






Comparing fear responses of two lizard species across habitats varying in human impact

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Abstract

Animals that are successful in urban habitats often have reduced antipredator responses toward people (sometimes called “fear” responses). However, few studies test whether sympatric species differ in their responses to humans, which may explain differing sensitivities to urbanization. Here, we quantified the behavioral and physiological responses to humans in two lizard species, side-blotched lizards (*Uta stansburiana*) and western fence lizards (*Sceloporus occidentalis*), across three different habitat types that vary in human impact: natural habitats with low levels of human activity, natural habitats with high levels of human activity, and urban habitats. We found that side-blotched lizards had longer flight initiation distances, were found closer to a refuge, and were more likely to hide than fence lizards, behaviors that could indicate greater fearfulness. Both lizard species were found closer to a refuge and were also more likely to hide in the urban habitat than in the natural habitat with low human impact, which could represent adaptive behaviors for increased risks in urban areas (e.g. cats). Western fence lizards exhibited lower body sizes and conditions in the habitats with moderate and high levels of human activity, whereas these traits did not differ among habitats in side-blotched lizards. Baseline and stress-induced corticosterone concentrations did not differ across habitats for both species, suggesting that human-impacted habitats were not stressful or that lizards had undergone habituation-like processes in these habitats. Taken together, our results highlight the importance of standardized measurements across multiple species in the same habitats to understand differential responses to human-induced environmental change.

Key words: urban ecology, escape behavior, vigilance, glucocorticoids, Phrynosomatidae, refuge distance, FID, Los Angeles

Introduction

We live in the Anthropocene, an epoch during which human-induced environmental change threatens global biodiversity (Dirzo et al. 2014). As humans become more urban, and natural areas more fragmented, wildlife conservation efforts will increasingly shift toward cities (Dunn et al. 2006; Aronson et al. 2017). Yet, in order to achieve conservation goals, we need to identify the processes that allow animals to successfully persist in urban habitats (Lambert and Donihue 2020). Success, in terms of reproduction and survival, will depend on an animal's ability to respond appropriately to the abiotic and biotic changes that occur with urbanization (Donihue and Lambert 2015; Johnson and Munshi-South 2017). If animals are inflexible in responding to such changes, they may become locally extinct in urban environments (McDonnell and Hahs 2015).

Human presence in urban areas is generally more pronounced than in natural habitats as humans live and move around in cities. Humans are often viewed as predators by animals (Frid and Dill 2002) and can indirectly influence them by inducing behavioral and/or physiological responses. Animals might be more vigilant around humans, flee upon detecting humans, hide in the presence of humans, or shift activity cycles to avoid humans, all

of which can disrupt fitness-relevant activities such as foraging (e.g. Tadesse and Kotler 2011; Belotti et al. 2018). The effects of humans on animal behavior sometimes outweigh those of actual predators (Ciuti et al. 2012; Clinchy et al. 2016; Zanette et al. 2023). Humans can also be perceived as stressors, causing a physiological stress response in animals via activation of the hypothalamic-pituitary-adrenal axis (HPA axis; Angelier and Wingfield 2012; Bonier 2012). Chronic elevation of the products of the HPA axis, glucocorticoid hormones (often referred to as “stress” hormones), can cause downstream effects on immunity and reproduction (Tilbrook, Turner, and Clarke 2000; Padgett and Glaser 2003; Fardell, Pavey, and Dickman 2020). Human activity can have negative impacts on animals when running away and hiding from humans reduces time or energy that can be spent on other activities such as looking for mates or foraging. Heightened responses could therefore lead to reduced body sizes or conditions if animals feed less around people. In support of this, prior work has shown that lizards in tourist areas have lower body conditions and overall health due to constant flight away from humans (Amo, López, and Martín 2006; Garrido and Pérez-Mellado 2015). Thus, animals occupying cities or habitats with high levels of human activity should either undergo habituation-like processes to humans—that is, reduce their fear

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responses—to reduce fitness costs associated with over responding to a non-predatory stimulus (Vincze et al. 2016; Cavalli et al. 2018), or preferentially occupy places where their tolerance for humans matches human activities.

Indeed, urbanization and human contact often lead to a reduction in antipredator responses (Geffroy et al. 2020), supporting the prediction that animals undergo habituation-like processes to humans in urban areas (Blumstein 2016). Urban birds, one of the most studied taxonomic groups for these sorts of questions, generally have shorter flight initiation distances (the distance at which an animal flees from an approaching threat), and lower glucocorticoid reactivity than their non-urban counterparts (Samia et al. 2015b, 2017; Symonds et al. 2016; Tablado et al. 2021). Bolder birds that have reduced stress responses to humans exploit novel opportunities in urban areas (Atwell et al. 2012). But not all animals become more tolerant to humans in human-impacted habitats (Bjørnvik et al. 2015; Uchida and Blumstein 2021), and some show the opposite, an increase in fear responses after repeated human disturbances (known as sensitization; e.g. Moroni et al. 2017). Many studies also show an increase in stress-associated physiological responses (higher glucocorticoid levels and oxidative stress, reduced immune function) in human-impacted populations (Lucas and French 2012; French et al. 2017; Batabyal and Thaker 2019). However, a recent meta-analysis across vertebrate taxa found no consistent effect of urbanization on glucocorticoids (Iglesias-Carrasco et al. 2020), suggesting that physiological responses are variable among species and populations.

Most studies on animals' behavioral and physiological fear responses toward people compare urban and non-urban populations of one focal species. However, it is likely that at the species-level, those with a higher responsiveness to humans will be less likely to persist in urban areas than those that are less fearful of people (Vincze et al. 2016; Cavalli et al. 2018). Thus, species that have high fear responses in natural habitats with low levels of human activity may experience negative fitness consequences in urban habitats with higher levels of human activity if they do not modify these responses (McDonnell and Hahs 2015). Few studies to date have compared the responses to humans among species that live sympatrically in urban and non-urban habitats (but see Møller 2008; Møller 2010). Such research would increase our understanding of which aspects of an animal's biology makes it vulnerable or not to urbanization (Iglesias-Carrasco et al. 2020). Furthermore, it is often difficult to decouple the effects of human presence from the other changes that occur with urbanization, such as changes to substrate, habitat structure, available resources, and predator presence and abundance. That is, the different animal responses documented between urban and non-urban populations might be caused by other aspects of the urban environment besides increased human activity.

Here, we compared behavioral and physiological responses to human disturbance between two lizard species, side-blotched lizards (*Uta stansburiana*) and western fence lizards (*Sceloporus occidentalis*), across urban and natural habitats in the Greater Los Angeles Area. We specifically quantified escape and hiding responses as standard behavioral measures of animal risk assessment, and glucocorticoid hormone levels as indicators of a physiological response to perceived or physical stressors (Cockrem 2013). These two lizards are ideal for our comparisons because they are common and widespread in the region, but side-blotched lizards are less tolerant of urbanization than fence lizards (from personal observations by us and Delaney et al. 2021). Both species are in the family Phrynosomatidae and are

ecologically similar: they are terrestrial generalists, have the same suite of predators, consume mostly arthropods, bask out in the open, and males defend territories (two of the three color morphs for the side-blotched lizards). However, even though they are often sympatric across habitats in the western United States, they exhibit differences in microhabitat preferences that could affect how they respond to urbanization and human disturbances. Side-blotched lizards are less arboreal than fence lizards, preferring to perch on rocks (and sometimes logs) in open or disturbed sites with bare ground and sand (Davis and Verbeek 1972; Morrison and Hall 1999). They tend to avoid shaded woody areas with leaf litter (Davis and Verbeek 1972; Hibbitts et al. 2013). Fence lizards occur in a greater variety of habitats, often using trees as perches in addition to rocks and logs (Davis and Verbeek 1972). Prior studies showed reduced escape behaviors in fence lizards (Grolle, Lopez, and Gerson 2014; Sparkman et al. 2018), and a higher corticosterone response in side-blotched lizards (Lucas and French 2012) in more urbanized populations compared to non-urban ones, demonstrating the capacity of these species to behaviorally and physiologically respond to urbanization.

We examined behavioral, physiological, and morphometric traits of these two lizard species across three different habitat types in Los Angeles County: (1) natural habitat with low levels of human activity (~1 person/h), (2) natural habitat with high levels of human activity (~65 people/h), and (3) highly urbanized areas with moderate levels of human activity (~12 people/h). We included habitats that differed in level of human activity to help tease apart the effects of urbanization from the effects of human presence. If lizards are more affected by urban development than human presence, we expect their responsiveness to differ in the urban habitat from the two natural habitats. If lizards are more affected by human presence, we expect their responsiveness to either increase or decrease with level of human activity in this order: natural habitat with low level of human presence, urban habitat with moderate level of human presence, and natural habitat with high level of human presence. If lizards are more responsive to humans in urban areas or areas of high human activity, this could be associated with reduced foraging opportunities leading to smaller body sizes or lower body conditions. Thus, we predicted that lizard body size and/or condition would be lower in habitats in which their responsiveness to humans was highest.

