

You can't bask with us: Does urbanization affect response to invasive and native competitors in lizards?

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Urbanization impacts biodiversity, changing the breadth and depth of species interactions. Urban animals may experience more intraspecific interactions and fewer interspecific interactions than nonurban animals due to reduced biodiversity in urban areas. Interspecific interactions in urban areas may be with novel competitors as invasive species are commonly associated with urbanization. Here, we tested whether urbanization affects animal responses to inter- and intraspecific competitors by quantifying physiological and behavioural traits of male western fence lizards, *Sceloporus occidentalis*, when exposed to potential competitors. We filmed fence lizard behaviour both when individuals were alone and when they were paired with either a nonurban or an urban unfamiliar conspecific competitor, or with a novel heterospecific competitor (a non-native Italian wall lizard, *Podarcis siculus*). We also quantified stress responses (corticosterone concentrations, CORT) from blood samples. Overall, urbanization did not impact fence lizard responses to competitors. Instead, we found that regardless of habitat, lizards were the most stressed and exhibited the most visual displays and aggressive behaviours when encountering a conspecific. Lizards also reduced usage of the basking site in heterospecific trials, suggesting potential responses to novelty, body size differences or exploitation competition by Italian wall lizards. Lastly, urban lizards exhibited more information-seeking behaviours and higher body temperatures than their nonurban counterparts, which could be associated with different risks and thermal environments, respectively, between urban and nonurban habitats. Collectively, our findings suggest that urbanization does not strongly affect responses to competitors, contrary to expectations based on differences in population density and biodiversity between urban and nonurban environments.

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Nearly all animals compete for food, mates and/or habitat within and between species. It is well known that two species utilizing the same limiting resources cannot coexist indefinitely (Potapov, 2004; Tilman, 1981). As animals compete for resources in their environment, interactions may change as the environment changes. One of the most drastic forms of environmental change is urbanization, which is defined as when large amounts of people reside in areas that were once rural, modifying landscapes to suit human needs (Filazzola et al., 2024; Parmesan & Yohe, 2003; United States Environmental Protection Agency, 2022). Although the effects urbanization on the environment are well studied, few studies focus on how these changes may affect species interactions, especially among potential competitors (Boyer & Rivault, 2004; Ropars et al., 2019; Sedláček et al., 2004). The

composition and number of competitors an animal coexists with likely differ between urban and nonurban habitats.

Urbanization usually reduces biodiversity (e.g. species richness) as many species do not tolerate the drastic habitat changes associated with urban development (Buczowski and Richmond, 2012; Gray, 1989; McKinney, 2002; Vitousek et al., 1997). Therefore, differences in species composition between urban and nonurban areas may cause urban-residing species to experience a lower frequency or intensity of heterospecific interactions than their nonurban counterparts (i.e. interacting with fewer other species). Conversely, interactions with conspecifics may be more intense in urban areas due to habitat fragmentation. For instance, resources occur in small patches (Parker & Nilon, 2008; Prange et al., 2004), and urban animals experience reduced home range sizes (O'Donnell & Delbarco-Trillo, 2020; Rotem et al., 2011; Rutz, 2006; Šálek et al., 2015), leading to an increase in population densities within small areas (Baxter-Gilbert & Whiting, 2019; Walton et al., 2017; Šálek et al., 2015). Thus, individuals of the same

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species may interact with each other more often in urban areas than in nonurban areas, a pattern found in a recent study on common wall lizards, *Podarcis muralis* (Maune et al., 2025). Such interactions may lead to shifts in behaviours such as increased aggressiveness to access limited resources or alternatively, increased tolerance of conspecifics (Collie et al., 2020; Łopucki et al., 2021).

Introduced or invasive species are commonly found in urban areas, representing potentially novel competitors for urban-residing natives. Invasive species are introduced to urban areas due to high amounts of human goods transportation and human migration (Essl et al., 2024; Gotzek et al., 2015; Padayachee et al., 2017). Although some introduced species have minor effects on native wildlife, others can impact native populations through predation (Doherty et al., 2016), pathogen/parasite transmission (Crowl et al., 2008) and displacement via direct or indirect competition (Hernández-Brito et al., 2014; Ropars et al., 2019). When introduced species are potential competitors of natives, they may interfere directly with natives' access to resources through aggression and direct attacks (i.e. interference competition; Vahl et al., 2007). Indeed, invasives can have higher levels of aggression or boldness compared to native species (Chapple et al., 2011; Weis, 2010). More often though, introduced species affect natives through exploitation competition where their use of a shared resource reduces its availability (Page & Williams, 2023). For example, some invasive species are more efficient foragers, which may aid in their invasion success (Downes & Bauwens, 2002; Pintor & Sih, 2009; Weis, 2010). If urban animals experience fewer interspecific interactions (due to lower species richness), they may not have the proper tactics to handle competition with a heterospecific. This may make urban animals more sensitive to introduced competitors than their nonurban counterparts, but few studies have tested this idea.

