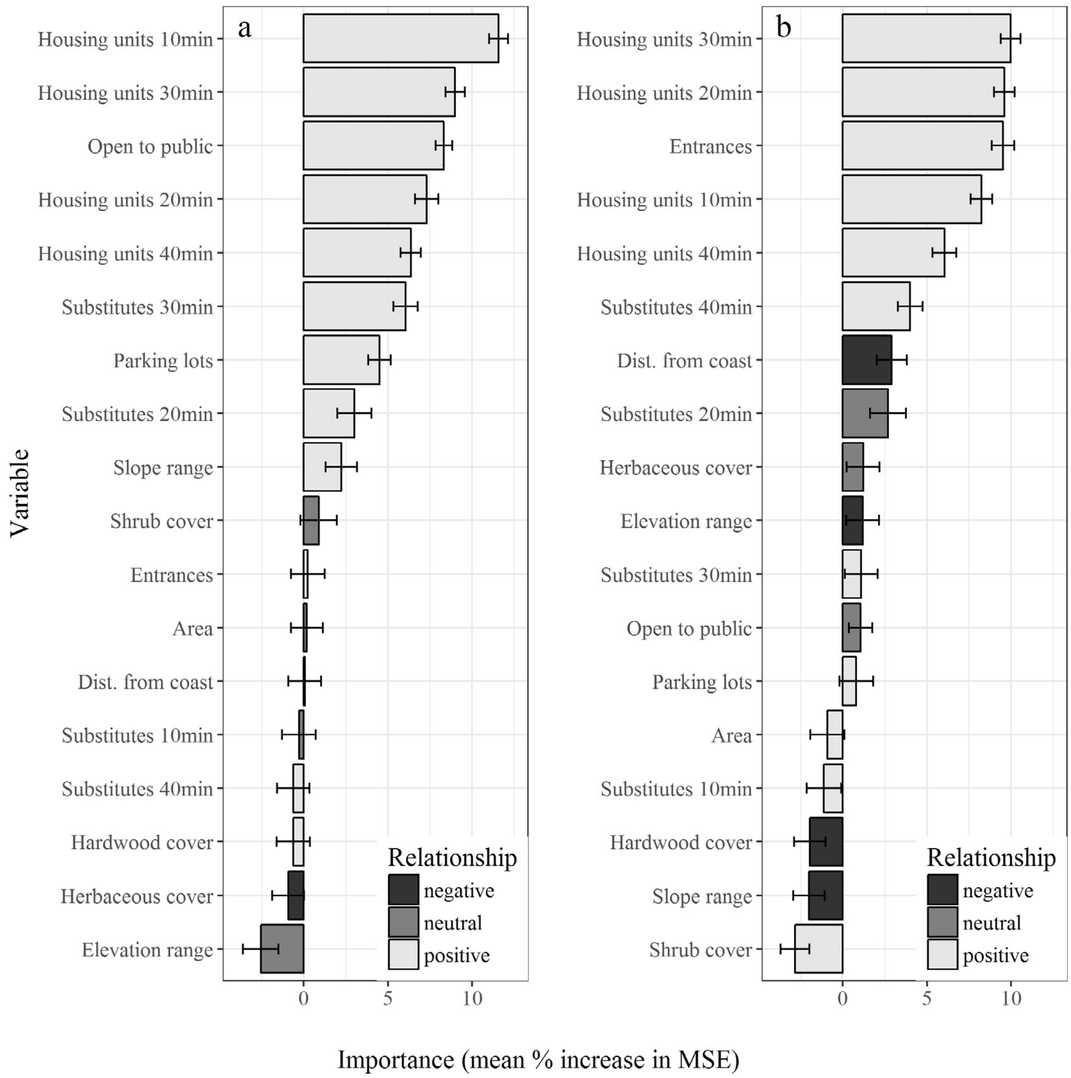

Fig. 2. Mean variable importance for a) hikers and b) bicyclists. A high value indicates that a variable is important to the random forest regression model because when this variable is randomly permuted, there is a relatively large change in the mean squared error (MSE) across all trees. A negative 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*; $\beta \pm SE = 0.026 \pm 0.009$, $p = 0.008$, $R^2 = 0.132$), orange-throated whiptail (*Aspidoscelis hyperythra*; $\beta \pm SE = 0.133 \pm 0.032$, $p < 0.001$, $R^2 = 0.275$), and coastal California gnatcatcher ($\beta \pm SE = 0.091 \pm 0.031$, $p = 0.005$, $R^2 = 0.147$). 