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Recreation and large mammal activity in an urban nature reserve

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ABSTRACT

Human recreation has immediate and long-term impacts on wildlife, and exposure to recreational activities might be particularly high in urban systems. We investigated the relationship between human recreation and the spatial and temporal activity patterns of large mammals in an urban nature reserve. Data from remotely triggered infra-red cameras (1999–2001) were used to assess activity for bobcat, coyote, mule deer, humans, and domestic dogs along paths in the Nature Reserve of Orange County (NROC), California. Forty-nine camera sites established across the NROC yielded 16,722 images of humans, dogs, and our three target large mammal species during 4232 observation nights. Results suggest that bobcats, and to a lesser degree coyotes, exhibited both spatial and temporal displacement in response to human recreation. Bobcats were not only detected less frequently along trails with higher human activity, but also appeared to shift their daily activity patterns to become more nocturnal in high human use areas; negative associations between bobcat and human activity were particularly evident for bikers, hikers, and domestic dogs. In general, both bobcats and coyotes displayed a relatively wide range of activity levels at sites with low human use, but a lower and markedly restricted range of activity at those sites with the highest levels of recreation. Although we did not find a clear and consistent pattern of avoidance of human recreation by deer, the probability of detecting deer during the day was lower with increasing levels of human recreation. Future studies that experimentally investigate the impacts of recreationists on wildlife, as well as relate behavioral responses to survival and reproduction, will allow further insight of the effects of urban recreation on large mammal populations.

1. Introduction

The impacts of human disturbance on animal behavior and conservation have received growing attention (Clemmons and Buchholz, 1997; Caro, 1998; Gosling and Sutherland, 2000; Frid and Dill, 2002; Kerley et al., 2002; Festa-Bianchet and Apollonio, 2003). One such disturbance, human recreation, may lead to an array of immediate and long-term impacts on the activity, reproduction, and survival of wildlife (Knight and Cole, 1991; Knight and Gutzwiller, 1995; Whittaker and Knight, 1998). Indeed, outdoor recreation is a primary cause of the decline of threatened and endangered species in the United States (Losos et al., 1995; Czech et al., 2000; Taylor and Knight, 2003). Studies have suggested that human recreational activities can impact a wide variety of species, including marine mammals (Allen et al., 1984),

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rodents (Mainini et al., 1993; Magle et al., 2005), birds (Yalden and Yalden, 1990; Miller et al., 1998; Stalmaster and Kaiser, 1998; Fernández-Juricic et al., 2005), herpetiles (Hecnar and M'Closkey, 1998; Lacy and Martins, 2003; Rodríquez-Prieto and Fernández-Juricic, 2005), and coral (Zakai and Chadwick-Furman, 2002).

Mammalian carnivores, given their low population densities, large area requirements, and historical and current persecution, may be especially sensitive to anthropogenic disturbances (Terborgh, 1974; Pimm et al., 1988; Breitenmoser, 1998; Woodroffe and Ginsberg, 1998; Woodroffe, 2000; Crooks, 2002; Gittleman et al., 2001; Ray et al., 2005), and prior studies have suggested human recreation can alter carnivore behavior and distribution (e.g. Aaris-Sorensen, 1987; Olson et al., 1997; White et al., 1999; Nevin and Gilbert, 2005a,b). Likewise, human recreation can also disturb ungulates, initiating alert and flush responses and potentially resulting in decreased foraging or reproduction, increased energetic costs or stress, and avoidance of recreational areas (Eckstein et al., 1979; MacArthur et al., 1982; Freddy et al., 1986; Yarmoloy et al., 1988; Papouchis et al., 2001; Miller et al., 2001; Taylor and Knight, 2003). Although most studies of recreational impacts on large mammal activity have occurred in relatively natural settings, wildlife in urban systems may be exposed to particularly high levels of human recreation. The consequences of increased exposure to recreation, however, remain unclear, in that wildlife may become desensitized to recurrent human disturbances in some situations but not others, and such habituation may have both beneficial and negative impacts (Knight and Gutzwiller, 1995; Whittaker and Knight, 1998; Taylor and Knight, 2003; Kloppers et al., 2005; Magle et al., 2005; Smith et al., 2005).

Highly urban regions are often characterized by rapid expansion, which leads to habitat loss and fragmentation, the primary threat to endangered species in the United States (Wilcove et al., 1998). Widespread urbanization, in combination with high levels of species endemism and diversity, has created a major 'hot-spot' of extinction in coastal southern Californian natural communities (Myers, 1990; Dobson et al., 1997). Orange County, California, is one such coastal region to experience massive human population growth. Between 1950 and 1990, Orange County's population increased 10-fold, from approximately 200,000 to over 2,400,000 (State of California, 2001), with a projected population of nearly 3.2 million in 2010 (State of California, 2004). In response to urban sprawl and resultant habitat fragmentation, The Nature Reserve of Orange County (NROC) was created to preserve some of the region's last remaining natural areas. Although the NROC protects over 150 km^2 of open space, housing and commercial units encircle and fragment the reserve, and development is continuing. The NROC is permeated by foot and bike trails, maintained dirt roads, and dry creek beds, which can serve, in varying degrees, as movement routes for local wildlife as well as human recreationists, such as hikers, bicyclists, horseback riders, and dog walkers.