As the types and intensity of species interactions shift with urbanization, animals may exhibit shifts in behavioural and/or physiological traits. Territorial and aggressive behaviours may intensify or animals may become more tolerant of interactions when conspecific densities increase, habitats become more fragmented or resources become limited (Barrero et al., 2024; Manenti et al., 2015; Maune et al., 2025; Stroud et al., 2019). In urban areas, some animals show no changes in territorial displays or aggression (Devitz & Dantzer, 2024; Grzywaczewski et al., 2024; Hurtado & Mabry, 2017; von Merten et al., 2022), while others exhibit an increase in these behaviours. For example, higher conspecific densities in urban areas are associated with higher wounding rates in water dragons, *Intellagama lesueurii* (Baxter-Gilbert & Whiting, 2019). Similarly, urban Cuban rock iguanas, *Cyclura nubila*, experience more aggressive male–male interactions (Lacy & Martins, 2003), and urban anoles exhibit higher dewlap display rates (territorial displays) than their nonurban counterparts (Stroud et al., 2019). Aside from behavioural responses, physiological stress can occur when an animal experiences a stressful encounter or physical wound from a competitor (Wingfield & Kitaysky, 2002). Stress is often measured by the concentration of glucocorticoid hormones (GCs, often called stress hormones) circulating in blood plasma. Baseline GC levels can differ between animals living urban and nonurban areas (Beaugeard et al., 2019; French et al., 2018; Gabor et al., 2018; Łopucki et al., 2019). This could potentially affect how GC levels are triggered when experiencing a stressor. High conspecific densities and increased social interactions are associated with heightened GC levels (Creel, 2001; Creel, Christianson, & Schuette, 2013; Creel, Dantzer, et al., 2013; Franchini et al., 2023; Zhao et al., 2021). Thus, because urban areas often have high conspecific density (Baxter-Gilbert & Whiting, 2019; Walton et al., 2017; Šálek et al., 2015), animals that

experience more conspecific interactions or crowding may have more frequent glucocorticoid release (Blondel et al., 2016). Notably, suburban male peninsular rock agamas, *Psammophilus dorsalis*, showed elevated GC levels in behavioural trials when paired with conspecific males and females, while rural lizards showed lower GCs during the same interactions (Batabyal & Thaker, 2019). Furthermore, GCs can be positively associated with aggression during species interactions (Mikics et al., 2004; Ros et al., 2014). Thus, if animals in urban and nonurban areas differ in their behavioural responses to competitors, this may be associated with underlying physiological responses, providing insight into the relationship between hormones, behaviour and species interactions.

Here, we evaluated the impact of urbanization on animal responses to potential competitors, both a conspecific and a novel heterospecific. Western fence lizards, *Sceloporus occidentalis*, are an ideal study organism for this work because they are found in habitats of varying degrees of urbanization across the western United States and males readily exhibit distinct and well-documented territorial display behaviours towards conspecific competitors (Carpenter, 1978). Furthermore, they reside in an area (California, U.S.A.) where invasive species are commonly introduced (California Invasive Species List, <https://calinvasives.ucdavis.edu/species>). One of these invasive species poses a threat to native western fence lizards. The Italian wall lizard, *Podarcis siculus*, was introduced to San Pedro, California in 1994 from Sicily, Italy (Burke, 2010). Like fence lizards, Italian wall lizards are heliothermic lizards that use exposed perches (wall, rocks, logs) for basking, and they consume a similar diet of arthropods (G. B. Pauly, personal communication). Western fence lizards were once abundant in San Pedro but now nearly none remain within the population range of the Italian wall lizards (G. Pauly & B. Putman, personal observations), suggesting they have been displaced by an introduced competitor. The question remains whether urbanization affects the response of western fence lizards to this invasive species.

For our study, we quantified the behavioural and stress responses of western fence lizards when paired with a competitor, either another western fence lizard or an Italian wall lizard. We predicted that lizards in urban areas would occur in higher population densities with their own species, which may lead to more frequent conspecific interactions and presumed competition. Thus, we predicted that urban lizards would exhibit different levels of responsiveness (aggression, display behaviours, CORT concentrations) when paired with a conspecific than would their nonurban counterparts. We also predicted that urban lizards would exhibit fewer aggressive or display behaviours when encountering a novel heterospecific competitor than would their nonurban counterparts due to less familiarity of heterospecifics resulting from lower species richness in urban areas.