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 ($\beta \pm SE = -0.076 \pm 0.030$, $p = 0.015$, $R^2 = 0.109$; 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

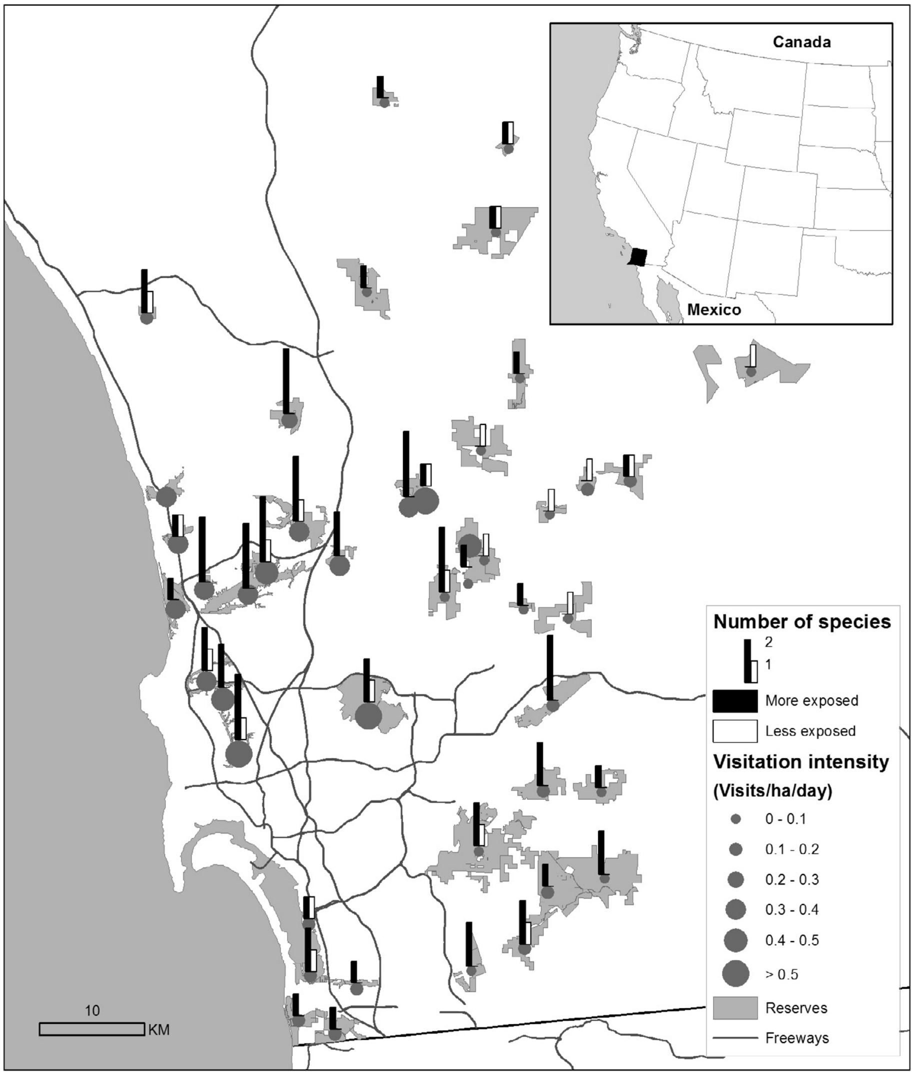

Fig. 3. Number of MSCP-listed species and subspecies that are likely to occur (i.e., have a predicted probability of presence at or above the median value for the reserve network) at each reserve. Only species with a statistically significant ($p \le 0.05$) linear relationship between predicted probability 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