Methods

We studied western fence lizards (*Sceloporus occidentalis*) and side-blotched lizards (*Uta stansburiana*) in 2017 and 2018. In the first year, we collected behavioral data, focusing on escape and hiding responses of the two species. We quantified flight initiation distances (a robust measure of animal risk assessment), distances to refuge, and hiding propensity upon a human approach. In both years, we collected blood samples from lizards to quantify baseline and stressed corticosterone concentrations. Finally, from all lizards captured across both years, we measured body size and estimated body condition.

Study species

Western fence lizards and side-blotched lizards are ideal for comparing species responses to human disturbances because they are within the same family, have similar behaviors and ecologies, and are widespread across habitats in the Western United States. Yet, the two differ in microhabitat preferences with fence

lizards being more arboreal, and side-blotched lizards preferring open areas with rocks and bare ground (Davis and Verbeek 1972; Morrison and Hall 1999). From personal observations (and see Delaney et al. 2021), western fence lizards appear more urban-tolerant than side-blotched lizards because they are found throughout more urbanized and residential areas in the region. We found further support for our observations using the location data from observations of lizards submitted to iNaturalist, a community science platform (www.inaturalist.org). Within Los Angeles County and during our study period (2017–2018), the majority of side-blotched lizard observations were from areas with low imperviousness (i.e. landcover impermeable to water, a measure of urbanization) and their mean percent impervious surface cover was much lower than that of fence lizards, suggesting a lower tolerance for urban areas in our study region (side-blotched lizards mean \pm SD = 8.43 ± 13.31 , median = 1.47, $n = 750$; western fence lizards mean \pm SD = 20.24 ± 19.28 , median = 16.16, $n = 750$; see [Supplementary Materials](#) and [Supplementary Fig. S1](#) for details).

Study sites

We studied the two lizard species across three different habitat types in Los Angeles County: (1) natural habitat with low levels of human activity (referred to as Natural-Low), (2) natural habitat with high levels of human activity (referred to as Natural-High), and (3) highly urbanized areas with moderate levels of human activity and no intact native natural habitat (referred to as Urban). We had two replicate sites per habitat type. The Natural-Low sites consisted of Stunt Ranch, a University of California Reserve in the Santa Monica Mountains (WGS84: 34.0943158° , -118.6567980°), and areas around the Oak Spring/Gold Creek trail on the southwest end of the San Gabriel Mountains (34.3172492° , -118.3366697°). The Natural-High sites consisted of Eaton Canyon, a popular hiking trail at the base of the San Gabriel Mountains (34.1835487° , -118.0977523°), and Baldwin Hills Scenic Overlook, another popular hiking area in Culver City (34.0180731° , -118.3818612°). Finally, the Urban sites consisted of paved walking/biking paths along channelized river drainages, one being the Bowtie Parcel along the Los Angeles River (34.1083775° , -118.2459009°) and the other being the San Gabriel River Trail on the border of El Monte and Baldwin Park (34.0734183° , -118.0023677°). The two natural habitat types all had relatively intact native vegetation that mostly consisted of oaks, sage scrub, and chaparral. The Natural-Low sites had exceptionally low human presence (~ 1 person/h) while the Natural-High sites contained hiking trails frequently visited by humans (~ 65 people/h; see below for calculation of this variable). For comparison, we estimated human activity at around 12 people/h in the Urban sites. The minimum distance between any two sites was ~ 15 km, much larger than the average home range sizes of the two lizard species (Tinkle, Mcgregor, and Dana 1962; Davis and Ford 1983).

We verified that replicate sites within each habitat type consistently varied in habitat characteristics and human activity levels. First, around each lizard capture locality (see below for capture methods), we estimated the mean percent tree cover and the mean percent impervious surface cover (a proxy for urbanization intensity) within a 100-m radius buffer. These data came from the 2016 National Land Cover Database. During our study, we also manually took ambient temperature recordings using a Kestrel Weather Meter (model 5500) after every lizard behavioral trial or capture attempt. We used these to determine whether

sites significantly differed in temperature during the study period. Finally, we also quantified level of human presence as number of persons encountered per hour during each field day. Qualitative examinations showed that replicate sites within each habitat type were more similar to each other than to sites of other habitat types ([Supplementary Fig. S2](#)).

Behavioral fear responses

Behavioral trials took place from July–September 2017 between 8:00–13:00 h and on clear, sunny days. To measure lizards' tolerance of human disturbance, we quantified their escape and hiding behaviors. First, we quantified the flight initiation distance (FID), which is the distance an animal will tolerate between it and an approaching threat before it flees. To measure FID, one person walked toward a focal lizard at a standardized walking pace (0.5 m/s) and noted when it fled (any movement away from its initial location), and the total distance between the lizard and the observer when the trial was started (termed the start distance, SD). FID and SD were measured using a measuring tape after each trial. We only conducted trials on adult lizards, and we alternated site visits to avoid sampling order effects. The same person (B.J.P.) conducted all trials.

After each FID trial, we also measured how lizards responded to the human approach—whether they sought refuge or remained out in the open. We defined seeking refuge as running to a location that completely concealed the lizard, for example, into a burrow or crevice, under a rock, or within thick vegetation. If the lizard sought refuge, we moved at least 5 m away and observed the refuge entrance with binoculars and from two different angles (we had two people performing these observations). We waited for 20 min to determine the time for the lizard to emerge from the refuge. Lizards that did not emerge within this timeframe were given the maximum time of 20 min. In most cases, we were able to confirm that the lizards that did not emerge within the 20-min time period were still within the refuge through visual identification (i.e. we could see them at the entrance of the refuge or we were able to lift the refuge—when it was a rock or log—and confirm the lizard's presence). Finally, for each lizard, we estimated the distance to the nearest refuge at the start of the FID trial. If the lizard sought refuge during the trial, we measured the distance from its initial location to its hiding place. If the lizard fled, but not to a refuge, we measured the distance from its initial location to the nearest location that could completely conceal the lizard. The behavioral fear responses outlined above are standard measures of assessing lizard responses to human disturbance (Cooper 2006, 2007; Samia et al. 2015a).

We attempted to capture lizards after each behavioral assay using a lasso tied to the end of an extendable fishing pole or by hand. Once captured, we immediately took the lizard's temperature using an infrared temperature gun (ennoLogic Dual Laser Infrared Thermometer et650D) held ~ 12.7 cm above the dorsum to measure an area with 1.27 cm diameter. We also collected data on sex, mass, and body size (as snout-vent length, SVL). Captured lizards were marked with a unique identifying number on their dorsal side using non-toxic white nail polish and then released at their place of capture; this was done to avoid repeat sampling.

The observers conducting behavioral trials attempted to test both lizard species (western fence lizards and side-blotched lizards) on the same days, and to alternate the testing of each species throughout the day (so species observations were not biased

toward time of day). The same two observers (B.J.P. and a field assistant) conducted these behavioral trials with one person always performing the human approach (B.J.P.) and the other standing back and taking notes. This reduced variation in lizard responses to differences in human body sizes, walking gaits, and other attributes to which lizards might be sensitive. These two observers always wore the same-colored T-shirt (orange with the Natural History Museum of Los Angeles County logo on it) during the trials to also reduce biases due to color sensitivities in the study animals (see Putman et al. 2017; Fondren, Swierk, and Putman 2020).

Physiological stress responses

We collected blood samples from which to compare baseline and stress-induced corticosterone concentrations across the three different habitat types in the two lizard species. These data were collected after behavioral trials, in September–October 2017, and in August–September 2018. The start of data collection for this part of the project occurred at least two weeks after the conclusion of the behavioral trials, so it is unlikely that human disturbances from the behavioral trials influenced hormonal responses. As above, we went to each site from 8:00–13:00 h and searched for both western fence lizards and side-blotched lizards. Time of sampling was limited to this five-hour window to reduce impacts on hormone concentrations; time of day was not a significant predictor in the statistical models (see results below). We captured lizards as above and took a blood sample either immediately upon capture (baseline sample) or 30 min after capture (stressed sample), a time period appropriate to show a stress response (Graham et al. 2012; Hews and Abell Baniki 2013). For baseline samples, we ensured that blood was drawn within 3 min of disturbance (i.e. attempt to capture) by using a stopwatch to quantify the latency to bleed. For stressed samples, lizards were kept in a shaded environment within breathable cotton bags prior to bleeding. Blood samples were drawn from the retro-orbital sinus using a 70 μ l heparinized microcapillary tube (Fisherbrand, Cat. No. 22–363–566), taking no more than 50 μ l or 10% of the total blood volume. We stored samples on ice in 1.5 ml microcentrifuge tubes in the field. Each lizard's body temperature was recorded at the time of sampling using the same temperature gun as above. Within the same day, blood samples from the field were centrifuged to separate plasma from the cellular fraction. Plasma was then stored in a -80°C freezer until further analyses. After blood samples were taken in the field, we recorded each lizard's sex, mass, and body size (as SVL).