METHODS

Study Subjects and Sites

We studied male western fence lizards from two replicate urban and nonurban sites in different cities in Southern California: San Bernardino and Claremont (Supplementary Fig. S1). At each location, one sample of lizards was taken from an urban area, which consisted of built-up college campuses with relatively high levels of human activity, and another sample was taken from a nonurban area, which consisted of mostly intact native chaparral and sage scrub habitat. Urban areas were located within the campuses of the Claremont Colleges (34.09859°N, 117.70286°W; WGS84 Coordinate System) and the California State University, San

Bernardino (CSUSB) campus (34.18436°N, 117.32459°W). The two nonurban areas were the Bernard Field Station in Claremont (34.10934°N, 117.71187°W) and an undeveloped area behind the CSUSB campus (34.18882°N, 117.31964°W). At both locations, lizard species diversity was lower at urban sites than at the nonurban sites based on personal observations (we have been working at these sites since 2020), iNaturalist observations and standardized cover board surveys (conducted in San Bernardino). In general, western fence lizards are the primary basking species inhabiting urban cores where they co-occur with nonbasking southern alligator lizards, *Elgaria multicarinata*. They also co-occur with side-blotched lizards, *Uta stansburiana*, at urban margins or in small patches of undeveloped land, but we did not collect lizards from these areas. At nonurban sites, western fence lizards co-occur with at least five other lizard species: *Anniella stebbinsi*, *Aspidoscelis tigris*, *Elgaria multicarinata*, *Plestiodon skiltonianus* and *U. stansburiana*.

We estimated western fence lizard population density within each habitat because differences in population densities might affect how they respond to competitors. We used the line transect sampling method (also known as distance sampling) to estimate population densities (Ruiz De Infante Anton et al., 2013; Vogt, 2010). This method estimates population density by considering how many lizards are seen during the transect (transect distance) and how far from the transect they are observed. We surveyed three 200 m transects in a randomized order within each site, for a total of 12 transects, six in urban habitats and six in nonurban habitats (3 transects for each of the four sites). We used an aerial map to determine five transects for each location, then picked three of the five based on walkability, distance between transects and proximity to roads. Following methods from past studies with minor modifications (Ruiz De Infante Anton et al., 2013; Vogt, 2010), we surveyed transects three times per year between June and July in 2022 and between May and June in 2023, for a total of 36 transect surveys per habitat type (6 transects over 6 days per habitat). Transects were surveyed during the regular activity times of lizards (0800–1300 hours). To account for temporal effects on lizard activity, we randomized the order in which sites were sampled, and we accounted for weather by only surveying on sunny days. For each survey, two people walked slowly to avoid scaring lizards over the length of the 200 m transect. The observers walked side by side and looked for lizards on each side of the transect. For each lizard sighted, we measured the perpendicular distance from the middle of the transect to where the lizard was first seen. Any lizards sighted outside of 20 m from the transect were not included to account for different visibility distances between the sites (we determined that we could reliably see lizards within 20 m at each site).

We used the unmarked package in R (Fiske & Chandler, 2011; Kellner et al., 2023) to estimate lizard population density within each habitat. This method accounts for variation in the probability that animals are detected or not detected along the transect through a detection probability function, estimated via transect distance length, number of lizard observations, and how far the lizards were from the transect line (up to 20 m). We estimated population density within each site (Claremont nonurban, Claremont urban, San Bernardino nonurban, San Bernardino urban) for each transect survey day ($N = 6$ days) by incorporating the survey data from the 12 transects into the distance sampling model. Using the 'distsamp' function in the unmarked package, we fitted a half-normal detection function to model the density in lizards/ha, incorporating site as a covariate. We did this for each day of surveys (for a total of 6 days) to account for potential differences observed due to weather or time of surveying.

We collected a total of 52 adult male western fence lizards between 16 May and 8 June 2022. Of these, 26 lizards were caught from urban habitats and 26 were caught from nonurban habitats (13 lizards from each of the four sites). We caught lizards with fishing line that was tied into a slipknot and attached to a fishing pole. We took a blood sample immediately upon capture via puncture of the post-orbital sinus using a heparinized micro-capillary tube. The blood samples were used to determine whether baseline corticosterone levels differed between urban and nonurban populations. We only captured male lizards to narrow the variability in responses, and because males are primarily the territorial sex often seen engaging in competitive displays (Carpenter, 1978). Twelve of the 52 lizards (three from each location) were used as stimulus lizards in the behavioural trials (detailed below), and no behavioural data were collected on these lizards (leaving 40 lizards for behavioural trials). After capture, lizards were transported to California State University, San Bernardino.

