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Reserves as double-edged sword: Avoidance behavior in an urban-adjacent wildland

Michael A. Patten[a,*], Jutta C. Burger[b,c]

[a] Oklahoma Biological Survey and Department of Biology, University of Oklahoma, Norman, OK 73019, USA
[b] Irvine Ranch Conservancy, Irvine, CA 92620, USA
[c] Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92620, USA

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ABSTRACT

Human activities affect wildlife in a variety of direct (e.g., hunting, supplemental feeding, and culling) and indirect (e.g., displacement from habitat loss, competition with introduced invasive species, and avoidance of human-dominated landscapes) ways. Even ostensibly benign activities such as hiking or horseback riding in established parks may affect the spatial and temporal activity patterns of wildlife species. Characterization and quantification of effects is essential if parks and other protected areas are to balance the dual needs to nurture an appreciation of wildlands or satisfy a need to encounter nature (sensu the biophilia hypotheses) and to ensure that wild animals can survive and reproduce. We explored how human presence affects wildlife presence in a spatially extensive system of camera traps established in various protected areas in coastal southern California. To characterize and quantify effects we developed a conceptual framework on the basis of joint probabilities of occurrence on a per-camera basis and created a novel statistical approach to assess whether observed probabilities of co-occurrence differed from expected probabilities of co-occurrence. We found that same-day co-occurrence of wildlife and humans was significantly lower than expected at > 90% of the cameras established. This pattern held across sites, across the seven species of large and medium-sized mammals (Bobcat *Lynx rufus*, Mountain Lion *Puma concolor*, Gray Fox *Urocyon cinereoargenteus*, Coyote *Canis latrans*, Striped Skunk *Mephitis mephitis*, Northern Raccoon *Procyon lotor*, and Mule Deer *Odocoileis hemionus*), and across the five types of human disturbance examined (hikers, bicyclists, domestic dogs, vehicles, and equestrians). Our results demonstrate that human presence acutely affects same-day wildlife detections in protected areas, supporting the hypothesis that avoidance behaviour is a type of "mortality-free predation." Adaptive and flexible management plans need to be established, evaluated, and updated regularly to facilitate the human nature experience while lessening as much as possible long-term degradation of wildlife habitat. Wildlife in urban-adjacent preserves constitute a major part of the nature experience by humans and require effective management of pressures for use and recreation along aside those for wildlife habitat needs.

1. Introduction

Wildlife species exhibit a variety of responses to human presence, ranging from attraction to habituation to avoidance, with the majority of documented responses being negative (Boyle and Sampson, 1985; Whittaker and Knight, 1998; Gil and Sutherland, 2000; Boarman et al., 2006; Steidl and Powell, 2006; Pruett et al., 2009). A firm understanding of wildlife responses to disturbance is essential to manage conflict, however conflict is defined (Peterson et al., 2010). Ongoing anthropogenic encroachment on habitats increases human–wildlife interaction, whether direct or indirect. Encroachment and interaction are guaranteed even in parks and reserves, which are, in many regions worldwide, increasingly embedded within a matrix of urban or suburban development that often is unsuitable for wildlife persistence (Gehrt et al., 2010). Human access increases with proximity of reserves to development, which can lead to detrimental effects on wildlife via habitat fragmentation (e.g., disruption of dispersal corridors or home range needs), decreased use of co-occupied areas, effects on food resources, introduction of disease vectors, competition from feral cats and dogs, and pest control, poaching, light pollution, and roadkill (Woodroffe et al., 2005; Smith-Patten and Patten, 2008; White and Ward, 2011; Barua et al., 2013). In many cases population-level and demographic effects of human disturbance are poorly known, although it is assumed that avoidance leads to energetic costs that affects an

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[*] Corresponding author at: Oklahoma Biological Survey, University of Oklahoma, 111 E. Chesapeake Street, Norman, OK 73019, USA.
E-mail address: mpatten@ou.edu (M.A. Patten).

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animal's health and reproduction or may ultimately lead to a perceptual trap, in which misleading cues cause an organism to avoid otherwise suitable habitat (Patten and Kelly, 2010).

The type of human activity affects how wildlife will respond. Domestic dogs that accompany hikers may have an additive effect on wildlife displacement relative to hikers without dogs (Miller et al., 2001; cf. Reed and Merenlender, 2011). A mix of hikers and bicyclists has a similar additive or interactive effect (Taylor and Knight, 2008). Off-trail hiking relative to on-trail hiking affects flight response of ungulates, with flight initiation distance higher for off-trail hikers (Stankowich, 2008). Response also depends on approach angle, wind direction, and hunting prevalence (Behrend and Lubeck, 1968; LaGory, 1987; de Boer et al., 2004; Stankowich and Coss, 2005). An animal cannot avoid human-use areas if accessible alternative habitat does not exist, in which case an animal may not flee because it cannot flee (Stankowich, 2008), an inability to disperse that may isolate populations (e.g., Riley et al., 2014).

