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Human presence and human footprint have non-equivalent effects on wildlife spatiotemporal habitat use

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ABSTRACT

Human impacts on wildlife stem from both our footprint on the landscape and the presence of people in wildlife habitat. Each may influence wildlife at very different spatial and temporal scales, yet efforts to disentangle these two classes of anthropogenic disturbance in their effects on wildlife have remained limited, as have efforts to predict the spatial extent of human presence and its impacts independently of human footprint. We used camera trap data from a 1400-km² grid spanning wildlands and residential development in central California to compare the effects of human presence (human detections on camera) and footprint (building density) on mammalian predators. We then developed a model predicting the spatial extent of human presence and its impacts across the broader landscape. Occupancy modeling and temporal activity analyses showed that human presence and footprint had non-equivalent and often opposing effects on wildlife. Larger predators (pumas *Puma concolor*, bobcats *Lynx rufus*, coyotes *Canis latrans*) were less active where human footprint was high but avoided high human presence temporally rather than spatially. Smaller predators (striped skunks *Mephitis mephitis*, Virginia opossums *Didelphis virginiana*) preferred developed areas but exhibited reduced activity where human presence was high. A spatial model, based on readily available landscape covariates (parking lots, trails, topography), performed well in predicting human activity outside of developed areas, and revealed high human presence even in remote protected areas that provide otherwise intact wildlife habitat. This work highlights the need to integrate multiple disturbance types when evaluating the impacts of anthropogenic activity on wildlife.

1. Introduction

The expanding influence of humans has greatly impacted wildlife by disrupting the distribution and activity patterns of animals globally (Dirzo et al., 2014; Gaynor et al., 2018; Tucker et al., 2018). The increasing human footprint on the landscape (i.e., urbanization, land use change) is a key threat to wildlife across virtually all taxonomic groups, not only through habitat loss and fragmentation (Hansen et al., 2005; Fischer and Lindenmayer, 2007), but also because urbanized areas represent concentrations of anthropogenic “disturbance” (i.e., real or perceived threats that elicit antipredator responses (Frid and Dill, 2002)), which may be actively avoided by wildlife. However, human impacts are not restricted to developed areas only, as the mere presence of humans has been shown to impact wildlife behavior and activity even in wildland areas (Suraci et al., 2019a). The latter is particularly salient given the rapid expansion of outdoor recreation into previously undisturbed landscapes (Cordell et al., 2008) and its potential negative

effect on many wildlife species (Larson et al., 2016).

Wildlife species respond to human activities in complex ways, ranging from acute behavioral changes to chronic distributional effects, which may depend on the type, intensity, and frequency of disturbance (Larson et al., 2016; Tablado and Jenni, 2017; Gaynor et al., 2018; Tucker et al., 2018). Humans are a major source of mortality for many wildlife species, particularly mammalian predators (Darimont et al., 2015), and recent experimental work confirms that many species therefore exhibit strong fear responses to human presence (Clinchy et al., 2016; Smith et al., 2017; Suraci et al., 2019a). The fear induced by human presence has correspondingly been shown to affect behavior and activity patterns of wildlife at the landscape scale (Suraci et al., 2019a), and fear may therefore mediate many of the impacts associated with recreational activity in wildland areas (Larson et al., 2016; Tablado and Jenni, 2017). When compared to the relatively transient presence (and associated fear) of humans in wildlife habitat (e.g., during recreation), sustained and high-intensity disturbance associated

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with long-term land use changes (e.g., housing developments) may be expected to exert even greater impacts on wildlife habitat use. Yet many synanthropic species (e.g., mesopredators like striped skunks, *Mephitis mephitis*, and Virginia opossums, *Didelphis virginiana*) appear to benefit from increased human footprint on the landscape, taking advantage of resource subsidies such as food waste (Ordeñana et al., 2010; Wang et al., 2015) and/or decreased risk from other predators where human activity is high (Muhly et al., 2011). Indeed, multiple anthropogenic influences may simultaneously affect wildlife, potentially in opposition, if for instance some species avoid risky interactions with people but take advantage of human infrastructure or resources (Beckmann and Berger, 2003; Bateman and Fleming, 2012; Suraci et al., 2019a).

An animal's response to a particular anthropogenic disturbance may additionally depend upon the relative constancy or regularity of the disturbance type in space and time and thus the animal's ability to predict when and where potential threats from humans are likely to occur. Predator-prey theory suggests that long-term, consistent spatial variation in risk should lead to outright avoidance and thus changes in prey space use (e.g., the "risky places hypothesis") (Creel et al., 2008; Dröge et al., 2017). Alternatively, predation risk that is more spatially variable but exhibits regular temporal fluctuations (e.g., due to the predator's daily activity cycle; Kohl et al., 2018) may lead to temporal partitioning, where prey avoid predators in time by increasing activity at times of day when the predator is less active (Suraci et al., 2019b). Thus, it is possible that human development as a long-term, spatially constant source of risk may be more likely to induce spatial displacement and altered habitat use for wildlife species (i.e., avoidance of risky places) (Frid and Dill, 2002; Tucker et al., 2018), while human presence in wildlife habitat, which is less constant and largely restricted to diurnal periods, may prompt shifts in temporal activity (Gaynor et al., 2018).

Despite ample reason to expect that human footprint and human presence will differ in their impacts on wildlife behavior and habitat use, ambiguity exists in how wildlife species respond to these two categories of anthropogenic disturbance. One reason for such ambiguity is that human footprint is often used as a proxy for multiple forms of anthropogenic disturbance, due in part to the ease of acquiring landscape level data on, e.g., land cover, human population density, and built infrastructure (Venter et al., 2016). However, such variables may be poor predictors of human presence across the landscape, particularly in wildland areas where outdoor recreation is growing (Cordell et al., 2008; Balmford et al., 2015). Using the human footprint as a proxy for human presence may therefore conflate the effects of different types of human disturbance on wildlife (Tablado and Jenni, 2017). However, measuring the spatial extent of human presence outside of developed areas, and thus the area over which human activity is likely to impact wildlife, remains a challenge. Studies of human presence in wildland areas typically rely on the localized deployment of sensors (e.g., camera traps) in the environment, a site-specific approach that may not be representative of landscape-scale patterns of human presence (Larson et al., 2016; Gutzwiller et al., 2017) and may therefore overlook human disturbance and its impacts in parts of the landscape not directly covered by camera trapping surveys (Monz et al., 2013). Thus, there is a need to predict human presence in wildland areas from readily available landscape-level variables, allowing estimation of broad-scale spatial patterns of human activity and associated impacts on wildlife beyond sites at which on-the-ground surveys have been conducted (Ladle et al., 2017).

Here we use a network of camera-traps deployed across a gradient of human recreational use and development in the Santa Cruz Mountains of California to quantify the effects of both human footprint (building density) and actual human presence (occurrence of people on camera traps) on wildlife behavior and habitat use. We then model where and when the observed impacts of human presence are likely to be greatest on the landscape using a suite of spatial predictors of human activity. We focus our analyses on large and medium-sized mammalian

predators, which experience the highest per capita risk of human-caused mortality (Darimont et al., 2015) and are correspondingly known to exhibit strong behavioral responses to the immediate presence of people (Clinchy et al., 2016; Smith et al., 2017; Suraci et al., 2019a), but which also represent a range of responses to human development, from reclusive large carnivores to synanthropic mesopredators. This work was conducted in areas of the Santa Cruz Mountains ranging from undeveloped tracts of forest to moderately developed rural and exurban areas, thus typifying the mosaic of wildlife habitat and human development characteristic of the wildland-urban interface (WUI) (Radeloff et al., 2005, 2010).

2. Methods

2.1. Study area

The Santa Cruz Mountains (37° 10' N, 122° 3' W) encompass a diverse landscape comprised of large tracts of relatively undisturbed native vegetation intermixed with low- and intermediate-density development that are surrounded by heavily developed areas along the fringe. One-third of the landscape falls within the wildland-urban interface (Martinuzzi et al., 2015) with a substantial portion of more remote public lands being available for recreational activities (e.g., biking, hiking, dog walking). The study area is crisscrossed by highways and numerous smaller roads providing access to rural houses and developments. The region thus provides marked gradients of development and human recreational pressures.