This work was funded by the California Department of Fish and Wildlife (Local Assistance Grant P1182112). We thank R. Rempel, Y. Moore, and E. Perkins (San Diego Management and Monitoring Program) for their assistance during the project, and R. Fisher, J. Tracey, and K. Preston (U.S. Geological Survey) and J. Franklin (Arizona State University) for sharing the species models used in our analyses. Many rangers and reserve managers assisted with fieldwork logistics and responded to our expert opinion survey, for which we are grateful. The survey was deemed exempt by the Colorado State University Research Integrity & Compliance Review Office (IRB ID: 070-14H). A. Bontrager (Wildlife Conservation Society) digitized recreational trails, and A. Hess (Colorado State University) provided helpful statistical advice.

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.

References

Arlettaz, R., Patthey, P., Baltic, M., Leu, T., Schaub, M., Palme, R., et al. (2007). Spreading free-riding snow sports represent a novel serious threat for wildlife. *Proceedings of the Royal Society B: Biological Sciences, 274*, 1219–1224.

Arnberger, A., Haider, W., & Brandenburg, C. (2005). Evaluating visitor-monitoring techniques: a comparison of counting and video observation data. *Environmental Management, 36*, 317–327.

Balmford, A., Green, J. M. H., Anderson, M., Beresford, J., Huang, C., Naidoo, R., et al. (2015). Walk on the wild side: Estimating the global magnitude of visits to protected areas. *PLOS Biology, 13*, e1002074.

Barros, A., Monz, C., & Pickering, C. (2014). Is tourism damaging ecosystems in the Andes? Current knowledge and an agenda for future research. *AMBIO*, 1–17.

Beale, C. M., & Monaghan, P. (2005). Modeling the effects of limiting the number of visitors on failure rates of seabird nests. *Conservation Biology, 19*, 2015–2019.

Becken, S., & Job, H. (2014). Protected areas in an era of global-local change. *Journal of Sustainable Tourism, 22*, 507–527.

Beeco, J. A., Hallo, J. C., & Brownlee, M. T. J. (2014). GPS visitor tracking and recreation suitability mapping: Tools for understanding and managing visitor use. *Landscape and Urban Planning, 127*, 136–145.

Bergstrom, J. C., & Cordell, H. K. (1991). An analysis of the demand for and value of outdoor recreation in the United States. *Journal of Leisure Research, 23*, 67.

Boll, T., von Haaren, C., & von Ruschkowski, E. (2014). The preference and actual use of different types of rural recreation areas by Urban Dwellers—The Hamburg case study. *PLoS ONE, 9*, e108638.

Braunisch, V., Patthey, P., & Arlettaz, R. (2011). Spatially explicit modeling of conflict zones between wildlife and snow sports: prioritizing areas for winter refuges. *Ecological Applications, 21*, 955–967.

Breiman, L. (2001). Random forests. *Machine Learning, 45*, 5–32.

CA Department of Fish and Game (2012). Summary of Natural Community Conservation Plans (NCCPs).

Cessford, G., & Muhar, A. (2003). Monitoring options for visitor numbers in national parks and natural areas. *Journal for Nature Conservation, 11*, 240–250.

Chan, K. M. A., Guerry, A. D., Balvanera, P., Klain, S., Satterfield, T., Basurto, X., et al. (2012). Where are cultural and social in ecosystem services? A framework for constructive engagement. *BioScience, 62*, 744–756.

Cisneros-Montemayor, A. M., & Sumaila, U. R. (2010). A global estimate of benefits from ecosystem-based marine recreation: Potential impacts and implications for management. *Journal of Bioeconomics, 12*, 245–268.

Cordell, H.K. (2012). Outdoor recreation trends and futures. U.S. Department of Agriculture Forest Service, Southern Research Station, Asheville, NC, USA.