We used an ELISA kit (Enzo Life Sciences, Inc., Correlate-EIATM Corticosterone kit 900-097) to determine plasma corticosterone concentrations in western fence lizards. These tests were done in the Schlinger Lab at UCLA as done previously for other species (Rensel et al. 2014). We optimized and validated this kit for western fence lizards, demonstrating parallelism and acceptable quantitative recoveries (see Supplementary Materials and Supplementary Fig. S3 for details). Based on these results, we diluted each sample 1:40 with a 1% concentration (of raw plasma volume) of steroid displacement buffer. Samples were run in duplicate and read at 405 nm after a 60-min incubation period. The minimum level of detection was 0.032 ng/ml, and samples that fell below this concentration were assigned this minimum level of detectability ($n = 22$ out of 132; Gangloff et al. 2016; Landau et al. 2019). Intraassay coefficients of variation (CV) ranged from 8.8 to 12.9% with an average intraassay CV of 10.4% ($n = 5$ plates). The interassay CV was 17.6% (four corticosterone standards per plate).

All side-blotched lizard samples were run at Utah State University following a protocol outlined in French et al. (2017). Briefly, we conducted a radioimmunoassay on each side-blotched lizard plasma sample (10 μ l) to analyze corticosterone concentrations (Ab: #07-120016; MP Biomedicals). We extracted samples with 30% ethyl acetate: isooctane and ran each sample in duplicate for the assay. Individual recoveries for each sample were used to adjust for the loss of any sample during the extraction and to calculate the final sample concentrations. The minimum level of detection was 0.3 ng/ml and the intraassay coefficient of variation (CV) was 7.4%.

Body size and condition

We used data from all lizards captured during this study (i.e. from those used in the behavioral trials and from those used to quantify plasma corticosterone levels) to calculate body sizes and estimate conditions of each species across each habitat. Snout-to-vent length (SVL) was used as a standard measure of body size while body condition was calculated by taking the residuals from a linear regression of log SVL on log of cube-root body mass.

Statistical analyses

We conducted all analyses in R (v 4.1.1, R Core Team 2021) and set alpha to 0.05. We used linear mixed models through the package lme4 (Bates et al. 2015) to evaluate whether the two lizard species differed in behavioral responses, corticosterone concentrations, body condition and body size across the three habitats. For all models, we included species (western fence lizard or side-blotched lizard), habitat type (Natural-Low, Natural-High, or Urban), and their interaction as main fixed factors and site as a random factor. If the interaction term was non-significant, it was removed from the model and only the main effects were assessed. Corticosterone concentrations from western fence lizards and side-blotched lizards were analyzed separately because they were quantified using different assays in different labs for each species (hence species is not in these models as a fixed factor). Because we ran multiple statistical tests on the same individual lizards, we report P -values adjusted by the false discovery rate method (Benjamini and Hochberg 1995) in all tests of main effects. When applicable, we also conducted pairwise comparisons among habitats using the multcomp package in R (Hothorn, Bretz, and Westfall 2008) and P -values were adjusted by the false discovery rate method. Assumptions of models were assessed through residual plots.

Behavioral fear responses

Lizard behavioral responses (FID and distance to refuge) were square root transformed to meet model assumptions. For the model on FID, we included starting distance as a covariate as this is known to significantly explain variation in FID (Blumstein 2003) and for the model on distance to refuge we included ambient temperature as a covariate because a preliminary likelihood ratio test showed that temperature was important in influencing this behavior ($X^2 = 18.64$, $df = 1$, $P < 0.001$). Ambient temperature did not have large impacts on FID or lizards seeking refuge based on preliminary analyses (FID: $X^2 = 1.32$, $df = 1$, $P = 0.251$; seek refuge: $X^2 = 1.36$, $df = 1$, $P = 0.243$) and so this was not included as a factor in the models explaining these behaviors. In addition to the mixed models examining variation in behavioral responses, we fitted a Cox mixed-effects survival model (coxme package in

R; [Therneau 2012](#)) with site as a random factor to evaluate whether habitat affected latency to emerge from a refuge. We only included data from side-blotched lizards in this survival analysis because too few fence lizards sought refuge during the human approach ($n=8$). We could not include sex of the lizards in the models on behavioral responses because we did not capture every individual after each FID trial so we lack data on sex for many observations. Because of this, we also lacked data on lizard body temperatures for most observations; however, using all capture data (from lizards in behavioral trials and those captured to take blood samples), we fitted a general linear model to examine whether body temperature significantly varied between the two lizard species and among the three habitat types. If body temperatures significantly differed between species or among habitats, this could partially explain our results for the above-measured behavioral traits.

Physiological stress responses

Prior to fitting the mixed models on corticosterone concentrations, we verified whether baseline concentrations (ln-transformed) were positively influenced by the time to collect the blood sample after disturbing the lizard using linear regression models. We found that the time to bleed did not affect baseline corticosterone levels in western fence lizards ($n=66$, Estimate \pm SE = 0.003 ± 0.003 , $t=0.946$, $P=0.348$), but there was a positive relationship in side-blotched lizards ($n=37$, Estimate \pm SE = 0.008 ± 0.003 , $t=2.59$, $P=0.014$), although the strength of this relationship was relatively low ($R^2=0.165$). Even though we found this relationship in side-blotched lizards, we still categorized these samples, taken within three minutes of disturbance, into the baseline treatment in comparison to the samples taken 30 min post-capture, but recognize that they might not all truly represent basal circulating levels of hormone ([Small et al. 2017](#)).

For the mixed models of the two lizard species, we set the natural log of corticosterone concentration (ng/mL) as the dependent variable and included the following predictors: habitat (Natural-Low, Natural-High, or Urban), treatment (baseline or stressed), lizard sex, lizard body size (as SVL), lizard body condition, lizard body temperature at time of blood collection, time of day that the blood was collected, and the year that the blood was collected. We were mainly interested in the effects of habitat and treatment but included the other variables as covariates because of their potential to influence corticosterone levels. These covariates were removed if they did not explain a significant amount of variation based on likelihood ratio tests. Thus, for the model on western fence lizard corticosterone, we retained body condition and body temperature as covariates, and for the model on side-blotched lizards, we retained body size as a covariate. For both models, we looked for an interaction between habitat type and treatment (baseline vs. stressed), and if this interaction term was non-significant, it was removed from the model and only the main effects were assessed.

Body size and condition

We evaluated whether habitat type was associated with differences in body size or condition, traits that are relevant to lizards' fitness ([Olsson 1993](#); [Radder and Shanbhag 2004](#); [Hofmann and Henle 2006](#); [Kingsolver and Huey 2008](#)). We fitted linear mixed models as described above and included sex as an additional covariate in these models to account for the known sexual dimorphism in these species. We also used Pearson's correlations to examine whether body size was correlated with body condition in each species.

Results

Behavioral fear responses

We collected behavioral data on 119 western fence lizards (41 from Natural-Low, 45 from Natural-High, and 33 from Urban) and 120 side-blotched lizards (38 from Natural-Low, 44 from Natural-High, and 38 from Urban). For the model on the probability of lizards seeking refuge upon a human approach, we had two fewer western fence lizard observations ($n=117$) and one fewer side-blotched lizard observation ($n=119$) because we could not determine where the lizard ran to during the FID trial. Side-blotched lizards had significantly higher FIDs ($X^2=6.23$, $df=1$, $P=0.015$, [Fig. 1A](#) and [Supplementary Tables S1 and S2](#)), were found closer to a refuge ($X^2=61.94$, $df=1$, $P<0.001$, [Fig. 1B](#) and [Supplementary Tables S3 and S4](#)), and were more likely to seek refuge upon a human approach ($X^2=9.29$, $df=1$, $P=0.003$, [Fig. 1C](#) and [Supplementary Tables S5 and S6](#)) compared to western fence lizards. Across all habitats, 25% of side-blotched lizards fled to a refuge compared to only 9% of western fence lizards.