The goal of this study was to investigate the relationship between large mammal activity patterns and human recreation in an urban nature reserve. We assessed the spatial and temporal activity patterns of bobcat (*Lynx rufus*), coyote (*Canis latrans*), and mule deer (*Odocoileus hemionus*), as well as humans and domestic dogs, using infra-red remotely triggered cameras, valuable survey tools because they can record daily activity patterns for an extended period of time with minimal supervision (Carthew and Slater, 1991; Cutler and Swann, 1999; Carbone et al., 2001). We hypothesized that in areas of higher human recreation, large mammals would exhibit lower trail use, particularly during the daytime when human recreationists are most active.

2. Methods

2.1. Study area

The NROC is a reserve system spanning the central portion of Orange County, California. Human recreation in the reserve varies due to differing restrictions. Many parcels allow recreation on a daily basis and often year-round. Human recreation activity is consistently high in these areas, both throughout the daytime hours and throughout the year. Other parcels are limited to docent-led tours (e.g. lands managed by The Nature Conservancy) or completely closed to the general public. These areas typically receive relatively low levels of human activity throughout the year, although trespassing does occur. Much of the NROC, including areas with both high and low levels of human recreation, supports native habitat and wildlife communities.

The reserve is divided into two core areas: the coastal sub-region (ca. 73 km^2) and the central sub-region (ca. 77 km^2). The coastal sub-region is bordered by the Pacific Ocean to the southwest and by cities in all other directions. The central sub-region is located at the northwestern terminal portion of the Santa Ana Mountain range. It is connected to the Cleveland National Forest to the east and bordered by cities in all other directions. The city of Irvine and major freeway systems separate the two sub-regions and, at present, there are few to no viable habitat corridors for large mammals connecting the two portions of the reserve.

Coastal southern California has a Mediterranean type climate with an average annual precipitation level of less than 38 cm per year and two seasons: dry (June–November) and wet (December–May). The majority of our large mammal surveys (86% of sampling effort) occurred in the dry season, although some sampling at some sites continued into the early wet season. Coastal sage scrub, chaparral, and oak woodlands are the dominant habitat types within the NROC, although open grasslands and riparian habitat also exist. Percent cover of native and exotic plant species was estimated within a 20-m radius of each sampling station by following a modified Braun-Blanquet categorical scale (Kent and Coker, 1992). The cover scale was 0 (absent), 1 (<1%), 2 (1–5%), 3 (6–25%), 4 (26–50%), 5 (51–75%), and 6 (76–100%). Cover types were categorized as: (1) trees, including both native and non-native species; (2) native shrubs; and (3) exotic vegetation.

2.2. Spatial displacement (relative activity)

During 1999–2001, we used remotely triggered cameras (CamTrakker, Inc., Watkinsville, GA) to record the presence of wildlife and humans in order to determine their spatial and temporal activity patterns. We focused our analyses on three large mammals – bobcat, coyote, and mule deer – that occurred throughout the Nature Reserve of Orange County and were potentially responsive to human disturbances.

Forty-nine camera sites were established along dirt roads and major game trails throughout the NROC, with each site separated by a minimum of 750 m. Camera locations were restricted to relatively concealed areas to reduce theft and vandalism. In regions considered high risk for theft, cameras were placed in locking steel containers attached to metal posts. In low risk areas, cameras were attached to an anchor (tree, post, etc.), and secured to the anchor by a cable and lock. Cameras were set to delay 3 min between successive photographs, were equipped with a 35 mm auto-focusing lens and an auto flash mechanism, and have shooting distances of 0.35–6.00 m. Date and time (Pacific Standard Time, PST) of photographs were automatically burned onto the negatives. Infrared sensors have a maximum detection distance of 18.3 m, with an optimal distance of 0.3–9.1 m. Each camera was set for continuous action throughout the day and night, and was positioned facing the road or trail to ensure documentation of associated wildlife and human recreational activity. Data collection began in June and ended no later than February from 1999 to 2001, and cameras were checked once per calendar week unless site activity required them to be checked more frequently (shortest interval was once per day). Each year a camera remained at a site for an average of 53.6 nights (SD = 19.9, range: 21–114 nights).

An index of relative activity (RA) was estimated for each camera station by calculating the number of images of a species detected in a photograph divided by the number of nights the camera operated at that station. We used RA as measure of the spatial displacement of wildlife species in response to human recreationists across the 49 camera stations. Although we did not individually identify animals in photographs and thus cannot measure absolute densities, the camera index can provide a useful measure of the relative activity of species at each sampling point (Cutler and Swann, 1999; Carbone et al., 2001). If multiple individuals (images) were captured within a single photograph, each individual (image) was counted singularly. Relative activity indices for wildlife species conformed to the assumption of a normal distribution, whereas human indices did not and thus were log transformed in subsequent analyses.

2.3. *Temporal displacement (percent daytime activity)*

For each target species detected, percent daytime activity (PDA) was calculated by collapsing images taken 0600–1759 (PST) into a diurnal category and images taken 1800–0559 (PST) into a nocturnal category. This allowed for an overall estimation of PDA per species and at each site. PDA was calculated per species only for sites with a minimum of five images. We used PDA as a measure of the temporal displacement of wildlife to human recreationists. The proportion of daytime activity was arcsin square root transformed for statistical analyses.