Italian wall lizards are an invasive species in California that have been displacing western fence lizards in urban areas where they have been introduced (G. Pauly & B. Putman, personal observations). On 30 March 2022, we captured five adult male Italian wall lizards in San Pedro, California (33.71545°N, 118.30340°W) where they were introduced in 1994. These lizards were used as novel heterospecific stimulus lizards in the behavioural trials (detailed below).

Lizard Processing and Housing

We housed captured lizards in an isolated room on campus. They were kept individually in plastic containers ($L \times W \times H$: 43 × 30 × 33 cm) equipped with a 25 W spotlight overhead (lit for 6 h per day) in a room with a 12:12 h light:dark cycle. Each enclosure contained play sand as substrate and a plastic refuge for shelter. The sides were covered in butcher paper to obstruct view of neighbouring lizards. All lizards were given food (dubia roaches, *Blaptica dubia*, and/or mealworms, *Tenebrio molitor*) and water ad libitum every other day. We also removed ticks and mites from lizards prior to housing. The Italian wall lizards were kept in 10-gallon (37.85-litre) glass terrariums (51 × 26.4 × 31 cm) with a 40 W spotlight for a heat source. All other housing protocols were identical to the western fence lizards. We gave the lizards a 1-week acclimation period before testing them in behavioural trials.

Behavioural Trials

To quantify how urbanization affects native species' responses to potential competitors, we ran behavioural trials pairing western fence lizards with either a conspecific lizard, a novel heterospecific lizard or no other lizard (as a control, Fig. 1). Trials were held between 0900 and 1300 hours, which is within the regular activity time of this species, and occurred between 5 June 2022 and 9 July 2022. Trials were conducted in a separate room from where lizards were housed in an arena constructed of white corrugated plastic. Arenas were 1 × 0.6 m and 1 m tall. Using similar methods to a past study (Damas-Moreira et al., 2020), each arena included a heated perch/refuge site at one side and a nonheated perch/refuge site on the opposite side (Fig. 1). Perches were composed of three stacked bricks, two on the bottom, slightly separated, and one on top, forming a shelter underneath. The heated perch was heated overhead by an overhanging 125 W spotlight, providing a valuable resource in the arena for basking that the lizards could compete over. The heated perch temperature ranged from 45 to 48 °C, and the unheated perch maintained a temperature between 20 and 25 °C. Fence lizard body temperature prior to trials ranged from 23°C

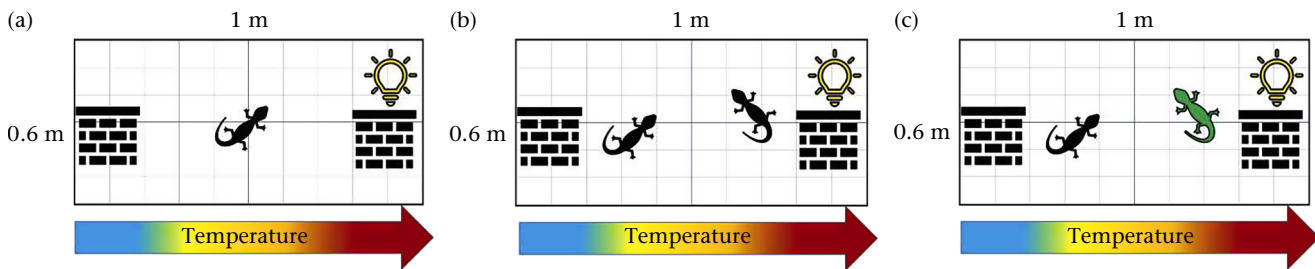


Figure 1. Trial types used to study behaviour. One side of the arena had a heated brick refuge, and the opposite side was not heated. This created a temperature gradient with preferred conditions for lizards on the warmer side. We tested focal lizards under three conditions: (a) control: a focal western fence lizard alone; (b) conspecific: a focal western fence lizard and a stimulus western fence lizard (size-matched); (c) heterospecific: a focal western fence lizard and a stimulus Italian wall lizard (size-matched).

to 34 °C, with an average of 27.5 °C, which is lower than their preferred temperature of 35 °C (McGinnis, 1966), so there should have been strong motivation to bask under the light to reach preferred temperatures.

Before each trial, we took the temperature of the room, which ranged from 22.8 °C to 24.6 °C, the arena and the focal lizard's body temperature. We took the room temperature using a digital thermometer (ThermoPro TP49, <https://tempopro.com>), and both the arena and body temperature with an infrared temperature gun (Etekcity Lasergrip 774, <https://etekcity.com>). An Akaso action camera (model EK7000, <https://www.akasotech.com>) was used to film the trial from directly overhead. Two trials were held in the same room at the same time, and motions of human observers conducting the trials were similar across all trial types to ensure each focal lizard was given the same triggers. Humans were not present during the trials and were only in the room to introduce the focal and stimulus lizards. Arenas and bricks were cleaned using animal-safe disinfecting wipes between trials.

