Reptile responses to outdoor recreation in urban habitat fragments

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Abstract

The world is urbanizing rapidly, resulting in increasing rates of habitat loss and fragmentation. Protected areas are commonly established to restrict development and conserve native ecological communities. Yet urban protected areas often receive high levels of recreational activity, which can reduce their conservation effectiveness because of disturbance to animals. Recreation has negative consequences for many animal species, but its effects on reptiles are largely unknown. We evaluated the effects of non-consumptive recreation on reptiles within urban protected areas in a fragmented landscape in coastal southern California, USA. We surveyed lizards and snakes along a gradient of recreation intensity and modeled species richness, community composition, and occupancy in relation to human activity along with other variables known to affect reptile distributions. We observed a decline in lizard species richness in association with human activity. Richness of habitat specialists was not related to recreation, but smaller-bodied lizards and lizards with narrower active temperature ranges were less common at sites with high human activity. Human activity was associated with a decline in occupancy of the common side-blotched lizard (*Uta stansburiana*), no meaningful relationship with occupancy of the orange-throated whiptail (*Aspidoscelis hyperythra*) and a positive relationship with western fence lizard (*Sceloporus occidentalis*) occupancy and/or detection probability. Our study demonstrates that increasing rates of recreation activity can reduce the ability of urban protected areas to conserve diverse reptile assemblages.

Keywords Reptile · Recreation · Species richness · Occurrence · Urban protected areas · Human activity

Introduction

The global human footprint is extensive and increasing rapidly, with 75% of the Earth's land surface currently experiencing measurable human pressures (Venter et al. 2016). This human pressure has had dramatic negative effects on wildlife populations worldwide, threatening at least 40% of the world's mammal species (Schipper et al. 2008). In addition to landscape modification, human activity on the landscape (e.g., recreation, hunting and gathering) can also affect wildlife (Suraci et al. 2019) and it is much more difficult to measure. However, it is important to quantify the effects of human activity on wildlife because they can vary

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in type and magnitude from the effects of landscape modification (Nickel et al. 2020).

Both landscape modification and human activity occur at high rates in and around urban areas. Protected areas are commonly established in urban areas to restrict development and conserve native ecological communities threatened by habitat loss and fragmentation (Watson et al. 2014). However, urban protected areas often face increased pressures compared to rural protected areas, such as fragmentation and edge effects (Woodroffe and Ginsberg 1998), loss of connectivity (Braaker et al. 2014), invasive species (Riley et al. 2005) and pollution (Grimm et al. 2008). These threats are growing as residential development intensifies around protected areas (Mcdonald et al. 2008; Radeloff et al. 2010). In addition, urban protected areas often have high rates of human activity within their boundaries resulting from large numbers of people living nearby (Larson et al. 2018; Chung et al. 2018; Weitowitz et al. 2019). Despite these threats, some species with small home ranges may be able to persist in urban habitat fragments and maintain sufficient population size (Shafer 1995; Delaney et al. 2021). Alternatively,



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parks and preserves with high levels of human activity could be ecological traps (Schlaepfer et al. 2002) if animal populations are declining due to human activity, but individuals are not able to move to alternate habitat because of the impermeability of the urban matrix (Delaney et al. 2010).

Recreation has negative effects on many animal species (Martínez-Abraín et al. 2010; Sato et al. 2013; Larson et al. 2016, 2019). However, reptile responses to recreation are not well understood; fewer than 6% of published studies of recreation impacts on animals focus on reptiles, but they are frequently impacted, with 63% of studies observing significant effects (Larson et al. 2016). Reptiles are likely to be vulnerable because they are targets of unsustainable collection (Gibbons et al. 2000), they may be drawn to trails for thermoregulation (Mccardle and Fontenot 2016), human activity can be a source of direct mortality along roads and trails (Rochester et al. 2001), and they are sensitive to displacement by competitor and predator species adapted to human activity (Spinks et al. 2003). Prior studies have shown that recreation can affect the survival (Iverson et al. 2006), population size (Garber and Burger 1995), and physiological condition (Amo et al. 2006) of reptiles. However, most studies focus on individual reptile species; we are not aware of prior studies on the effects of recreation on reptiles at the community level.

We evaluated the effects of non-consumptive recreation on the species richness, community composition, and occurrence of reptiles within habitat fragments in an urbanized landscape. We hypothesized that in urban reserves with higher recreational activity, sensitive species would disappear, thereby reducing species richness and shifting community composition. We expected smaller and more specialized species, and species with a narrower active temperature range, to be more sensitive to recreation. Since thermoregulation is highly important to ectotherms' ability to forage (Sinervo et al. 2010), a narrow range of temperatures in which a species is active may mean that their foraging timing is less flexible, limiting their ability to shift activity to times of day with lower human activity. To test our hypotheses, we measured recreational activity and reptile occurrence in parks and open space preserves along a gradient of human disturbance in San Diego County, California, USA. We modeled reptile species richness, community composition, and occupancy as a factor of human activity as well as other variables known to affect reptile distributions, such as habitat characteristics and topography.

Our findings help evaluate the degree to which recreation is a significant concern for the conservation of reptiles in urbanized landscapes. Understanding the effects of human disturbance on reptiles in urban areas may be critical for their conservation since they depend on remaining intact habitat and have limited ability to move to alternative suitable habitat. Our conclusions about the traits that influence reptile responses to recreation can also help researchers and managers identify the species that are the most likely to be affected in other systems.