Habitat type had no effect on FID in both species ($X^2=5.60$, $df=2$, $P=0.097$, [Supplementary Tables S1 and S2](#)), but affected distance to refuge ($X^2=8.97$, $df=2$, $P=0.030$, [Fig. 2A](#) and [Supplementary Tables S3 and S4](#)) and the proportion of lizards seeking refuge upon a human approach ($X^2=7.88$, $df=2$, $P=0.039$, [Fig. 2B](#) and [Supplementary Tables S5 and S6](#)). Lizards of both species were found closer to a refuge and more likely to seek refuge in the Urban habitat compared to in the Natural-Low habitat (refuge distance: $P=0.009$; proportion seeking refuge: $P=0.017$). Refuge distance and the proportion of lizards seeking refuge in the Natural-High habitat were intermediate and not significantly different from Urban (refuge distance: $P=0.228$; proportion seeking refuge: $P=0.136$) or Natural-Low (refuge distance: $P=0.102$; proportion seeking refuge: $P=0.136$). Because so few western fence lizards sought refuge ($n=8$), we could only include data from side-blotched lizards in the survival analysis on time to emerge (with right-censoring occurring at 20 min). Habitat did not significantly affect time to emerge in side-blotched lizards (integrated log likelihood: $X^2=6.20$, $df=3$, $P=0.102$, $n=27$).

Body temperatures upon capture significantly differed between the two lizard species ($X^2=15.14$, $df=1$, $P<0.001$, [Supplementary Fig. S4](#) and [Supplementary Tables S7 and S8](#)), but not among habitats ($X^2=3.26$, $df=2$, $P=0.261$). Side-blotched lizards were on average 1.4°C warmer than western fence lizards.

Physiological stress responses

From western fence lizards, we collected 66 baseline blood samples (23 from Natural-Low, 21 from Natural-High, and 22 from Urban) and 66 stressed blood samples (21 from Natural-Low, 23 from Natural-High, and 22 from Urban, [Table 1](#)). From side-blotched lizards, we collected 37 baseline blood samples (12 from Natural-Low, 10 from Natural-High, and 15 from Urban) and 34 stressed samples (11 from Natural-Low, 12 from Natural-High, and 11 from Urban, [Table 1](#)). Habitat did not affect corticosterone concentrations in western fence lizards ($X^2=0.108$, $df=2$, $P=0.948$, [Supplementary Tables S9 and S10](#)) or side-blotched lizards ($X^2=0.550$, $df=2$, $P=0.868$, [Supplementary Tables S11 and S12](#)). Both species showed a significant stress response with concentrations of the stressed samples being higher than the baseline samples (western fence lizards: $X^2=191.60$, $df=1$, $P<0.001$; side-blotched lizards: $X^2=257.08$, $df=1$, $P<0.001$, [Table 1](#)). Corticosterone concentrations increased with body temperature ($X^2=12.26$, $df=1$, $P=0.001$) and decreased with body condition

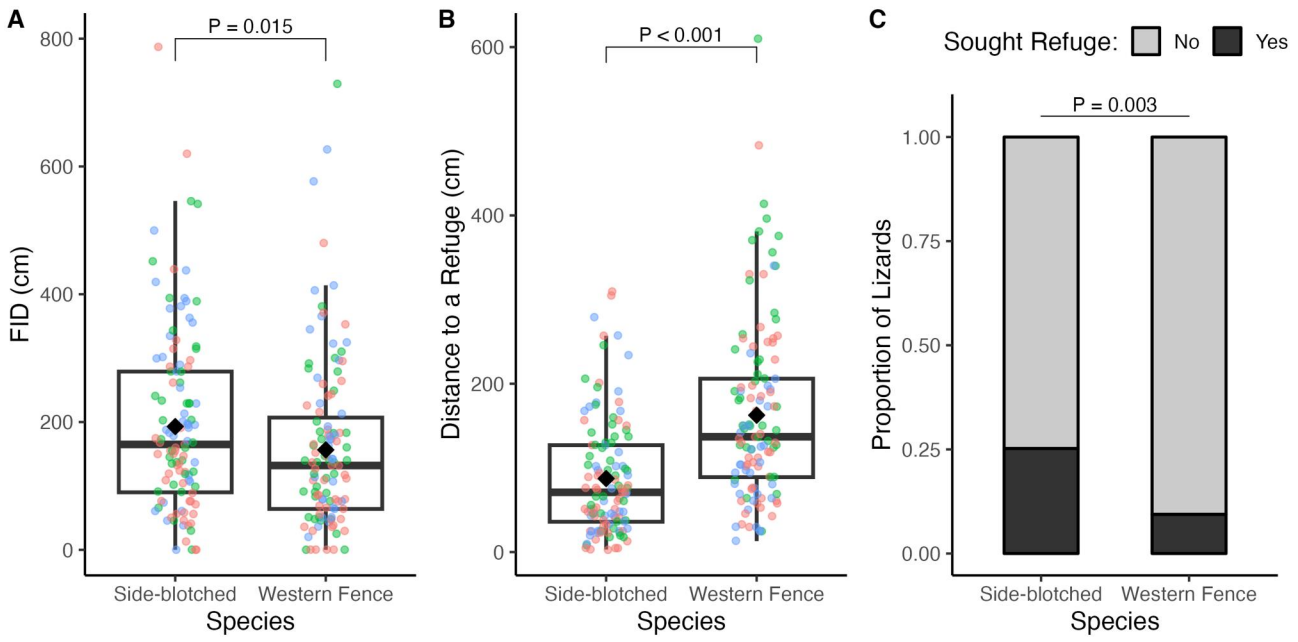


Figure 1: Differences in behavioral fear responses between side-blotched lizards and western fence lizards. **(A)** Flight initiation distances, the distance at which lizards fled from an approaching human. **(B)** The distance to the closest refuge when the lizard was found. **(C)** The proportion of lizards that sought refuge during the human approach. Boxplots show median and interquartile range, mean values are represented by black diamonds, and raw data are jittered on top with colors indicating habitat type: green = Natural-Low, red = Natural-High, blue = Urban.

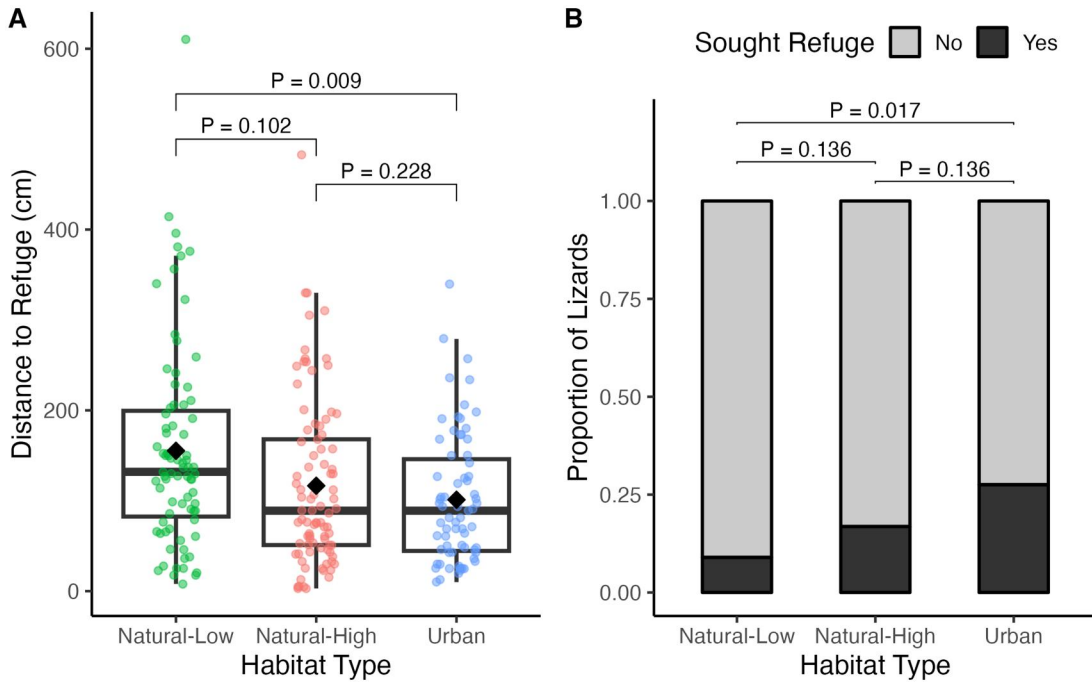


Figure 2: The effect of habitat on western fence lizard and side-blotched lizard behaviors: **(A)** distance to the closest refuge when the lizard was found, and **(B)** the proportion of lizards seeking refuge upon a human approach; 9% of lizards sought refuge in Natural-Low, 17% in Natural-High, and 28% in Urban. Boxplots show median and interquartile range, mean values are represented by black diamonds, and raw data are jittered on top.

($X^2 = 9.06$, $df = 1$, $P = 0.003$) in western fence lizards, and increased with body size in side-blotched lizards ($X^2 = 27.63$, $df = 1$, $P < 0.001$, [Supplementary Fig. S5](#)).