To start a trial, a focal western fence lizard was put in the arena alone and given a 20 min acclimation period. After 20 min, either a stimulus lizard was introduced, or the human observer mimicked introducing a lizard into the arena (for the control), and the trial ran for another 20 min. Each lizard experienced three different trial types, with one trial per week: (1) novel heterospecific lizard, (2) unfamiliar conspecific lizard and (3) a control of no other lizard (Fig. 1). Each lizard had a 1-week rest period between trials. The trial orders for each lizard were balanced by habitat (urban or nonurban) and trial type. Heterospecific trials consisted of introducing a non-native Italian wall lizard into the arena with the native western fence lizard. Italian wall lizards represented a novel heterospecific competitor to all the focal western fence lizards because none of the focal lizards were from locations where Italian wall lizards occur. The conspecific trials consisted of introducing an unfamiliar western fence lizard into the arena. Three of the western fence lizards caught at each site (as detailed above) were reserved as stimulus lizards for the trials. Stimulus western fence lizards were not tested as focal lizards, and all lizards were matched from the same habitat types (i.e. urban lizards paired with urban lizards and nonurban lizards paired with nonurban lizards), but from opposite locations (San Bernardino or Claremont) to account for familiarity. Lastly, the control had no stimulus introduced during the trial, but researchers mimicked introducing a stimulus lizard to the arena after the acclimation period to account for the effect of human disturbance on lizard responses.

All heterospecific and conspecific stimulus lizards were size-matched as close as possible to the focal lizard (Damas-Moreira et al., 2020). The average (\pm SE) percentage difference in body size for conspecific pairs was $1.97 \pm 0.42\%$ ($N = 40$). The maximum percentage difference was 14.29% and the minimum difference

was 0%. Among pairings of lizards from nonurban areas, six focal lizards were larger than the stimulus, six focal lizards were smaller than the stimulus and eight were the same size. For urban pairings, nine focal lizards were larger than the stimulus, six focal lizards were smaller than the stimulus and five were the same size. The average (\pm SE) percentage difference in body size for lizards paired in heterospecific trials was $6.35 \pm 1.07\%$ ($N = 38$). The maximum percentage difference between heterospecific pairs was 26.79% and the minimum was 0%. The difference between heterospecific pairs was greater as Italian wall lizards are a larger-bodied species than western fence lizards and were more difficult to size-match. Among heterospecific pairings for nonurban lizards, 17 lizards were smaller than the stimulus, two were larger than the stimulus and none was the same size. For urban heterospecific pairings, 16 lizards were smaller than the stimulus, one was larger than the stimulus and two were the same size. We ensured that stimulus lizards were used evenly across trials (i.e. we did not repeatedly pair the same heterospecific individual with all urban lizards or use a single conspecific for all nonurban lizards; [Supplementary Table S2](#)).

After the 20 min trial period, the focal lizard was removed from the arena and a blood sample was immediately taken from the post-orbital sinus using a heparinized microcapillary tube, and the body temperature of the lizard was taken again. We did not take pretrial blood samples to avoid altering the behaviour of lizards and to limit the amount of blood samples per individual across the study duration. Samples were kept on ice in microcentrifuge tubes until we returned to the laboratory. In the laboratory, blood samples were spun down in a centrifuge at 3.0 g (29.4 m/s^2) for 10 min. We used a Hamilton syringe to collect the plasma, which was then transferred to a cryotube for storage in a -80 °C freezer. We quantified CORT levels using an ELISA kit (ADI-901-097, Enzo Life Sciences, <https://www.enzo.com/>), which has been optimized and validated previously for use in western fence lizards (Putman et al., 2024). Plasma samples were diluted at a 1:40 ratio with a 1% concentration (of raw plasma volume) of steroid displacement buffer and tested on a 96-well plate in duplicate. We used a Byonoy absorbance reader (Byonoy, <https://byonoy.com/absorbance-96/>) set to read at 405 nm to analyse the samples after a 60 min incubation period. We calculated the concentration of CORT using the absorbance readings by taking the average of the duplicate samples. The minimum level of detection for this kit is 0.032 ng/ml, so any samples that were lower than this concentration were assigned this minimum concentration ($N = 2$). Baseline blood samples (from Putman et al., 2025) and post-trial blood samples were randomized on plates to reduce biases associated with date of collection. Intraassay coefficients of variation (CV) ranged from 10% to 26%, with an average of 17% ($N = 8$ plates). The interassay CV was 16% (with 4 CORT standards on each plate).