2.2. Camera trap study design

We deployed a grid of camera traps (Bushnell Trophy Cameras) across approximately 1400 km² of the Santa Cruz Mountains, CA, USA, focusing on undeveloped and moderately developed areas that still provide substantial wildlife habitat (Fig. 1). We created a grid for 100 camera traps, with 4 km between the center of each grid cell. This systematic sampling approach was chosen to facilitate accurate estimates of habitat use by a range of species that differ in average home range size and movement patterns (Efford and Dawson, 2012; Neilson et al., 2018). We placed camera traps within 400 m of the center of each grid cell along landscape features likely to maximize detection of mammalian predators. We were unable to place 12 cameras due to land access or safety issues, leading to a total deployment of 88 cameras. Cameras were deployed using standardized procedures (O'Connell et al., 2011; Burton et al., 2015), being placed at a height of 30–90 cm and oriented along hiking trails, forest roads, or game trails used by wildlife to increase the probability of detection. We programmed cameras to take 3 photos per detection event, with at least a 1 min delay between subsequent detections.

Camera traps were deployed for five to seven weeks during three separate study periods: Spring 2015 (10 March to 13 April), Autumn 2015 (23 August to 10 October), and Spring 2016 (4 March to 21 April). During each study period, we deployed and retrieved camera traps on a rolling basis, and the date ranges noted above correspond to the weeks when at least 80% of the 88 camera traps were active. We scored all camera trap images for the presence of mammalian predator species including the sole large carnivore in the Santa Cruz Mountains, the puma (*Puma concolor*), and a suite of mammalian mesopredators (coyote *Canis latrans*, bobcat *Lynx rufus*, gray fox *Urocyon cinereoargenteus*, northern raccoon *Procyon lotor*, striped skunk, and Virginia opossum). We also scored all detections of humans on camera traps. All images of the same species (including humans) on the same camera were considered independent occurrences if separated by at least 30 min (Wang et al., 2015).

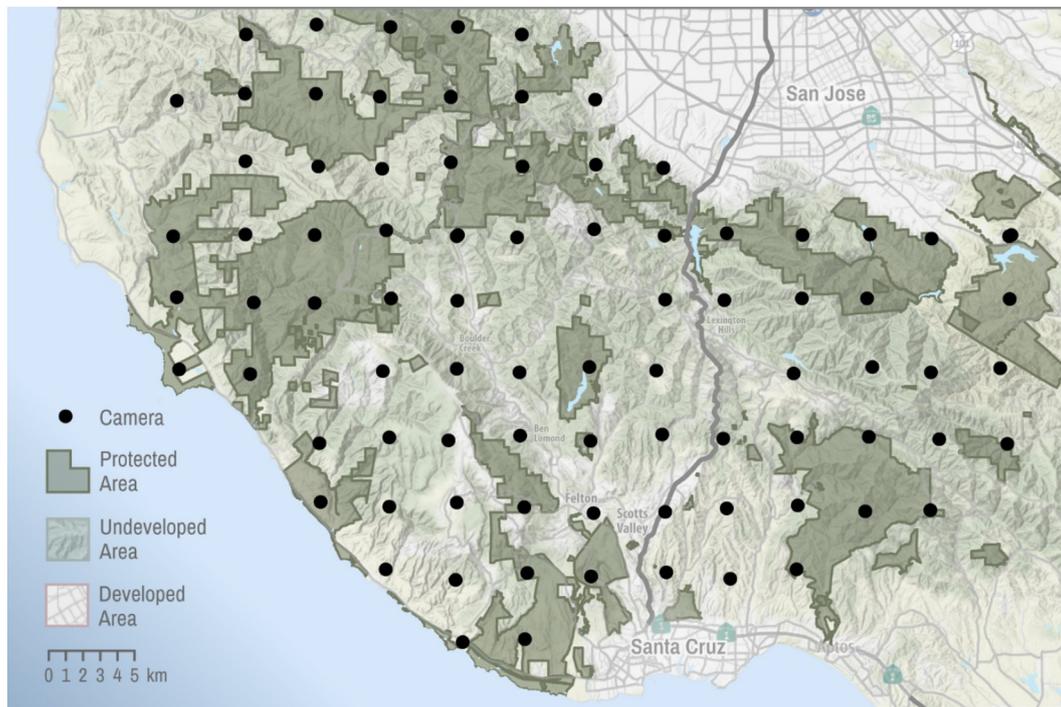


Fig. 1. The study area in the Santa Cruz Mountains, California, USA, displaying the locations of camera traps (black dots), protected areas (dark green shading), undeveloped areas (light green), and developed areas (light gray) across the region. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.3. Anthropogenic and habitat covariates

For each camera site, we measured several anthropogenic and habitat covariates that could potentially affect both human and wildlife activity, including building density (BUILDING), road density (ROAD), trail density (TRAIL), distance to urban area (URBAN), distance to public open space (i.e., state and local parks, outdoor recreation areas; OPEN), distance to parking lot (a proxy for accessibility; ACCESS), proportion of forest cover (FOREST), elevation gradient (ELEV), proportion of visible landscape (i.e., vista opportunities; VIEW), ruggedness (RUGGED), topographic position index (TPI), and amount of wildland-urban interface within 1 km (WUI). All covariates are presented in Table 1 and described in detail in the Supplementary methods. All GIS analyses were performed using the Python programming language (v. 2.7.9; Python Software Foundation, Wilmington, DE, USA) and ArcGIS for Desktop (v. 10.6.1; ESRI Inc., Redlands, CA, USA).

Our camera grid spanned a substantial gradient of both human presence and human footprint. The average number of independent

(i.e., separated by 30 min) human groups detected per day across the 88 camera sites ranged from 0 to 6 (mean ± SD = 1.2 ± 1.8 human groups per day), with 12 of 88 sites experiencing an average of 0 visitors per day. The largest total number of independent human groups detected in single day was 13. Building density ranged from 0 to 568 buildings within 1 km of the camera site (mean ± SD = 60.5 ± 100.2 buildings). Importantly, these two forms of human disturbance were not strongly correlated across camera sites (Pearson's correlation coefficient = -0.22, p = 0.058).

2.4. Comparing the effects of human presence and human footprint on wildlife habitat use

For each camera trap, we derived estimates of human presence at both the daily and study period (i.e., Spring 2015, Autumn 2015, or Spring 2016) levels from images of humans recorded on camera traps. Daily estimates were simply the total number of independent human detections during each calendar day on a given camera trap (humans

Table 1
Environmental variables measured for each camera site and data sources from which variables were derived.

Variable	Description	Data source
Anthropogenic		
BUILDING	# of buildings within a 1 km radius	Municipal, county, and state agencies; Microsoft Building Footprint, 2018 (Martinuzzi et al., 2015)
WUI	# of wildland-urban interface parcels within a 1 km radius	(Martinuzzi et al., 2015)
URBAN	Euclidean distance to the nearest medium to high density urban areas	California Protected Areas Database; GreenInfo Network, 2017
OPEN	Euclidean distance to the nearest public open space	Municipal, county, and state agencies
ROAD	Length of road network within a 1 km radius	Municipal, county, and state agencies; OpenStreetMap, 2017
TRAIL	Length of trail network within a 1 km radius	Municipal, county, and state agencies; OpenStreetMap, 2017
ACCESS	Euclidean distance to the nearest parking lot or campground	Municipal, county, and state agencies; OpenStreetMap, 2017
WEEKEND	Day of the week, coded as weekend (Saturday, Sunday) or weekday	-
Habitat		
FOREST	% of forested landscape within a 1 km radius	National Land Cover, v2 (30m); US Geological Survey 2011
VIEW	% of visible landscape within a 1 km radius	Digital Elevation Model (30 m); US Geological Survey 2011
ELEV	Elevation range within a 1 km radius	Digital Elevation Model (30 m); US Geological Survey 2011
RUGGED	Surface roughness within a 1 km radius	Digital Elevation Model (30 m); US Geological Survey 2011
TPI	Topographic position relative to ridges and valleys within 1 km	Digital Elevation Model (30 m); US Geological Survey 2011

per day, or HPD). Study period-level estimates were the number of humans detected per day on a given camera averaged across each study period (meanHPD). We used building density (i.e., BUILDING, described above) as our estimate of human footprint at each camera site.

To estimate the effects of the two forms of human disturbance on wildlife habitat use and behavior, we fit multi-species occupancy models (Burton et al., 2012; Broms et al., 2016) to camera trap data on detections of the seven mammalian predators described above. Occupancy models estimate two parameters, both of which may be affected by human disturbance: site occupancy (ψ) and detection probability (p). As originally formulated (e.g., MacKenzie et al., 2003), occupancy and detection probability depend on an assumption of closure, i.e., that an individual that uses a given camera site will always be present and available for sampling. This assumption may be violated in camera trap studies when the actual area sampled by a camera is substantially smaller than the home ranges of the animals surveyed (Efford and Dawson, 2012; Burton et al., 2015; Neilson et al., 2018). We therefore treated the occupancy (ψ) and detection probability (p) parameters estimated from our models as proxies for the probability of occurrence (i.e., whether a given species occurred at a site during sampling) and intensity of use (i.e., the overall activity of a species at a given site) respectively. Species occurrence is likely to be lower where high human disturbance reduces habitat suitability. Intensity of use is a function of both animal behavior and the density of individuals using the area sampled by the camera trap. Thus, if fewer individuals occur in disturbed habitats and/or if individuals reduce their activity levels or increased cryptic behavior where disturbance is high, this will lead to fewer detections on camera and lower estimates of intensity of use.