Methods

Study sites

We conducted our study in 14 publicly-owned parks and preserves ("reserves") in coastal San Diego County, California, all of which are part of the San Diego County Multiple Species Conservation Program (Online Resource 1 Table S1). Previous recreation monitoring in the region showed variation in recreation activity ranging from zero to over 1,800 people per day at the reserve level (Larson et al. 2018). Based on this work, we selected reserves from a pool of potential study areas to span a gradient in expected human activity, including two reserves closed to the public. Reserves ranged from 284 to 8324 ha in size. The vegetation communities varied within and among study reserves and included chaparral, coastal sage scrub, native and nonnative grasslands, oak and sycamore woodlands, and riparian habitats. While none of the reserves allowed recreational motorized use, motorized vehicles were occasionally present (e.g., rangers, utility workers, unauthorized recreational users).

We located 92 sampling points along official and unofficial trails within the study reserves. Points were allocated to reserves proportionally based on length of the total trail network and reserve area, such that a minimum of three and a maximum of 12 points were located within each reserve, spaced at least 500 m apart. The point locations were selected using a spatially balanced random design using the RRQRR algorithm on the rasterized trail network (Theobald et al. 2007). Visitation rates can be highly variable within a single reserve (Taczanowska et al. 2014), and even reserves with high total visitation rates likely have low-use areas within them. Therefore, to ensure that our study included sampling points with high levels of human use, we allocated greater weight to trail cells expected to receive higher use, based on (a) distance from the nearest trailhead and (b) estimates of daily human use at trailheads from Larson et al. (2018). We removed trail cells within 100 m of a road or residential parcel to avoid confounding the effects of recreation with those of roads and development. We generated 296 points and screened potential points using aerial imagery and initial field visits, removing point locations that were not located on human trails (e.g., ridgelines, streambeds) and points with excessively steep slopes or thick vegetation such that coverboards could not be placed and visual surveys could not be conducted. In closed reserves, we ensured that sampling points were located on service roads or wildlife trails similar in structure (e.g., width) to recreational trails.

Sampling methods

We sampled the reptile community with a combination of artificial cover surveys and visual encounter surveys. Artificial cover objects (e.g., plywood, carpet, or tin sheets) mimic natural cover such as rocks and logs, create microhabitats sought out by reptiles for thermoregulation and refugia, can be easily surveyed without damaging natural habitat, and detect both surface-dwelling and fossorial reptile species (Ryan et al. 2002; Willson 2016). Each sampling point had an array of four coverboards varying in size and material to maximize detections of different species (Grant et al. 1992) and consisted of one new 61 × 122 cm, 1.59 cm thick plywood board; two old 61×61 cm plywood or OSB boards ranging in thickness from 0.95 to 2.4 cm; and one 61×61 cm piece of carpet. Coverboards were aged in place for a minimum of five weeks, and then were checked 14-17 times between January 2017 and June 2018. In combination with coverboard checks, we conducted visual transect surveys in which an observer slowly walked a 400 m transect along the trail, centered at the sampling point, scanning for reptiles. We did not capture animals, but rather identified individuals to species by sight with the aid of digital photos for later review if necessary. We rotated the order in which points were sampled and recorded the time, air temperature, cloud cover, and wind speed at the start of each survey. Since we were most interested in surveying species that would be affected by human activity, we did not conduct nighttime surveys that would detect primarily nocturnal species. Detections from the coverboards and the visual encounter survey were pooled for each survey visit.

To monitor human activity, we installed a motion-triggered camera (Bushnell TrophyCam HD Aggressor) at each sampling point. Cameras were housed in locked metal security boxes and affixed to metal posts pounded into the soil facing recreational trails. Cameras were programmed to take two pictures per trigger with a five second delay between triggers. Sampling periods were four weeks, with a check after approximately two weeks, and sampling periods were repeated four times between January 2017 and February 2018 to capture seasonal variability in human use. High temperatures, rapidly growing vegetation, and wind led to large numbers of false triggers at many camera locations, mostly in the mid-morning to late afternoon. Therefore, we randomly selected 20% of photos taken between 11:00 am and 5:00 pm for viewing and identification to reduce time spent sorting photos. We viewed and identified the contents of all photos taken during other hours of the day, when false triggers were less prevalent. Photos and metadata were stored and organized in the Colorado Parks and Wildlife Photo Warehouse (Ivan and Newkirk 2016). Humans appearing in photos were categorized by activity (pedestrian, cyclist, equestrian, vehicle). While we recognize that the effects of domestic dogs on reptiles likely vary from the effects of recreationists (Doherty et al. 2017), given the high correlation between daily counts of dogs and humans (r=0.85) we were not able to separately analyze domestic dog effects. We summed counts of all human activities (including dogs) as a measure of total overall human activity and used the mean daily counts as our primary human activity variable. For dates in April-June 2018, when we conducted reptile surveys but the camera traps were not operational, we used human activity data from similar dates in 2017 in our analyses.

We surveyed vegetation at each sampling point using a point-intercept transect technique modified from Fisher et al. (2008). We established two transects originating at the edge of the trail and extending 10 m into the vegetation on the side of the trail where the coverboards were located. If boards were on both sides of the trail, one transect was established on each side. At 0.5 m intervals, we held a measuring rod vertically to the ground and recorded each plant species that touched the rod and their heights, using general categories for grasses and forbs, and also recording bare ground or rock cover. After completing the transects, we recorded any incidental plant species in the general area of the sampling point (roughly within 10 m on either side of transects) that were not recorded at any point on the transects. All vegetation surveys were conducted between mid-May and mid-June when most vegetation was at its maximum height and greenness.

