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Spatial and temporal response of wildlife to recreational activities in the San Francisco Bay ecoregion

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ABSTRACT

Non-motorized human recreation may displace animals from otherwise suitable habitat; in addition, animals may alter their activity patterns to reduce (or increase) interactions with recreationists. We investigated how hiking, mountain biking, equestrians, and recreationists with domestic dogs affected habitat use and diel activity patterns of ten species of medium and large-sized mammals in the San Francisco Bay ecoregion. We used camera traps to quantify habitat use and activity patterns of wild mammals and human recreationists at 241 locations in 87 protected areas. We modeled habitat use with a multi-species occupancy model. Species habitat use was most closely associated with environmental covariates such as landcover, precipitation, and elevation. Although recreation had less influence on habitat use, the presence of domestic dogs was negatively associated with habitat use of mountain lions and Virginia opossum. We also compared diel activity patterns of species at sites with no observed recreation to the activity patterns of species at sites with high (≥eight per day) levels of non-motorized recreation. Coyotes were more active at night and less active during the day in areas with high levels of recreation. Striped skunks were slightly more active later into the morning in areas that allowed human recreation. Smaller carnivores with nocturnal activity patterns may not be directly affected by recreational activities that are limited to daylight hours. We suggest that by maintaining habitat free of domestic dogs, and creating trail-free buffers, land managers can manage recreation in a way that minimizes impacts to wildlife habitat and preserves the value of protected areas to people and wildlife.

1. Introduction

Managers of many parks and protected areas seek to protect natural resources while simultaneously providing opportunities for non-motorized recreation. Non-motorized recreation by humans, and associated domestic animals such as dogs and horses, can impact wildlife by disrupting normal maintenance routines (Sime, 1999; Lenth et al., 2008), reducing feeding times (Cassirer et al., 1992), displacing them from suitable habitat (Papouchis et al., 2001; Lenth et al., 2008), increasing adrenal stress hormones (Barja et al., 2007), and provoking flight responses (Taylor and Knight, 2003). Wildlife species can respond by avoiding (sensitive species) or seeking areas of human activity (human-associated species) (Frid and Dill, 2002; Tigas et al., 2002; Reed and Merenlender, 2008). In coastal southern California, Ordeñana et al. (2010) found coyote (*Canis latrans*) and raccoon (*Procyon lotor*) occurrences increased, and bobcat (*Lynx rufus*), grey fox (*Urocyon cinereoargenteus*), and mountain lion (*Puma concolor*) occurrences decreased, with both proximity to and intensity of urbanization. Bighorn sheep (*Ovis canadensis*) avoid habitat with human activity in Canyonlands National Park, Utah (Papouchis et al., 2001) and the development of an extensive trail network used by many hikers and domestic dogs is thought to be the major factor in the extirpation of desert bighorn sheep from the Santa Catalina Mountains, Arizona (Krausman et al., 1995a,b).

In addition to altering habitat use and wildlife abundance, human activities can also change animal activity patterns. For example, artificial night lighting altered the activity patterns of wallabies in a way that disrupted the population's breeding synchrony (Robert et al., 2015). However, remarkably little research has attempted to document whether non-motorized human recreation alters animal activity patterns (but see Wang et al., 2015).

Because of its 7.5 million human residents (U.S. Census Bureau 2014), 4800 km^2 (1.2 million acres) of open space (BAOSC, 2011), and diversity of protected area management agendas, the San Francisco Bay Area is an ideal laboratory to study impacts of non-motorized recreation on wildlife. In one such study of recreation impacts in Bay Area oak woodlands, coyote and bobcat scat densities were more than five times lower in 14 Bay Area protected areas that permitted non-motorized

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recreation than in 14 paired protected areas that did not (Reed and Merenlender, 2008). However, use of carnivore scats as a proxy for carnivore population size is problematic because domestic dogs accompanying human recreationists can consume and disturb scat of bobcats and coyotes, decreasing detection probabilities and likely lead to underestimation of carnivore populations.

Camera traps are an efficient tool for detecting medium and large-sized terrestrial mammals (Tobler et al., 2008) and have been widely used to study their occupancy and habitat use (e.g. Linkie et al., 2007; Tobler et al., 2009; Ahumada et al., 2013). Camera traps were three times more likely to detect coyote, striped skunk, cottontail, and raccoon than hair traps or track plates in a coastal ecosystem (O'Connell et al., 2006) and we believe that they provide better estimates of recreational activity and habitat use by a broad array of medium to large-sized mammals in our study area compared to other methods. We used camera traps to estimate numbers and activity patterns of ten mammal species (mule deer, mountain lions, coyote, bobcat, raccoon, grey fox, opossum, striped skunk, rabbit, feral pigs) and hikers, cyclists, equestrians, and recreationists with dogs in eight counties of the SF Bay Area. Based on results from previous studies, we expected species' response to human recreation to vary by species and type of recreation (Crooks, 2002; Wang et al., 2015; Wilmers et al., 2013).

Land managers face pressure to create trails and accommodate more users (Dolton-Thorton, 2015; M. Savidge, Golden Gate National Recreation Area, pers. comm., April 21, 2015). The goal of our study was to provide land managers with information that can help them manage recreation in a way that minimizes impacts to wildlife habitat and preserves the value of protected areas to people and wildlife. Results could also assist in the planning and management of wildlife corridors. Our specific objectives were to 1) quantify how non-motorized recreation (hiking, cycling, horse-riding, and dog-walking) affects occupancy for ten species of mammals (accounting for environmental variables), 2) determine if non-motorized recreation is associated with shifts in activities patterns of wildlife, and 3) describe temporal patterns of non-motorized recreation in protected areas in the San Francisco Bay area.

2. Methods

2.1. Study area

This study was carried out in the San Francisco Bay Area (Fig. 1). This region has a Mediterranean climate with numerous microclimates (NOAA, 1995). Cool marine air and persistent coastal fog keep temperatures along the coast 10–21 °C year-round (National Oceanic and Atmospheric Association, 1995). Inland temperatures can reach 32 °C. The Bay Area is part of the California Floristic Province and a biodiversity hotspot (Bay Area Open Space Council, BAOSC, 2011). Our study area includes diverse plant communities. We studied wildlife and recreation in the Bay Area's four dominant woodland types (Bay Area Open Space Council, BAOSC, 2011), namely redwood forests, Douglas-fir forests, montane hardwood forests, oak savannas and woodlands.