Body size and condition

We collected morphometric data on 221 western fence lizards (90 from Natural-Low, 72 from Natural-High, and 59 from Urban)

and 137 side-blotched lizards (53 from Natural-Low, 39 from Natural-High, and 45 from Urban). For both models on body size and condition, we found significant species*habitat interactions (body size: $X^2 = 11.23$, $df = 2$, $P = 0.022$, [Supplementary Tables S13 and S14](#); condition: $X^2 = 8.13$, $df = 2$, $P = 0.037$, [Supplementary Table S15 and S16](#)). Western fence lizards' body size and condition were affected by habitat with lizards in the Natural-Low

habitat having larger body sizes and being in better condition compared to lizards in the Natural-High and Urban habitats (body size contrasts: Natural-Low/Natural-High: $P < 0.001$, Natural-Low/Urban: $P < 0.001$, Natural-High/Urban: $P = 0.090$; condition contrasts: Natural-Low/Natural-High: $P < 0.001$, Natural-Low/Urban: $P < 0.001$, Natural-High/Urban: $P = 0.656$, Fig. 3). For side-blotched lizards, body size and condition were similar across all habitats (all contrasts with $P > 0.05$). In both species, males were larger (as expected based on the sexual dimorphism that characterizes these species) and in better condition than females (body size: $X^2 = 27.44$, $df = 1$, $P < 0.001$; condition: $X^2 = 25.56$, $df = 1$, $P < 0.001$). Body size and body condition were not correlated in western fence lizards ($r = 0.024$, 95% CI = -0.108 – 0.156 , $t = 0.361$, $df = 219$, $P = 0.719$) or side-blotched lizards ($r = 0.009$, 95% CI = -0.177 – 0.159 , $t = -0.109$, $df = 135$, $P = 0.914$).

Discussion

Side-blotched lizards responded differently to human disturbances than western fence lizards across sites of varying human

impact in the Greater Los Angeles Area. They exhibited behaviors that could be considered more fearful such as having longer flight initiation distances, being found closer to a refuge, and more likely seeking a refuge upon a human approach compared to western fence lizards. Within both species, urban populations were found closer to a refuge and more readily fled to a refuge upon a human approach than populations found in natural sites with low levels of human activity. However, these behavioral differences across habitats were not associated with differences in glucocorticoid concentrations in either species. Although we documented differences in behaviors across habitats of varying human impact in both species, only western fence lizards had lower body sizes and body conditions in the habitats impacted by people: the urban sites and natural sites with high levels of human activity.

Thus, two ecologically similar lizards living in sympatry across urban and natural habitats differed in their responses to human disturbances. Side-blotched lizards were not as tolerant of human approaches as western fence lizards. They fled from an approaching human from a larger distance, were found closer to a refuge, and were more likely to seek refuge than fence lizards,

Table 1: Summary statistics for raw corticosterone concentrations (ng/ml) among the three habitats for each lizard species

Lizard species	Habitat type	Basal mean \pm SE (N)	Basal range	Stressed mean \pm SE (N)	Stressed range
<i>Sceloporus occidentalis</i> (western fence lizard)	Natural-Low	4.32 \pm 0.16 (23)	1.28–13.15	21.81 \pm 0.69 (21)	5.32–53.70
	Natural-High	3.51 \pm 0.18 (21)	1.28–13.49	29.68 \pm 0.95 (23)	1.35–82.57
	Urban	5.49 \pm 0.32 (22)	1.28–33.07	22.55 \pm 0.72 (22)	2.75–54.27
<i>Uta stansburiana</i> (side-blotched lizard)	Natural-Low	7.98 \pm 0.57 (12)	0.45–23.97	77.08 \pm 4.51 (11)	26.52–150.72
	Natural-High	5.45 \pm 0.48 (10)	1.14–14.66	100.33 \pm 6.40 (12)	14.68–249.90
	Urban	6.52 \pm 0.29 (15)	0.94–14.15	68.36 \pm 5.49 (11)	21.65–232.14

Corticosterone concentrations were ln-transformed for statistical analyses.

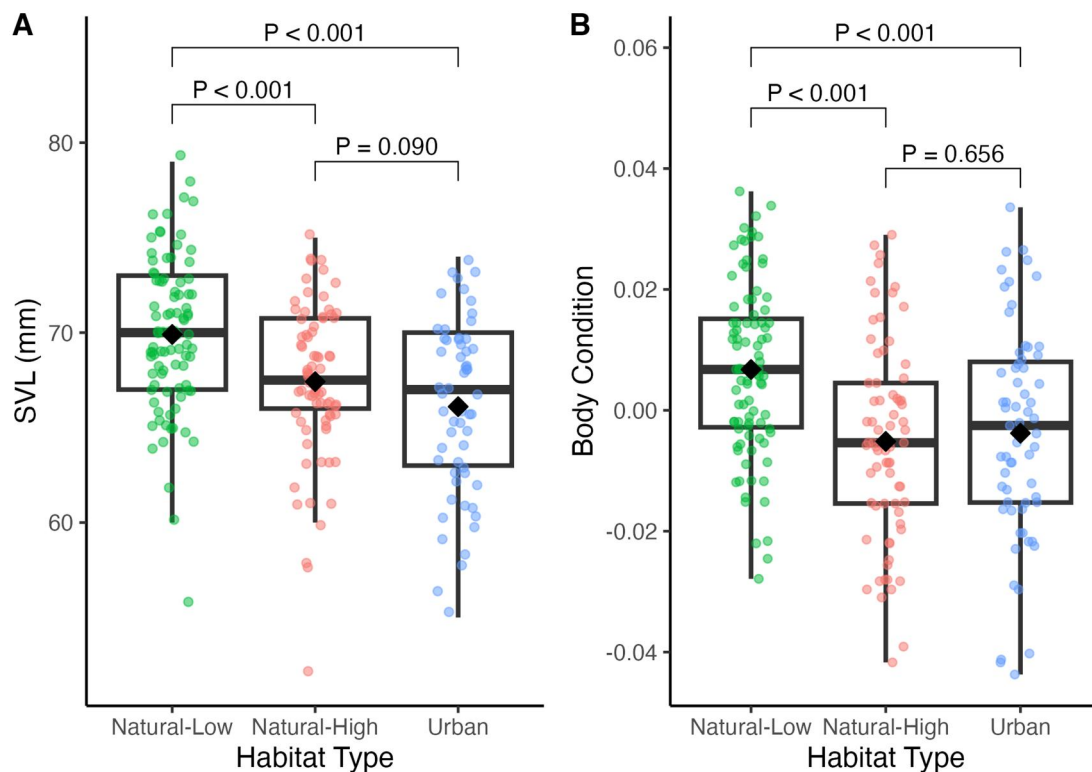


Figure 3: The effect of habitat on western fence lizards' (A) body size, measured as SVL, and (B) body condition. Boxplots show median and interquartile range, mean values are represented by black diamonds, and raw data are jittered on top.

behavioral differences that were consistent across all habitats. Such responses could make side-blotched lizards more sensitive to urbanization if lizards in urban areas spend less time foraging, looking for mates, and/or defending territories due to constant escape and increased time spent hiding from humans. However, we did not detect differences in body size or body condition in side-blotched lizards among habitats (detailed further below). The differences in behaviors between the two species could be due to their differences in microhabitat preferences, specifically side-blotched lizards' greater reliance on rock and burrow refuges and on their ground-dwelling lifestyle. Side-blotched lizards prefer relatively open sandy areas (Davis and Verbeek 1972; Morrison and Hall 1999), and large areas of this habitat type are often developed or landscaped in urban areas. In natural areas, western fence lizards bask upon woody vegetation (shrubs and trees), but in urban areas increasingly rely upon built structures with this habitat shift correlated with changes in morphology (Sparkman et al. 2018; Putman et al. 2019). Built structures (e.g. walls and buildings), especially those recently constructed, often lack retreat sites. Thus, decreased availability of habitat and/or retreat sites (see Rurik et al. 2022) could lead to behavioral differences between the two species and make side-blotched lizards more sensitive to urbanization.

Both side-blotched lizards and western fence lizards were found closer to a refuge and were more likely to seek refuge upon a human approach in the urban habitat compared to the habitat with low levels of human activity. These differences could be due to varying refuge types and availabilities between the two habitats (Rurik et al. 2022). Urban habitats may be more heterogenous in the types of perches and refuges available for lizards to use (Putman et al. 2019), and they may be more spread out or fragmented due to roads, sidewalks, or buildings separating them. We cannot say whether lizards are actively selecting sites based on refuge distance because we did not measure refuge availability, but prior research suggests that being found close to a hiding place may be a behavioral adaptation to urban life. Urban populations of lizards are often found closer to refuge than their non-urban counterparts (Batabyal, Balakrishna, and Thaker 2017; Putman et al. 2019; Álvarez-Ruiz et al. 2023) and invasive species that exploit urban habitats ("urban exploiters") are also found closer to refuge than less urban-tolerant native species (Putman, Pauly, and Blumstein 2020). Urban lizards may stay closer to refuge to avoid harm from urban associated risks such as humans, motorized vehicles, and/or bicycles, which increase mortality or injuries in lizards (Putman et al. 2021). Predation risk for lizards can also be greater in urban areas than in less developed areas (Tyler et al. 2016; Putman et al. 2021). This is likely due to increased numbers of outdoor cats and other human-subsidized predator populations. These higher risks in urban habitats may explain urban lizards' greater likelihood to completely hide in a refuge upon a human approach. Our urban sites also had the lowest tree cover (Supplementary Fig. S2), which could associate with a higher risk perception in lizards if they are more exposed to potential predators at these sites.