These problems are exacerbated in regions that have been developed extensively for housing and infrastructure, such as in coastal southern California, where the human population continues to grow. In this region the species-level response to human activity or encroachment is idiosyncratic, with both acute behavioral changes and chronic distributional effects. Camera trap studies in southern California revealed that populations of the Coyote (see Table 1 for scientific names) and Northern Raccoon increased with proximity and intensity of urbanization whereas populations of the Bobcat, Gray Fox, and Mountain Lion decreased (Riley et al., 2003; Ordeñana et al., 2010). Behavioral changes regionally are such that medium- to large-bodied mammal species, such as the Coyote, Bobcat, and Mule Deer, generally avoid areas of high human use (George and Crooks, 2006) and shift activity to night-time hours along recreational trails. Other studies have documented proportionally higher nocturnal occurrence in areas of high human use than in areas of low use (Tigas et al., 2002; Riley et al., 2003; George and Crooks, 2006).

Most behavioral studies have been based on relatively limited data sets spanning either short time frames or a limited number of cameras and have not taken the spatially discrete response patterns across study landscapes into account or clearly quantified human activity. The generality, intensity, and persistence of a negative response to human presence or activity level remains unclear. We addressed these needs with a spatially extensive camera-trap study established both to provide long-term data on wildlife activity patterns as well as on wildlife response to human activity in managed protected areas. Our goal is to help guide management recommendations on how to minimize any observed negative effects. Moreover, we provide a novel analysis of patterns of human detections, wildlife detections, and their intersection in that we conceptualize the question as one of joint probability of occurrence tested against a null of a product of independent probabilities. This conceptual framework is more appropriate for the standard question asked of such data, which typically is some variant of "Does the presence of humans affect the presence of wildlife?" We argue that such a question is answered directly once it is reworded as "Is the probability of wildlife occurrence independent of the probability of human occurrence?" If anthropogenic disturbance, in the form of hikers, bicyclists, vehicles, domestic dogs, and equestrians, affects wildlife then the probability of joint occurrence ought to be lower than the expectation under an assumption of independence. We tested observed joint probabilities against expected joint probabilities with a Monte Carlo statistic we created and for which we generated estimates of type I error (i.e., *P*-values) by means of bootstrap resampling. This approach not only provided clear results but is transferable to any system for which there is a question of whether human presence affects wildlife presence.

Table 1
Total mammal detections, grouped by taxonomic order, at camera traps in Orange County, California, from June 2007 to December 2011. Domesticated animals were treated as a component of human disturbance.

Scientific name	English name	detections	percent
Didelphimorphia			
Didelphis virginiana Kerr, 1792	Virginia opossum	97	0.41
Lagomorpha			
Sylvilagus audubonii (Baird, 1858)	Desert cottontail	102	0.43
Rodentia			
Spermophilus beecheyi (Richardson, 1829)	California ground squirrel	21	0.09
Carnivora			
Felis catus Linnaeus, 1758	domestic cat	5	0.02
Lynx rufus (Schreber, 1777)	Bobcat	2369	9.98
Puma concolor (Linnaeus, 1758)	Mountain lion	455	1.92
Urocyon cinereoargenteus (Schreber, 1775)	Gray fox	1152	4.85
Canis lupus Linnaeus, 1758	domestic dog	545	2.30
Canis latrans Say, 1823	Coyote	4973	20.95
Mephitis mephitis (Schreber, 1776)	Striped skunk	358	1.51
Procyon lotor (Linnaeus, 1758)	Northern raccoon	590	2.49
Artiodactyla			
Odocoileus hemionus (Rafinesque, 1817)	Mule deer	13,065	55.05

2. Methods

2.1. Study area and management regime

The study was conducted in Orange County, California, within a complex of urban and urban-adjacent reserves once privately owned and now publicly owned by the County of Orange, City of Irvine, and City of Newport Beach (Fig. 1). Reserves in our study span approximately 15,000 ha (37,000 acres) in central and coastal Orange County and are protected further through either the Orange County Central and Coastal Natural Community Conservation Plan (NCCP) or by conservation easements, as well as deed restrictions, park abandonment ordinances, and other legal mechanisms. Lands are adjacent both to a heavily urbanized landscape, which supports > 3 million people, and to ~28,300 ha (70,000 acres) of U.S. National Forest land. Areas included in this study span from urban-adjacent coastal canyons that no longer support the Mountain Lion or Gray Fox to more remote foothills and steep canyons of the Santa Ana Mountains. The region is in a Mediterranean ecosystem, known for its high biodiversity and its limited spatial extent worldwide; habitats consist of coastal sage scrub, chaparral, grassland and oak woodland with few ephemeral streams and permanent water sources (natural and man-made). At the time of the study, public access was controlled across most of the study area via permit-only entry as well as regular docent-led programs and monthly self-guided wilderness access days. Managed access parks provide an ideal arena to assess patterns of wildlife use in relation to human activity and to develop an adaptive management program to minimize conflict in that they allow direct control over human activity. Dogs are not permitted on managed-access lands.