2.4. *Data analysis*

2.4.1. *Sub-region, season, vegetation*

Preliminary analyses were conducted to evaluate the potential effects of sub-region (coastal and central reserve), season (wet and dry), and vegetative cover (trees, native shrubs, and exotic vegetation) on relative activity and circadian activity of wildlife and humans. Relative activity did not differ between sub-regions for bobcats, mule deer, and humans (all $t < 0.613$, all $P > 0.543$), although RA was higher in the coastal sub-region for coyotes (mean coastal ± SD = 0.276 ± 0.234, $n = 24$; mean central = 0.160 ± 0.124, $n = 20$; $t = 2.097$, $P = 0.043$). PDA for mule deer did not significantly differ between sub-regions (mean coastal = 0.412 ± 0.410, $n = 16$; mean central = 0.679 ± 0.492, $n = 16$; $t = 1.699$, $P = 0.105$), however, PDA was higher in the coastal sub-region for bobcats (mean coastal = 0.731 ± 0.231, $n = 11$; mean central = 0.420 ± 0.278, $n = 13$; $t = 2.945$, $P = 0.007$) and coyotes (mean coastal = 0.500 ± 0.246, $n = 19$; mean central = 0.264 ± 0.233, $n = 17$; $t = 2.950$, $P = 0.006$). To account for sub-regional effects in subsequent statistical analyses of human recreational impacts, RA for coyotes and PDA for both coyotes and bobcats were standardized by taking the standard normal Z scores within each sub-region.

Although log transformed human RA indices tended to be higher in the dry season (mean dry = 0.385 ± 1.022, mean wet = −0.011 ± 1.245, $n = 14$ sites sampled in both the wet and dry season within the same year; paired $t = 2.085$, $P = 0.057$), RA did not differ by season for bobcats, coyotes and mule deer (all paired $t < 1.164$, all $P > 0.275$) nor did PDA differ by season for these three target species (all paired $t < 1.154$, all $P > 0.292$) and the majority (86%) of sampling occurred during the dry season. Thus, season was not included in further analyses. Likewise, vegetative cover of trees, native shrubs and exotic vegetation did not differ between sub-regions (all $t < 1.770$, $P > 0.083$, n coastal = 24, n central = 24) or between areas of high and low human use (all $t < 0.731$, $P > 0.473$, n high = 14, n low = 34; see below for definition of high and low human use sites). Further, preliminary tests revealed few significant relationships between vegetative cover and RA or PDA of wildlife (George, unpublished data). Thus, vegetative cover was also not included in further analyses.

2.4.2. *Human recreation*

The relationships between recreation and wildlife activity were assessed in multiple steps. First, logistic regressions were performed to determine if overall human activity was a significant predictor of the probability of a species using a monitored trail (for all 49 camera stations) as well as the probability of exhibiting daytime activity at a site (for all stations with a minimum of five images for each species). For the logistic regression models, the response variable was input as a 1 (or 0) if a species was detected (or not) at a camera station or during the day.

Second, each camera site was categorized as either "high" or "low" based on overall levels of human recreation. A visual inspection of the human RA distribution indicated a natural break at a camera index of about 4.0 (i.e. four images of recreationists per sampling day), corresponding to approximately 30% of the most highly used sites by recreationists. This division resulted in 14 "high" (4.2–39.1 recreationists per sampling day) and 35 "low" (0.2–2.9 recreationists per day) human use sites. *T*-tests were used to investigate the differences in species RA and PDA in areas of high versus low human use.

Third, we developed regression models with wildlife RA or PDA as the response variable and overall human activity as the predictor variable. Four candidate models were compared: (1) Null: an intercept only model where human activity was not considered; (2) Log Human: representing a linear, 1st order relationship between human and wildlife activity; (3) (Log Human)^2: representing a non-linear relationship between human and wildlife activity; and (4) Log Human Polynomial: a global model representing a non-linear 2nd order polynomial incorporating both (Log Human) and (Log Human)^2. Akaike's Information Criterion (AIC) was used for model selection; the model with the minimum AIC was considered the best approximating model and models within two AIC units of the minimum AIC model were considered competitive models with some support from the data (Burnham and Anderson, 2002).

Finally, to further explore the relationship between wildlife activity and various types of human recreation, we also constructed linear regression models of large mammal relative activity and circadian activity using specific recreational categories as predictor variables: overall human activity, hikers (including joggers), bicyclists, equestrians, and motorized vehicles (including automobiles, motorbikes, and all-terrain vehicles). Because domestic dogs were highly correlated to human visitations (George, unpublished data), we also analyzed dog visitations, exclusive of any other recreational category, as a predictor variable of large mammal activity. Camera indices for all recreational categories were log-transformed for statistical analyses.

3. Results

3.1. *Spatial displacement*

From 1999 to 2001, cameras stationed across 49 sites operated for a total of 4232 camera nights, yielding 16,722 images of humans, domestic dogs, and our three target large mammal species (Table 1). Coyotes were the most frequently detected large mammal, followed closely by mule deer, and then bobcats (Table 1); all three species were detected at most camera stations in the NROC. Humans were the most detected species overall, occurring throughout the reserve. Hikers were the most common recreational category, followed by bikers, vehicles, and equestrians. Domestic dogs also were frequently detected.