Vegetation data were summarized into percent cover by species at each sampling point. Plants incidentally recorded at the site but not the sampling transects were assigned a percent cover value of 1% (Fisher et al. 2008). Plant cover often summed to >100% because multiple plants could be recorded at the same transect point. We removed plant species that we found at fewer than five sampling points, then used principal coordinate analysis to reduce the number of dimensions of the data while preserving as much information as possible (Anderson and Willis 2003), using the vegan package for R (Oksanen et al. 2018). We used the Bray-Curtis distance measure and reduced to two dimensions. To interpret the resulting multi-dimensional scaling (MDS) dimensions, we examined the highest and lowest scores of individual plant species on each MDS dimension and qualitatively described the associations of these species.

Model covariates

We hypothesized that reptile species richness, community composition, and occupancy were primarily driven by habitat characteristics, topography, and human activity. Specifically, to describe habitat we used vegetation composition as represented by the two dimensions from the MDS analysis, plant greenness as measured by the normalized difference vegetation index (NDVI), and years since the last recorded fire (Table 1). For topography, we included solar radiation and elevation, and we eliminated slope and aspect after preliminary analysis showed that they had little relationship reptile species richness, community composition, or occupancy. For human activity, we used mean daily counts of pedestrians, cyclists, and total human activity (maximum one human activity type per model). Due to low counts of equestrians and vehicles, we did not separately model relationships between these activities and our response variables, but did include them in counts of total human activity. To assess whether urbanization had a confounding effect, we measured housing density within 500 m of each sampling point using county parcel data (SanGIS and SANDAG 2018). No pairs of predictor variables had a correlation coefficient greater than 0.6. All variables were scaled (by subtracting the mean and dividing by the standard deviation) to allow for comparisons among regression coefficients.

Species richness and community composition analysis

We used species accumulation models to estimate the number of undetected species at each sampling point. These models use counts of individuals and assume that the number of undetected species is related to the number of species detected only once or twice (Chiu et al. 2014). We used the Chao estimator with the small-sample correction term, implemented with the vegan package for R (Oksanen et al. 2018). We then used linear regression models to assess the relationships between estimated species richness and habitat, topography, and human activity variables.

To assess whether species traits influence their response to human activity rates, we assigned each species to categories describing their habitat specificity (specialist or generalist, Franklin et al. 2009) and the most common method of detection (coverboard or visual transect); nocturnal and/or fossorial species were detected primarily via coverboards while diurnal and/or surface-active species were detected primarily via visual transects. We also gathered data from the literature on two traits that may influence species sensitivity: body size (mean adult snout-vent length [SVL]; Amburgey et al. 2021) and body temperature range (range of temperatures of active lizards recorded in the field; Meiri 2018; Table 2). We recognize that these traits can vary by

Covariate	Covariate category	Description	Data	Observed	Parameter
		-		range/count	
				by category	
Pedestrians	human	Mean per day	field	0–2,826	ψ , SR, CC
Cyclists	human	Mean per day	field	0-101.6	ψ, SR, CC
Total human	human	Mean per day of combined cyclists, pedestrians, dogs, equestrians, and vehicles	field	0–2,949	ψ, p, SR, CC
MDS1	habitat	MDS axis from vegetation community data; low values interpreted as grassland/oak woodland, high values interpreted as open chaparral	field	-0.15-0.18	ψ, SR, CC
MDS2	habitat	MDS axis from vegetation composition data; low values interpreted as chaparral, high values interpreted as coastal sage scrub	field	-0.19-0.25	ψ, SR, CC
NDVI	habitat	Index (0-1), mean value within 10 m of point	GIS	0.2-0.62	ψ, SR, CC
Fire	habitat	Years since fire	GIS	3–139	ψ, SR, CC
Elevation	topography	Meters, mean value within 10 m of point	GIS	17.3-666.5	ψ, SR, CC
Solar radiation	topography	Index (0-255; very cool to very warm), mean value within 10 m of point	GIS	163.9–241.4	ψ, SR, CC
Temperature	weather	°C, measured at start of survey	field	4.4-41.1	р
Wind speed	weather	Km/hr, measured at start of survey	field	0-16.7	р
Cloud cover	weather	Categorical: sunny (0–50% cloud cover), cloudy (50–100% cloud cover)	field	sunny: 1081 cloudy: 224	р
Julian date	temporal	Day of year	field	5-358	р
Time of day	temporal	Decimal hours, recorded at start of survey	field	8.0-20.1	р
Observer	observation process	Categorical: CLL or other (field assistant or volunteer)	field	CLL: 654 other: 662	р
Search effort	observation process	Number of observers	field	1–3	р
Trail width	observation process	Meters	field	1-8.3	р

Table 2 Characteristics of the reptile species detected. SVL is lizard body size as measured by mean adult snout-vent length. Temperature range
is the difference between the highest and lowest reported mean body temperatures of active lizards recorded in the field. Board, transect, and total
detections are counts of reptiles detected via coverboards, visual transects, and their sum