2.2. Data set

Fixed location digital wildlife cameras (Cuddeback Expert Model #3300, Non Typical, Inc., Green Bay, Wisconsin) were installed throughout an approximately 11,530 ha (28,300 acre) managed-access to monitor human and wildlife occurrence concurrently on a long-term basis across the reserve system (Fig. 1). Only ten cameras were placed in 7-day access areas (within parks owned by the City of Newport Beach and the City of Irvine); all others were placed in areas in which human access was limited. All cameras had a flash range of 18 m and were equipped with an instant trigger tripped by motion (6–30 m distance) and heat. Their detection angle is narrow, 2 m wide at 10 m distance,

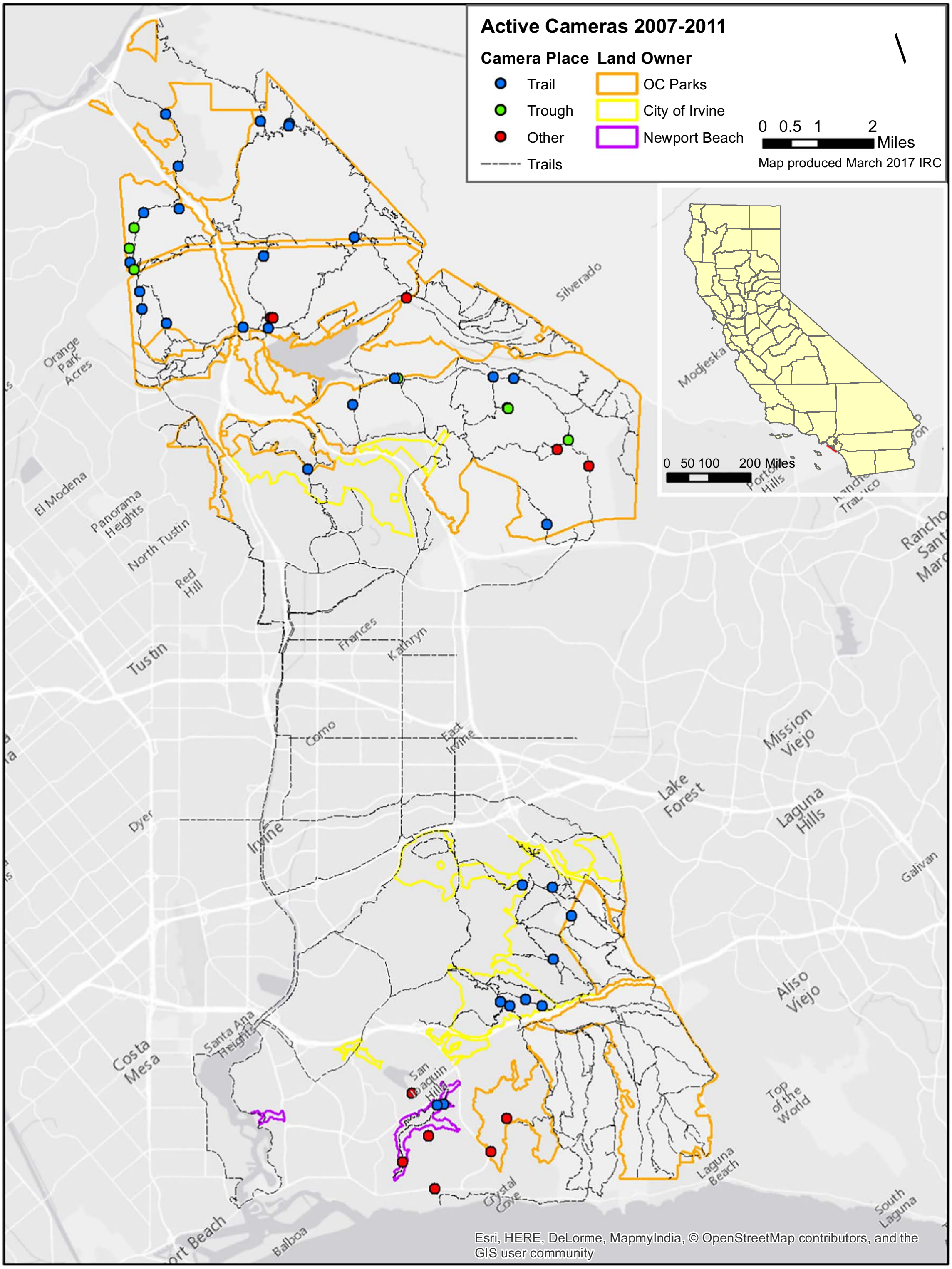

Fig. 1. The study area in Orange County, California, including the Irvine Ranch Open Space (Orange County Parks), the City of Irvine Open Space Preserve (City of Irvine) and Buck Gully Reserve (City of Newport Beach).

compared to other recent models. The sensitivity of each camera was adjusted to maximize the probability of species detections but minimize the number of extraneous photographs of moving vegetation. Each camera was set for a one-minute delay between photographs to minimize duplicates of the same object. Cameras were positioned along trails or roads where wildlife activity was likely, as well as by active water troughs, future recreational trail locations, and established animal trails. Images were stamped with date and time on one-gigabyte compact flash cards, which were collected every two weeks.