Logistic regression models indicated that the probability of detection at a camera station was negatively related to human activity for bobcats (coefficient = −0.584, $\chi^2 = 6.459$, $P = 0.011$). The probability of detection at a camera station was not significantly related to human activity for coyote (coefficient = −0.471, $\chi^2 = 2.344$, $P = 0.126$) and mule deer (coefficient = −0.139, $\chi^2 = 0.287$, $P = 0.592$).

When comparing high versus low human use sites, RA indices were significantly lower in areas of high overall human use for bobcats (mean high = 0.061 ± 0.036, $n = 8$; mean low = 0.143 ± 0.103, $n = 29$; $t = 2.192$, $P = 0.035$) and coyotes (standardized mean high = −0.454 ± 0.293, $n = 11$; standardized mean low = 0.302 ± 1.059, $n = 33$; $t = 2.322$, $P = 0.025$). Mule deer RA indices did not differ between areas of high and low human use (mean high = 0.218 ± 0.211, $n = 11$; mean low = 0.186 ± 0.267, $n = 29$; $t = 0.370$, $P = 0.713$).

Across all 49 sampling stations, the negative non-linear model ["(Log Human)^2"] between bobcat RA and overall human activity had the strongest support from the data, with a model weight of 0.456; the linear model ("Log Human") was also competitive (Table 2). The null model was supported by the data for coyotes and mule deer with no other competing models. When viewed graphically, negative relationships between overall human recreation and bobcat and coyote activity were similar in appearance (Fig. 1). Both species demonstrated a wide range of activity levels at sites with lower human use, from zero relative activity to the highest RA index recorded for each species. In contrast, bobcats and coyotes displayed a lower and markedly restricted range of activity in those sites with the highest levels of human recreation.

When analyzing specific recreational categories at all 49 camera stations, bobcat RA was negatively related to the activity of all humans, bikers, and hikers, but not equestrians,

Table 1 – Camera station visits from 1999 to 2001 during 4232 camera observation nights across 49 sites in the Nature Reserve of Orange County, California

Species	Number of images	Number of observed sites	Mean relative activity (SE)	Overall % daytime activity
Coyote	874	44	0.200 (0.029)	23.16
Mule deer	813	41	0.164 (0.034)	25.19
Bobcat	458	37	0.095 (0.014)	31.83
All humans	14,101	49	5.257 (1.345)	94.43
Hikers	8217	49	3.004 (0.877)	92.72
Bikers	3562	34	1.725 (0.671)	98.00
Vehicles	1758	42	0.407 (0.091)	95.17
Equestrians	564	21	0.122 (0.036)	94.25
Domestic dog	476	30	0.169 (0.065)	83.37

Images are the count of individuals captured in all photographs during the study. Observed sites indicates the number of camera stations in which at least one individual of the species was detected. The mean relative activity index (standard error) is derived from all sites and across all years. Overall percent daytime activity represents the proportion of a species images recorded between the hours of 0600–1759 (PST) across all sites and all years.

Table 2 – AIC results for species relative activity indices across all 49 sites

Species	Model	log(Lhood)	K	$\Delta_i AIC_c$	W_i
Bobcat	$(\text{Log Human})^2$	115.897	3	0	0.456
	Log Human	115.594	3	0.607	0.337
	Log Human + $(\text{Log Human})^2$	116.061	4	2.425	0.136
	Null	112.768	2	3.714	0.071
Coyote[a]	Null	4.367	2	0	0.870
	Log Human	3.100	3	5.078	0.069
	$(\text{Log Human})^2$	2.647	3	5.984	0.044
	Log Human + $(\text{Log Human})^2$	3.124	4	7.782	0.018
Mule deer	Null	70.576	2	0	0.606
	Log Human	70.619	3	2.458	0.177
	$(\text{Log Human})^2$	70.578	3	2.541	0.170
	Log Human + $(\text{Log Human})^2$	70.672	4	5.105	0.047

The models examined were: (1) Null, in which humans were excluded from analysis; (2) Log Human, representing a linear relationship between humans and wildlife species; (3) $(\text{Log Human})^2$, which represents a non-linear relationship between human and wildlife indices; and (4) Log Human + $(\text{Log Human})^2$, a non-linear 2nd order polynomial model.
a Standard normal (Z) scores.

vehicles, or dogs (Table 3). Similarly, coyote RA was negatively related to overall human and hiker activity, and there was a trend for a negative relationship with bikers, but was not related to equestrians, vehicles, or dogs. Mule deer RA was not related to any recreational group.

3.2. *Temporal displacement*

Almost all human activity was recorded between the hours of 0600 and 1800 (Table 1). Domestic dogs also showed a high PDA (Table 1), revealing their strong association with human activity. Bobcats, coyotes, and mule deer showed similar degrees of nocturnality, primarily nocturnal with some diurnal activity (Table 1).

Logistic regression models indicated that the probability of daytime activity at a camera station was negatively related to human RA indices for bobcats (coefficient = −1.421, $\chi^2 = 5.352$, $n = 24$, $P = 0.021$) and mule deer (coefficient = −0.583, $\chi^2 = 3.879$, $n = 32$, P = 0.049). The probability of detecting coyotes during the day was not significantly related to human activity (coefficient = −0.252, $\chi^2 = 0.858$, $n = 36$, $P = 0.354$).