As all of our target wildlife species are at least partially nocturnal, particularly where humans are present (Wang et al., 2015), we defined each night that a camera was active as a survey (Burton et al., 2012), and recorded whether a given species was detected (1) or not (0) over a 24-hour period spanning each night (from noon to noon). Our estimates of wildlife species detection were therefore offset (by 12 h) from our daily estimates of human activity on camera such that detection of a wildlife species during a given nocturnal period is modeled as a function of the number of humans present during the immediately preceding diurnal period.

We formulated our occupancy models as hierarchical zero-inflated binomial models with separate binomial submodels describing ψ and p (MacKenzie et al., 2002; Royle and Dorazio, 2008). We fit two occupancy models varying only in the type of human disturbance used to model ψ and p , i.e., human footprint (building density) or human presence (meanHPD and HPD for ψ and p respectively). Each model also included environmental covariates that could affect occupancy and detection probability at camera sites (i.e., FOREST, RUGGED, and TPI), as well as an interaction between FOREST and human disturbance (presence or footprint) to account for potential changes in wildlife responsiveness to human disturbance with varying levels of protective cover. All covariates were normalized (mean centered and scaled by one standard deviation) prior to model fitting. Full details of the multi-species occupancy model are provided in the Supplementary methods.

We analyzed the occupancy models in a Bayesian framework using the JAGS language called through the package R2jags in R (v. 3.4.2; R Core Team, 2019). For each model, we ran three Markov Chain Monte Carlo (MCMC) chains of 20,000 iterations each and made inference from 1000 samples from the posterior distribution of each chain after a burn in of 15,000 and a thinning rate of 5. We chose vague priors for all variables and random starting values for all chains. We confirmed the convergence of MCMC chains by visually inspecting trace plots, and via the Gelman-Rubin statistic (\hat{R}) (Hobbs and Hooten, 2015). We assessed model fit using Bayesian p -values (Hobbs and Hooten, 2015) calculated from the Freeman-Tukey and chi-squared statistics (Royle and Dorazio, 2008). In describing the effect of model covariates on ψ and p below, we report the posterior probability that the coefficient estimate for a given covariate is more extreme (greater or less) than zero (hereafter,

'posterior probability').

2.5. Comparing the effects of human presence and human footprint on wildlife nocturnality

We estimated the degree to which wildlife activity was concentrated during nocturnal hours by calculating the time difference in hours between noon and each detection of a wildlife species on camera. We used the absolute value of this "hours to noon" estimate as a measure of nocturnality such that we considered detections occurring farther from noon (i.e., closer to the middle of the night) to exhibit greater nocturnality. We then calculated the average nocturnality value for each species at each camera site, as well as the total number of independent detections of that species at each site. We used linear regression to compare the effects of human presence and human footprint on species nocturnality. We estimated camera site-level human presence as human detections per week (HPW), averaged across all three study periods (see above) at a site, and estimated site-level human footprint from building density (BUILDING) as described above. Both HPW and BUILDING were normalized to permit direct comparison of coefficient estimates, and log transformed to account for heterogeneity of variances. For each wildlife species, we fit a single, weighted linear regression model including both HPW and BUILDING as covariates and total detections of the species as a weighting term. We confirmed model fit by inspecting residual vs. fitted value and quantile-quantile plots.

2.6. Predicting the intensity of human presence across the landscape

We evaluated landscape scale predictors of human activity to determine where and when human presence would be concentrated on the landscape beyond developed areas. We estimated camera site-level human presence based on daily counts of humans detected at each camera, as described above. We expected temporal variation in human activity due to a "day-of-the-week effect" (WEEKEND), given that outdoor activity is typically greater on weekends when recreational opportunities are greatest (Nix et al., 2018). We therefore summed human counts for each camera site based on day of the week, creating two estimates per site corresponding to expected low and high human activity, i.e., counts during the 5 days in the middle of the week (Monday–Friday; low activity) and those during the 2 days on the weekend (Saturday and Sunday; high activity). To account for uneven sampling effort between level of activity (weekday versus weekend), we included the total number of weekday or weekend days a camera was active as an offset in models described below, resulting in a response of humans per day (HPD). We modeled HPD as a function of multiple anthropogenic covariates related to human activity and accessibility (ROAD, BUILD, URBAN, WUI, TRAIL, OPEN, and ACCESS), as well as natural features that may drive recreational use (FOREST, RUGGED, ELEV and VIEW). To evaluate whether any landscape characteristics associated with human activity varied between weekends versus weekdays, we included a 2-way interaction between WEEKEND and all other covariates. We normalized all covariates to improve model convergence and to facilitate comparison of model coefficients among covariates (Gelman, 2008).

All pairs of covariates were tested for collinearity by examining Pearson correlation coefficients (r_p) and three pairs were found to be relatively strongly correlated ($r_p > 0.7$). ELEV and RUGGED showed substantial collinearity ($r_p = 0.94$) and, because RUGGED provided a meaningful measure of terrain complexity assumed to influence recreational activity such as hiking, ELEV was dropped from the analysis. ROAD and BUILD were also found to be strongly correlated with WUI ($r_p = 0.78$ and $r_p = 0.87$, respectively) and given that WUI is determined, in part, by both BUILD and ROAD (see Supplementary methods), we only retained WUI in the model. All other pairs of covariates exhibited limited correlation ($r_p \leq 0.4$).

Based on Vuong closeness tests (Vuong, 1989), we formulated our

model as a zero-inflated Poisson (ZIP) model, as data were skewed towards counts of zero humans per camera day. ZIP model and Vuong closeness tests were fit using the R package `pscl`. Beginning with a full model that included all covariates just described (except those excluded for collinearity), we determined the best supported ZIP model via backward stepwise elimination of variables based on AICc (calculated using the R package `MuMIn`). Model quality and goodness of fit was assessed using adjusted pseudo- R^2 as proposed by Martin and Hall (2016). We performed all analyses in R (v. 3.4.2; R Development Core Team, 2010).

Finally, to illustrate the relative intensity of human presence across the broader landscape, we used the suite of spatial covariates retained in the best supported zero-inflated Poisson model to project model predictions across the Santa Cruz Mountains study area. Spatial predictions were only made for areas characterized by relatively low development (≤ 120 buildings km^{-2} , constituting wildland to exurban areas, see Fig. S1), as human presence in heavily developed areas (i.e., the cities of Santa Cruz and San Jose and major suburbs) is assumed to be consistently high. We limited our prediction area to a 2-km buffer (half the distance between neighboring camera traps) surrounding the minimum convex polygon of all camera trap locations such that predictions were restricted to the area actually sampled by camera traps (Fig. S1).

3. Results

3.1. Effects of human presence and human footprint on wildlife habitat use

Our multi-species occupancy models revealed that human presence and human footprint are not equivalent in their effects on wildlife habitat use (Fig. 2, Tables S1 and S2), with the magnitude and sign of the effect of each human disturbance type varying substantially between species. Both human presence and human footprint models exhibited successful convergence ($\hat{R} < 1.1$ for all model terms) and excellent fit (Bayesian p -values: $0.445 \leq p \leq 0.499$). Several species exhibited a positive relationship between the probability of occurring at a camera site (ψ) and human presence (average human detections per day) at that site (pumas, bobcats, and foxes; posterior probability for all species ≥ 0.99 ; Table S1). By contrast human footprint (building density) had a strong negative effect on fox occurrence probability (posterior

probability = 1; Fig. 2, Table S2). Several well-known synanthropic species (coyotes, skunks, and opossums) exhibited relatively strong positive associations between occurrence probability and footprint (posterior probability: coyotes = 0.99, skunks = 0.96, opossums = 0.92).

Human presence and human footprint had similarly non-equivalent effects on the intensity with which wildlife used the camera sites (i.e., overall activity level, p). The number of human detections per day had a strong negative effect on the intensity of use by skunks and opossums (posterior probability = 0.99 and 0.97, respectively), with bobcats and foxes showing the opposite pattern (posterior probability = 1 for both species; Fig. 2, Table S1). Pumas (0.97), bobcats (0.99), and foxes (1.0) were all less active with increasing human footprint, while common synanthropic species showed increasing intensity of use with increasing footprint (skunks and raccoons, posterior probability = 1.0 for both species; Fig. 2, Table S2).