Data from 50 cameras were analyzed from June 2007–December 2011; 28 cameras operated continuously from September 2007 onward. Data from one camera could not be analyzed fully because there were solely human detections (i.e., no wildlife was detected). Of the remaining 49 cameras, 30 were positioned along trails, 6 were directly adjacent to water troughs or water sources, and 13 were off-trail. The data set used represented a total of 40,149 trap-days (mean: 803 trap-days/camera; range: 113–1120 trap-days/camera), for which "day" refers to a calendar day. Each photograph was viewed by a technician, who recorded the species, date, time, and location into the relational biodiversity database program Biota 2.04®. If a human, bicycle, or vehicle detection occurred within 1 h, then all photos within that hour were treated as a single record. If a wildlife species occurred repeatedly within a 5-min period, then these photos were treated as a single record. We did not estimate detection probability of the cameras (see below).

General relationships between wildlife and humans were analyzed using the full set of data from June 2007–December 2011. Prior to analysis, we collapsed camera trap data by calendar day to two columns of information. The first column was the amount of human-activity, described here as "disturbance," an index that included all photographs of humans on foot, vehicles, bicyclists, and domestic cats, domestic dogs, and horses. The second was the amount of mammal detections (taken here as a broader indicator of wildlife occurrence), which we restricted to mean photographs of seven species (Table 1). We did not consider in our analyses of birds, small mammals that camera traps sample poorly (e.g., the Desert Cottontail or California Ground Squirrel), animals we could not identify to species, or the Virginia Opossum, which is introduced to California. For either column we summed individuals in the photograph; hence, one photograph of seven people was recorded as "7" not "1" for the number of records. We did not weight level of human disturbance: a vehicle counted as "1" even though we recognize that disturbance from a vehicle differs from a single person on foot.

2.3. Analyses

To address the basic question of whether human disturbance has an effect on mammal detection, we developed a novel randomization test against the H_0 of no effect with a focus on joint probability of occurrence. We used presence–absence data per camera trap for all days a given trap obtained a useable photograph, meaning a photo in which one of the seven focal species or one of the five types of human activity could be identified unambiguously. We used these data to calculate a per-camera probability, defined as the number of occurrences (e.g., days with photos of Bobcats) over the total number of events (i.e., days with useable photos). Calendar days on which a given species or disturbance type was not detected were treated as "absence" for the sake of probability trials. We calculated probabilities in this way to avoid biasing results to a finding of no effect, which would occur if there were numerous days of no mammals and no humans (i.e., days when both had 0). Inclusion of 0/0 days would increase the denominator but leave the numerator unchanged, even though the basic pattern of days or 0/1 vs. 1/0 vs. 1/1 is unchanged; it is the latter pattern that is of biological interest. We did not build an occupancy model to adjust occupancy (Ψ) for detection probability (p); i.e., we used naive occupancy $\Pr(\Psi)$ rather than conditional occupancy $\Pr(\Psi|p)$. Naive occupancy underestimates true occupancy (MacKenzie et al., 2006), but this bias only makes our analysis conservative because $\Pr(\Psi|p) \geq \Pr(\Psi)$. We accept this bias because a) it is conservative, b) we do not ask questions about relative occupancy, whether among species or disturbance types, and c) we do not use estimates as a response variable in subsequent analyses (e.g., linear regression). We do not argue that our method replaces occupancy modeling but that is it a straightforward, easily presented alternative that many stakeholders grasp readily and that provides clearly interpretable results.

Under the H_0, the probability of mammal detection is independent of amount of human disturbance. As such, we calculated an expected probability of joint occurrence—both detection and disturbance will be recorded on the same calendar day—as the product of the probability of disturbance and of detection. This probability need only be multiplied by the total number of days a camera obtained a useable photo to have an expected number of days (E) both a mammal and a human or human commensal would be recorded by that camera. This expected value is compared to the observed number of days (O) both detection and disturbance were recorded. If H_0 holds, then E and O will be similar; if the H_A of human effect holds, then O would be significantly less than E (or significantly greater if wildlife are attracted to humans). We tested goodness of fit of O for each trap by means of a bootstrap for that trap to get a spread of E values. We ran bootstrapped resampling 1000 times in a C program we wrote for this purpose (available from the authors). As is standard for randomization tests, the final P for the test was taken to be the number of times a bootstrapped E was less than or equal to the O, divided by the number of bootstrap replicates. (Note that use of $\Pr(\Psi|p)$ would increase E but leave O unchanged, which would place O farther out in the tail of a randomized distribution.) We ran such randomization tests, and calculated Spearman rank correlations (r_s) as a measure of effect size, for species-specific responses to human disturbance under the H_0 that a given species' occurrence was independent of the presence of humans on any given calendar day.