Bobcats tended to have a lower PDA (20.8%) in sites with the highest human recreation compared to their PDA (33.2%) in sites with lower human activity (standardized mean high = −0.337 ± 0.917, $n = 3$; standardized mean low = 0.483 ± 0.716, $n = 21$; $t = 1.803$, $P = 0.085$). The PDA of mule deer (mean high = 0.493 ± 0.646, $n = 9$; mean low = 0.566 ± 0.390, $n = 23$; $t = 0.391$, $P = 0.699$) and coyotes (standardized mean high = −0.236 ± 0.759, $n = 7$; standardized mean low = 0.109 ± 0.821, $n = 29$; $t = 1.010$, $P = 0.320$) did not differ between areas of high and low human use.

There was a negative linear relationship between bobcat PDA and human RA, with a relatively high model weight (0.642) and no other competing models (Table 4). For coyote PDA, the non-linear model was supported, with both the null and linear as competitive models. The null model was the minimum AIC model for mule deer PDA, with no other competing models. As with relative activity, bobcats and coyotes exhibited a greater range of daytime activity in areas with less recreation and showed less daytime activity, and a more restricted range of PDA, in areas highly used by humans (Fig. 2a and b).

When analyzing specific recreational categories, the proportion of daytime activity for bobcats was negatively related to overall human, biker, hiker, and dog activity, but not equestrians and vehicles (Table 3). Coyote PDA was not significantly related to any recreational category, although there was a negative trend with dog activity. Deer PDA was not related to any recreation groups.

4. Discussion

Bobcats appeared most responsive to recreation in the Nature Reserve of Orange County. Bobcats not only were detected less frequently along trails with higher human activity, but also appeared to shift their daily activity patterns to become more nocturnal in high human use areas, suggesting both spatial and temporal displacement in response to human recreation. Specifically, we found: (1) the probability of recording bobcats at camera stations, as well as the probability of detecting them during the day, decreased with increasing human recreation; (2) bobcat camera indices and proportion of daytime activity were relatively low in the sites with the highest human activity; and (3) statistical support for models describing negative relationships between recreational activity and bobcat relative activity and proportion of daytime activity. Negative associations between bobcat activity and specific recreational categories suggested spatial displacement in response to bikers and hikers and temporal displacement in response to bikers, hikers, and dogs, but no displacement in response to equestrians or motorized vehicles. Although to a lesser degree than bobcats, coyotes also appeared to exhibit spatial displacement in that coyote activity was lower in the sites with the most recreation and was negatively related to overall human, hiker, and biker visitations; a trend of temporal displacement in response to dogs also was evident.

Previous research also has found that pedestrians, mountain bikers, and domestic dogs can disturb wildlife, although