For several species, the effects of human presence on habitat use were mediated by the availability of forest cover. Both foxes and opossums were increasingly likely to occur at sites with high human presence as the availability of forest cover increased (Fig. 3a,b; Table S1). Coyotes similarly exhibited increased occurrence probability at high building density sites where high forest cover was available, while bobcats showed the opposite pattern, though with substantial variability (Fig. 3c,d; Table S2). Full results of the human presence and human footprint occupancy models are presented in Tables S1 and S2. Estimates of average use intensity (p) and probability of occurrence (ψ) for each species are presented in Table S3.

3.2. Effects of human presence and human footprint on wildlife nocturnality

Several wildlife species exhibited significant temporal shifts in their diel activity patterns across the gradients of human presence and/or footprint. Pumas (weighted linear regression: $F_{1,67} = 17.22$, $p < 0.001$), bobcats ($F_{1,67} = 3.81$, $p = 0.05$), and coyotes ($F_{1,67} = 8.47$, $p = 0.007$) exhibited increased nocturnality as human presence at a site increased. Bobcats also exhibited increased nocturnality with increasing building density ($F_{1,67} = 9.51$, $p = 0.003$) while foxes were moderately less nocturnal at increasing levels of building density ($F_{1,67} = 8.38$, $p = 0.005$; Fig. 4, Table S4).

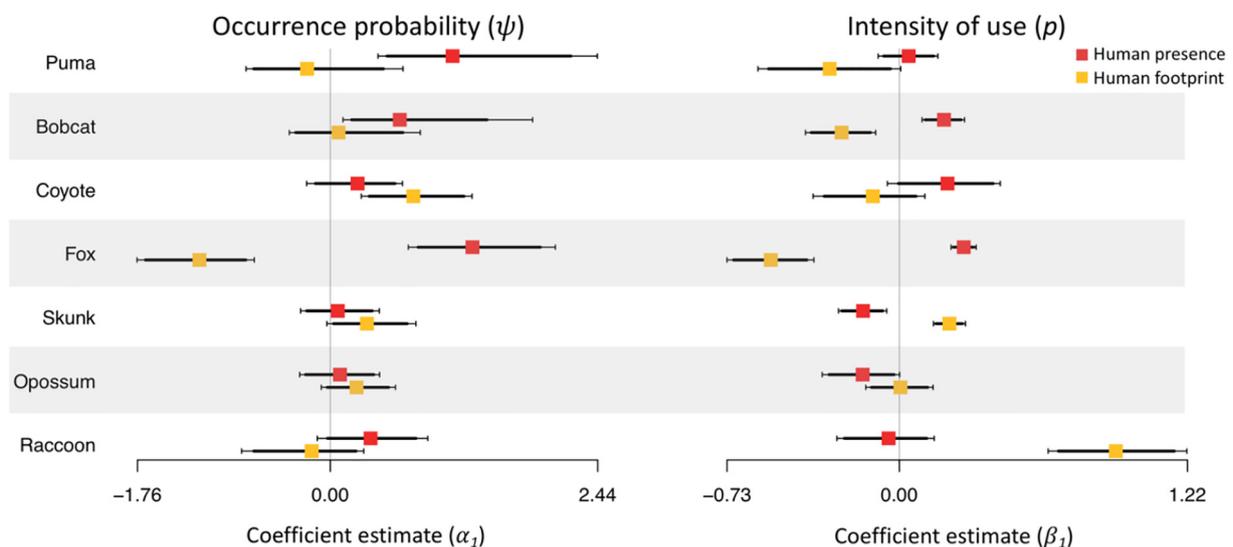


Fig. 2. Coefficient estimates from the multispecies occupancy models showing the effect of human presence (detections on camera; red) and human footprint (building density; yellow) on occurrence probability (ψ) and intensity of use (p) for each wildlife species. Symbols to the right of zero (vertical line) indicate a positive effect of the human disturbance metric on occurrence or intensity of use, and symbols to the left of zero indicate a negative effect. Thick horizontal lines are 90% Bayesian credible intervals, and thin horizontal lines are 95% credible intervals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

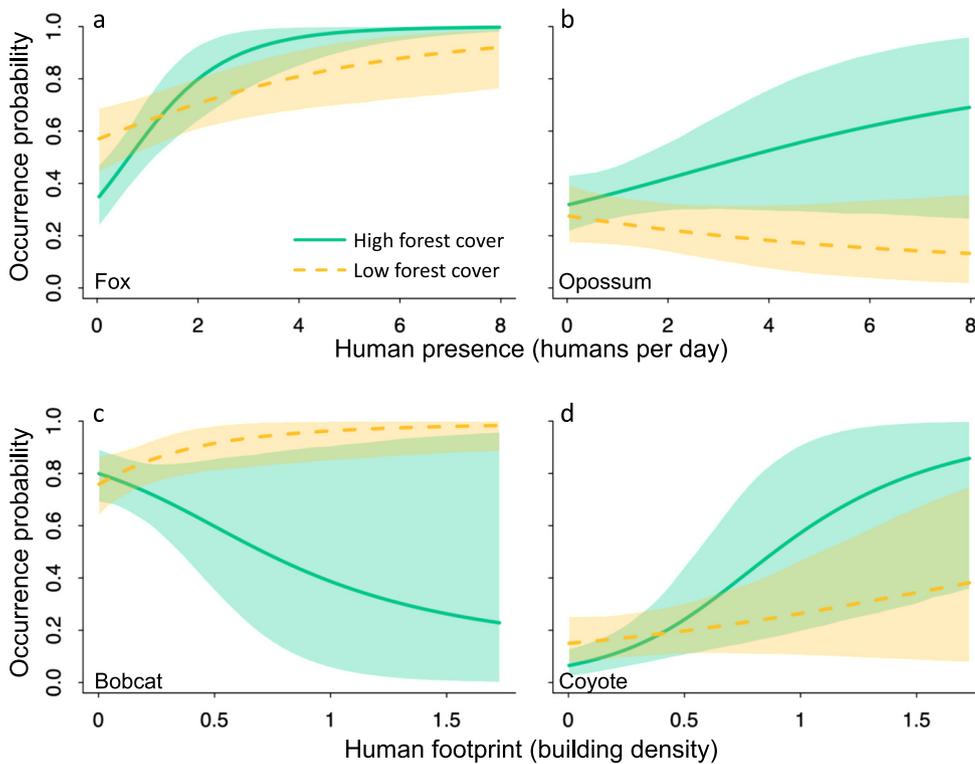


Fig. 3. Human disturbance interacts with forest cover to affect wildlife species occurrence probability. The effect of human presence (detections on camera; a,b) and human footprint (building density; c,d) on occurrence probability are shown for (a) foxes, (b) opossums, (c) bobcats, and (d) coyotes at both low (yellow) and high (green) levels of forest cover. Low and high forest cover are here defined as the 20% and 80% quantiles, respectively, of forest cover across all camera sites. Lines and shaded areas are predictions and 95% Bayesian credible intervals from the multi-species occupancy model. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.3. Predicting the intensity of human presence across the landscape

The ZIP model revealed a strong association between several landscape-level variables and the intensity of human activity outside of developed areas ($\chi_{11,176}^2 = 1163$, $p < 0.001$; Pseudo $R^2 = 0.63$; Table 2; Fig. 5a). As expected, human activity (i.e., humans per day, HPD) varied depending on the time of the week with increased activity on weekends ($\beta_{\text{WEEKEND}} = 0.29$, $p < 0.001$) compared to weekday use. HPD also increased significantly in areas with greater opportunities for recreational activities, including proximity to public open space ($\beta_{\text{OPEN}} = -0.77$, $p < 0.001$), higher trail density ($\beta_{\text{TRAIL}} = 0.99$, $p < 0.001$), greater proportion of vista opportunities ($\beta_{\text{VIEW}} = 0.10$, $p < 0.001$), and adjacency to recreational access points ($\beta_{\text{ACCESS}} = -0.89$, $p < 0.001$). Additionally, HPD was greater in proximity to highly developed urban areas ($\beta_{\text{URBAN}} = -0.16$, $p = 0.04$) as well as those dominated by exurban expansion into rural landscapes ($\beta_{\text{WUI}} = 0.11$, $p < 0.001$). However, an interaction with weekend ($\beta_{\text{URBAN:WEEKEND}} = 0.46$, $p < 0.001$) suggests activity is more prevalent in areas farther away from developed areas on the weekend, with use localized to areas near development during weekdays. The surrounding natural characteristics of a site also influenced HPD with decreased activity in more rugged landscapes ($\beta_{\text{RUGGED}} = -0.14$, $p < 0.001$), though human use of rugged areas increased on weekends ($\beta_{\text{RUGGED:WEEKEND}} = 0.2$, $p = 0.004$). We did not find significant correlations for the remainder of the variables. The Vuong test suggested that the ZIP model was a significant improvement over a standard Poisson regression model ($p < 0.0001$).