We did not find support for a habituation-like process occurring in areas of moderate (i.e. Urban) or high human activity levels (i.e. Natural-High) in either lizard species, corroborating prior work on western fence lizards that showed no habituation to humans (i.e. lower FIDs) along moderately used hiking trails (Putman et al. 2017). Lizard FIDs were similar across all habitat types, whereas lizard hiding responses (i.e. seeking refuge) were highest in the urban habitat. Despite this, side-blotched lizards did not exhibit differences in body sizes or conditions as expected

with constant flight away from humans or more time spent hiding in urban habitats. Western fence lizards, on the other hand, seemed to suffer negative consequences of not modifying behavioral responses in the human-impacted habitats (Urban and Natural-High). They had smaller body sizes and were in worse condition in these habitats. These reductions in size and condition could be associated with heightened responsiveness to human approaches leading to lost foraging opportunities and/or higher energy expenditures (Amo, López, and Martín 2006; Garrido and Pérez-Mellado 2015). On the other hand, the small body sizes exhibited by fence lizards in these habitats might be due to differences in food availability or to differences in thermal resources (e.g. access to radiant heat), two environmental factors that affect lizard growth (Sinervo and Adolph 1989; Tracy 1999; Mugabo et al. 2010). Some studies report increased population densities and conspecific competition in urban areas, which could alter an individual lizard's access to such resources (Baxter-Gilbert and Whiting 2019; de Andrade 2020; Lailvaux 2020). There could also be selective pressures driving shifts in body size for lizards living in human-impacted environments. Prior work has shown reduced post-maturational growth in lizards living in environments with high and unpredictable probabilities of unsuccessful annual reproduction, leading to different life history strategies (Tracy 1999). Yet, a recent meta-analysis showed that most lizard species exhibit an increase in body size in urban areas compared to their non-urban counterparts (Putman and Tippie 2020). Further work will need to determine whether body size differences among these populations are due to proximate differences in environmental conditions or genetic causes (e.g. selection or drift).

Corticosterone concentrations in both lizard species were unaffected by habitat. We found a clear difference between baseline samples taken within three minutes of disturbance and samples taken 30 min after capture, showing that the two species mount a stress response when handled and confined by humans. However, human impacts on the habitats such as increased human activity, increased impervious surface cover (i.e. changes to the structural components of the environment), and reduced tree cover did not affect these hormone concentrations, even though prior studies have shown effects of urbanization on lizard glucocorticoids (French, Fokidis, and Moore 2008; Lucas and French 2012; Batabyal and Thaker 2019). These lack of differences in corticosterone concentrations across habitats could be due to lizards in human-impacted habitats undergoing habituation-like processes to the challenges encountered in these habitats. Yet, side-blotched lizards showed a significant increase in corticosterone concentration with time since disturbance even under a three-minute period, suggesting a more rapid stress response toward humans than fence lizards (although this is inconclusive as we were not able to directly compare fence to side-blotched lizard corticosterone in our analyses). As we only took a single blood sample from each lizard, future work could opt for repeated sampling and/or characterization of stress response curves over multiple timepoints post-capture as another way to assess variation in HPA axis between species and habitats. This could assess whether a species' corticosterone response peaks earlier in urban habitats, or if there is a difference in when peak levels are achieved.

We also found that western fence lizards in worse body condition and those with warmer body temperatures had higher corticosterone levels, suggesting that corticosterone may be more related to energy status than fear (for the effect of body condition). These results corroborate a general trend observed in other

species of higher corticosterone being correlated with lower body conditions (Moore et al. 2000; Romero and Wikelski 2001; Rensel et al. 2011; DeSimone et al. 2020). Prior work on other lizard species has also found a positive relationship between temperature and corticosterone (Telemeco and Addis 2014; Racic, Tylan, and Langkilde 2020). Although we did not find an effect of urbanization on corticosteroids in our study, if urban lizards persist at warm temperatures (i.e. due to the urban heat island effect—Hall and Warner 2018; Campbell-Staton et al. 2020) and continue to have lower body conditions (as documented for fence lizards in this study), these could be associated with higher stress hormone values. It is important to recognize these relationships are correlative and have not been causally linked to fitness consequences.

It is possible that the behavioral differences between side-blotched lizards and western fence lizards are due to differences in body temperature. Side-blotched lizards were significantly warmer than fence lizards across all habitat types. However, prior research has reported a negative association with FID and temperature where warmer lizards tend to tolerate closer approaches from people presumably because warmer lizards are physiologically capable of a quicker, more coordinated retreat (Cooper 2006; Samia et al. 2015a). This would presumably allow lizards to be active farther away from refuge. Another potential factor that could explain our results is differences in predation risk between the two species. Side-blotched lizards largely use the ground or habitat near the ground, and are thus likely more exposed to diurnal predators than western fence lizards which have greater use of vertical habitat (e.g. trees and buildings). This increased predation risk may explain side-blotched lizards more wary responses compared to fence lizards, although this hypothesis needs further testing.

Overall, our study highlights the importance of studying multiple species responses in the same habitats to understand the impacts of humans on animals. Even though these lizards are sympatric, we show important differences in their behavioral responses to humans and in changes in body size and body condition across the three habitats, and a lack of differences in corticosteroid hormones across the habitats. Thus, not all animals respond similarly to the same disturbances. Our work sets the stage for understanding whether lizards with different microhabitat preferences consistently differ in their responses to humans, such as ground-dwelling species (like side-blotched lizards) being more wary than more arboreal species (like western fence lizards). This could help determine whether certain species are “pre-adapted” to existing in urban habitats. Lizards within the family Phrynosomatidae are an excellent system in which to study these questions as closely related species with different microhabitat preferences often occur in sympatry. Multi-species approaches will be necessary for creating a general framework for predicting how species may respond to human-induced habitat changes.

Supplementary data

Supplementary data are available at JUECOL online.

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Author contributions

Breanna Putman (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Funding acquisition [equal], Investigation [equal], Methodology [equal], Project administration [equal], Writing—original draft [equal]), Michelle Rensel (Methodology [equal], Resources [equal], Writing—review & editing [equal]), Barney A. Schlinger (Methodology [equal], Resources [equal], Supervision [equal], Writing—review & editing [equal]), Susannah French (Project administration [equal], Resources [equal], Writing—review & editing [equal]), Daniel Thomas Blumstein (Conceptualization [equal], Methodology [equal], Supervision [equal], Writing—review & editing [equal]), and Gregory B. Pauly (Conceptualization [equal], Methodology [equal], Resources [equal], Supervision [equal], Writing—review & editing [equal])

Conflict of interest statement

None declared.

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Data availability

All data used in this study will be made freely available upon request.

References

- Álvarez-Ruiz, L. et al. (2023) ‘Lizards’ Response to the Sound of Fire is Modified by Fire History’, *Animal Behaviour*, **196**: 91–102.
- Amo, L., López, P., and Martó'n, J. (2006) ‘Nature-Based Tourism as a Form of Predation Risk Affects Body Condition and Health State of *Podarcis muralis* Lizards’, *Biological Conservation*, **131**: 402–9.
- de Andrade, A. C. (2020) ‘Metropolitan Lizards? Urbanization Gradient and the Density of *Lagartixas (Tropidurus hispidus)* in a Tropical City’, *Ecology and Evolution*, **10**: 1740–50.
- Angelier, F., and Wingfield, J. C. (2012) ‘Importance of the Glucocorticoid Stress Response in a Changing World: Theory, Hypotheses and Perspectives’, *General and Comparative Endocrinology*, **190**: 118–28.
- Aronson, M. F. J. et al. (2017) ‘Biodiversity in the City: Key Challenges for Urban Green Space Management’, *Frontiers in Ecology and the Environment*, **15**: 189–96.
- Atwell, J. W. et al. (2012) ‘Boldness Behavior and Stress Physiology in a Novel Urban Environment Suggest Rapid Correlated Evolutionary Adaptation’, *Behavioral Ecology: official Journal of the International Society for Behavioral Ecology*, **23**: 960–9.
- Batabyal, A., Balakrishna, S., and Thaker, M. (2017) ‘A Multivariate Approach to Understanding Shifts in Escape Strategies of Urban Lizards’, *Behavioral Ecology and Sociobiology*, **71**: 83.