We used an ethogram to quantify behaviours of the focal lizards from video recordings (Table 1). We coded for behaviours that represent territorial displays (push-ups, headbobs), aggression (approaches, biting), displacement or submission (hiding), or behaviours that allow the lizard to gain information from the environment (head scanning, tongue flicks). We also recorded time spent on the basking perch, which was the limiting resource in the arena. Behaviours were split into two categories: events and states (Table 1). Events included behaviours that could be counted within a certain time period (i.e. number of push-ups, number of head scans, etc.), while states were durations of behaviour (i.e. time spent hiding, etc.). Events could occur at the same time as states, but states were mutually exclusive (i.e. only one state could happen at a time). We utilized JWatcher (version 1.0, <https://www.jwatcher.ucla.edu>), a behaviour recording software, to quantitatively record the events and states of the lizards. The video reviewer was blind to habitat type and source location of each lizard, but not to treatment (trial type).

Statistical Analyses

We analysed data using R (version 4.3.0) with alpha set to 0.05. We used the emmeans package (Lenth, 2022) to generate predicted responses with 95% confidence levels (based on the estimated marginal means for dependent variables in the models) and to estimate pairwise differences adjusted by the false discovery rate method. Assumptions of models were met, verified through examination of residual plots. We used likelihood ratio tests to determine whether interactions were important, and if these tests were nonsignificant, interaction terms were removed and only main effects were assessed. Not all lizards were included in analyses due to logistical constraints (e.g. camera malfunctions, issues with taking blood samples immediately after a trial). Therefore, we analysed lizard behaviours from 118 trials (59 nonurban, 59 urban) and analysed CORT concentrations from 113 trials (58 nonurban, 55 urban).

Table 1
Ethogram used to quantify behaviours from videos

Behaviour	Definition	Behaviour type
Head scans	How many times the focal lizard moves its head fully in one direction	Information-seeking event
Tongue flicks	How many times the focal lizard sticks its tongue out	Information-seeking event
Headbobs	How many times the focal lizard moves its head up and down	Display behaviour event
Push-ups	How many times the focal lizard moves its body up or down in a push-up formation	Display behaviour event
Biting	How many times the focal lizard bites the stimulus lizard	Aggressive behaviour event
Approach	How many times the focal lizard quickly moves in the direction of the stimulus lizard	Aggressive behaviour event
Basking	How much time the focal lizard spends basking on the heated perch	Undisturbed state
Hiding	How much time the focal lizard spends hiding under a refuge or staying in place with its head facing the corner	Displacement response state

Behavioural states were calculated in minutes, while events were calculated as counts. Only the behaviour of the focal lizard was recorded over the 20 min trial period.

First, to determine whether lizard population densities differed between habitat types or locations, we ran a linear model with the daily average density estimates per site set as the dependent variable and habitat type (nonurban versus urban), location (San Bernardino or Claremont) and their interaction set as the independent variables. The interaction term was not significant ($P > 0.05$), so it was not included in the final model. We were unable to run a linear mixed effects model with site as a random effect because with so few sites, the model would not converge.

To determine whether urbanization affects how native western fence lizards behaviourally respond to potential competitors, we used generalized linear mixed models with a negative binomial distribution through the glmmTMB package in R (Brooks et al., 2017) to account for zero inflation and overdispersion. We did this because the behavioural data were right-skewed with many zero values. In these models, we included focal lizard ID nested within site as a random factor to account for repeated measures, and trial type (conspecific, heterospecific, or control), habitat (nonurban or urban) and their interaction as fixed factors. The interaction between trial type and habitat was nonsignificant for all models ($P > 0.05$) and was removed from final analyses. We analysed time spent basking and hiding separately. We acknowledge that these two behaviours are negatively correlated because they are mutually exclusive, but we elected to analyse them separately because they may represent different functional responses to the arena stimuli (submission versus motivation to thermoregulate). The six behavioural events were collapsed into three different measures that also represent different functional responses: information seeking, visual displays and aggression. Information-seeking behaviours were calculated as the summation of all head scans and tongue flicks, display behaviours were calculated as the summation of all push-ups and headbobs and aggression behaviours were calculated as the summation of all bite attempts and quick approaches towards the stimulus lizard. Information-seeking behaviours and displays were analysed with the full data set as we recorded these behaviours across all trial types, whereas aggression was analysed using only data from conspecific and heterospecific trials as these behaviours could not be observed during the control trial. In the GLMM on aggression, stimulus ID nested within trial type was added as a random factor.