Scientific name	Common name	Habitat specificity ^a	SVL (cm) ^b	Temp. range (°C) ^c	Board detections	Transect detections	Total detec- tions
Lizards							
Uta stansburiana	Common side-blotched lizard	generalist	5.05	4.0	50	381	431
Sceloporus occidentalis	Western fence lizard	generalist	7.3	5.5	30	217	247
Aspidoscelis hyperythra beldingi	Orange-throated whiptail	specialist	6.05	1.4	2	203	205
Aspidoscelis tigris	San Diegan tiger whiptail	generalist	9.35	4.2	3	50	53
Plestiodon skiltonianus	Western skink	generalist	7.0	4.8	34	1	35
Phrynosoma blainvillii	Blainville's horned lizard	specialist	8.0	2.5	0	23	23
Sceloporus orcutti	Granite spiny lizard	specialist	9.95	9.1	2	16	18
Plestiodon gilberti	Gilbert's skink	specialist	8.85	4.9	9	1	10
Anniella stebbinsi	California legless lizard	specialist	14.45	3.6	8	0	8
Elgaria multicarinata	Southern alligator lizard	generalist	12.55	7.0	6	1	7
Coleonyx variegatus	San Diego banded gecko	specialist	6.75	13.4	1	0	1
Snakes							
Crotalus oreganus helleri	Southern Pacific rattlesnake	generalist			4	7	11
Pituophis catenifer	Gopher snake	generalist			3	3	6
Coluber lateralis	California striped racer	generalist			2	3	5
Lampropeltis californiae	California kingsnake	generalist			2	3	5
Hypsiglena ochrorhyncha	Coast night snake	generalist			3	0	3
Thamnophis hammondii	Two-striped garter snake	specialist			0	3	3
Crotalus ruber	Red diamond rattlesnake	specialist			0	2	2
Coluber flagellum	Red racer	specialist			0	1	1
Diadophis punctatus	Ring-necked snake	generalist			1	0	1
Rhinocheilus lecontei	Long-nosed snake	generalist			1	0	1
Salvadora hexalepis	Patch-nosed snake	specialist			0	1	1

^a Franklin et al. (2009)

^b Amburgey et al. (2021)

^c Meiri (2018)

sex, age, climatic conditions, and other factors (Mesquita et al. 2016; Stanley et al. 2020); however, our comparisons are among species rather than individuals. We restricted these analyses to lizards since we rarely detected snakes. For each sampling point, we calculated two measures of mean lizard body size: the mean of all species detected, and the mean weighted by the frequency of detection of each species; and two measures of mean range in body temperature: the mean difference between minimum and maximum body temperature of all species detected, and the mean difference weighted by the frequency of detection of each species. We then used a set of linear regression models to evaluate how richness of each category of reptiles, snake and lizard richness, mean lizard body size, and mean range in body temperature varied in response to human and environmental variables.

For each of the trait analyses, our set of linear regression models contained all combinations of variables with a maximum of two habitat variables and one topography variable. We used Akaike's information criterion corrected for small sample size (AIC_c) to rank and compare models (Burnham and Anderson 2002) using the R package *AIC-cmodavg* (Mazerolle 2019), and then added each human activity covariate (singly) to each of the models with $\leq 2 \Delta AIC_c$. We considered human activity to have an important effect if models containing human activity variables were included in the top-ranked model set ($\Delta AIC_c \leq 2$) and 95% confidence intervals did not include zero. We also examined the effect size of human activity compared to other variables by comparing regression coefficients and their confidence intervals.

Single-species occupancy analysis

We had enough detections to model occupancy of three lizard species: the orange-throated whiptail (*Aspidoscelis hyperythra*), western fence lizard (*Sceloporus occidenta-lis*), and common side-blotched lizard (*Uta stansburiana*). Though selected for modeling because of greater numbers of detections, these species vary in their degree of

habitat specialization, body size, and range of temperatures at which they are active. Side-blotched lizards are the smallest and are intermediate in terms of specialization and range of active temperatures, orange-throated whiptails are small, the most specialized, and have the narrowest active temperature range; and western fence lizards are a medium-sized and highly generalist species with a fairly wide active temperature range (Table 2; Lemm 2006; Meiri 2018; Amburgey et al. 2021).

We modeled the occurrence of these three lizards using single-species, single-season occupancy models with implicit dynamics (MacKenzie et al. 2017) using the R package unmarked (Fiske and Chandler 2011). Each combination of sampling point and sampling period was treated as an independent data point (O'Connell et al. 2006). This allowed us to use mean human activity during the four-week camera rotations as a predictor of occupancy rather than mean human activity across the duration of the study, which was important because of seasonal increases in human activity at many of our sampling locations that coincided with the breeding season of most reptile species. To avoid inflating our sample size as a consequence of this approach, we used the number of sampling points (n = 92) as the effective sample size in model comparison and selection. We removed reptile and human data from late October to mid-February when the focal species are relatively inactive and difficult to detect, so each sampling point had data from 10 to 12 repeat surveys in total (2-3 per camera rotation).

We hypothesized that lizard occupancy was related to habitat characteristics, topography, and human activity, and we used the same list of variables from the species richness and composition analyses (Table 1). We expected that lizard detection probability was a function of weather (i.e., cloud cover, wind speed, and temperature), temporal variability (i.e., Julian date and survey time of day), and the observation process (i.e., observer, survey effort, and trail width; Table 1). We also included total human activity as a predictor of detection probability because lizards may respond to humans behaviorally in a way that affects their detectability (e.g., hiding or fleeing), or use the habitat less frequently. Human activity could also influence local abundance at occupied sampling points, which would affect detection probability (Royle and Nichols 2003).

We used a multi-stage model building procedure (Lebreton et al. 1992), first running models to determine the environmental variables that best explained detection probability (p) while holding occupancy (ψ) at a global structure, constant across all species, that included vegetation composition, elevation, years since fire, NDVI, and solar radiation. We used Akaike's information criterion corrected for small sample size (AIC_c) to rank and compare occupancy models (Burnham and Anderson 2002). We used

combinations of variables for detection probability from all models with $\leq 2 \Delta AIC_c$ in the next stage, assessing how occupancy varied in relationship to habitat and topography variables. We limited occupancy structures to two habitat variables and one topography variable and ran all possible combinations of additive models (30 models for each detection structure). Finally, we added each of the human activity covariates (singly) to each of the models with $\leq 2 \Delta AIC_c$ as a covariate on occupancy and both occupancy and detection probability, and again ranked and compared models. We considered human activity to be an important predictor if models containing human activity variables were selected as well-supported models ($\leq 2 \Delta AIC_c$). We also examined the direction and magnitude of the human activity effect by comparing the regression coefficients and their confidence intervals to those of other variables and assessing whether the 95% confidence intervals included zero. In text and figures, we report results for the best-supported models containing the specified covariate(s). We used a parametric bootstrapping procedure to evaluate goodness-of-fit and overdispersion of the occupancy models (MacKenzie and Bailey 2004). When the results of this procedure showed that there was overdispersion in the data, we adjusted the model selection results using the estimated overdispersion parameter (\hat{c}) , resulting in a QAIC_c value.