4. Discussion

Although a growing body of research demonstrates that both human footprint and human presence (including recreation) can have negative impacts on wildlife (Larson et al., 2016; Gaynor et al., 2018; Tucker et al., 2018), studies aimed at disentangling the concurrent effect of both forms of disturbance on wildlife behavior are surprisingly rare. Our results demonstrate that human presence and human footprint have differing, and in some cases opposite, effects on wildlife habitat

use and activity patterns. These effects are likely widespread, as modeling results indicated that human presence outside of developed areas was extensive, particularly in protected areas with high recreational potential. Moreover, we were able to predict the intensity of human presence from landscape-level variables, demonstrating a methodology that can be used by other researchers to estimate human impacts on wildlife outside of developed areas. Together, these results refine our understanding of how both human activity and development drive changes in wildlife behavior and demonstrate that solely focusing on one type of anthropogenic disturbance may lead to erroneous conclusions regarding the way human-induced risk affects wildlife.

4.1. Contrasting effects of human presence and human footprint on wildlife habitat use and behavior

Our results demonstrate that human presence and human footprint are not equivalent in their impacts on wildlife habitat use and behavior. Building density and other forms of development represent long-term and spatially constant sources of disturbance, and several sensitive wildlife species have been shown to avoid these risky places (Riley, 2006; Ordeñana et al., 2010; Wilmers et al., 2013). We correspondingly found negative effects of building density on the habitat use of several mammalian predators. Pumas and bobcats exhibited strong decreases in intensity of use with increasing building density, though occurrence probability was unaffected (Fig. 2), suggesting that these species reduced their overall activity levels in areas of high human footprint, but still occasionally use habitat with moderate levels of development. Gray foxes appeared to be particularly sensitive to human footprint, with building density having a strong negative effect on fox occurrence probability and intensity of use (Fig. 2). Thus, foxes tended to avoid high human footprint and exhibited lower activity levels when present in these areas.

By contrast, these same three predators (and to a lesser extent, coyotes) exhibited increased occurrence and/or activity with increasing human presence, despite growing experimental evidence that several large and medium-sized predator species (including pumas and bobcats) exhibit strong fear responses to humans (Clinchy et al., 2016;

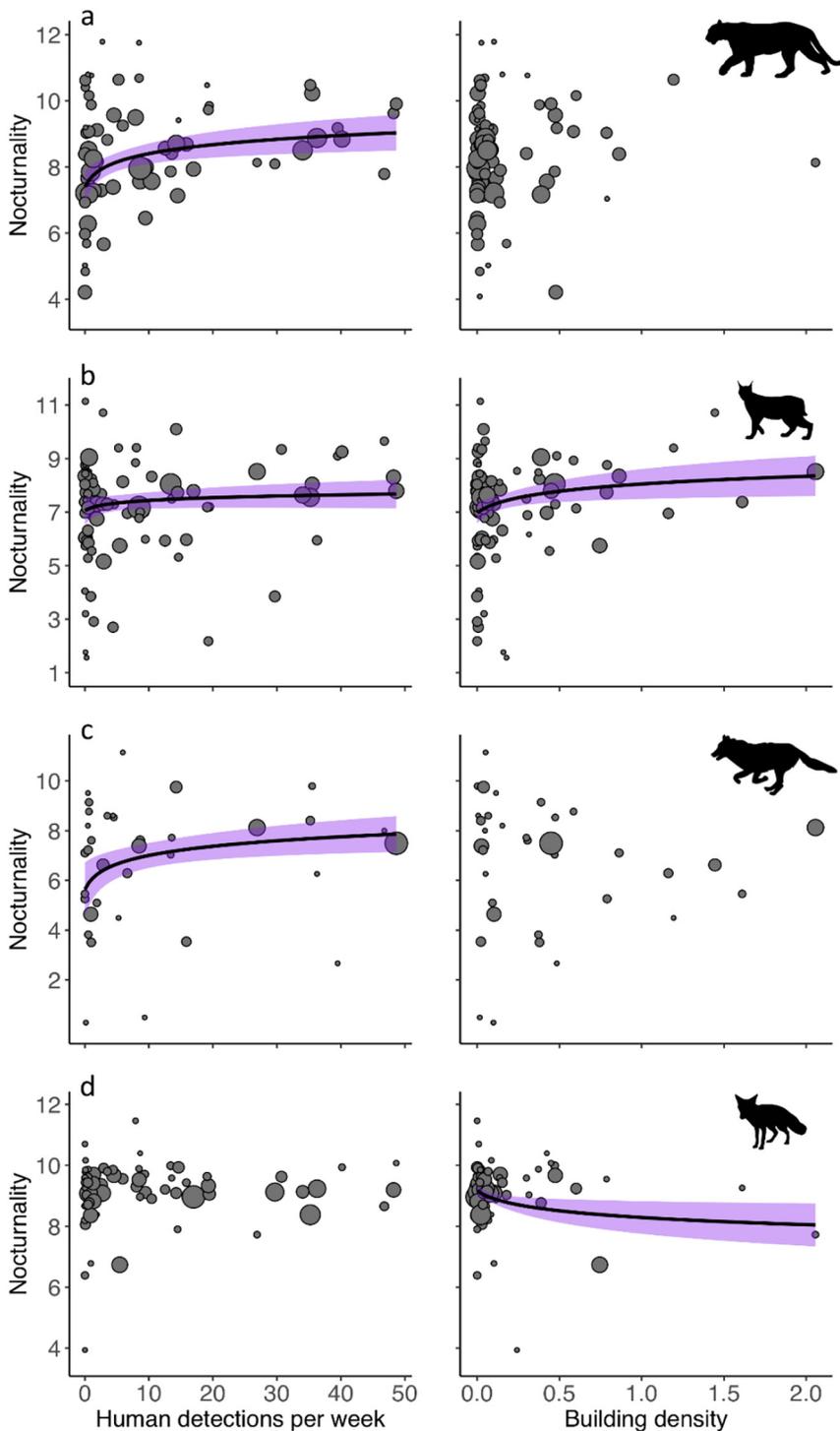


Fig. 4. The effect of human disturbance on wildlife nocturnality. Nocturnality estimates (i.e., average time of detections on camera expressed as hours from noon) at a given camera site are plotted against human detections per week and building density at that camera site for (a) pumas, (b) bobcats, (c) coyotes, and (d) foxes. Fitted lines and shaded areas represent the predicted effect, \pm 95% confidence intervals, of human disturbance on nocturnality. Absence of a fitted line indicates no significant effect of disturbance on nocturnality. Only those wildlife species for which at least one human disturbance type significantly affected nocturnality are shown.

Smith et al., 2017; Suraci et al., 2019a). Previous observational studies examining the impacts of recreationalists on mammalian predators have found mixed results, ranging from a negative effect of human presence on predator detections to neutral or positive effects on predator habitat use (Reed and Merenlender, 2008; Reilly et al., 2017; Kays et al., 2017). We suggest that these differences may be due in part to the spatial distribution of human presence on the landscape. Our spatial modeling results (Fig. 5) revealed that human presence is relatively high throughout many of the protected areas in the Santa Cruz Mountains, and thus likely overlaps with high-quality habitat for many species, potentially making the outright avoidance of human presence in wildland areas overly costly. Additionally, highly mobile species

such as pumas, bobcats, and coyotes, may be positively associated with areas of high human presence because, like humans, these species are attracted to trails through wooded areas (Kays et al., 2017), which provide energetically efficient movement pathways across relatively large home ranges (Dickie et al., 2017). Our results indicate that, instead of avoiding humans in space, these species take advantage of the high temporal predictability of human activity to avoid humans in time, becoming increasingly nocturnal as human presence increases (Fig. 4). Increased wildlife nocturnality as a response to increasing human disturbance has been demonstrated for many wildlife species globally (Gaynor et al., 2018) and has been associated with both human footprint (Beckmann and Berger, 2003; Díaz-Ruiz et al., 2016) and high

Table 2
Fixed effects terms from the best-supported model for predicting human presence on the landscape.