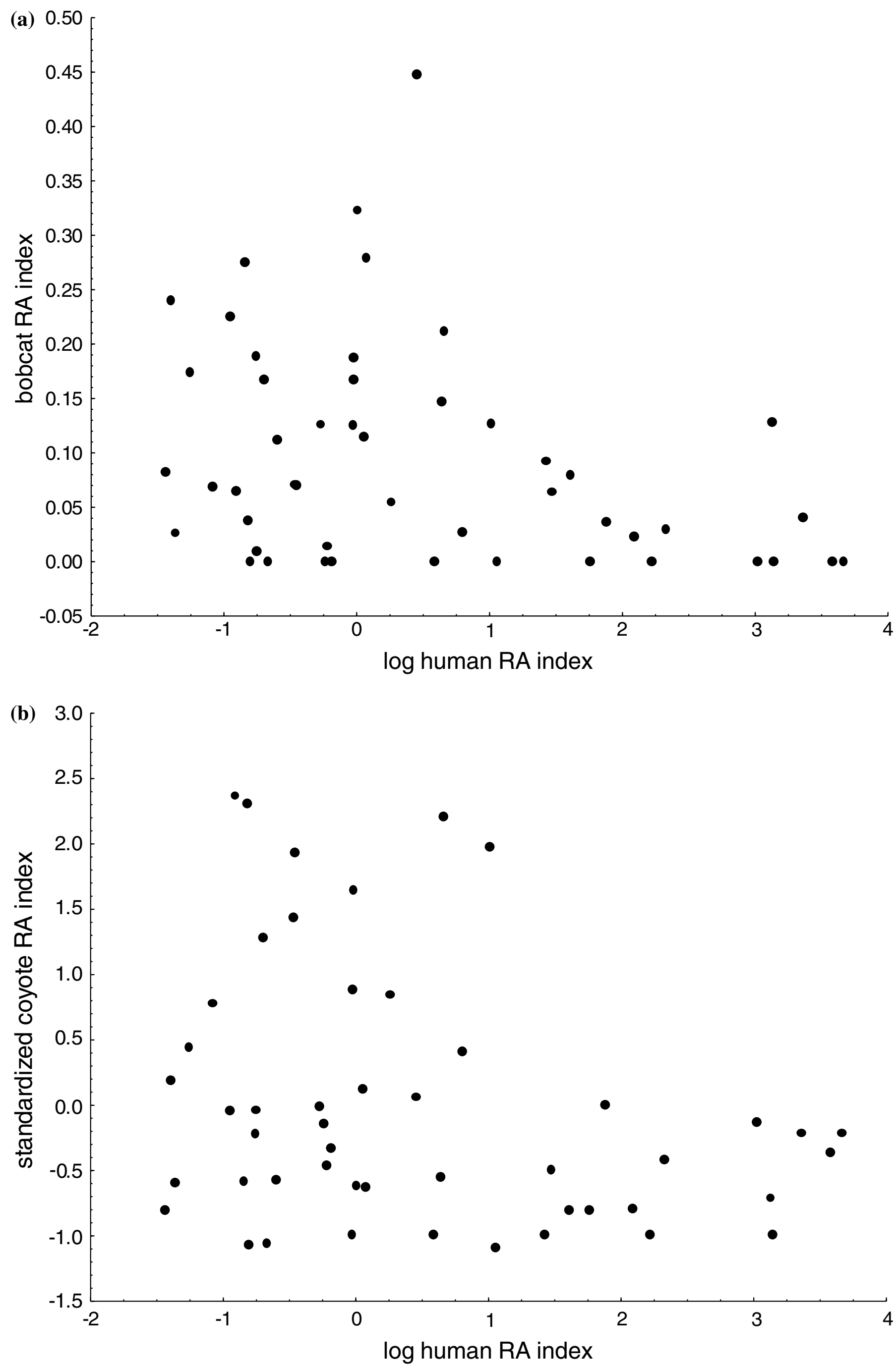


Fig. 1 – (a and b) The relationship between log human relative activity (RA) indices and RA indices of (a) bobcat and (b) coyote across all 49 camera sampling sites. Coyote RA represent standard normal Z scores (see text).

relatively little is known about their impacts on mammalian carnivores. Because wildlife tend to be particularly responsive to the human form (Taylor and Knight, 2003), pedestrians can elicit more intense reactions than motorized vehicles (Eckstein et al., 1979; MacArthur et al., 1982; Freddy et al., 1986), especially when accompanied by domestic dogs (MacArthur et al., 1982; Yalden and Yalden, 1990; Mainini et al., 1993; Miller et al., 2001). Impacts of dogs on native carnivores are not well understood, but may include disruption of carnivore behavior through chasing, barking, and scent marking via urine and scat. In comparison to pedestrians, mountain bikers move quickly and quietly, and in the NROC also travel off designated trails, and thus may be especially unpredictable and hence disruptive to wildlife (MacArthur et al., 1982; Knight and Gutzwiller, 1995; Miller et al., 2001; Taylor and Knight, 2003). The degree of spatial and temporal displacement of wildlife by different forms of human recreation can help guide management strategies to mitigate recreational impacts. For instance, spatial displacement of bobcat and coyotes by hikers and bikers might warrant greater enforcement of existing off-trail and

Table 3 – Relationship between wildlife relative activity (RA) and percent daytime activity (PDA) and human recreational categories

	Bobcat			Coyote			Mule deer		
	Coefficient	*r*	*P*	Coefficient	*r*	*P*	Coefficient	*r*	*P*
RA[*]									
Overall human	−0.023	−0.33	0.021	−0.193	−0.29	0.047	0.007	0.04	0.775
Hiker	−0.038	−0.34	0.016	−0.371	−0.34	0.017	−0.012	−0.05	0.756
Biker	−0.045	−0.36	0.010	−0.307	−0.26	0.076	0.051	0.18	0.229
Vehicles	−0.039	−0.11	0.433	0.555	0.17	0.250	0.008	0.01	0.947
Equestrian	0.040	0.07	0.629	−0.240	−0.04	0.764	−0.221	−0.17	0.252
Dog	−0.028	−0.07	0.633	−0.318	−0.08	0.578	−0.128	−0.14	0.352
PDA[**]									
Overall human	−0.369	−0.50	0.013	−0.127	−0.22	0.193	−0.042	−0.13	0.480
Hiker	−0.618	−0.54	0.006	−0.243	−0.27	0.108	−0.108	−0.18	0.329
Biker	−2.367	−0.45	0.028	−0.229	0.22	0.193	−0.021	−0.04	0.819
Vehicles	−0.100	−0.03	0.882	−0.407	−0.16	0.366	0.087	0.05	0.806
Equestrian	0.485	0.10	0.654	0.354	0.07	0.671	−0.749	−0.25	0.173
Dog	−1.574	−0.51	0.012	−1.078	−0.29	0.081	0.129	0.04	0.849

* All $n = 49$.
** All $n = 24$ for bobcats; all $n = 36$ for coyotes; all $n = 32$ for mule deer.

Table 4 – AIC results for wildlife percent daytime activity (PDA)