We used beta regression (Ferrari and Cribari-Neto, 2004), a technique in which the response variable a probability or proportion, to examine how human disturbance is associated with mammal detection across all cameras. We used a Bayesian approach to estimate regression parameters (i.e., slope, β_1, and intercept, β_0). Our likelihood was $y_i \sim \text{beta}(\mu_i\varphi, [1 - \mu_i]\varphi)$, with the line fit as $\text{logit}(\mu_i) = \beta_0 + \beta_1 x_i$. Priors were flat and set as $\beta_0, \beta_1 \sim N(0,0.000001)$ and φ (precision) $\sim \text{gamma}(0.001,0.001)$. The Markov chain Monte Carlo algorithm to estimate β_0 and β_1 was run for 10,000 iterations after a burn-in of 1000. We implemented the model in JAGS 4.3.0, as run via R. We estimated a correlation coefficient between probabilities of disturbance and mammal detection as the square root of the coefficient of determination (i.e., "pseudo-R^2") from the resultant regression equation.

We did not conduct formal threshold analyses to determine the critical mass of human disturbance at which mammal detection declined, but as a first pass we plotted disturbance per day against mammal species detections per day across the whole of the study area and ran two-segment piecewise regressions, in SigmaPlot 12.0, to identify a potential thresholds (Toms and Lesperance, 2003). Furthermore, we ran a second beta regression, constructed as described above, but with the predictor as mean human activity/day at each camera and the response variable as the expected joint probability of occurrence.

3. Results

A total of 12 mammal species were recorded in 59,483 records of wildlife and humans across the 50 cameras (Table 2). Of this total, we obtained 23,608 records of larger mammals, including dogs, most often as unauthorized accompaniment of humans; moreover, on 37.8% of camera-days (i.e., a calendar day for a given camera) we detected no humans. Across the entire landscape of 50 camera traps, there was no relation between the total number of mammals recorded and the amount of human activity (Fig. 2); i.e., camera trap locations with high overall human activity did not predictably also have few wildlife detections. By contrast, wildlife were negatively associated with human disturbance on a camera-by-camera basis, in that there were significant departures from expectations of independence for 92% (45 of 49) of cameras (Table 2).

Null-model probability distributions calculated for mammals co-occurring on the same day as humans, under the H_0 of no association between the number of days mammals co-occur with humans (Fig. 3), consistently showed that the observed number of days on which both mammals and humans occurred was significantly less than expected (Table 2). Each of the seven large and medium-sized mammals detected in the study area responded negatively to human disturbance (Table 3). Parsing human disturbance into its five constituent types—pedestrians, bicycles, motorized vehicles, horses, and domestic dogs—revealed that

Table 2
Avoidance behavior of large and medium-sized mammals relative to human activity at each of the 50 camera traps. Legend: *n* = sample size (number of days); pDist = probability of human disturbance (i.e., number of human detections at a camera trap divided by *n*); pMamm = probability of a mammal detection; pBoth = joint probability of human disturbance and mammal detection under the H_0 of independence (i.e., pBoth = pDist × pMamm); exp = expected number of detections of both humans and mammals under the H_0 of independence; obs = observed number of detections of both humans and mammals; *P* = probability of the observed count against a null distribution from Monte Carlo randomization of data. Note that the observed number of joint detections consistently is lower than expected and that cameras with high human disturbance have low mammal detections and vice versa (Pearson correlation: $r_{48} = -0.91$, $P < 0.0001$). No mammals were detected at camera #20, precluding statistical analyses, yet human disturbance was present there every day, so the general pattern held at that camera trap, too.