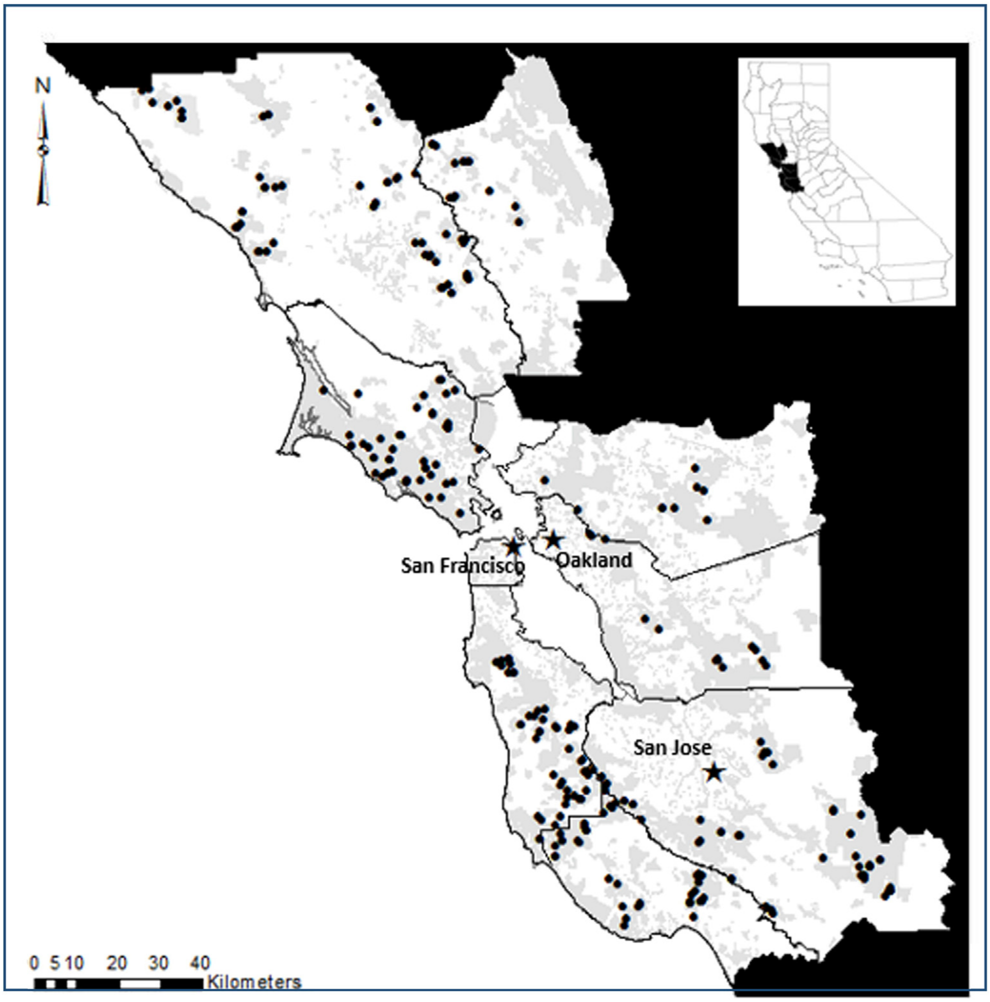

Fig. 1. Study area in the San Francisco Bay Area, including sites in Marin, Sonoma, Napa, Alameda, Contra Costa, Santa Clara, Santa Cruz, and San Mateo Counties. Location of sites sampled from 2011 to 2013 is denoted by black points. Grey shading in the background indicates protected areas designated in the California Protected Areas Database.

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2.2. Location of study sites

We sampled a total of 241 study sites in 87 parcels owned by government, non-profit, and private entities and protected as open-space, including small and large urban parks, national forests, private ecological preserves, and lands owned by land trusts, water districts, universities, and public utilities (California Protected Area Database (CPAD) version 1.7). Many of these protected areas receive high levels of human visitation, while several are closed to the public and others allow only docent-led tours or limit recreation opportunities to those who attend a certification course. We considered only parcels with at least a 240 × 240-m area mapped as woodlands in the Bay Area Open Space Council and Conservation Lands Network Bay Area Protected Areas database (Bay Area Open Space Council, BAOSC, 2011) in order to accommodate our study site design.

We obtained GIS shapefiles of trails from the State of California Geoportal (Cal Atlas, 2011), local and regional land management offices, and nonprofit agencies. We randomly generated potential study site locations along trails in protected areas using ArcGIS 10.0 (ESRI, 2010). Random site generation was not stratified by covariates but was restricted so that no sites would be located within 350 m of another site. In an attempt to control for potential differences in water availability throughout the field season, sites could not be located within 350 m of a body of water or waterway.

2.3. Field data collection

A study site consisted of two 30-m radius circular plots (Supplementary material Fig. S1a), one on-trail and one 120 m from the trail, with two cameras per plot (Fig. S1b); the plot size and camera orientation minimized overlap between the fields of view. We use Reconyx HC600 camera traps (Reconyx Inc., Holmen, WI) that use a no-glow infrared technology, which reduces disturbance to wildlife and makes the unit less conspicuous to humans. Each time a camera was triggered, it took a burst of three photos, 1 s apart with no delay between consecutive bursts. The trigger speed of 1/5 s maximizes the probability that an animal, or fast moving cyclist, will be photographed before moving out of the field of view.

Camera traps were deployed during May to August of 2012, 2013, and 2014, for 15 days at each site. Because few species in our survey area are considered rare and most are large-bodied, we assumed detection probabilities would be high enough to estimate occupancy using a 15-day sampling period, thus allowing us to sample more sites than would have been possible with a longer sampling period.

Cameras were placed on trees approximately 20 cm above ground level with the field of view parallel to the ground. Cameras were placed inside security boxes and locked to the tree with steel cables. Placards on the camera alerted people of the CodeLoc® antitheft system and provided additional study and contact information. We recorded each camera location with a GPS. We stored all photos and data in Camera Base 1.6 (Tobler, 2012).

2.4. Site covariates

We characterized each site by woodland type, proximity to urban edge, trail density within one kilometer of the on-trail plot center, road density within two kilometers of the on-trail plot center, size of the protected area, annual precipitation, July maximum temperature, January minimum temperature, and elevation. We included these covariates in our occupancy model to enhance our ability to separate the influence of recreation from potentially confounding variables that may affect wildlife habitat use and distribution (Zipkin et al., 2010). An explanation of how these covariates were quantified is included in the Supplementary material (Supplement S-2).