R Core Team (2015). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Crain, B. J., & White, J. W. (2013). A checklist and floristic summary of the vascular plants of Napa County, California. *Phytotaxa, 95*, 1–60.

Cutler, D. R., Edwards, T. C., Beard, K. H., Cutler, A., Hess, K. T., Gibson, J., et al. (2007). Random forests for classification in ecology. *Ecology, 88*, 2783–2792.

De Valck, J., Broekx, S., Liekens, I., De Nocker, L., Van Orshoven, J., & Vranken, L. (2016). Contrasting collective preferences for outdoor recreation and substitutability of nature areas using hot spot mapping. *Landscape and Urban Planning, 151*, 64–78.

Degenhardt, B., Frick, J., Buchecker, M., & Gutscher, H. (2011). Influences of personal, social, and environmental factors on workday use frequency of the nearby outdoor recreation areas by working people. *Leisure Science, 33*, 420–440.

Dobson, A. P., Rodriguez, J. P., Roberts, W. M., & Wilcove, D. S. (1997). Geographic distribution of endangered species in the United States. *Science, 275*, 550–553.

Eagles, P.F.J., McCool, Stephen F, Haynes, C.D. (2002). United Nations Environment Programme, World Tourism Organization, International Union for Conservation of Nature and Natural Resources. Sustainable tourism in protected areas: guidelines for planning and management. IUCN–the World Conservation Union, Gland, Switzerland.

Ekkel, E. D., & de Vries, S. (2017). Nearby green space and human health: Evaluating accessibility metrics. *Landscape and Urban Planning, 157*, 214–220.

Ficetola, G. F., Sacchi, R., Scali, S., Gentilli, A., De Bernardi, F., & Galeotti, P. (2007). Vertebrates respond differently to human disturbance: Implications for the use of a focal species approach. *Acta Oecologica, 31*, 109–118.

Finney, S. K., Pearce-Higgins, J. W., & Yalden, D. W. (2005). The effect of recreational disturbance on an upland breeding bird, the golden plover Pluvialis apricaria. *Biological Conservation, 121*, 53–63.

Fisher, R., Stokes, D., Rochester, C.J., Brehme, C.S., Hathaway, S.A., Case, T.J. (2008). Herpetological monitoring using a pitfall trapping design in Southern California (No. 2–A5), Techniques and Methods. U.S. Geological Survey, Reston, VA.

Franklin, J., Wejnert, K. E., Hathaway, S. A., Rochester, C. J., & Fisher, R. N. (2009). Effect of species rarity on the accuracy of species distribution models for reptiles and amphibians in southern California. *Diversity and Distributions, 15*, 167–177.

George, S. L., & Crooks, K. R. (2006). Recreation and large mammal activity in an urban nature reserve. *Biological Conservation, 133*, 107–117.

Gutzwiller, K. J., Riffell, S. K., & Anderson, S. H. (2002). Repeated human intrusion and the potential for nest predation by gray jays. *The Journal of Wildlife Management, 66*(2), 372–380.

Hadwen, W. L., Hill, W., & Pickering, C. M. (2007). Icons under threat: Why monitoring visitors and their ecological impacts in protected areas matters. *Ecological Management and Restoration, 8*, 177–181.

Hill, G. W., & Courtney, P. R. (2006). Demand analysis projections for recreational visits to countryside woodlands in Great Britain. *Forestry, 79*(2), 185–200.

Hochachka, W. M., Caruana, R., Fink, D., Munson, A., Riedewald, M., Sorokina, D., et al. (2007). Data-mining discovery of pattern and process in ecological systems. *The Journal of Wildlife Management, 71*, 2427–2437.

Ikuta, L. A., & Blumstein, D. T. (2003). Do fences protect birds from human disturbance? *Biological Conservation, 112*(3), 447–452.

IUCN UNEP (2014). *The world database on protected areas (WDPA)*. Cambridge, UK: UNEP-WCMC.