To determine whether urbanization affects how native western fence lizards physiologically respond to competitors, we used a linear mixed effects model with focal lizard ID nested within site as a random factor, and trial type (conspecific, heterospecific, control), habitat (nonurban, urban) and their interaction as fixed factors. CORT concentration (ln-transformed) was set as the dependent variable. The interaction between habitat and trial type was verified to be nonsignificant ($P > 0.05$) through a likelihood ratio test, so it was removed from the final model. We also added the temperature of the lizard during blood sampling as a fixed factor because prior research has shown this to significantly influence CORT (Putman et al., 2024). Population differences in baseline CORT were not analysed here as these results have been published elsewhere (Putman et al., 2025). There was no significant difference in baseline CORT between urban and nonurban populations.

Because we were interested in lizards' use of the basking site in response to potential competitors, we also looked at whether their body temperatures were affected by trial type. To evaluate this, we used a linear mixed effects model with lizard body temperature as the dependent variable, time point of temperature measurement (pretrial versus post-trial) to estimate the change in temperature over the course of the trial, trial type (conspecific, heterospecific, control) and habitat (nonurban, urban) as fixed factors and focal lizard ID nested within site as a random factor. We also ran

additional models to determine whether stimulus lizard ID could have affected our overall results and conclusions. For every model run above, we ran an additional model with stimulus ID nested within trial type as a random factor and qualitatively compared these results to those of models without this random factor (Supplementary Table S3). Models with stimulus ID as a random factor did not include the control treatment and therefore had lower power to detect significant results.

Ethical Note

This study conformed to the legal requirements of the United States. Lizards were collected under a California Department of Fish and Wildlife (CDFW) permit (S-19280001-19282-001), and work with lizards was ethically performed under an Institutional Animal Care and Use protocol approved by California State University, San Bernardino (IACUC number 19-019) that ensured methods minimized stress and discomfort. At the end of the study lizards were humanely euthanized via sodium pentobarbital following both CDFW and IACUC guidelines. Because they interacted with invasive Italian wall lizards, the native fence lizards had to be euthanized to prevent spread of parasites and diseases that they could have contracted from the invasive species. All lizards were donated to the Natural History Museum of Los Angeles County to be used in future research.

RESULTS

Western fence lizard population density differed between our urban and natural habitats, with more dense populations occurring in urban habitats (estimated mean nonurban density = 4.48 lizards/ha [95% CL = 2.38–6.58], estimated mean urban density = 11.51 lizards/ha [95% CL = 9.42–13.61]; linear model results: estimate \pm SE = 7.032 ± 1.427 , $t = 4.930$, $P < 0.001$; Supplementary Table S1, Fig. S3).

For all behaviours analysed, we found no significant interactions between habitat and trial type (all $P > 0.05$), suggesting that although lizards responded differently to heterospecific versus conspecific competitors, habitat of origin (urban versus nonurban) did not affect the direction or magnitude of this difference. Thus, we report the results of main effects. For time spent basking, we did not find a significant difference between urban and nonurban lizards ($\chi^2_1 = 0.54$, $P = 0.465$), but there was a difference in basking times among trial types ($\chi^2_2 = 9.98$, $P = 0.007$; Fig. 2a). Post hoc comparisons via the emmeans package with model-adjusted predicted responses (Lenth, 2022) revealed that fence lizards basked less during heterospecific trials than during conspecific trials ($P = 0.026$) and control trials ($P = 0.006$). There was no significant difference in time spent basking between conspecific and control trials ($P = 0.377$). The predicted average time basking during heterospecific trials was 11.5 min