- , and Thaker, M. (2019) 'Social Coping Styles of Lizards Are Reactive and Not Proactive in Urban Areas', *General and Comparative Endocrinology*, **270**: 67–74.
- Bates, D. et al. (2015) 'Fitting Linear Mixed-Effects Models Using lme4', *Journal of Statistical Software*, **67**: 1–48.
- Baxter-Gilbert, J. H., and Whiting, M. J. (2019) 'Street Fighters: Bite Force, Injury Rates, and Density of Urban Australian Water Dragons (*Intellagama lesueurii*)', *Austral Ecology*, **44**: 255–64.
- Belotti, E. et al. (2018) 'Recreational Activities Affect Resting Site Selection and Foraging Time of Eurasian Lynx (*Lynx lynx*)', *Hystrix, Italian Journal of Mammalogy*, **29**: 3–10.
- Benjamini, Y., and Hochberg, Y. (1995) 'Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing', *Journal of the Royal Statistical Society: Series B (Methodological)*, **57**: 289–300.
- Bjørnvik, L. M. et al. (2015) 'Bird Flight Initiation Distances in Relation to Distance from Human Settlements in a Tanzanian Floodplain Habitat', *Journal of Ornithology*, **156**: 239–46.
- Blumstein, D. T. (2003) 'Flight-Initiation Distance in Birds is Dependent on Intruder Starting Distance', *The Journal of Wildlife Management*, **67**: 852.
- (2016) 'Habituation and Sensitization: New Thoughts about Old Ideas', *Animal Behaviour*, **120**: 255–62.
- Bonier, F. (2012) 'Hormones in the City: Endocrine Ecology of Urban Birds', *Hormones and Behavior*, **61**: 763–72.
- Campbell-Staton, S. C. et al. (2020) 'Parallel Selection on Thermal Physiology Facilitates Repeated Adaptation of City Lizards to Urban Heat Islands', *Nature Ecology & Evolution*, **4**: 652–8.
- Cavalli, M. et al. (2018) 'The Role of Habituation in the Adjustment to Urban Life: An Experimental Approach with Burrowing Owls', *Behavioural Processes*, **157**: 250–5.
- Ciuti, S. et al. (2012) 'Effects of Humans on Behaviour of Wildlife Exceed Those of Natural Predators in a Landscape of Fear', *PLoS One*, **7**: e50611.
- Clinchy, M. et al. (2016) 'Fear of the Human "Super Predator" Far Exceeds the Fear of Large Carnivores in a Model Mesocarnivore', *Behavioral Ecology*, **27**: arw117.
- Cockrem, J. F. (2013) 'Individual Variation in Glucocorticoid Stress Responses in Animals', *General and Comparative Endocrinology*, **181**: 45–58.
- Cooper, W. E. (2006) 'Risk Factors Affecting Escape Behaviour by Puerto Rican *Anolis* Lizards', *Canadian Journal of Zoology*, **84**: 495–504.
- Cooper, W. E. (2007) 'Compensatory Changes in Escape and Refuge Use following Autotomy in the Lizard *Sceloporus virgatus*', *Canadian Journal of Zoology*, **85**: 99–107.
- Davis, J., and Ford, R. G. (1983) 'Home Range in the Western Fence Lizard (*Sceloporus occidentalis occidentalis*)', *Copeia*, **1983**: 933–40.
- , and Verbeek, N. A. M. (1972) 'Habitat Preferences and the Distribution of *Uta stansburiana* and *Sceloporus occidentalis* in Coastal California', *Copeia*, **1972**: 643–9.
- Delaney, K. S. et al. (2021) 'Reptile and Amphibian Diversity and Abundance in an Urban Landscape: Impacts of Fragmentation and the Conservation Value of Small Patches', *Ichthyology & Herpetology*, **109**: 424–35.
- DeSimone, J. G. et al. (2020) 'Developing a Stopover-CORT Hypothesis: Corticosterone Predicts Body Composition and Refueling Rate in Gray Catbirds during Migratory Stopover', *Hormones and Behavior*, **124**: 104776.
- Dirzo, R. et al. (2014) 'Defaunation in the Anthropocene', *Science*, **345**: 401–6.
- Donihue, C. M., and Lambert, M. R. (2015) 'Adaptive Evolution in Urban Ecosystems', *Ambio*, **44**: 194–203.
- Dunn, R. R. et al. (2006) 'The Pigeon Paradox: Dependence of Global Conservation on Urban Nature', *Conservation Biology*, **20**: 1814–6.
- Fardell, L. L., Pavey, C. R., and Dickman, C. R. (2020) 'Fear and Stressing in Predator-Prey Ecology: Considering the Twin Stressors of Predators and People on Mammals', *PeerJ*, **8**: 1–35.
- Fondren, A., Swierk, L., and Putman, B. J. (2020) 'Clothing Color Mediates Lizard Responses to Humans in a Tropical Forest', *Biotropica*, **52**: 172–81.
- French, S. S., Fokidis, H. B., and Moore, M. C. (2008) 'Variation in Stress and Innate Immunity in the Tree Lizard (*Urosaurus ornatus*) across an Urban-Rural Gradient', *Journal of Comparative Physiology B*, **178**: 997–1005.
- et al. (2017) 'Too Much of a Good Thing? Human Disturbance Linked to Ecotourism Has a "Dose-Dependent" Impact on Innate Immunity and Oxidative Stress in Marine Iguanas, *Amblyrhynchus cristatus*', *Biological Conservation*, **210**: 37–47.
- Frid, A., and Dill, L. (2002) 'Human-Caused Disturbance Stimuli as a Form of Predation Risk', *Conservation Ecology*, **6**: 11.
- Gangloff, E. J. et al. (2016) 'Hormonal and Metabolic Responses to Upper Temperature Extremes in Divergent Life-History Ecotypes of a Garter Snake', *Journal of Experimental Biology*, **219**: 2944–54.
- Garrido, M., and Pérez-Mellado, V. (2015) 'Human Pressure, Parasitism and Body Condition in an Insular Population of a Mediterranean Lizard', *European Journal of Wildlife Research*, **61**: 617–21.
- Geffroy, B. et al. (2020) 'Evolutionary Dynamics in the Anthropocene: Life History and Intensity of Human Contact Shape Antipredator Responses', *PLOS Biology*, **18**: e3000818.
- Graham, S. P. N. A. et al. (2012) 'The Impacts of Invaders: Basal and Acute Stress Glucocorticoid Profiles and Immune Function in Native Lizards Threatened by Invasive Ants', *General and Comparative Endocrinology*, **176**: 400–8.
- Grolle, E. K., Lopez, M. C., and Gerson, M. M. (2014) 'Flight Initiation Distance Differs between Populations of Western Fence Lizards (*Sceloporus occidentalis*) at a Rural and an Urban Site', *Bulletin of the Southern California Academy of Sciences*, **113**: 42–6.
- Hall, J. M., and Warner, D. A. (2018) 'Thermal Spikes from the Urban Heat Island Increase Mortality and Alter Physiology of Lizard Embryos', *Journal of Experimental Biology*, **221**: jeb181552.
- Hews, D. K., and Abell Baniki, A. J. (2013) 'The Breeding Season Duration Hypothesis: Acute Handling Stress and Total Plasma Concentrations of Corticosterone and Androgens in Male and Female Striped Plateau Lizards (*Sceloporus virgatus*)', *Journal of Comparative Physiology B*, **183**: 933–46.
- Hibbitts, T. J. et al. (2013) 'Microhabitat Selection by a Habitat Specialist and a Generalist in Both Fragmented and Unfragmented Landscapes', *Herpetological Conservation and Biology*, **8**: 104–13.
- Hofmann, S., and Henle, K. (2006) 'Male Reproductive Success and Intrasexual Selection in the Common Lizard Determined by DNA-Microsatellites', *Journal of Herpetology*, **40**: 1–6.
- Hothorn, T., Bretz, F., and Westfall, P. (2008) 'Simultaneous Inference in General Parametric Models', *Biometrical Journal*, **50**: 346–63.
- Iglesias-Carrasco, M. et al. (2020) 'Stress in the City: meta-Analysis Indicates No Overall Evidence for Stress in Urban Vertebrates. Proceedings of the Royal Society', *B: Biological Sciences*, **287**: 20201754.
- Johnson, M. T. J., and Munshi-South, J. (2017) 'Evolution of Life in Urban Environments', *Science*, **358**: eaam8327.
- Kingsolver, J. G., and Huey, R. B. (2008) 'Size, Temperature, and Fitness: three Rules', *Evolutionary Ecology Research*, **10**: 251–68.
- Lailvaux, S. P. (2020) 'It's Not Easy Being Green: Behavior, Morphology, and Population Structure in Urban and Natural