We defined an occurrence of a hiker, equestrian, or cyclist as a photo captured at least 20 s (5 s for a cyclist) after a previous photo of the same type of individual on either of the two cameras in the on-trail plot at a site (no recreationists were detected on the off-trail plots). We counted the number of recreationists engaged in each of three types of recreation and calculated the average number per day that a camera was functional at that site. For sites that had dog activity, dog abundance was highly correlated with hiker abundance (Supplement S-3), and we therefore only included a binary variable indicating whether dogs were present at a site or not.

2.5. Occupancy modeling

Occupancy models describe the probability Ψ that a species is present at a site while accounting for the fact that detection probabilities are often smaller than one (MacKenzie et al., 2002). They incorporate covariates that can affect occupancy and detection probability. We used a multi-species variation of the Royle-Nichols (RN) occupancy model (Royle and Nichols, 2003, Yamaura et al., 2012, Tobler et al., 2015) to analyze how recreation (hikers, cyclists, equestrians, and domestic dogs) and environmental covariates (elevation, temperature, precipitation, trail density, woodland type, size of protected area, distance to urban edge, and road density) affect occupancy and habitat use of each species.

We chose the RN model over a standard occupancy model because camera trap data often exhibit a high level of heterogeneity in the detection history and the RN model generally performs better under those circumstances (Tobler et al., 2015). We use the model only to cope with heterogeneity in the detection history (Royle and Nichols, 2003) and do not perform any inference on the estimated abundances.

We briefly describe our model, which closely follows the extensive literature on occupancy models in wildlife research (MacKenzie et al., 2006; Karanth et al., 2009; Mordecai et al., 2011; Royle and Dorazio, 2008; Tobler et al., 2015).

Instead of modeling the observed occurrence z_{ijk} of each species i at each site j and camera k, the multi-species RN model models the species' unobserved site abundances (a_{ij}) using a Poisson distribution with an expected value of λ_{ij}, that is a_{ij}~*Poisson* (λ_{ij}). The probability that site is occupied (Ψ_{ij}) is calculated as:

$$\Psi_{ij} = \Pr(a_{ij}>0) = 1 - exp(-\lambda_{ij})$$

The expected abundances (λ_{ij}) are related to the site covariates via a log-link linear form:

$$\begin{gathered}\log(\lambda_{ij}) = \mathbf{X}_j\beta_i \\ = \beta_{i0} + \beta_{i,Habitat(j)} + X_{j,Hiker}\beta_{i,Hiker} + X_{j,Dogs}\beta_{i,Dogs} + X_{j,Cyclists}\beta_{i,Cyclists} \\ + X_{j,Equestrian}\beta_{i,Equestrian} + X_{j,DistToUrban}\beta_{i,DistToUrban} + X_{j,Size}\beta_{i,Size} \\ + X_{j,RoadDensity}\beta_{i,RoadDensity} + X_{j,TrailDensity}\beta_{i,TrailDensity} \\ + X_{j,Elevation}\beta_{i,Elevation} + X^2_{j,Elevation}\beta_{i,Elevation2} \\ + X_{j,JanTemp}\beta_{i,JanTemp} + X_{j,JulyTemp}\beta_{i,JulyTemp}\end{gathered}$$

where X terms denote observed standardized covariate data at site j and the β terms denote the regression parameters. To improve parameter estimates for species with few detections we modeled all regression parameters as random effects across species (Zipkin et al., 2010) by using a hierarchical method. The species level terms (generically indexed by *) are modeled

$$\beta_{i,*} \sim N(\mu_*, \sigma^2_*)$$

where

$$\mu_* \sim N(0, 1000) \text{ and } \sigma^2_* \sim Uniform(0, 10).$$

We standardized all covariates by subtracting the mean and dividing by the standard deviation. Standardizing the covariates leads to better model convergence and facilitates interpretation of coefficients because

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effects can be directly compared. Pairwise correlations (Supplementary Table S-3) between recreation covariates were low ($r < 0.10$, except $r = 0.18$ between hikers and equestrians), and all variance inflection factors were ≤1.7, indicating a low level of collinearity (Supplementary Table S-4).

The observed detections are assumed to be a function of the unobserved abundance term based on the assumption of independent detections among all a_{ij} individuals at the site. Letting r_{ijk} be the detection probability of an individual of species i at site j and plot k, the probability of detecting at least one individual, on a given day, for a given plot, is $\pi_{ijk} = 1 - (1 - r_{ijk})^{a_{ij}}$. Finally the daily detections are modeled as $z_{ijk} \sim Binomial(n_{jk},\ \pi_{ijk})$ where n_{jk} is the number of days that camera jk were operational at each plot. We allow the detection probabilities to vary if the plot was on or off trail: $\text{logit}(r_{ijk}) = \gamma_0 + \gamma_{TrailType(jk)}$.

We modeled the individual species detection probabilities r_{ijk} independently for each of the two plots at a site but assumed that occupancy Ψ_{ij} was the same for both plots as they were only 120 m apart.

While sampling occurred over three years, the majority of sites were only sampled once. Of the sites that were sampled multiple times, we saw little evidence of year effects (either local extinctions or colonizations). When year was included in the model, it was non-significant and did not affect model inferences.

We implemented the model in a Bayesian framework utilizing JAGS (Plummer, 2003) via the R2Jags (Su and Yajima, 2015) package in Program R. The model ran with three parallel chains with a length of 50,000 after a burn-in of 30,000 iterations and a thinning rate of 20. We assessed convergence by visually inspecting the chains and by examining the R-hat values for each parameter estimate.

2.6. Diel activity patterns

For diel activity pattern analysis, we defined a 'high' level of recreation as an average of more than eight recreationists per day, which corresponds to a natural break in recreationists per day in our data. Previous studies of the influence of recreation on mammal activity patterns considered four and two recreationists per day as a high level of use (George and Crooks, 2006; Wang et al., 2015, respectively). Our results did not differ substantially when we used a threshold of 20 recreationists per day. Areas categorized as no recreation (29 sites total) were sites that had zero photographs of humans during the 15-day sampling period. We defined an event of a wildlife species as a photo taken by a camera at least 1 h after any previous photo of the same species at either plot camera (Bowkett et al., 2007).