Camera	*n*	pDist	pMamm	pBoth	exp	obs	*P*
1	119	0.185	0.933	0.172	21	14	0.055
2	484	0.074	0.959	0.071	35	16	0.0001
3	402	0.888	0.239	0.212	85	51	0.0001
4	20	0.550	0.550	0.303	6	2	0.0001
5	21	0.333	0.714	0.238	5	1	0.006
6	377	0.332	0.793	0.263	99	47	0.0001
7	206	0.204	0.864	0.176	36	14	0.0001
8	296	0.324	0.784	0.254	75	32	0.0001
9	94	0.245	0.819	0.200	19	6	0.0001
10	262	0.515	0.676	0.348	91	50	0.0001
11	154	0.455	0.604	0.274	42	9	0.0001
12	384	0.091	0.930	0.085	33	8	0.0001
13	526	0.492	0.705	0.347	183	104	0.0001
14	609	0.898	0.223	0.201	122	74	0.0001
15	479	0.380	0.789	0.300	144	81	0.0001
16	154	0.539	0.552	0.297	46	14	0.0001
17	51	0.196	0.843	0.165	8	2	0.0001
18	400	0.647	0.482	0.312	125	52	0.0001
19	72	0.750	0.306	0.229	17	4	0.0001
20	162	1.000	0.000	0.000	0	0	
21	739	0.706	0.594	0.420	310	222	0.0001
22	162	0.593	0.728	0.432	70	52	0.0001
23	941	0.913	0.601	0.549	517	484	0.009
24	280	0.204	0.857	0.174	49	17	0.0001
25	179	0.341	0.883	0.301	54	40	0.006
26	480	0.594	0.544	0.323	155	66	0.0001
27	599	0.910	0.182	0.166	99	55	0.0001
28	70	0.714	0.443	0.316	22	11	0.0001
29	574	0.927	0.213	0.197	113	80	0.0001
30	882	0.765	0.732	0.561	494	439	0.0001
31	831	0.996	0.043	0.043	36	33	0.319
32	200	0.265	0.785	0.208	42	10	0.0001
33	32	1.000	0.031	0.031	1	1	0.997
34	191	0.644	0.419	0.270	52	12	0.0001
35	912	0.798	0.822	0.656	599	566	0.002
36	158	0.576	0.475	0.273	43	8	0.0001
37	352	0.108	0.932	0.101	35	14	0.0001
38	83	0.916	0.181	0.165	14	8	0.024
39	425	0.922	0.144	0.132	56	28	0.0001
40	237	0.662	0.409	0.271	64	17	0.0001
41	843	0.986	0.197	0.194	164	154	0.194
42	409	0.421	0.702	0.295	121	50	0.0001
43	330	0.918	0.100	0.092	30	6	0.0001
44	618	0.921	0.217	0.200	123	85	0.0001
45	370	0.959	0.103	0.099	36	23	0.003
46	330	0.155	0.891	0.138	45	15	0.0001
47	606	0.380	0.817	0.310	188	119	0.0001
48	479	0.113	0.939	0.106	51	25	0.0001
49	102	0.078	0.941	0.074	8	2	0.014
50	327	0.688	0.385	0.265	87	24	0.0001

same-day avoidance behavior by focal wildlife species was markedly higher in the presence of pedestrians, bicycles, and vehicles than of dogs and horses (Table 4).

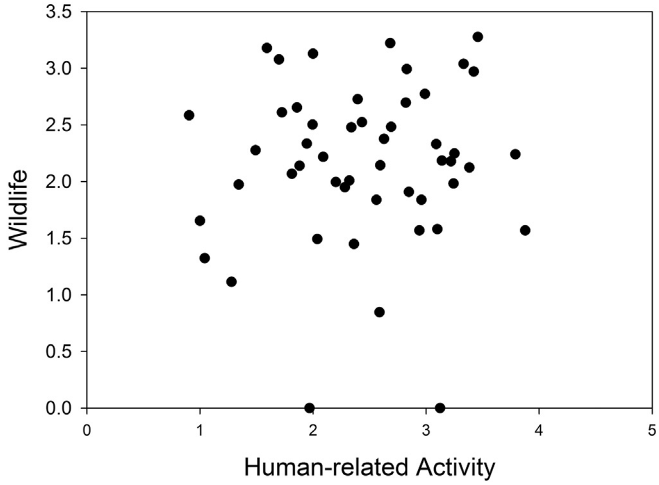

Fig. 2. A $\log_{10}$–$\log_{10}$ plot of total number of human detections against total number of wildlife detections across fifty camera traps in Orange County, California. At this gross scale, there is no correlation ($r = 0.07$).

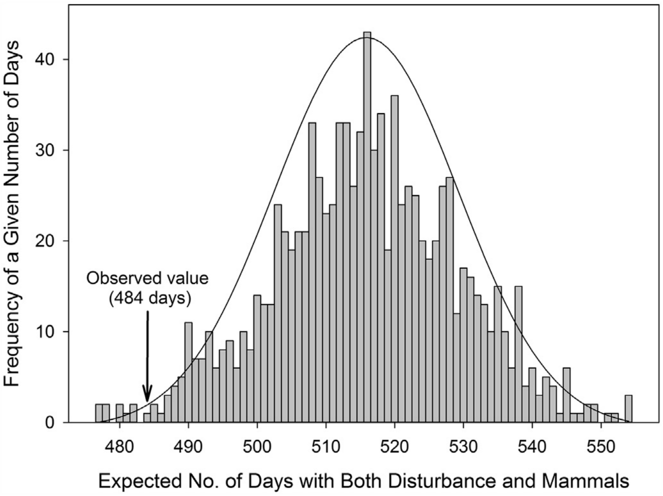

Fig. 3. An example of a probability distribution of expected number of days that both mammals and humans would co-occur if humans had no effect on mammals, with the observed number of days that both occurred. In this case the observed number of days of co-occurrence was substantially lower than expected under the H_0 of no effect.

Table 3
Avoidance behavior of each of seven large and medium-sized mammal species across all types of human activity. Legend: r_s = Spearman rank correlation between mammal detection and human presence (a measure of effect size); see Table 2 for definitions of other headings. Note that for each species the observed number of join detections was far less than the expected number under the H_0 of independence (i.e., no relationship between the presence of humans and presence of mammals). All statistical tests of observed vs. expected rejected the H_0 at $P < 0.0001$.