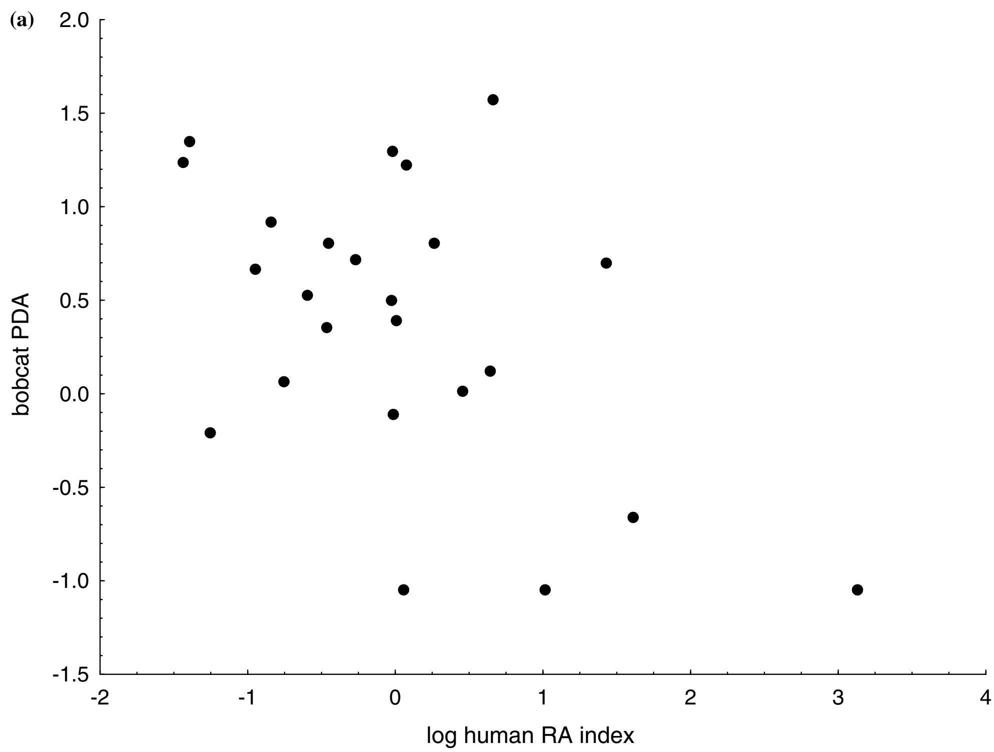
Species	Model	log(Lhood)	K	$\Delta_i AIC_c$	W_i
Bobcat[a]	Log Human	10.168	3	0	0.642
	(Log Human)^2	8.633	3	3.070	0.138
	Log Human + (Log Human)^2	10.370	4	3.406	0.117
	Null	6.715	2	3.650	0.103
Coyote[a]	(Log Human)^2	9.812	3	0	0.423
	Null	8.067	2	0.714	0.296
	Log Human	8.979	3	1.667	0.184
	Log Human + (Log Human)^2	9.885	4	2.935	0.097
Mule deer	Null	24.958	2	0	0.614
	Log Human	25.228	3	2.347	0.190
	(Log Human)^2	25.026	3	2.750	0.155
	Log Human + (Log Human)^2	25.306	4	5.439	0.040

Four models were examined: (1) Null, in which humans were excluded from analysis; (2) Log Human, representing a linear relationship between human relative activity indices and wildlife percent daytime activity; (3) (Log Human)^2, which represents a non-linear relationship between human indices and wildlife percent daytime activity; and (4) Log Human + (Log Human)^2, a non-linear 2nd order polynomial model. Sites with five images or more were included for species PDA analyses (see text).
a Standard normal (Z) scores.

trespassing regulations, or even setting aside new areas that restrict recreation. Alternatively, temporal displacement by domestic dogs may suggest limiting the hours in which a reserve is open to dog walking.

Our findings that bobcats appeared more responsive to human disturbances than did coyotes are consistent with prior studies in the region. For instance, Crooks (2002) examined the effects of habitat fragmentation on carnivores in coastal southern California and concluded that bobcats were more sensitive to landscape variables such as fragment size and isolation than coyotes. Tigas et al. (2002) studied the responses of radio-collared bobcats and coyotes to fragmentation and corridors in an urban area northwest of Los Angeles and suggested that although both species partially adjusted to habitat fragmentation through spatial and temporal avoidance, coyotes tended to be relatively more tolerant of human development. In the same system, Riley et al. (2003) found that some bobcats incorporated partially developed lands into their home ranges, but to a lesser extent than coyotes. Consistent with our findings, Tigas et al. (2002) and Riley et al. (2003) also found that bobcats and coyotes tended to shift towards nocturnal use of more fragmented, developed areas; studies in other systems have also suggested that coyotes in urban areas shift their activity to times when humans are less active (Andelt and Mahan, 1980; Quinn, 1997a; Grinder and Krausman, 2001; McClennen et al., 2001).

Research on urban deer typically has focused on topics such as space use (Kilpatrick and Spohr, 2000), movement patterns (Grund et al., 2002), human conflicts (McCullough et al., 1997; Wagner et al., 1997), and responses to hunting pressures (Kilpatrick and Lima, 1999), but fewer studies have investigated possible recreational impacts on urban deer