We used kernel density estimates in the package 'overlap' (Meredith and Ridout, 2014) in Program R (R Core Development Team) to compare temporal activity patterns in areas with no and high recreation. By considering capture times as random variables from a continuous circular distribution we can use kernel density estimation to create a probability density function for the two populations we wanted to compare. These density functions ($f()$ and $g()$), are interpreted as the activity patterns for the two populations and the coefficient of overlap (Δ) (Linkie and Ridout, 2011) describes the concordance between the two. The coefficient of overlap (Δ) can be interpreted as the integrated difference in estimated density functions for two distributions and thus ranges from zero (no overlap) to one (complete overlap) (Ridout and Linkie, 2009). For each species, we calculated the coefficient of overlap between activity patterns in areas with no recreation and areas of high recreation. We calculated $\hat{\Delta}_1$ (see Supplement S-5 for alternative measures) which is recommended for small sample sizes (Ridout and Linkie, 2009). $\hat{\Delta}_1$ is the integral of the minimum and is defined as

$$\hat{\Delta}_1 = \int_0^1 min\{\hat{f}(t), \hat{g}(t)\}dt$$

To test if species change their activity patterns in response to recreational activities, we examined how active species were during times recreationists are typically active. First, we calculated the overlap between each species' activity pattern at sites with high recreational activities and the observed activity pattern of recreationists from all sites combined. We then did the same for sites with no recreational activity, again comparing each species' activity pattern to the typical activity pattern of recreationists across sites. If animals respond negatively to recreational activities, they move their activities away form times when recreationists are active and we expect less overlap for sites with recreation (Fig. 3).

To determine if the activity patterns of species differed between areas with recreation and without recreation, we performed permutation tests with 10,000 replicates. Permutation datasets were generated by randomly shuffling the recreation level labels and then we calculated the difference of coefficients of overlap with the recreationists. The reported p-value is the percent of simulated differences of larger magnitude than what was actually observed.

To determine if the activity patterns of species and recreation types differed between weekdays and weekends, we performed permutation tests to test if an overlap was significantly different from what is expected under the null hypothesis of no difference between the groups. One thousand permuted datasets were created by randomly shuffling the group labels and then calculating the coefficient of overlap. The α-quantile of this permutation distribution is the threshold for an α-level hypothesis test (with values of $\hat{\Delta}_1$ smaller than the α-quantile being statistically significant).

3. Results

We detected 15 native and 3 non-native species of mammals (Table 1) from 9099 independent images in 20,574 trap days over three field seasons. Over 95% of the camera placements functioned for the full 15 days. Because we could not reliably distinguish between photographs of brush rabbits (*Sylvilagus bachmani*) and desert cottontails (*Sylvilagus audubonii*), we treated them as a combined *Sylvilagus* spp. group for analysis. Coyote, bobcat, striped skunk, grey fox, and mule deer were detected at >47% of the sites (Table 1). Raccoon, mountain lion, Virginia opossum, *Sylvilagus* spp., and feral pig were detected at 13–38% of sites. American badger, ringtail, spotted skunk, black bear, red fox, river otter, and black-tailed jackrabbits were detected at ≤7% of sites.

Across 284 samples (Fig. 1) we detected on average over the 15-day session 25 hikers (range: 0–456), two dogs (range: 0–25), one equestrian (range: 0–28), and two cyclists (range: 0–263) per day at a site (Supplement S-6). About 150 sites had fewer than five hikers per day on average; 39 of these sites were in reserves closed to public use. Over 99% of detections of hikers and cyclists occurred between sunrise and 60 min after sunset. Mean group size of both hikers and cyclists was two. All but one of the detections of dogs were on trails and 100% of dog detections occurred within 5 min of a hiker. We had only five detections of house cats and thus, did not include house cats in analysis.

3.1. Associations between mammal habitat use and recreation

We analyzed the effects of recreation on the ten species that were detected at ≥30 sites (Table 1). For each of these species, detection probabilities on-trail were 1.5 to 7 times higher than off-trail (Table 1).

There were only two significant associations between recreation and species occupancy (Table 2). Mountain lions and Virginia opossum were both negatively associated with presence of domestic dogs. Hikers, cyclists, and equestrians were not significantly negatively or positively associated with habitat use of any of the ten species in our analysis.

3.2. Associations between mammal habitat use and other covariates

Each of the ten environmental variables (temperature (January min), precipitation, elevation, elevation squared, landcover type, distance to urban edge, size of the protected area, road density, and trail density) were significantly associated with habitat use of at least one

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Table 1
Number of detections and individual detection probabilities for 18 species of mammals in the San Francisco Bay area.

Species	No. of surveys detected (% of 284 surveys)	Number of detections		Detection probability (r)	
		Off trail	On trail	Off trail	On trail
American badger *Taxidea taxus*	6 (2.1%)	1	5	*	*
Black bear *Ursus americanus*	10 (3.5%)	5	18	*	*
Black-tailed jackrabbit *Lepus californicus*	20 (7.0%)	6	67	*	*
Bobcat *Lynx rufus*	224 (78.9%)	90	777	0.009	0.061
Coyote *Canis latrans*	135 (47.5%)	62	428	0.014	0.082
Grey fox *Urocyon cinereoargenteus*	211 (74.3%)	204	1568	0.023	0.166
Mountain lion *Puma concolor*	64 (22.5%)	12	80	0.004	0.024
Mule deer *Odocoileus hemionus*	264 (92.3%)	953	1436	0.068	0.098
Raccoon *Procyon lotor*	103 (36.3%)	92	268	0.024	0.059
Red fox *Vulpes vulpes*	1 (0.4%)	0	1	*	*
Ringtail *Bassariscus astutus*	1 (0.4%)	0	1	*	*
River otter *Lontra canadensis*	1 (0.4%)	0	1	*	*
Striped skunk *Mephitis mephitis*	162 (57.0%)	169	411	0.03	0.066
Sylvilagus spp. *Sylvilagus* spp.	37 (13.0%)	52	75	0.059	0.093
Virginia opossum *Didelphis virginiana*	70 (24.6%)	63	145	0.033	0.069
Western spotted skunk *Spilogale gracilis*	3 (1.0%)	1	3	*	*
Feral pig *Sus scrofa*	33 (11.6%)	23	68	0.021	0.060
Mean				0.029	0.078

All species except red fox, Virginia opossum, and feral pig are native to the study area.

* Indicates detection probability was not calculated and the species was not included in multi-species model.

species; landcover type and elevation (Table 3) were significantly associated with the largest numbers of species. Coyotes, mule deer, raccoon, *Sylvilagus* spp., and opossums were all negatively associated with elevation. Bobcat, *Sylvilagus* spp., and feral pig were negatively associated with annual precipitation while grey fox was positively associated with precipitation. For coyotes and mule deer there was a significant difference in occupancy probability for multiple landcover types. Bobcat, striped skunk, and feral pigs showed a preference for oak woodlands while raccoons tended to avoid redwoods.