Results

We collected 1077 detections of 11 lizard and 11 snake species over 1305 survey occasions (Table 2). Visual transect surveys accounted for 85.1% of total detections, and coverboard and transect methods detected 17 species each, with 12 species detected using both survey methods. The distribution of species detections was skewed; we detected the three most commonly observed species more than 200 times (common side-blotched lizard [431 detections], western fence lizard [247], orange-throated whiptail [205]), a middle group of six species between 10 and 53 times, and 13 species less than 10 times. We detected a mean (\pm SD) of 3.6 \pm 1.5 species per sampling point (range: 0–8) over the course of the study.

Overall mean (\pm SD) human activity across all sites was 41.8 \pm 144.9 (range: 0–3401) people, vehicles, and dogs per day. Pedestrians were the most common human activity with a mean daily count of 33.3 \pm 134.5 (range: 0–3249) and were present at 97.8% of sites, followed by dogs, which averaged 4.1 \pm 10.2 per day (range: 0–173) and were present at 89.1% of sites. Cyclists averaged 3.2 \pm 11.6 per day (range: 0–303) and were present at 83.7% of sites, equestrians averaged 0.6 \pm 2.9 per day (range: 0–67) and were present at 50.0% of sites, and motorized vehicles averaged 0.5 \pm 2.4 per day

(range: 0–46) and were present at 63.0% of sites. The correlation between overall human activity and nearby housing density was very low (r=0.04), which provides confidence that our results are related to the level of human activity rather than confounding effects of urbanization.

Twenty-six plant species, genera, and general categories (e.g., grass, forb) were observed at more than five of the sampling points and were used in our vegetation analysis. The categories with the highest scores on MDS dimension 1 were chamise (Adenostoma fasciculatum), bare ground, and black sage (Salvia mellifera), which are associated with chaparral communities, especially open chamise chaparral. The lowest scores were assigned to grasses, oaks (Quercus spp.), and thistles. Species with high scores on MDS dimension 2 were buckwheat (Erigonum fasciculatum) and California sagebrush (Artemesia californica), which are typical coastal sage scrub species. Plants with the lowest scores on MDS dimension 2 were chamise, grasses, and black sage. Therefore, we interpret MDS1 as a continuum between chaparral and grassland/oak woodlands, and MDS2 as separating coastal sage scrub from chaparral communities.

Species richness and composition

The total number of species across all sampling points, including undetected species, was estimated to be 26 ± 5.2 using the Chao estimator, compared to 22 species detected. Human activity was associated with a weak trend toward reduced estimated species richness; while the beta coefficient was negative, the 95% confidence interval included zero (Fig. 1). Total human, pedestrian, or cyclist activity were included in eight of thirteen top models with ΔAIC_c \leq 2 (Online Resource 1 Table S2), and the best-supported regression model contained total human activity rates, though a model without human activity had equal AIC. weight. Cyclist activity had a weaker negative relationship with estimated species richness ($\beta \pm SE = -0.28 \pm 0.26$) than pedestrian ($\beta \pm SE = -0.41 \pm 0.26$) and total human activity $(\beta \pm SE = -0.45 \pm 0.26;$ Fig. 1); each of these had 95% confidence intervals that included zero. Species richness was positively related to NDVI ($\beta \pm SE = 0.75 \pm 0.27$; Fig. 1), which was included in all thirteen best-supported models (Online Resource 1 Table S2). Elevation was included in six of the thirteen top models and had a positive association with species richness ($\beta \pm SE = 0.71 \pm 0.29$). Years since fire also was included in six of the top models and had a negative association with species richness ($\beta \pm SE = -0.40 \pm 0.25$) and MDS1 was included in four of the top models and had a negative association with species richness ($\beta \pm SE =$ -0.48 ± 0.30), but 95% confidence intervals for both variables overlapped zero. The magnitude of the human activity effect size was similar to or greater than all other covariate effect sizes except for the effect sizes of NDVI and elevation (Fig. 1).

Lizard richness declined in association with human activity ($\beta \pm SE = -0.46 \pm 0.18$), whereas snake richness was not related to human activity ($\beta \pm SE = 0.07 \pm 0.08$; Fig. 2a). Richness of species detected primarily with coverboards (n=9) declined slightly ($\beta \pm SE = -0.14 \pm 0.11$) whereas species detected primarily with visual transects (n=13) did not change substantially as human activity increased ($\beta \pm SE$ = -0.04 ± 0.18; Fig. 2b). Specialist richness remained unchanged ($\beta \pm SE = 0.02 \pm 0.11$) while generalist richness declined slightly as human activity increased ($\beta \pm SE =$ -0.14 ± 0.22; Fig. 2c). Of these models, lizard richness was the only one in which the 95% confidence interval for the human activity coefficient did not include zero. Lizard richness was more strongly related to total human and pedestrian activity than any of the environmental covariates (Fig. 2d).