Model parameter	β	SE	t	p
Pseudo R ² = 0.63				
TRAIL	0.99	0.004	7.53	< 0.001
ACCESS	-0.89	0.006	5.73	< 0.001
OPEN	-0.77	0.004	14.64	< 0.001
WEEKEND	0.29	0.004	12.92	< 0.001
RUGGED	-0.14	0.004	4.89	< 0.001
WUI	0.11	0.005	-4.68	< 0.001
VIEW	0.10	0.004	-2.21	0.05
URBAN	-0.16	0.004	-2.12	0.03
URBAN:WEEKEND	0.46	0.004	-2.43	0.004
RUGGED:WEEKEND	0.20	0.004	-2.21	0.02

human presence (e.g., recreation) in wildland areas (Wang et al., 2015; Reilly et al., 2017). Restricting activity to nocturnal hours may involve substantial costs for some wildlife species, e.g., by interfering with foraging behavior or increasing overlap with predators or competitors (Gaynor et al., 2018; Smith et al., 2018), but may nonetheless promote coexistence by allowing humans and wildlife to use the same habitat (Carter et al., 2012; Suraci et al., 2019b).

Human presence and human footprint also had opposing effects on habitat use by skunks and opossums, synanthropic species which commonly take advantage of human resource subsidies (e.g., food waste) in developed areas (Bateman and Fleming, 2012). Recent experimental work demonstrates that, despite their strong association with human development, these species are nonetheless fearful of immediate human presence, reducing activity and foraging behavior when perceived human presence was experimentally increased (Suraci et al., 2019a). The present study confirms that these experimental results are relevant at the regional scale. Despite exhibiting increased occupancy (skunks and opossums) and detection probability (skunks) with increasing building density, both skunks and opossums were substantially less detectable in areas with high human presence, consistent with reduced activity levels in the presence of people. Taken together, these findings suggest that, even for synanthropic species, human presence is potentially costly, and that the benefits of exploiting anthropogenic environments (e.g., resources subsidies) must be traded off against the risks of a potentially dangerous direct encounter with humans.

For several predator species, occupancy of habitats with either high human presence (foxes and opossums) or high human footprint (coyotes) increased with increasing forest cover, indicating that the availability of protective cover reduces the risk that some wildlife species perceive from humans. Previous studies have similarly demonstrated increased use of human-dominated landscapes by mammalian predators when the availability of protective cover is high (Boydston et al., 2003; Ordiz et al., 2011; Suraci et al., 2019b), suggesting that cover availability plays a key role in mediating coexistence between humans and predators by reducing the impacts of anthropogenic disturbance on predator behavior.

4.2. Predicting the intensity of human presence across the landscape

Projecting the predictions of our human presence model across the broader landscape (Fig. 5A) reveals that human activity outside of developed areas is pervasive throughout the Santa Cruz Mountains region, with several major protected areas (composed of otherwise high-quality wildlife habitat) predicted to have relatively high levels of human use intensity. Comparing the spatial distribution of human presence with that of human footprint (Fig. 5B) highlights the fact that human presence (and its associated impacts on wildlife habitat use and temporal activity) is not necessarily spatially linked to development, with areas of high human presence intensity extending well beyond the heavily developed cities and suburbs (Fig. 5). Indeed, relatively little land area

in the Santa Cruz Mountains is expected to experience low levels of both human presence and human footprint. Completely “undisturbed” habitat – areas predicted to experience zero human presence and to be at least 1 km from the nearest building – accounts for only 1.14% of the study area.

Human presence beyond heavily developed areas varied widely across the region with the most important drivers of use related to variation in accessibility and demand for recreation. In particular, human presence was higher in conserved lands with infrastructure providing access to recreational opportunities. Proximity to public open space, vehicle access, and trail density were the strongest predictors of human presence at a site, consistent with previous findings suggesting that access to dense trail networks is correlated with significantly higher visitation rates (Reed and Merenlender, 2008, 2011; Larson et al., 2018). Similarly, ruggedness and the scenic potential of a site were positively associated with human use. As such, human presence was predicted to be regular and widespread in protected areas with high recreation potential and where recreation infrastructure is well-developed. Given that protected lands often overlap with high-quality habitat for many species, elevated human activity in these areas likely leads to substantial, yet unintended, impacts on wildlife from disturbance.

We found higher levels of human presence at sites adjacent to urban development as well as those immediately surrounded by the wildland-urban interface (Patten and Burger, 2018; Larson et al., 2018). This pattern is particularly significant for urban-adjacent reserves as the potential for human-wildlife interactions and thus negative impacts is likely greatest given the already elevated presence of humans in protected areas of the region. However, we detected a significant interaction between distance to urban center and weekend (Table 1), indicating that human presence in protected areas shifted depending on the day of the week with greater concentrations of activity at sites further away from developed areas on weekends (Rossi et al., 2015; Larson et al., 2018). This shift in human activity depending on day of the week meant that even relatively remote areas of the Santa Cruz Mountains were exposed to substantial human presence during some time periods.

4.3. Conservation and management implications

Our approach to modeling human presence and evaluating species response to human activity can be used to guide future research and inform guidelines for the management of non-consumptive recreation in open space lands. For example, landscape level measures of the human footprint, such as land cover, population density, and built infrastructure, are well developed and readily available (Venter et al., 2016), however spatially explicit data on human presence outside of developed areas are notably absent (but see Gutzwiller et al., 2017). Our approach helps address this gap and demonstrates that the intensity of human presence on the landscape (including in wildland areas) can be predicted from landscape-level variables, allowing estimation of human impacts on wildlife even outside of developed areas. Further, we showed that modeling human presence is possible using increasingly available sources of spatial data (e.g., parking lots, elevation, trails) allowing for projecting or forecasting the intensity of human activity at the landscape scale (Fig. 5). Predictive models of this nature could be used to improve landscape-wide management of non-consumptive forms of human disturbance. For example, when planning for future recreation uses of an area, land-use managers could predict human activity, and thus disturbance potential, based on where they place trails and parking lots.

Taken together, our research demonstrates that in many cases the human footprint on the landscape is unlikely to be an adequate predictor of total anthropogenic impacts on wildlife communities given that (i) human presence and development differ in their effects on wildlife behavior and habitat use (Fig. 2), and (ii) the potential impacts