Road density (a proxy for human population density) was negatively associated with habitat use of grey foxes (Table 3). Size of the protected area was negatively associated with habitat use of striped skunks and

Table 2
Mean β estimates (and 95% credible intervals) from the multi-species model.

	No. of sites	Hikers	Bikers	Domestic dogs	Equestrians
Bobcat	224	0.009 (−0.087, 0.086)	−0.036 (−0.138, 0.03)	−0.156 (−0.381, 0.066)	0.075 (−0.02, 0.167)
Coyote	135	0.027 (−0.07, 0.122)	−0.015 (−0.105, 0.07)	0.19 (−0.113, 0.502)	0.026 (−0.076, 0.132)
Grey fox	211	0.043 (−0.039, 0.132)	−0.048 (−0.19, 0.031)	0.092 (−0.123, 0.311)	−0.037 (−0.14, 0.042)
Mountain lion	64	−0.037 (−0.363, 0.097)	−0.003 (−0.097, 0.114)	−0.893* (−1.526, −0.342)	−0.023 (−0.196, 0.113)
Mule deer	264	0.009 (−0.056, 0.067)	−0.025 (−0.091, 0.028)	0.017 (−0.151, 0.191)	−0.034 (−0.13, 0.045)
Raccoon	103	0.04 (−0.043, 0.132)	−0.047 (−0.212, 0.042)	0.318 (−0.035, 0.675)	−0.034 (−0.16, 0.058)
Striped skunk	162	−0.002 (−0.157, 0.097)	−0.019 (−0.103, 0.063)	−0.131 (−0.408, 0.156)	−0.03 (−0.183, 0.08)
Sylvilagus spp.	37	0.015 (−0.157, 0.149)	−0.034 (−0.203, 0.074)	−0.076 (−0.605, 0.458)	0.001 (−0.149, 0.152)
Virginia opossum	70	0.091 (−0.017, 0.245)	−0.01 (−0.108, 0.097)	−0.701* (−1.15, −0.263)	−0.03 (−0.211, 0.103)
Feral pig	33	−0.041 (−0.447, 0.109)	−0.037 (−0.194, 0.066)	−0.163 (−0.758, 0.403)	−0.048 (−0.282, 0.104)

* Indicates that the 95% credible interval for β did not overlap zero.

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Table 3
β estimates (and 95% credible intervals) from the multi-species model.

	No. of sites	Trail density	Road density	Annual precip	Jan min temp	July max temp	Distance to urban	Elevation	Elevation^2	Size of protected area
Bobcat *Lynx rufus*	122	0.001 (−0.098, 0.11)	−0.05 (−0.15, 0.06)	−0.154* (−0.35, −0.10)	0.064 (−0.02, 0.20)	0.027 (−0.09, 0.15)	−0.112 (−0.22, 0.01)	0.036 (−0.07, 0.20)	−0.019 (−0.10, 0.05)	0.085 (−0.03, 0.20)
Coyote *Canis latrans*	192	−0.045 (−0.17, 0.08)	0.02 (−0.11, 0.16)	−0.13 (−0.30, 0.04)	0.04 (−0.08, 0.16)	0.015 (−0.10, 0.14)	−0.069 (−0.24, 0.07)	−0.21* (−0.39, −0.01)	0.009 (−0.09, 0.099)	0.188* (0.03, 0.34)
Gray fox *Urocyon cinereoargenteus*	184	−0.093 (−0.21, 0.004)	−0.127* (−0.26, −0.003)	0.265 (0.15, 0.37)	0.041 (−0.08, 0.14)	−0.027 (−0.15, 0.07)	0.024 (−0.08, 0.13)	0.093 (−0.05, 0.23)	0.074 (−0.003, 0.16)	0.274* (0.16, 0.38)
Mountain lion *Puma concolor*	86	−0.076 (−0.26, 0.07)	−0.053 (−0.28, 0.14)	−0.216* (−0.48, 0.01)	0.074 (−0.06, 0.22)	−0.045 (−0.26, 0.09)	−0.006 (−0.18, 0.18)	0.152 (−0.12, 0.44)	−0.015 (−0.16, 0.09)	−0.165 (−0.44, 0.10)
Mule deer *Odocoileus hemionus*	225	0.01 (−0.07, 0.09)	0.065 (−0.02, 0.15)	−0.056 (−0.15, 0.04)	0.103* (0.01, 0.21)	0.006 (−0.08, 0.099)	−0.094 (−0.21, 0.005)	−0.149* (−0.26, −0.04)	0.028 (−0.04, 0.095)	−0.058 (−0.15, 0.03)
Raccoon *Procyon lotor*	92	0.049 (−0.09, 0.24)	0.024 (−0.09, 0.15)	0.115 (−0.08, 0.30)	0.092 (−0.02, 0.25)	−0.023 (−0.18, 0.1)	−0.048 (−0.22, 0.11)	−0.782* (−1.03, −0.54)	0.023 (−0.098, 0.15)	0.364* (0.22, 0.51)
Striped skunk *Mephitis mephitis*	150	−0.115 (−0.26, 0.005)	0.065 (−0.06, 0.21)	−0.074 (−0.23, 0.08)	0.04 (−0.10, 0.15)	0.034 (−0.07, 0.17)	−0.012 (−0.14, 0.12)	0.061 (−0.10, 0.23)	−0.013 (−0.12, 0.70)	−0.261* (−0.44, −0.10)
Sylvilagus spp.	36	−0.07 (−0.28, 0.096)	−0.025 (−0.23, 0.16)	−0.364* (−0.72, −0.05)	0.041 (−0.15, 0.18)	−0.042 (−0.28, 0.09)	−0.015 (−0.22, 0.21)	−0.398* (−0.75, −0.07)	−0.049 (−0.26, 0.08)	0.15 (−0.12, 0.43)
Virginia opossum *Didelphis virginiana*	58	−0.055 (−0.21, 0.09)	−0.061 (−0.25, 0.11)	−0.132 (−0.38, 0.09)	0.088 (−0.04, 0.25)	0 (−0.15, 0.15)	−0.05 (−0.24, 0.12)	−0.545* (−0.83, −0.26)	−0.036 (−0.22, 0.09)	−0.512 (−0.84, −0.23)
Wild pig *Sus scrofa*	31	−0.064 (−0.28, 0.11)	−0.148 (−0.52, 0.07)	−0.372* (−0.73, −0.06)	0.063 (−0.1, 0.22)	0.085 (−0.06, 0.44)	0.105 (−0.09, 0.43)	0.268 (−0.08, 0.66)	−0.056 (−0.25, 0.06)	−0.081 (−0.42, 0.24)

* Indicates that the credible interval for β did not overlap zero.