Species	*n*	r_s	pDist	pMamm	pBoth	exp	obs
Canis latrans	11,133	− 0.372	0.865	0.268	0.232	2581	1480
Urocyon cinereoargenteus	8981	− 0.362	0.937	0.093	0.087	780	266
Lynx rufus	9939	− 0.390	0.893	0.180	0.161	1600	729
Puma concolor	8518	− 0.259	0.970	0.043	0.042	359	117
Mephitis mephitis	8455	− 0.202	0.978	0.036	0.036	300	120
Procyon lotor	8518	− 0.314	0.963	0.043	0.042	356	54
Odocoileus hemionus	13,016	− 0.660	0.722	0.374	0.270	3516	1254

Across sites, the probability of mammal detection was correlated strongly and negatively ($r \approx -0.91$) with the probability of human presence (Fig. 4). The back-transformed slope of the relationship is $\beta_1 \approx -0.0148$, a drop in detections from an average of 2.46/d on days without human disturbance to 0.62/d in the presence of any instance of human disturbance. Nevertheless, the amount ("intensity") of human disturbance has additional explanatory value: with $P = 0.99$, the true and underlying slope is negative of a beta regression of joint probability

Table 4
Avoidance behavior across seven large and medium-sized mammal species relative to type of human activity. See Tables 2 and 3 for definitions of headings. Note that for each species the observed number of join detections was far less than the expected number under the H_0 of independence (i.e., no relationship between the presence of humans and presence of mammals). All statistical tests of observed vs. expected rejected the H_0 at $P < 0.0001$.

Disturbance type	*n*	r_s	pDist	pMamm	pBoth	exp	obs
Pedestrian	11,769	− 0.646	0.449	0.667	0.299	3523	1362
Bicycle	8611	− 0.594	0.247	0.812	0.200	1724	503
Motorized vehicle	14,032	− 0.579	0.538	0.626	0.337	4726	2302
Domestic dog	6828	− 0.326	0.050	0.962	0.048	328	82
Horse	6826	− 0.253	0.050	0.967	0.048	328	112

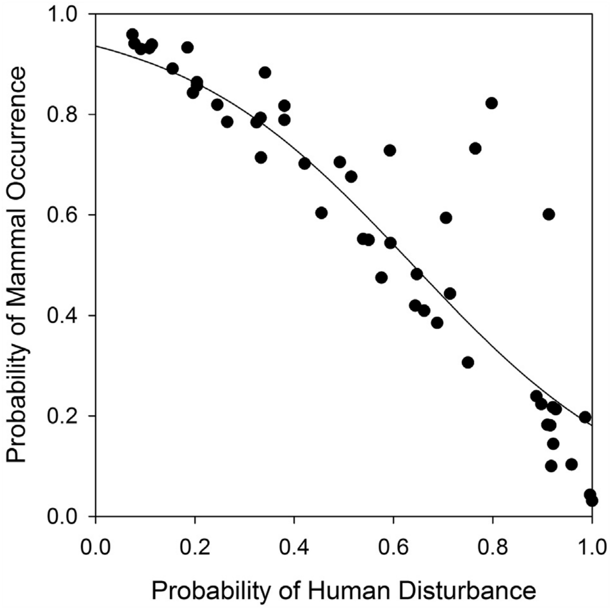

Fig. 4. The probability of mammal occurrence against the probability of human disturbance (data are from the third and fourth columns of Table 2). The fitted line is from a beta regression with parameters generated via Bayesian estimation (see text). The approximate correlation, from the pseudo-coefficient of determination of the regression, is $r = -0.91$.

of occurrence against mean human activity (back-transformed $\beta_1 \approx -0.48$, roughly a drop of two units of joint probability for every additional unit of mean human activity). Approximate disturbance thresholds (*T*, rounded up to the nearest whole number of humans) varied among focal species, with *Lynx rufus*, *Canis latrans*, *Urocyon cinereoargenteus*, and *Procyon lotor* apparently sensitive to mere presence of human disturbance ($T = 1$), whereas *Mephitis mephitis* ($T = 3$), *Odocoileus hemionus* ($T = 5$), and *Puma concolor* ($T = 10$) apparently were less sensitive.

4. Discussion

Response of large and medium-sized mammals to human activity may be difficult to characterize because that response varies in time and space (e.g., Vistnes and Nellemann, 2008) and with species and type of activity. Moreover, response is likely to be threshold-dependent, species specific, and subject to feedbacks and interactions with other factors (e.g., edge effects, availability of cover, exposure to disturbance, or time since fire). We assessed the general pattern of wildlife detections in the broadest sense and its response to human disturbance by compiling data from fifty fixed locations across four-and-a-half years. We did not observe an effect of human activity on wildlife on a landscape scale, over which there was a range of background human disturbance levels and local environments (Fig. 2). We could interpret this pattern to mean that human use of reserves had not changed wildlife use fundamentally, in contrast to findings of depauperate diversity of native fauna at urban edges relative to interior habitats (e.g., Ordeñana et al., 2010), but we feel it is more likely a statistical artifact that results from pooling data in the standard way many researchers would. For example, some of our cameras in highly urbanized areas failed to detect two of the seven target species, Mountain Lion and Gray Fox (unpubl. data), suggesting extirpation where surrounding development has been extensive and connectivity has been severed. Our findings underscore the value of large protected areas that allow human and wildlife use to covary in space and time.