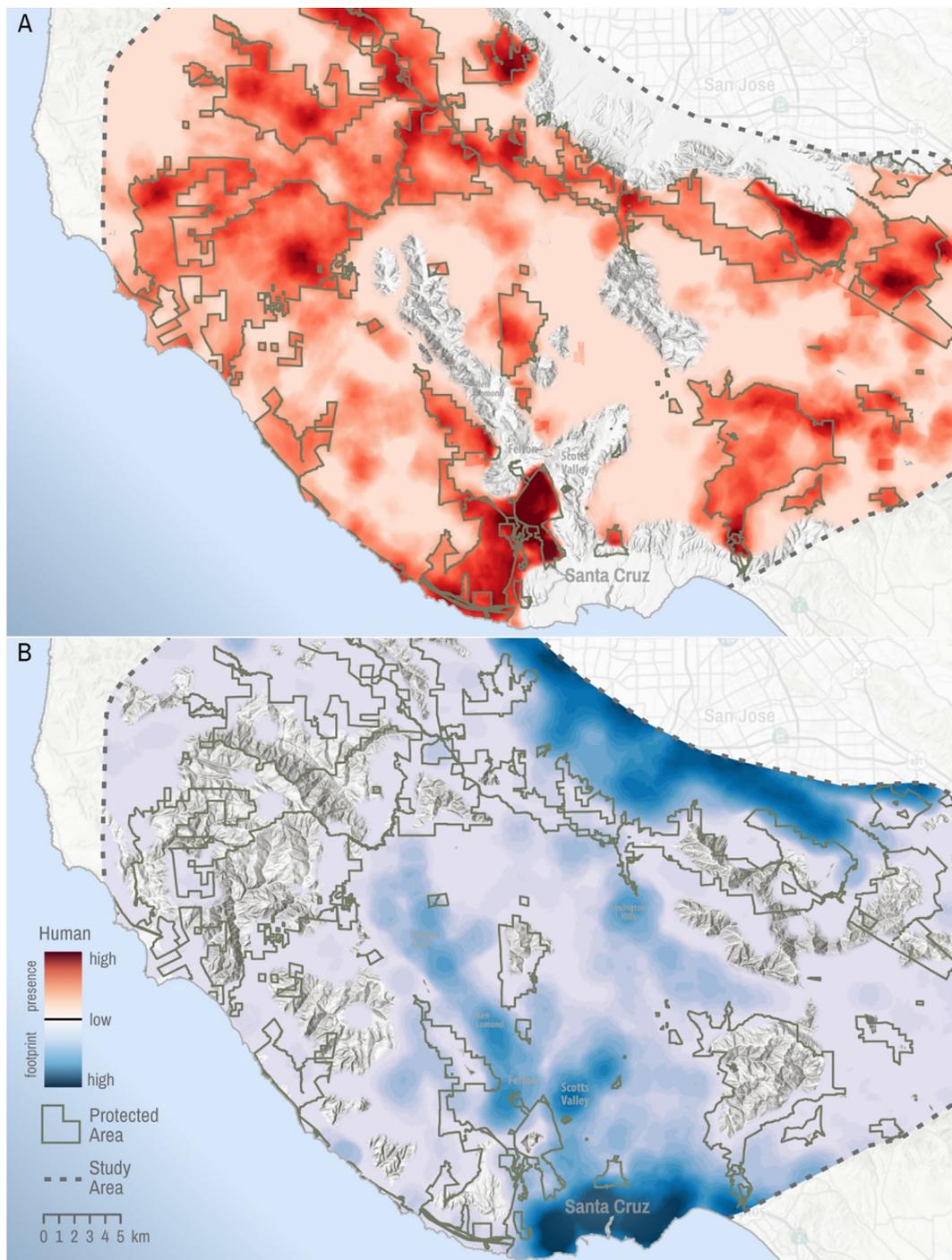


Fig. 5. Comparing human presence and human footprint across the broader landscape. (A) The relative intensity of human presence, ranging from low (light pink) to high (dark red), is derived from our modeling results (Table 2) using publicly available sources of spatial data. Human presence is projected across areas of the Santa Cruz Mountains (SCM) characterized by relatively low development (≤ 120 buildings km^{-2} ; see Methods and Fig. S1 for details). (B) Human footprint (low = light blue, high = dark blue) is derived from the density of all building points, estimated using a Gaussian kernel with 1-km bandwidth, and is plotted for all areas of SCM with building density ≥ 1 building km^{-2} . Human presence and human footprint surfaces are truncated to within 2 km of the extent of our camera trap grid. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

of human presence extend well beyond the spatial footprint of developed areas (Fig. 5). Occupancy modeling results revealed that several wildlife species avoided human development overall, meaning that projected increases in development (Smith et al., 2019) will only increase the importance of protected areas in providing wildlife habitat. However, as development intensifies so will human activity and the associated costs to wildlife in terms of changes in behavior and activity patterns, posing serious challenges for landscape management and

conservation. This is especially true in and around protected areas where recreation activity is often greatest but not always compatible with conservation objectives (Larson et al., 2016). Conservation planning should thus take into account not only wildlife distributions but also the spatial extent of human activities, including recreational demand, and its compatibility with conservation goals and other land-management objectives.

CRediT authorship contribution statement

Barry A. Nickel: Conceptualization, Methodology, Formal analysis, Writing - original draft, Visualization. **Justin P. Suraci:** Conceptualization, Methodology, Formal analysis, Writing - original draft, Visualization. **Maximilian L. Allen:** Conceptualization, Methodology, Investigation, Writing - review & editing. **Christopher C. Wilmers:** Conceptualization, Methodology, Writing - review & editing, Project administration, Funding acquisition.

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None of the funding sources played any role in study design; in the collection, analysis, and interpretation of data; in the writing of the report; or in the decision to submit the paper for publication.

Declaration of competing interest

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Appendix A. Supplementary material

Supplementary methods, tables and figures for this article can be found online at <https://doi.org/10.1016/j.biocon.2019.108383>.

References

- Balmford, A., Green, J.M.H., Anderson, M., Beresford, J., Huang, C., Naidoo, R., Walpole, M., Manica, A., 2015. Walk on the wild side: estimating the global magnitude of visits to protected areas. *PLoS Biol.* 13, e1002074.
- Bateman, P.W., Fleming, P.A., 2012. Big city life: carnivores in urban environments. *J. Zool.* 287, 1–23.
- Beckmann, J.P., Berger, J., 2003. Rapid ecological and behavioural changes in carnivores: the responses of black bears (*Ursus americanus*) to altered food. *J. Zool.* 261, 207–212.
- Boydston, E.E., Kapheim, K.M., Watts, H.E., Szykman, M., Holekamp, K.E., 2003. Altered behaviour in spotted hyenas associated with increased human activity. *Anim. Conserv.* 6, 207–219.
- Broms, K.M., Hooten, M.B., Fitzpatrick, R.M., 2016. Model selection and assessment for multi-species occupancy models. *Ecology* 97, 1759–1770.
- Burton, A.C., Sam, M.K., Balangtaa, C., Brashares, J.S., 2012. Hierarchical multi-species modeling of carnivore responses to hunting, habitat and prey in a West African protected area. *PLoS One* 7.
- Burton, A.C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J.T., Bayne, E., Boutin, S., 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *J. Appl. Ecol.* 52, 675–685.
- Carter, N.H., Shrestha, B.K., Karki, J.B., Man, N., Pradhan, B., Liu, J., 2012. Coexistence between wildlife and humans at fine spatial scales. *Proc. Natl. Acad. Sci.* 109, 15360–15365.
- Clinchy, M., Zanette, L.Y., Roberts, D., Suraci, J.P., Buesching, C.D., Newman, C., Macdonald, D.W., 2016. Fear of the human “super predator” far exceeds the fear of large carnivores in a model mesocarnivore. *Behav. Ecol.* 27, arw117.
- Cordell, H.K., Betz, C.J., Green, G.T., 2008. Nature-based outdoor recreation trends and wilderness. *Int. J. Wildland Fire* 14, 7–10.
- Creel, S., Winnie, J.A., Christianson, D., Liley, S., 2008. Time and space in general models of antipredator response: tests with wolves and elk. *Anim. Behav.* 76, 1139–1146.
- Darimont, C.T., Fox, C.H., Bryan, H.M., Reimchen, T.E., 2015. The unique ecology of human predators. *Science* 349, 858–861.
- Díaz-Ruiz, F., Caro, J., Delibes-Mateos, M., Arroyo, B., Ferreras, P., 2016. Drivers of red