Virginia opossums and positively associated with habitat use of coyotes, grey fox, and raccoons.

3.3. Activity patterns

The diel activity of non-motorized recreation differed between weekdays and weekends with a higher peak density of all recreation types on the weekends (Fig. 2). On weekends, there were about 48% more recreationists per day than on weekdays. All types of recreation peaked at midday, but there was a smaller early evening peak for cyclists, hikers, and dog walkers during weekdays. We found no significant difference in activity patterns of mammals on weekends compared to weekdays in areas with human recreation.

Coyotes and mule deer in areas of high recreation were less active during the day and more active at night compared to areas with no recreation (Fig. 3). Striped skunk in areas that allowed recreation was

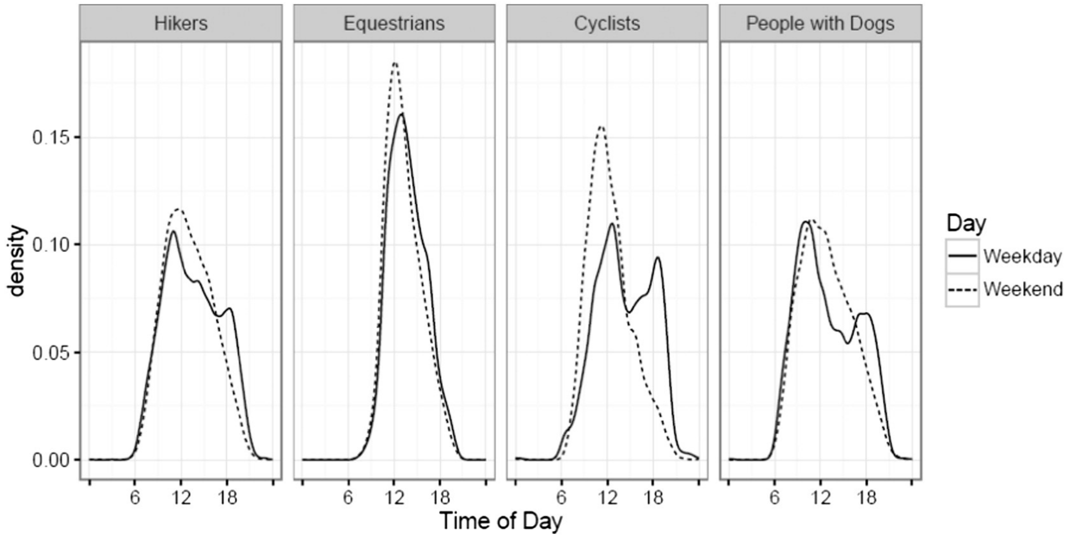

Fig. 2. Weekend (dotted) and weekday (solid) activity patterns of hikers ($n = 4815$ weekday and 5593 weekend observations, coefficient of overlap, $\hat{\Delta}_1 = 0.74$), equestrians ($n = 1219$ weekday and 897 weekend observations, coefficient of overlap, $\hat{\Delta}_1 = 0.91$), cyclists ($n = 27{,}433$ weekday and 22,821 weekend observations, coefficient of overlap, $\hat{\Delta}_1 = 0.89$), and recreationists with domestic dogs ($n = 3656$ weekday and 2705 weekend observations, coefficient of overlap, $\hat{\Delta}_1 = 0.88$). All $\hat{\Delta}_1$ indicated significantly different patterns between weekdays and weekends ($P < 0.001$).

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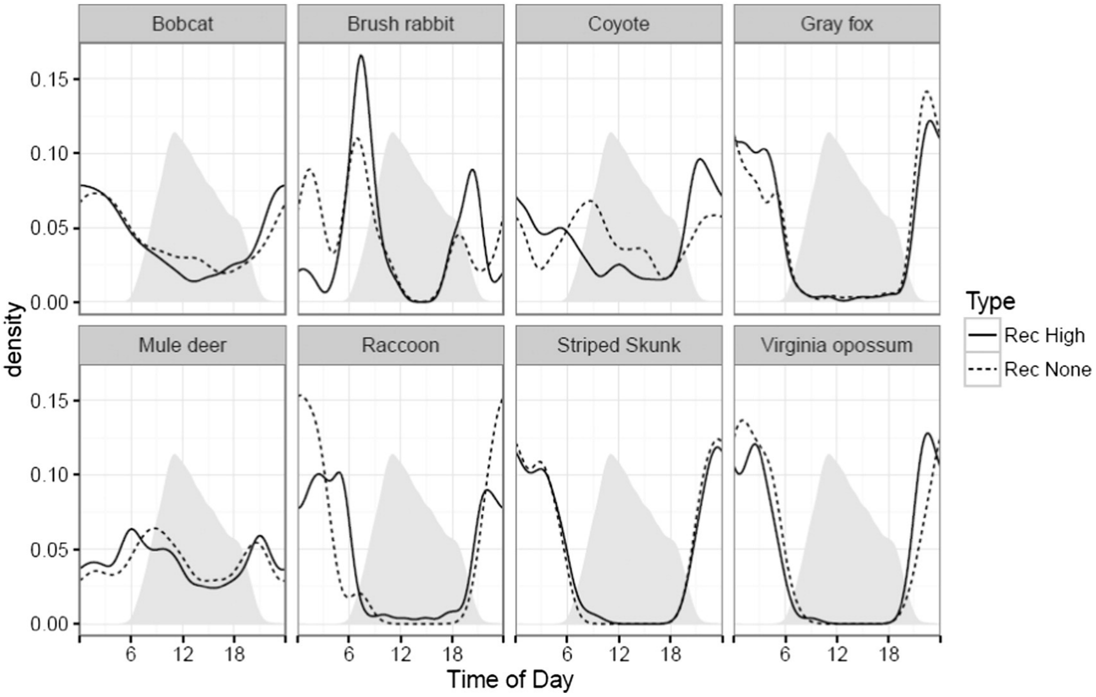

Fig. 3. Activity patterns of eight species and recreationists in areas with high recreation (solid line), the activity patterns of species and recreationist in areas with no recreation (dotted line), and the activity patterns of recreationists (grey shading). The activity pattern of coyotes in areas with high levels of recreation differed from the activity patterns of coyotes in areas with no recreation (significant *p*-value; bootstrap CI did not overlap). Coyotes in areas with high levels of recreation were less active throughout the day and more active at night than coyotes in areas with no recreation. The activity patterns of mountain lions and feral pigs is not shown due to small sample size as indicated in the text.

slightly more active in the morning than striped skunk in area without recreation (Fig. 3). None of the other species showed a significant change in activity patterns.