Mean lizard body size increased as human activity increased ($\beta \pm SE = 0.16 \pm 0.11$), more strongly when it was calculated as an average weighted by detection rate ($\beta \pm SE = 0.38 \pm 0.10$; Fig. 3a and b). Human activity variables were included in most of the best-supported linear regression models for unweighted mean body size (including each of the top three models), and all the best-supported models for weighted mean body size (Online Resource 1 Table S3). The top linear regression models had an R² of 0.18 for the unweighted mean body size and 0.29 for the weighted mean body size and 0.29 for the weighted mean body size included MDS1 (negative effect), NDVI (positive), elevation (positive), and years since fire (positive).

The mean range in lizard body temperature increased as human activity increased ($\beta \pm SE = 0.18 \pm 0.10$), more strongly when calculated as an average weighted by detection rate ($\beta \pm SE = 0.27 \pm 0.09$; Fig. 3c and d). Human activity variables were included in six of eight best-supported models for unweighted mean range in body temperature, and both best-supported models for weighted mean range in temperature (Online Resource 1 Table S3). The top linear regression models had an R² of 0.11 for the average range in body temperature and 0.27 for the average range in body temperature weighted by species detection rate. MDS1 and MDS2 were the other covariates related to mean range in body temperature, both with negative effects.

Single-species occupancy

Human activity was an important predictor of common side-blotched lizard occupancy. Each of the seven bestsupported occupancy models contained either total human or pedestrian activity rates (Online Resource 1 Table S4). Common side-blotched lizard occupancy was negatively related to all three human activity variables, most strongly



Fig. 1 Estimated sampling-point level species richness (Chao estimator) in relation to daily counts of (**a**) pedestrian (**b**) cyclist, and (**c**) total human activity. The shaded areas show 95% confidence intervals. Panel (**d**) shows beta coefficients and 95% confidence intervals for the

relationships between habitat, topography, and human covariates and estimated reptile species richness. All panels show results from linear regression models selected as the best model containing the specified predictors

for total human ($\beta \pm SE = -0.69 \pm 0.18$) and pedestrian activity ($\beta \pm SE = -0.68 \pm 0.17$; Figs. 4 and 5); these effect sizes were larger than any other covariate except years since fire (Fig. 5). Years since fire had a strong negative relationship with occupancy, while MDS2, elevation, and solar radiation had positive relationships with occupancy (but 95% confidence intervals included zero; Fig. 5). Common sideblotched lizard detection probability was higher in sunny conditions, varied among observers, and was lower when human activity was higher (Online Resource 1 Table S4).

Orange-throated whiptail occupancy models that included human activity did not outperform those built with environmental variables only, appearing in only one of the nine best-supported models (Online Resource 1 Table S4). While total human ($\beta \pm SE = -0.12 \pm 0.17$) and pedestrian activity ($\beta \pm SE = -0.15 \pm 0.17$) had weak negative relationships and cyclist activity had a weak positive relationship with occupancy ($\beta \pm SE = 0.07 \pm 0.20$; Fig. 4), the 95% confidence intervals substantially overlapped zero, indicating no meaningful relationship (Fig. 5). The effect sizes of environmental covariates were larger than the effect of human activity (Fig. 5). Orange-throated whiptail occupancy was negatively related to years since fire and elevation, and positively related to MDS1 and MDS2 (Fig. 5), although MDS2 was the only variable whose 95% confidence interval did not overlap zero in the top-performing model. Orangethroated whiptail detection probability was higher in sunny



Fig. 2 Estimated sampling-point level richness (Chao estimator) of (a) lizards and snakes, (b) species grouped by their primary detection method (coverboards or visual transects), and (c) specialists and generalists in relation to daily counts of total human activity, from the best-supported linear regression models that included total human activity.

conditions, in summer months (June-August), and with greater search effort (>1 observer; Online Resource 1 Table S4).

Western fence lizard occupancy and detectability had a complex relationship with human activity. Each of the twelve best-supported models included total human activity as a predictor of occupancy, often with human activity as a predictor of detection probability as well (Online Resource 1 Table S4). Occupancy was positively related to total human activity ($\beta \pm SE = 0.67 \pm 0.25$; Fig. 4), but the effect size was reduced considerably when human activity was included as a predictor of detection probability within the same model. This difference is apparent in comparing results from the best-supported model that contained total human activity (which did not include human activity as a predictor of detection probability) and the best-supported model that

The shaded areas show 95% confidence intervals. Panel (d) shows beta coefficients and 95% confidence intervals for the relationships between habitat, topography, and human covariates and estimated lizard species richness. All panels show results from linear regression models selected as the best model containing the specified predictors

contained pedestrian activity (which included human activity as a predictor of detection probability; Online Resource 1 Table S4, Fig. 4). Detection probability and occupancy were both positively correlated with total human and pedestrian activity, but due to model selection uncertainty it is difficult to tell which parameter was most strongly associated with human activity. On the other hand, cyclist activity was somewhat negatively related to western fence lizard occupancy ($\beta \pm SE = -0.47 \pm 0.37$; Fig. 4), although the 95% confidence interval included zero. Occupancy was positively related to NDVI and negatively related to MDS1 and elevation; these effects sizes were similar in magnitude to the effect size of total human activity, but only NDVI and human activity had 95% confidence intervals that did not include zero (Fig. 5). In addition to human activity, detection probability was higher in late spring and early summer,



Fig. 3 Lizard body size as (a) the mean of all species detected and (b) the mean weighted by the frequency of detection of each species, and range in lizard body temperature as (c) the mean of all species detected and (d) the mean weighted by the frequency of detection of each species, in relation to daily counts of total human activity. Mod-

and in moderately warm temperatures (21–27 degrees C; Online Resource 1 Table S4).