- fox (*Vulpes vulpes*) daily activity: prey availability, human disturbance or habitat structure? *J. Zool.* 298, 128–138.
- Dickie, M., Serrouya, R., McNay, R.S., Boutin, S., 2017. Faster and farther: wolf movement on linear features and implications for hunting behaviour. *J. Appl. Ecol.* 54, 253–263.
- Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the Anthropocene. *Science* 345 (401 LP – 406).
- Dröge, E., Creel, S., Becker, M.S., M’soka, J., 2017. Risky times and risky places interact to affect prey behaviour. *Nature Ecology & Evolution* 1, 1123–1128.
- Efford, M.G., Dawson, D.K., 2012. Occupancy in continuous habitat. *Ecosphere* 3, art32.
- Fischer, J., Lindenmayer, D.B., 2007. Landscape modification and habitat fragmentation: a synthesis. *Glob. Ecol. Biogeogr.* 16, 265–280.
- Frid, A., Dill, L., 2002. Human-caused disturbance stimuli as a form of predation risk. *Conserv. Ecol.* 6, 11.
- Gaynor, K.M., Hohnowski, C.E., Carter, N.H., Brashares, J.S., 2018. The influence of human disturbance on wildlife nocturnality. *Science* 360, 1232–1235.
- Gelman, A., 2008. Scaling regression inputs by dividing by two standard deviations. *Stat. Med.* 27, 2865–2873.
- Gutzwiller, K.J., D’Antonio, A.L., Monz, C.A., 2017. Wildland recreation disturbance: broad-scale spatial analysis and management. *Front. Ecol. Environ.* 15, 517–524.
- Hansen, A.J., Knight, R.L., Marzluff, J.M., Powell, S., Brown, K., Gude, P.H., Jones, K., 2005. Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. *Ecol. Appl.* 15, 1893–1905.
- Hobbs, N.T., Hooten, M.B., 2015. *Bayesian Models: A Statistical Primer for Ecologists*. Princeton University Press, Princeton.
- Kays, R., Parsons, A.W., Baker, M.C., Kalies, E.L., Forrester, T., Costello, R., Rota, C.T., Millsbaugh, J.J., McShea, W.J., 2017. Does hunting or hiking affect wildlife communities in protected areas? *J. Appl. Ecol.* 54, 242–252.
- Kohl, M.T., Stahler, D.R., Metz, M.C., Forester, J.D., Kauffman, M.J., Varley, N., White, P.J., Smith, D.W., MacNulty, D.R., 2018. Diel predator activity drives a dynamic landscape of fear. *Ecol. Monogr.* 88, 638–652.
- Ladle, A., Avgar, T., Wheatley, M., Boyce, M.S., 2017. Predictive modelling of ecological patterns along linear-feature networks. *Methods Ecol. Evol.* 8, 329–338.
- Larson, C.L., Reed, S.E., Merenlender, A.M., Crooks, K.R., 2016. Effects of recreation on animals revealed as widespread through a global systematic review. *PLoS One* 11, e0167259.
- Larson, C.L., Reed, S.E., Merenlender, A.M., Crooks, K.R., 2018. Accessibility drives species exposure to recreation in a fragmented urban reserve network. *Landsc. Urban Plan.* 175, 62–71.
- MacKenzie, D., Nichols, J., Lachman, G., 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83, 2248–2255.
- MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G., Franklin, A.B., 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84, 2200–2207.
- Martin, J., Hall, D.B., 2016. R2 measures for zero-inflated regression models for count data with excess zeros. *J. Stat. Comput. Simul.* 86, 3777–3790.
- Martinuzzi, S., Stewart, S.L., Helmers, D.P., Mockrin, M.H., Hammer, R.B., Radeloff, V.C., 2015. The 2010 wildland-urban interface of the conterminous United States. In: *Research Map NRS-8*. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA.
- Monz, C.A., Pickering, C.M., Hadwen, W.L., 2013. Recent advances in recreation ecology and the implications of different relationships between recreation use and ecological impacts. *Front. Ecol. Environ.* 11, 441–446.
- Muhly, T.B., Semeniuk, C., Massolo, A., Hickman, L., Musiani, M., 2011. Human activity helps prey win the predator-prey space race. *PLoS One* 6, e17050.
- Neilson, E.W., Avgar, T., Burton, A.C., Broadley, R., Boutin, S., 2018. Animal movement affects interpretation of occupancy models from camera-trap surveys of unmarked animals. *Ecosphere* 9, e02092.
- Nix, J.H., Howell, R.G., Hall, L.K., McMillan, B.R., 2018. The influence of periodic increases of human activity on crepuscular and nocturnal mammals: testing the weekend effect. *Behav. Process.* 146, 16–21.
- O’Connell, A.F., Nichols, J.D., Karanth, K.U. (Eds.), 2011. *Camera Traps in Animal Ecology: Methods and Analyses*. Springer, Japan.
- Ordeñana, M.A., Crooks, K.R., Boydston, E.E., Fisher, R.N., Lyren, L.M., Siudyla, S., Haas, C.D., Harris, S., Hathaway, S.A., Turschak, G.M., Keith, A., Van Vuren, D.H., 2010. Effects of urbanization on carnivore species distribution and richness. *J. Mammal.* 91, 1322–1331.
- Ordiz, A., Støen, O.-G., Delibes, M., Swenson, J.E., 2011. Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia* 166, 59–67.
- Patten, M.A., Burger, J.C., 2018. Reserves as double-edged sword: avoidance behavior in an urban-adjacent wildland. *Biol. Conserv.* 218, 233–239.
- Radeloff, V.C., Hammer, R.B., Stewart, J.S.F., Holcomb, S.S., McKeefry, J.F., 2005. The wildland-urban interface in the United States. *Ecol. Appl.* 15, 799–805.
- Radeloff, V.C., Stewart, S.L., Hawbaker, T.J., Gimmi, U., Pidgeon, A.M., Flather, C.H., Hammer, R.B., Helmers, D.P., 2010. Housing growth in and near United States protected areas limits their conservation value. *Proc. Natl. Acad. Sci.* 107, 940–945.
- R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.** <https://www.R-project.org/>.
- Reed, S.E., Merenlender, A.M., 2008. Quiet, nonconsumptive recreation reduces protected area effectiveness. *Conserv. Lett.* 1, 146–154.
- Reed, S.E., Merenlender, A.M., 2011. Effects of management of domestic dogs and recreation on carnivores in protected areas in northern California. *Conserv. Biol.* 25, 504–513.
- Reilly, M.L., Tobler, M.W., Sonderegger, D.L., Beier, P., 2017. Spatial and temporal response of wildlife to recreational activities in the San Francisco Bay ecoregion. *Biol.*

- Conserv. 207, 117–126.
- Riley, S.P.D., 2006. Spatial ecology of bobcats and gray foxes in urban and rural zones of a national park. *J. Wildl. Manag.* 70, 1425–1435.
- Rossi, S.D., Byrne, J.A., Pickering, C.M., 2015. The role of distance in peri-urban national park use: who visits them and how far do they travel? *Appl. Geogr.* 63, 77–88.
- Royle, J.A., Dorazio, R.M., 2008. Hierarchical Models of Animal Abundance and Occurrence in Ecology: The Analysis of Data From Populations, Metapopulations and Communities. Academic Press, London, UK.
- Smith, J.A., Suraci, J.P., Clinchy, M., Crawford, A., Roberts, D., Zanette, L.Y., Wilmers, C.C., 2017. Fear of the human 'super predator' reduces feeding time in large carnivores. *Proc. R. Soc. B Biol. Sci.* 284, 20170433.
- Smith, J.A., Thomas, A.C., Levi, T., Wang, Y., Wilmers, C.C., 2018. Human activity reduces niche partitioning among three widespread mesocarnivores. *Oikos* 127, 890–901.
- Smith, J.A., Duane, T.P., Wilmers, C.C., 2019. Moving through the matrix: promoting permeability for large carnivores in a human-dominated landscape. *Landsc. Urban Plan.* 183, 50–58.
- Suraci, J.P., Clinchy, M., Zanette, L.Y., Wilmers, C.C., 2019a. Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecol. Lett.* 22, 1578–1586.
- Suraci, J.P., Frank, L.G., Oriol-Cotterill, A., Ekwanga, S., Williams, T.M., Wilmers, C.C., 2019b. Behavior-specific habitat selection by African lions may promote their persistence in a human-dominated landscape. *Ecology* 100 (4), e02644.
- Tablado, Z., Jenni, L., 2017. Determinants of uncertainty in wildlife responses to human disturbance. *Biol. Rev.* 92, 216–233.
- Tucker, M.A., Böhning-Gaese, K., Fagan, W.F., Fryxell, J.M., Van Moorter, B., Alberts, S.C., Ali, A.H., Allen, A.M., Attias, N., Avgar, T., Bartlam-brooks, H., Bayarbaatar, B., Belant, J.L., Bertassoni, A., Beyer, D., Bidner, L., Van Beest, F.M., Blake, S., Blaum, N., Bracis, C., Brown, D., De Bruyn, P.J.N., Cagnacci, F., Diefenbach, D., Douglas-hamilton, I., Fennessy, J., Fichtel, C., Fiedler, W., Fischer, C., Fischhoff, I., Fleming, C.H., Ford, A.T., Fritz, S.A., Gehr, B., Goheen, J.R., Gurarie, E., Hebblewhite, M., Heurich, M., Hewison, A.J.M., Hof, C., Hurme, E., Isbell, L.A., Janssen, R., Jeltsch, F., Kaczensky, P., Kane, A., Kappeler, P.M., Kauffman, M., Kays, R., Kimuyu, D., Koch, F., Kranstauber, B., Lapoint, S., Mattisson, J., Medici, E.P., Mellone, U., Merrill, E., Morrison, T.A., Díaz-muñoz, S.L., Mysterud, A., Nandintsetseg, D., Nathan, R., Niamir, A., Odden, J., Hara, R.B.O., Oliveira-santos, L.G.R., Olson, K.A., Patterson, B.D., De Paula, R.C., Pedrotti, L., Reineking, B., Rimmler, M., 2018. Moving in the Anthropocene: global reductions in terrestrial mammalian movements. *Science* 359, 466–469.
- Venter, O., Sanderson, E.W., Magrath, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., Levy, M.A., Watson, J.E.M., 2016. Data descriptor: global terrestrial human footprint maps for 1993 and 2009. *Scientific Data* 3, 160067.
- Vuong, Q.H., 1989. Likelihood ratio tests for model selection and non-nested hypotheses. *Econometrica* 57, 307.
- Wang, Y., Allen, M.L., Wilmers, C.C., 2015. Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. *Biol. Conserv.* 190, 23–33.
- Wilmers, C.C., Wang, Y., Nickel, B., Houghtaling, P., Shakeri, Y., Allen, M.L., Kermish-Wells, J., Yovovich, V., Williams, T., 2013. Scale dependent behavioral responses to human development by a large predator, the puma. *PLoS One* 8, e60590.