4. Discussion

We observed only two significant associations between recreation and wildlife habitat use, namely that presence of domestic dogs was negatively associated with mountain lions and Virginia opossums (Table 2). The negative association was stronger for mountain lions (β: −0.893). Of the 87 protected areas sampled, 34 permitted dogs on all trails, 20 permitted dogs on some trails, and 26 prohibited dogs. Thus, domestic dogs were allowed on 63% of the area we sampled; they were detected at 59% (141 of 241) of our sites. Mountain lions are often considered elusive (Busch, 2004), and avoid human-dominated landscapes (Dickson and Beier, 2002) and human-modified vegetation types and paved roads (Dickson et al., 2005). Our data suggest mountain lions may also avoid protected areas that allow domestic dog use.

Strikingly, there was no negative association between recreation and habitat use by bobcats and coyotes, the two species for which Reed and Merenlender (2008, 2011) documented strong negative responses in the same study area. Reed and Merenlender (2008) used scat detections as an index of species densities; this index may have violated the fundamental assumption that detection probabilities (when the species is present) are constant across sites (Harmsen et al., 2010). Domestic dogs were regularly detected in areas that allowed human recreation (Reed and Merenlender, 2008), and they often consume and disturb scat of other carnivores (Mackay et al., 2008), decreasing detection of scat without necessarily decreasing abundance of the wild carnivores.

Our occupancy model provides estimates of detection and habitat use for all species and allows for the inclusion of site-level and species-specific covariates. Failure to incorporate imperfect detection in logistic regression models will lead to biased estimates of habitat relationships (Tyre et al., 2003, Gu and Swihart, 2003). Although occupancy models are a useful metric for comparing landscape-scale trends between sites, potential limitations exist. The short duration of the surveys used to estimate detection probabilities may not provide reliable estimate for wide-ranging species such as mountain lions; mountain lions may be undetected at highly suitable sites. Additionally, animals face competing demands that influence behavior and ultimately fitness (Beyers et al., 2010). Occupancy—or as interpreted in our analysis, habitat use—does not provide complete information on the value of that habitat. Occupancy may fail to differentiate between habitat at locations that are actively selected for and those that are used incidentally (Beyers et al., 2010).

Because occupancy is only one indicator of animal response to recreation, we also examined if animal activity patterns differed between areas with or without recreation. In our study, coyotes shifted their activity away from daylight hours and toward crepuscular or nighttime hours (Fig. 3) in high recreation areas. In our spatial analysis, coyotes did not avoid sites as recreational use increased; they responded by temporal rather than spatial shifts in habitat use. This is consistent with results from similar research on carnivore activity patterns in the Santa Cruz Mountains (Wang et al., 2015) and with other research that found shifts in diel activity patterns of wild canid species in the presence of humans (Kitchen et al., 2000; McClennen et al., 2001; Rasmussen and Macdonald, 2012). Near Los Angeles California, coyotes are able to persist in urban fragments by shifting activity patterns to avoid human contact (Tigas et al., 2002). Shifts in diel activity to avoid recreation may result in less time available for foraging and breeding and an increase in encounters with competitors (Rasmussen and Macdonald, 2012). High levels of human activity in the Santa Cruz Mountains, CA, increased the temporal overlap between several species of native carnivores potentially increasing interspecific competition (Wang et al., 2015). Future research should investigate potential differences in fitness and population persistence due to temporal or spatial avoidance of non-motorized recreation as well as other consequences associated with shifts in temporal activity patterns among species.

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Mule deer showed a slight reduction in activity during daylight hours in areas with recreational activities but they had still a large overlap with humans. Mule deer were the most readily detected species (92% of surveys) in our study area and are known to exhibit fidelity to specific sites (Krausman et al., 2008). Previous research in urban nature reserves, reported lower probabilities of detection for deer in areas with higher levels of recreation during the day but also found no spatial avoidance of deer to recreation (George and Crooks, 2006). We found that mule deer continue to exist even in areas with high levels of recreation by making slight shifts to their diel activity patterns.

Striped skunk in areas with recreation was slightly more active in the morning than striped skunk in areas without recreation (Fig. 3). In Indiana, the presence of striped skunk is positively correlated with a greater proportion of human dwellings (Gehring and Swihart, 2002). Results suggest striped skunk may be attracted to human presence and habituated to human disturbances such as high-level of recreation in the morning hours. Additionally, shifts in the diel activity patterns of predators may cause shifts in the diel activity of prey species. In our study area, the activity patterns of skunks have a lower level of overlap with the activity patterns of coyote than the patterns of coyote and other mesocarnivores (Reilly et al. in preparation).

We found no significant difference in the activity patterns of grey fox, raccoon, or opossums (Table 4). These species have nocturnal activity patterns that do not coincide with activity patterns of recreationists (Fig. 3), thus we would not expect them to change their activity patterns in areas with recreation.

We found no significant difference in the activity patterns of bobcats, or *Sylvilagus* spp., or mule deer, in areas with and without recreation (Table 4). Activity patterns of these species coincide with the activity patterns of recreationists (Fig. 3) indicating they may have adapted to the presence of recreation. Human influence on bobcats is not great (Ray, 2000). In southern California, bobcats were not significantly correlated with human disturbance levels in open spaces or parklands (Markovchick Nicholls et al., 2008). Thus our results are consistent with past research that suggest this species has already habituated or responded to human disturbances such as recreation.

Mountain lions and feral pigs had small sample sizes throughout the study. Of the 29 sites without recreation 38% of those had lion captures compared to 20% of sites with recreation. Similarly, 28% of sites without recreation had feral pigs whereas only 10% with recreation had feral pigs. Because only 11 and 8 sites without recreation had lion and pig captures (respectively), we did not have enough data to detect a significant difference in activity patterns in areas with recreation compared to areas without recreation. In the Santa Cruz Mountains, mountain lions increased nighttime activity and decreased daytime activity in areas with more human presence (Wang et al., 2015). In Montana, mountain lions adopt more nocturnal feeding behaviors in areas with human disturbance to avoid humans on trails (Jalkosky et al., 1997). Feral pigs are considered a nuisance species in the Bay Area and are persecuted by humans both on private lands outside Bay Area parks and in some of the parks in our study area (M. Gillogly, Pepperwood Ecological Preserve, pers. comm., September 29, 2015; C. Freeman, California Department of Parks and Recreation, pers. comm, October 1, 2015). Our small sample size for feral pigs may reflect eradication efforts. It is therefore likely that feral pigs learned to avoid areas with many humans.