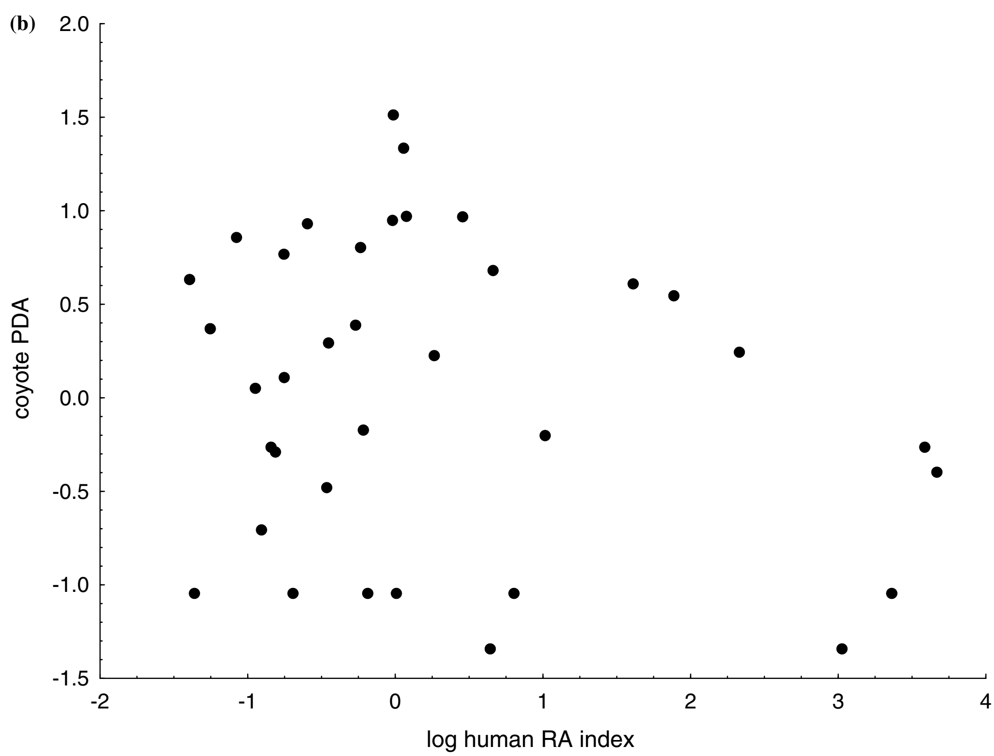


Fig. 2 – (a and b) The relationship between log human relative activity (RA) indices and percent daytime activity (PDA) of (a) bobcat and (b) coyote. PDA was determined by taking the proportion of daytime (0600–1759) images recorded amongst all images for each species and was calculated only for sites with a minimum of five images. PDA proportions were arc sin square root transformed and represent standard normal Z scores (see text).

populations. Mule deer are known to behaviorally respond to human recreationists, including both mountain bikers and hikers (Taylor and Knight, 2003) but more so to pedestrians than to motorized vehicles (Freddy et al., 1986), and particularly during daylight compared to evening hours (Altmann, 1958; Taylor and Knight, 2003) or when a dog was present

(Miller et al., 2001). Although we did not find a clear and consistent pattern of avoidance of human recreation by deer, the probability of detecting deer during the day was lower with increasing levels of human recreation.

If large mammals are somewhat tolerant, albeit in differing degrees, to human intrusion within the NROC, this may partially result from lack of hunting or trapping in the reserve, activities that can result in the increased wariness of both deer (Kufeld et al., 1988; Naugle et al., 1997; Kilpatrick and Lima, 1999) and carnivores (Andelt, 1985; McClennen and Shackleton, 1989; Frank and Woodroffe, 2001). Indeed, desensitization of large mammals to human recreation may result from habituation, defined as decreased responsiveness resulting from repeated applications of neutral stimuli (Whittaker and Knight, 1998). The ability to habituate to predictable and recurrent human use of recreational trails may be an important behavioral adaptation for wildlife in urban areas, allowing them to continue normal behaviors, such as resting, foraging or breeding, when confronted with continued human activity (Whittaker and Knight, 1998). However, habituated urban wildlife might be less likely to avoid contact with humans, and thus may be more likely to be attracted to anthropogenic food sources such as lawns or gardens for ungulates (Lubow et al., 2002; Rubin et al., 2002) or pets, trash, and cultivated fruits for carnivores (MacCracken, 1982; McClure et al., 1995; Quinn, 1997b; Crooks and Soulé, 1999; Fedriani et al., 2001). Habituation may also increase wildlife aggression towards humans, or render wildlife more vulnerable to hunters, poaching, or road-kill (Jones and Witham, 1990; Knight and Gutzwiller, 1995; Whittaker and Knight, 1998; Kloppers et al., 2005). Because habituation can increase the probability of human-wildlife conflicts, it is considered an emerging problem in many urban areas (Thompson and Henderson, 1998; Kloppers et al., 2005).

A priority for future research is experimental studies to further explore potential relationships between human recreation and wildlife in metropolitan reserve systems. For example, experimentally examining wildlife activity prior to and after the admittance or cessation of specific recreational activities in an area, preferentially with control areas with no such treatment, would help identify causal mechanisms and hence allow stronger inference regarding species-specific responses to recreational groups. Further, when interpreting wildlife responses to human intrusion, it is also important to consider the costs and benefits associated with avoiding human disturbance. Benefits include avoiding the disturbance, but costs might include energy expenditures and risks of predation while moving to do so. It is often assumed that species behaviorally avoiding disturbances are most susceptible to them, but behavioral avoidance may not always be the best predictor of which species are adversely affected by disturbance (Gill and Sutherland, 2000; Gill et al., 2001). For example, species that do not exhibit strong behavioral avoidance of humans, such as mule deer in this study, may still suffer fitness impacts if the costs of moving to avoid human recreation are overly high. Conversely, although we expect spatial and temporal displacement by bobcats and coyotes to human recreation to be associated with real costs in terms of energetic losses or increased stress levels, more research is necessary to determine how such avoidance actually translates into changes in survival, reproduction, and ultimately population persistence.

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