Kangas, K., Luoto, M., Ihantola, A., Tomppo, E., & Siikamäki, P. (2010). Recreation-induced changes in boreal bird communities in protected areas. *Ecological Applications, 20*(6), 1775–1786.

Kerbiriou, C., Le Viol, I., Robert, A., Porcher, E., Gourmelon, F., & Julliard, R. (2009). Tourism in protected areas can threaten wild populations: From individual response to population viability of the chough *Pyrrhocorax pyrrhocorax*. *Journal of Applied Ecology, 46*, 657–665.

Knudby, A., Brenning, A., & LeDrew, E. (2010). New approaches to modelling fish–habitat relationships. *Ecological Modelling, 221*, 503–511.

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

Liaw, A., & Wiener, M. (2002). Classification and regression by randomForest. *R News, 2*, 18–22.

Mallord, J. W., Dolman, P. M., Brown, A. F., & Sutherland, W. J. (2007). Linking recreational disturbance to population size in a ground-nesting passerine. *Journal of Applied Ecology, 44*(1), 185–195.

Malo, J., Acebes, P., & Traba, J. (2011). Measuring ungulate tolerance to human with flight distance: A reliable visitor management tool? *Biodiversity and Conservation, 20*, 3477–3488.

McClaran, M.P., Cole, D.N. (1993). Packstock in wilderness: use, impacts, monitoring, and management. US Department of Agriculture, Forest Service, Intermountain Research Station.

Meijles, E. W., de Bakker, M., Groote, P. D., & Barske, R. (2014). Analysing hiker movement patterns using GPS data: Implications for park management. *Computers, Environment and Urban Systems, 47*(Supplement C), 44–57.

Monz, C. A., Cole, D. N., Leung, Y.-F., & Marion, J. L. (2010). Sustaining visitor use in protected areas: Future opportunities in recreation ecology research based on the USA experience. *Environmental Management, 45*, 551–562.

Monz, C. A., Pickering, C. M., & Hadwen, W. L. (2013). Recent advances in recreation ecology and the implications of different relationships between recreation use and ecological impacts. *Frontiers in Ecology and the Environment, 11*, 441–446.

MSCP Policy Committee, & MSCP Working Group (1998). Final Multiple Species Conservation Program Plan. San Diego, CA. Retrieved from http://www.sandiegocounty.gov/content/dam/sdc/pds/mscp/docs/SCMSCP/FinalMSCPProgramPlan.pdf.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature, 403*, 853–858.

Neuvonen, M., Pouta, E., Puustinen, J., & Sievänen, T. (2010). Visits to national parks: Effects of park characteristics and spatial demand. *Journal for Nature Conservation, 18*, 224–229.

Ode, Å., & Fry, G. (2006). A model for quantifying and predicting urban pressure on woodland. *Landscape and Urban Planning, 77*, 17–27.

Pettebone, D., Newman, P., & Lawson, S. R. (2010). Estimating visitor use at attraction sites and trailheads in Yosemite National Park using automated visitor counters. *Landscape and Urban Planning, 97*, 229–238.

Preston, K. L., Rotenberry, J. T., Redak, R. A., & Allen, M. F. (2008). Habitat shifts of endangered species under altered climate conditions: Importance of biotic interactions. *Global Change Biology, 14*, 2501–2515.

Reed, S. E., & Merenlender, A. M. (2008). Quiet, nonconsumptive recreation reduces protected area effectiveness. *Conservation Letters, 1*, 146–154.

Rösner, S., Mussard-Forster, E., Lorenc, T., & Müller, J. (2014). Recreation shapes a “landscape of fear” for a threatened forest bird species in Central Europe. *Landscape Ecology, 29*, 55–66.

Rotenberry, J. T., Preston, K. L., & Knick, S. T. (2006). GIS-based niche modeling for mapping species' habitat. *Ecology, 87*, 1458–1464.

San Diego Association of Governments (2010). 2050 regional growth forecast. San Diego, California.

SanGIS and SANDAG (2016). SanGIS/SANDAG Data Warehouse. http://sandag.org.