Table 4

Confidence intervals for coefficient of overlap (Δ) estimates for species activity patterns compared to recreation patterns in areas of zero and high levels of recreation. Significance test and CI (that do not include zero), indicate that the diel activity pattern in areas of high recreation differed from the activity pattern in areas with no recreation.

	Sample Size		Confidence interval		
Species	high rec	no rec	lower	upper	Est. *p*-value
coyote	61	194	−0.332	−0.086	0.002*
bobcats	95	367	−0.159	0.035	0.201
fox	727	220	−0.041	0.025	0.800
raccoon	232	16	−0.025	0.104	0.638
mule deer	1402	284	−0.141	−0.029	0.006*
skunk	92	220	0.008	0.059	0.050*
opossum	100	35	−0.026	0.046	0.993
Sylvilagus sp.	41	21	−0.163	0.171	0.930

Asterisks indicate species with a significant shift in their activity pattern in areas with no recreation compared to high recreation.

For all species in this study detection probability was higher on-trail than off-trail. Similarly, other studies found that detection probabilities were higher on trails for carnivores and some ungulates (Harmsen et al., 2010; Tobler et al., 2015; Kays et al., 2016), but many other species had a neutral or even negative response to trails. Differences in species use of trails depend on size variations and behavioral differences of the animals as well as permeability of the forest matrix adjacent to the trail (Harmsen et al., 2010). Pumas and jaguars in South America readily use trails (Harmsen et al., 2009) while smaller prey species may display avoidance behavior of predators in exposed areas such as trails. Our results indicate that in the San Francisco Bay area all medium and large-sized species use trails despite use of trails by recreationists and predators.

While new trails can result in habitat avoidance and a negative impact on wildlife (Jalkosky et al., 1997), animals habituated to roads or trails may be able to use suitable habitat that other animals avoid (Papouchis et al., 2001). Contrarily, habituation of adult individuals may be associated with negative consequences for their offspring as habituation of adult animals does not translate to immediate habituation of juveniles (Mullner et al., 2004; Ellenburg et al., 2007). Wildlife habituated to human presence and occurring near developed area may increase the probability of a human wildlife interactions and conflicts. Bobcats and coyotes in urban corridors have a greater risk of mortality caused by vehicular collisions (Tigas et al., 2002; Krausman et al., 2008).

4.1. Conclusion

Our goal is to provide managers with answers to questions related to the effects of non-motorized recreation on species habitat use and the utility of protected areas and corridors for these mammals. The lack of significant relationships between animal habitat use and human recreation in our study contrasts with important previous research on the effects of non-motorized human recreation on coyote and bobcat density and abundance (Reed and Merenlender, 2011) and on habitat use by mule deer, rabbits, and bobcats (Lenth et al., 2008). However, species vary widely in their responses to human activities. Analysis of 12 wildlife species in forested protected areas in eastern USA, showed that recreation affected habitat use of only coyotes (Kays et al. 2016). In the San Francisco Bay area, natural areas have long histories of human recreation and mammals in these areas may be habituated to recreation (Steidl and Powell, 2006).

Our data suggest that recreation can have negative impacts, but that these impacts are modest, and protected areas in urban matrices continue to provide habitat (LaPoint et al., 2014) to medium and large-sized mammals despite the presence of human recreation. Smaller protected areas in this matrix provide conservation benefits to smaller mammal species and can serve as a potential habitat linkage for larger species. We caution that some species may be more sensitive to recreation than the woodland species we studied; for example, recreation, especially recreation involving domestic dogs, may have strong impacts on pronghorn antelope or bighorn sheep in open habitats (Papouchis 2001; Krausman et al., 1995a,b; MacArthur et al., 1982).

Managers may also want to know if there is a “safe distance” from trails (at which animals are no longer impacted by recreation on the trail) that could inform where trails can be located in corridors and other protected areas. We found no evidence that animals were avoiding trails. Our results suggest that mountain lions and Virginia opossum may benefit from protected areas free of trails that allow domestic dogs. Coyotes in protected areas show temporal avoidance to

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specific levels of human recreation and may benefit from protected areas that incorporate wide undisturbed corridors that allow them to retreat from human recreation. Corridors for coyotes should contain densely mixed vegetation and forest and shrub habitat for hiding cover (Krausman et al., 2008).

Most mammals in our study area showed no negative spatial or temporal response suggesting that these species are able to habituate to predictable and recurrent human recreation. Habituation is a behavioral response that allows animals to dedicate energy toward fitness-enhancing behaviors such as foraging and mating instead of expending energy to flee activities that result in neutral outcomes (Brown et al., 2012). From a conservation perspective, the impacts of human recreation on wildlife are important if they cause a population to decline. Most species included in our analysis are widely distributed across the San Francisco Bay ecoregion suggesting that these species exhibit some level of adaptability.

Future research on the effects of human recreation or presence on wildlife should focus on populations of animals that are rare or declining and for which human recreation is a likely limiting factor. For example, black bears, spotted skunks, badgers, and ringtails have limited distributions in the Bay area and may be more affected by recreation than common species or species with wider distributions. Future research could also address two important limitations of our study. First, birds, reptiles, amphibians, and small mammals may respond differently than the large and medium-sized mammals we studied. Second, because we limited site selection to areas at least half a kilometer from water, our study did not indicate how location of trails in riparian corridors affects seasonal use by mammals.

One of the greatest threats to conservation is a decline in public support due to less engagement in outdoor recreation (Zaradic et al., 2009). One's experience with nature influences one's willingness to financially support conservation (Zaradic et al., 2009). Many conservation plans view management as balancing the losses and gains of species as an implicit part of managing biodiversity (Zipkin et al., 2010). Outdoor recreation has numerous benefits including those for human health and the economy (Reed et al., 2014) and influences support for land and wildlife conservation (Zaradic et al., 2009). Research suggests that people who engage in hiking and backpacking contribute roughly $200–$300 annually to conservation (Zaradic et al., 2009). Thus, limiting access of these groups to protected areas could negatively impact conservation. Of the species included in our analyses, none are categorized as sensitive, threatened, or endangered. It is therefore our stance that the impacts are small in relation to the multiple gains such as human health benefits and continued political and financial support for land and species conservation.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2016.11.003.

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