- Populations of Green Anole (*Anolis carolinensis*) Lizards', *Frontiers in Ecology and Evolution*, **8**: 1–13.
- Lambert, M. R., and Donihue, C. M. (2020) 'Urban Biodiversity Management Using Evolutionary Tools', *Nature Ecology and Evolution*, **4**: 903–10.
- Landau, E. R. et al. (2019) 'Salivary C-Reactive Protein among at-Risk Adolescents: A Methods Investigation of out of Range Immunoassay Data', *Psychoneuroendocrinology*, **99**: 104–11.
- Lucas, L. D., and French, S. S. (2012) 'Stress-Induced Tradeoffs in a Free-Living Lizard across a Variable Landscape: Consequences for Individuals and Populations', *PLoS ONE*, **7**: e49895.
- McDonnell, M. J., and Hahs, A. K. (2015) 'Adaptation and Adaptedness of Organisms to Urban Environments', *Annual Review of Ecology, Evolution, and Systematics*, **46**: 261–80.
- Møller, A. P. (2010) 'Interspecific Variation in Fear Responses Predicts Urbanization in Birds', *Behavioral Ecology*, **21**: 365–71.
- (2008) 'Flight Distance of Urban Birds, Predation, and Selection for Urban Life', *Behavioral Ecology and Sociobiology*, **63**: 63–75.
- Moore, I. T. et al. (2000) 'Relationships between Annual Cycles of Testosterone, Corticosterone, and Body Condition in Male Red-Spotted Garter Snakes, *Thamnophis sirtalis concinnus*', *Physiological and Biochemical Zoology*, **73**: 307–12.
- Moroni, E. et al. (2017) 'Increased Behavioural Responses to Human Disturbance in Breeding Burrowing Owls *Athene cunicularia*', *Ibis*, **159**: 854–9.
- Morrison, M. L., and Hall, L. S. (1999) 'Habitat Characteristics of Reptiles in Pinyon-Juniper Woodland', *The Great Basin Naturalist*, **59**: 288–91.
- Mugabo, M. et al. (2010) 'Immediate and Delayed Life History Effects Caused by Food Deprivation Early in Life in a Short-Lived Lizard', *Journal of Evolutionary Biology*, **23**: 1886–98.
- Olsson, M. (1993) 'Male Preference for Large Females and Assortative Mating for Body Size in the Sand Lizard (*Lacerta agilis*)', *Behavioral Ecology and Sociobiology*, **32**: 337–41.
- Padgett, D. A., and Glaser, R. (2003) 'How Stress Influences the Immune Response', *Trends in Immunology*, **24**: 444–8.
- Putman, B. J. et al. (2017) 'Fear No Colors? Observer Clothing Color Influences Lizard Escape Behavior', *Plos One*, **12**: e0182146.
- et al. (2019) 'Downsizing for Downtown: limb Lengths, Toe Lengths, and Scale Counts Decrease with Urbanization in Western Fence Lizards (*Sceloporus occidentalis*)', *Urban Ecosystems*, **22**: 1071–81.
- , Pauly, G. B., and Blumstein, D. T. (2020) 'Urban Invaders Are Not Bold Risk-Takers: A Study of 3 Invasive Lizards in Southern California', *Current Zoology*, **66**: 657–65.
- , and Tippie, Z. A. (2020) 'Big City Living: A Global Meta-Analysis Reveals Positive Impact of Urbanization on Body Size in Lizards', *Frontiers in Ecology and Evolution*, **8**: 1–13.
- et al. (2021) 'The Power of Community Science to Quantify Ecological Interactions in Cities', *Scientific Reports*, **11**: 3069.
- R Core Team. (2021) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. <https://www.R-project.org/>
- Racic, A., Tylan, C., and Langkilde, T. (2020) 'Effects of Temperature on Plasma Corticosterone in a Native Lizard', *Scientific Reports*, **10**: 16315.
- Radder, R. S., and Shanbhag, B. A. (2004) 'Factors Influencing Offspring Traits in the Oviparous Multi-Clutched Lizard, *Calotes versicolor* (Agamidae)', *Journal of Biosciences*, **29**: 105–10.
- Rensel, M. A. et al. (2014) 'Region-Specific Neural Corticosterone Patterns Differ from Plasma in a Male Songbird', *Endocrinology*, **155**: 3572–81.
- , Wilcoxon, T. E., and Schoech, S. J. (2011) 'Corticosterone, Brood Size, and Hatch Order in Free-Living Florida Scrub-Jay (*Aphelocoma coerulescens*) Nestlings', *General and Comparative Endocrinology*, **171**: 197–202.
- Romero, L. M., and Wikelski, M. (2001) 'Corticosterone Levels Predict Survival Probabilities of Galapagos Marine Iguanas during El Nino Events', *Proceedings of the National Academy of Sciences of the United States of America*, **98**: 7366–70.
- Rurik, A. J. et al. (2022) 'Rock Refuges Are Strongly Associated with Increased Urban Occupancy in the Western Fence Lizard, *Sceloporus occidentalis*', *Diversity*, **14**: 655.
- Samia, D. S. M. et al. (2017) 'Rural-Urban Differences in Escape Behavior of European Birds across a Latitudinal Gradient', *Frontiers in Ecology and Evolution*, **5**: 1–13.
- et al. (2015a) 'Fifty Years of Chasing Lizards: New Insights Advance Optimal Escape Theory', *Biological Reviews*, **91**: 349–66.
- et al. (2015b) 'Increased Tolerance to Humans among Disturbed Wildlife', *Nature Communications*, **6**: 8877.
- Sinervo, B., and Adolph, S. C. (1989) 'Thermal Sensitivity of Growth Rate in Hatchling *Sceloporus* Lizards: Environmental, Behavioral and Genetic Aspects', *Oecologia*, **78**: 411–9.
- Small, T. W. et al. (2017) 'Stress-Responsiveness Influences Baseline Glucocorticoid Levels: Revisiting the under 3 Min Sampling Rule', *General and Comparative Endocrinology*, **247**: 152–65.
- Sparkman, A. et al. (2018) 'Parallel Behavioral and Morphological Divergence in Fence Lizards on Two College Campuses', *Plos One*, **13**: e0191800.
- Symonds, M. R. et al. (2016) 'Time since Urbanisation but Not Encephalisation is Associated with Increased Tolerance of Human Proximity in Birds', *Frontiers in Ecology and Evolution*, **4**: 117.
- Tablado, Z. et al. (2021) 'Factors Modulating the Behavioral and Physiological Stress Responses: Do They Modify the Relationship between Flight Initiation Distance and Corticosterone Reactivity?', *Hormones and Behavior*, **132**: 104979.
- Tadesse, S., and Kotler, B. (2011) 'Seasonal Habitat Use by Nubian Ibex (*Capra nubiana*) Evaluated with Behavioral Indicators', *Israel Journal of Ecology and Evolution*, **57**: 223–46.
- Telemeco, R. S., and Addis, E. A. (2014) 'Temperature Has Species-Specific Effects on Corticosterone in Alligator Lizards', *General and Comparative Endocrinology*, **206**: 184–92.
- Therneau, T. (2012) *coxme: Mixed Effects Cox models. R package version 2.2-18.1*. Vienna, Austria: R Foundation for Statistical Computing.
- Tillbrook, A. J., Turner, A. I., and Clarke, I. J. (2000) 'Effects of Stress on Reproduction in Non-Rodent Mammals: The Role of Glucocorticoids and Sex Differences', *Reviews of Reproduction*, **5**: 105–13.
- Tinkle, D. W., Mcgregor, D., and Dana, S. (1962) 'Home Range Ecology of *Uta stansburiana stejnegeri*', *Ecology*, **43**: 223–9.
- Tracy, C. R. (1999) 'Differences in Body Size among Chuckwalla (*Sauromalus obesus*) Populations', *Ecology*, **80**: 259–71.
- Tyler, R. K., Winchell, K. M., and Revell, L. J. (2016) 'Tails of the City: caudal Autotomy in the Tropical Lizard, *Anolis cristatellus*, in Urban and Natural Areas of Puerto Rico', *Journal of Herpetology*, **50**: 435–41.
- Uchida, K., and Blumstein, D. T. (2021) 'Habituation or Sensitization? Long-Term Responses of Yellow-Bellied Marmots to Human Disturbance', *Behavioral Ecology*, **32**: 668–78.
- Vincze, E. et al. (2016) 'Habituation to Human Disturbance is Faster in Urban than Rural House Sparrows', *Behavioral Ecology*, **27**: arw047.
- Zanette, L. Y. et al. (2023) 'Fear of the Human "Super Predator" Pervades the South African Savanna', *Current Biology*, **33**: 4689–96.e4.