By contrast, short-term (single-day) patterns in wildlife detections were affected strongly by human presence at a given site: mammals were nearly four times as likely to be recorded on days with no human activity as on days that humans were recorded by a camera trap, and mammal detections decreased incrementally with increasing number of human activity (falling to a near-zero probability as counts of human counts reached > 60/day). Our data thus suggest multiple thresholds in wildlife response to human activity. A first and stronger threshold is determined by whether or not humans occur at all on a given day, whereas a second and weaker threshold relates to amount of human activity (i.e., number of visitors) on those days, with this secondary threshold varying among species. These findings jibe with theoretical expectations of how organisms perceive risk from with an increase in predators (Fig. 5), despite being conservative given that cameras yield only approximate levels of human activity because preset one-minute delays in photography underestimate counts of humans present.

Both the stronger and weaker thresholds could be influenced by type and timing of human activity, an important area for further study. Pedestrians (hikers and runners) had the greatest negative correlation with local wildlife detections ($r = -0.65$), whereas equestrians had the lowest ($r = -0.25$), yet all common recreational activities were correlated negatively with mammal detection, so differences among user groups are less important than the negative association of human presence, irrespective of type. We further noted that all seven mammal species we analyzed in detail responded negatively to human presence. It may be that avoidance behavior or flight initiation distance varies with species (Blumstein et al., 2003), and we found evidence that some species, most notably the Mule Deer, were affected more negatively than others (Table 3). Such a response could alter predator–prey dynamics (Muhly et al., 2011), for example by elevating encounter rates or altering perceived risk (sensu Beale and Monaghan, 2004).

We detected a strong local behavioral response of wildlife to human

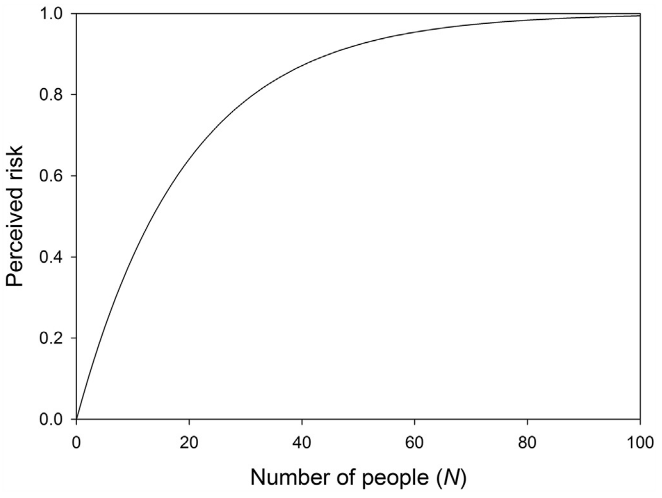

Fig. 5. Theoretical effect of increased human disturbance on perceived risk of predation, from the equation risk = $1 - [1 - 1/D]^N$ (Beale and Monaghan, 2004), for which distance to "predator" is assumed to be constant ($D = 20$).

activity ($r = -0.91$ correlation between the two probabilities), but we could not further explain avoidance response by a short-term temporal displacement of wildlife. For instance, in one study in southern California, mammals tended to be more nocturnal in areas of high human use (George and Crooks, 2006). Preliminary analyses of certain key species (unpubl. data) do indicate a temporal shift, although we do not know if effect size of daily spatial shifts vs. daily temporal shifts is greater in our study area. Future research and analyses ought to address both the duration of the effect of human activity and the spatial scale at which wildlife response occurs as well as their numeric effects on wildlife populations.

Our study supports the hypothesis that human presence triggers avoidance by wildlife, which ultimately lends support to the hypothesis that human disturbance can act as a kind of “predation” by reducing animal occurrence (Fig. 5; Beale and Monaghan, 2004). Nevertheless, with appropriate management avoidance behavior may be minimized because knowledge of this negative relationship can guide management decisions related to human access during sensitive periods for wildlife, such as during breeding season and when food and water resources may be limiting. Daily access was restricted on virtually all of the protected area during our study, yet human presence nevertheless led to measurable avoidance behavior across seven species or large to medium-sized mammal species, with expected joint probabilities under an assumption of independence met at a mere three of fifty cameras. Locally, guidelines for managed-access areas have been adjusted to cluster or zone human activities, to limit nighttime activity and the number of high-use days in sensitive areas, to enact and enforce rest periods immediately after high-use days, and to set recommended maxima for visitor numbers per day. New measures will require a balance of wildlife needs with recreational demands because human use of wildlands is essential to bolster or foster appreciation of wildlands, particularly in urbanized regions. In short, effective management of human access over time is essential to sustain natural communities and wildlife dynamics and to provide high quality visitor experiences on these lands in perpetuity.

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