eled relationships are from the best-supported linear regression models that included total human activity. Shaded areas show 95% confidence intervals. Note that the y-axes encompass only meaningful values for body size and temperature range

Discussion

Recreation was negatively related to lizard species richness in habitat fragments in an urbanized landscape, which contributed to a weak trend toward lower overall reptile richness. Richness of species classified as habitat specialists was not related to human activity, but small-bodied lizards

1

0

-1

Beta coefficient

Fig. 4 Probability of occupancy of common side-blotched lizard (Uta stansburiana), orangethroated whiptail (Aspidoscelis hyperythra), and western fence lizard (Sceloporus occidentalis) in relation to daily counts of pedestrian, cyclist, and total human activity, from the bestsupported single-species occupancy models that included the specified covariate. Shaded areas show 95% confidence intervals



Fig. 5 Beta coefficients and 95% confidence intervals for the relationship between habitat, topography, and human variables (number of pedestrians, cyclists, and total human activity) and occupancy of three

lizard species (common side-blotched lizard, orange-throated whiptail, and western fence lizard), from single-species occupancy models selected as the best model containing the specified covariate

and species with narrow body temperature ranges were less common in sites with more recreation. Human activity was also associated with declines in occupancy of the common side-blotched lizard. Western fence lizard occupancy and/ or detectability increased in association with pedestrian and total human activity, but model selection uncertainty makes it difficult to discern which parameter was more affected. Orange-throated whiptail occupancy was not meaningfully related to human activity; occupancy was better predicted by vegetation variables.

The decline in lizard richness associated with human activity parallels observed declines in bird and mammal richness in connection to human activity (e.g., Banks and Bryant 2007; Reed and Merenlender 2011; Bötsch et al. 2018). A recent meta-analysis found that vertebrate richness or abundance is reduced in association with higher recreation activity in approximately 7 of 10 cases (Larson et al. 2019). In addition, our results are consistent with the findings of Ficetola et al. (2007) who observed a decrease in reptile species richness in association with the presence of people in an urban park in northern Italy, though the assemblage comprised only four species of lizards and snakes. In our system, although the overall reptile community was quite diverse (22 observed species, 26 estimated species), the reptile community we were able to detect at individual sampling locations was much smaller. While this meant that the estimated difference in lizard richness between the site with lowest and highest human activity was only two species, this is a decline of approximately 50%.

We hypothesized that reptile richness would decline because sensitive species would disappear from sampling locations with higher human activity. Though we expected habitat specialists to be more sensitive, we found evidence for a slight decline in generalist richness as human activity increased, and no relationship between specialist richness and human activity. It is possible that our binary categorization of specialists and generalists was not sensitive enough to detect how smaller differences in habitat use (e.g., use of human-modified areas) influenced tolerance of recreation.

We also found evidence that small-bodied lizards may be more sensitive to human disturbance, since they were less likely to be found in areas with high levels of human activity. This relationship was more pronounced when we used a mean body size weighted by detection rate because of frequent detections of the common side-blotched lizard and orange-throated whiptail, both small-bodied species. Across several broad taxonomic groups, flight initiation distance (the distance from a stimulus at which an animal initiates an escape response) generally increases with body size, meaning that smaller species permit closer approaches by humans before fleeing (Piratelli et al. 2015; Samia et al. 2016; Dertien et al. 2021), possibly because smaller-bodied species are more sensitive to reduced foraging success than larger species (Møller 2009). However, smaller birds have been shown to be less tolerant of human disturbance than larger birds, meaning that they likely incur higher energetic costs from fleeing more frequently (Samia et al. 2015). If this is true for lizards, it could explain our finding that smallbodied lizards are more vulnerable to recreation if there are greater fitness costs associated with frequent flight. Further, smaller-bodied ecotherms must bask in the open more frequently to maintain optimal body temperature compared to larger-bodied species, increasing their exposure to disturbance from human activity (Asplund 1974).

As we predicted, species with narrower active temperature ranges occurred less frequently in areas with high human activity. Shifts in diel activity patterns are thought to be a primary mechanism allowing many mammal species to persist in areas with high levels of recreational use (George and Crooks 2006; Gaynor et al. 2018), but this mechanism is likely not available to ectotherms, which are highly sensitive to small changes in surface and air temperatures. Small body size and narrow active temperature ranges may also work synergistically. Small-bodied lizards are the first to start basking in the morning, often on or near trails where there is open sunshine, corresponding to times of high human recreational activity (early to mid-morning). Body temperatures of the common side-blotched lizard have been shown to increase over the morning hours and then stabilize throughout the rest of the day (Goller et al. 2014), meaning that they bask to raise their body temperature during the morning, which was the most popular time of day for recreationists in our study. Conversely, constrained thermal tolerances can also prevent exposure to human activity; for example, the two whiptail species in our study had narrow active temperature ranges but maintain very high body temperatures (median 39.2°C; Meiri 2018). This means they are most active mid-day in hot, sunny weather - conditions that many recreationists avoid.