Sato, C. F., Wood, J. T., & Lindenmayer, D. B. (2013). The effects of winter recreation on alpine and subalpine fauna: A systematic review and meta-analysis. *PLoS ONE, 8*, e64282.

Shanahan, D. F., Lin, B. B., Gaston, K. J., Bush, R., & Fuller, R. A. (2015). What is the role of trees and remnant vegetation in attracting people to urban parks? *Landscape Ecology, 30*, 153–165.

Siderelis, C., Moore, R. L., & Lee, J.-H. (2011). A mixed logit model of visitors' national park choices. *Society and Natural Resources, 24*, 799–813.

Siikamäki, P., Kangas, K., Paasivaara, A., & Schroderus, S. (2015). Biodiversity attracts visitors to national parks. *Biodiversity and Conservation, 24*(10), 2521–2534.

Steven, R., & Castley, J. G. (2013). Tourism as a threat to critically endangered and endangered birds: Global patterns and trends in conservation hotspots. *Biodiversity Conservation, 22*, 1063–1082.

Storch, I., & Leidenberger, C. (2003). Tourism, mountain huts and distribution of corvids in the Bavarian Alps, Germany. *Wildlife Biology, 9*(4), 301–308.

Taczanowska, K., González, L.-M., Garcia-Massó, X., Muhar, A., Brandenburg, C., et al. (2014). Evaluating the structure and use of hiking trails in recreational areas using a mixed GPS tracking and graph theory approach. *Applied Geography, 55*(Supplement C), 184–192.

Termansen, M., McClean, C. J., & Jensen, F. S. (2013). Modelling and mapping spatial heterogeneity in forest recreation services. *Ecological Economics, 92*, 48–57.

Termansen, M., McClean, C. J., & Skov-Petersen, H. (2004). Recreational site choice modelling using high-resolution spatial data. *Environment and Planning A: Economy and Space, 36*, 1085–1099.

Termansen, M., Zandersen, M., & McClean, C. J. (2008). Spatial substitution patterns in forest recreation. *Regional Science and Urban Economics, 38*, 81–97.

Theobald, D. M., Norman, J. B., & Newman, P. (2010). Estimating visitor use of protected areas by modeling accessibility: A case study in Rocky Mountain National Park, Colorado. *Journal of Conservation Planning, 6*, 1–20.

Thiel, D., Menoni, E., Brenot, J.-F., & Jenni, L. (2007). Effects of recreation and hunting on flushing distance of capercaillie. *Journal of Wildlife Management, 71*(6), 1784–1792.

Thompson, B. (2015). Recreational trails reduce the density of Ground-Dwelling Birds in protected areas. *Environmental Management, 55*(5), 1181–1190.

U.S. Census Bureau (1970). Census of Housing: Housing Characteristics for States, Cities, and Counties. https://www.census.gov/prod/www/decennial.html.

U.S. Census Bureau (2014). TIGER/line Shapefiles. https://www.census.gov/geo/maps-data/data/tiger-line.html.

U.S. Census Bureau (2015). 2011-2015 American Community Survey 5-Year Estimates: Selected Housing Characteristics. http://factfinder.census.gov.

U.S. Census Bureau (2016). 2012-2016 American Community Survey 5-Year Estimates: Total Population. http://factfinder.census.gov.

U.S. Fish and Wildlife Service, National Marine Fisheries Service (1996). Habitat conservation planning and incidental take permit processing handbook. U.S. Department of the Interior, U.S. Department of Commerce, Washington, D.C.

van der Zee, D. (1990). The complex relationship between landscape and recreation. *Landscape Ecology, 4*, 225–236.

Wade, A. A., & Theobald, D. M. (2010). Residential development encroachment on U.S. protected areas. *Conservation Biology, 24*, 151–161.

Wilmers, C. C., Wang, Y., Nickel, B., Houghtaling, P., Shakeri, Y., Allen, M. L., et al. (2013). Scale dependent behavioral responses to human development by a large predator, the puma. *PLoS ONE, 8*, e60590.