Most reptile species had insufficient detections to model the relationship between single-species occupancy and recreation activity. Of the three lizards for which we modeled occupancy, only the common side-blotched lizard exhibited a negative relationship with human activity. The common side-blotched lizard is the smallest lizard in the region and occurs in arid and semi-arid habitats including coastal scrub, chaparral, woodland, and grassland habitats (Jones and Lovich 2009). Though it can be locally abundant (Franklin et al. 2009), the common side-blotched lizard has lower survival rates in urban areas where physiological stress levels are higher compared to rural areas (Lucas and French 2012). However, Delaney et al. (2021) documented high abundance and population growth of side-blotched lizards in small habitat fragments in southern California. Therefore, our findings could indicate a potential ecological trap if survival is diminished in areas with high levels of human disturbance where the species could otherwise thrive. Although it is a relative generalist, the common side-blotched lizard is rarely found in highly altered greenspace such as mowed lawns and landscaped urban parks, and has limited dispersal ability (Doughty and Sinervo 1994). Its inability to move between isolated habitat fragments can result in substantial genetic isolation among populations (Delaney et al. 2010).

We expected that the orange-throated whiptail, a species of conservation concern listed under the San Diego County Multiple Species Conservation Plan (MSCP Policy Committee and MSCP Working Group 1998), would be more sensitive to human activity than the other lizard species. It has the most specialized habitat requirements of the three, occurring only in coastal sage scrub and chaparral, often in association with buckwheat, black sage, white sage, and chamise, and is rarely found in degraded or developed areas (Jones and Lovich 2009). We observed a slight trend toward a negative relationship between occupancy and human activity, but with considerable uncertainty. A lack of flexibility in habitat use may prevent the orange-throated whiptail from moving away from human activity if there is little suitable habitat nearby (Gill et al. 2001), as it is small and has limited dispersal ability (Delaney et al. 2010). Previous studies have shown that prey abundance, specifically abundance of Crematogaster ants, is an important predictor of orange-throated whiptail abundance (Ver Hoef et al. 2001). We did not quantify prey abundance, but native ant communities are known to decline in the presence of the exotic Argentine ant (Linepithema humile), which is more abundant near development and in areas with non-native vegetation (Suarez et al. 1998). Human activity also increases near residential development (Larson et al. 2018) and is associated with introduction of exotic plants (Anderson et al. 2015), and so disturbance from recreation could work synergistically with prey declines to decrease habitat suitability for the orange-throated whiptail.

The positive response of the western fence lizard to human activity was not surprising. It is a medium-sized habitat generalist that is tolerant of humans, inhabiting many types of natural habitat as well as backyards and highly modified urban parks (Jones and Lovich 2009). However, it did show a slight decline in occupancy in response to cyclist activity. Anecdotally, we observed several dead western fence lizards on trails frequented by cyclists, as did Rochester et al. (2001). The western fence lizard had a higher probability of detection associated with higher levels of human activity. One possible explanation is that western fence lizards, true to their name, are commonly found basking and foraging on fences (Jones and Lovich 2009) where they are easily detected, and fences may be more common in areas with higher human activity to prevent people from straying from authorized trails, or near the boundaries of reserves and private developments where human use is also higher. Another potential explanation is that lizards inhabiting areas with high human activity may habituate to human disturbance (Rodríguez-Prieto et al. 2010) and are therefore more detectable in higher-use areas. However, prior behavioral studies on this species show mixed results. Putman et al. (2017) found no differences in escape behavior between areas with high and low human activity, potentially indicating a lack of habituation. In contrast, Grolle et al. (2014) documented longer flight initiation distances in areas with low human activity compared to high, suggesting that western fence lizards do habituate to human presence.

Although we detected 22 reptile species, the numbers of detections were skewed, with many detections of a just few species, allowing us to model only the three most commonly-detected species in species-specific models. The varying responses of these three species to human activity may have limited the magnitude of the overall richness response and raises questions about how and why species responses to recreation differ. While threats to threatened and declining species with small population sizes are perhaps a more pressing conservation problem, it is also important to consider ecological effects of declines in abundant species (Adams et al. 2013; Baker et al. 2018). More than a quarter of species become functionally extinct before losing just 30% of the individuals in a population (Säterberg et al. 2013). In our system, the side-blotched lizard is an important prey species for a wide variety of species including other lizards, snakes, birds, and mammals (Jones and Lovich 2009), so its strong negative response to recreation could potentially affect species at higher trophic levels.

Our sampling points were all located on recreational trails, and we were not able to quantify the effect zone of recreational disturbance extending away from the trail. Accordingly, we cannot determine the total area of the study reserves in which reptile communities may be negatively affected by human disturbance. Behavioral metrics such as alert distance (the distance from a stimulus at which an animal initiates vigilance behavior) and flight initiation distance may provide insight into recreation effect zones (Guay et al. 2016). Investigating alert and flight distances of reptiles and translating them to disturbance effect zones would be valuable next step, as would sampling the reptile community at multiple distances from trails. However, we feel it is safe to conclude that reserves with less fragmentation from trails (Ballantyne et al. 2014) are likely to have more area where the negative effects of recreation are minimized and will be better able to support diverse animal communities in the long term.

The negative effects of recreation compound the numerous conservation challenges in fragmented landscapes, such as lack of connectivity and the resulting loss of genetic diversity in isolated populations (Aguilar et al. 2008; Haddad et al. 2015). This study shows that recreation can reduce the ability of urban habitat fragments to conserve a diverse reptile community, and it may particularly affect small-bodied lizard species with narrow active temperature ranges. At the same time, there was considerable variation in species responses to recreation, suggesting that some species may thrive in highly visited areas. Accordingly, we recommend that managers carefully plan public access to keep a diversity of areas trail-free and, at least to some extent, to separate high-intensity recreation areas from quality habitat harboring populations of sensitive species. Limiting the effects of recreation in urban protected areas helps ensure that they provide habitat for species whose could otherwise persist in urban habitat fragments, particularly for species unable to avoid humans temporally or disperse to alternative habitat elsewhere.

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Code Availability R code is available in Zenodo: https://doi. org/10.5281/zenodo.10079307.

Declarations

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