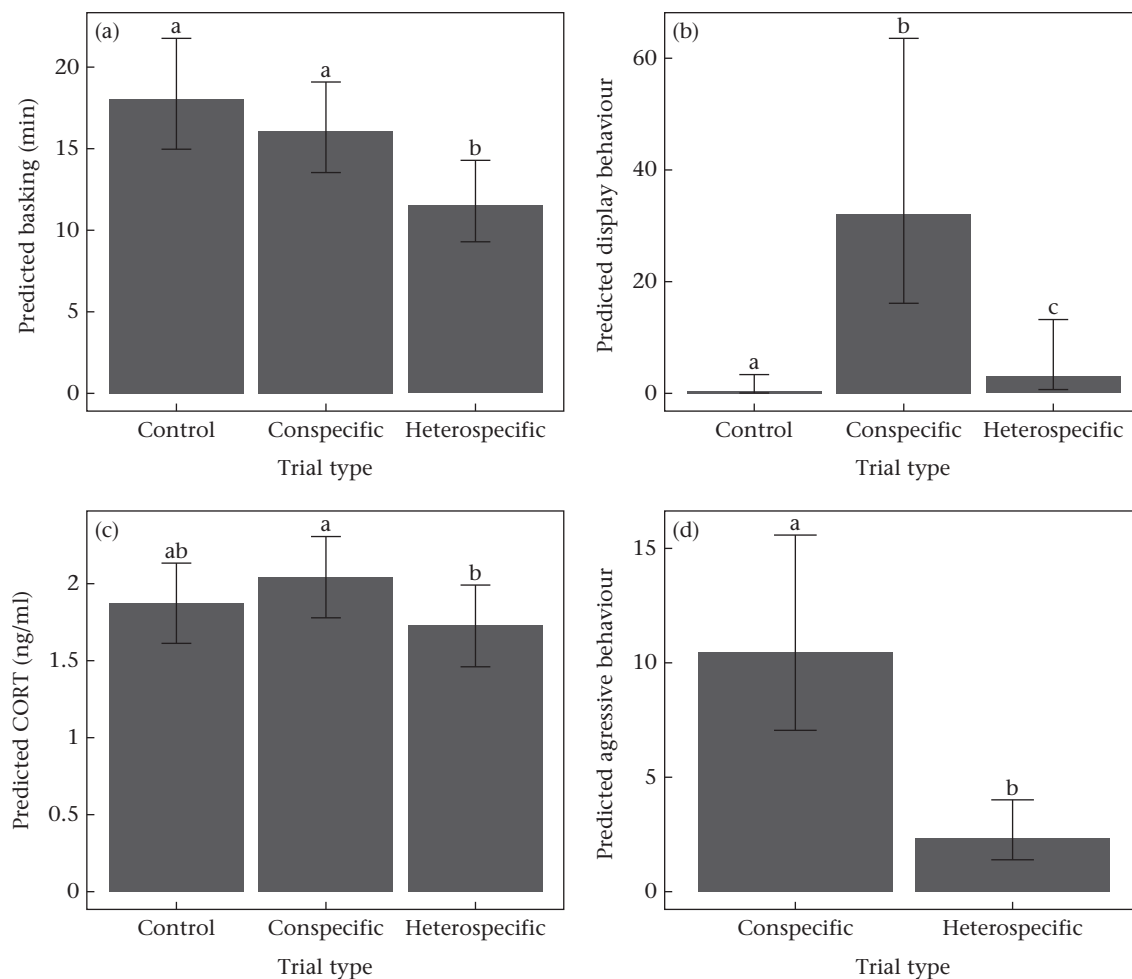


Figure 2. Predicted lizard behavioural and physiological responses (with 95% confidence levels) across trial types: (a) time spent basking; (b) number of display behaviours; (c) ln-transformed CORT after trials; (d) number of aggressive behaviours. Lower-case letters above bars represent statistically significant differences.

(95% CL = 9.27–14.3), while the predicted average basking time during conspecific trials was 16.1 min (95% CL = 13.54–19.1). We did not find an effect of urbanization or trial type for time spent hiding (habitat: $\chi^2_1 = 0.22$, $P = 0.642$; trial type: $\chi^2_2 = 0.25$, $P = 0.884$).

We also did not find a significant effect of urbanization on display behaviours (push-ups and headbobs) ($\chi^2_1 = 1.00$, $P = 0.316$) or aggression (biting and approaches) ($\chi^2_1 = 1.64$, $P = 0.201$). However, trial type influenced display behaviours ($\chi^2_2 = 15.80$, $P < 0.001$; Fig. 2b) and aggression ($\chi^2_1 = 21.13$, $P < 0.001$). Post hoc comparisons showed that western fence lizards were predicted to display more during conspecific trials compared to both control ($P < 0.001$) and heterospecific trials ($P = 0.004$). Western fence lizards also displayed more in heterospecific trials than in control trials ($P = 0.007$). Fence lizards were more aggressive in conspecific trials than in heterospecific trials ($\chi^2_1 = 21.13$, $P < 0.001$).

Urbanization affected information-seeking behaviours. Lizards from urban areas showed significantly more head scans and tongue flicks compared to lizards from nonurban areas ($\chi^2_1 = 6.58$, $P = 0.010$; Fig. 3). We did not find a significant difference in information-seeking behaviour among trial types ($\chi^2_2 = 0.22$, $P = 0.897$).

We did not find a difference in CORT concentrations between urban and nonurban lizards after the behavioural trials ($\chi^2_1 = 1.44$, $P = 0.231$). However, trial type had a significant effect on post-trial CORT ($\chi^2_2 = 6.54$, $P = 0.038$; Fig. 2c). Lizards were predicted to have higher CORT when paired with a conspecific compared to a heterospecific ($P = 0.044$). There was no difference in CORT when compared to the control trial for either heterospecific ($P = 0.229$) or conspecific ($P = 0.229$) trials. Lizard body temperature did not affect post-trial CORT ($\chi^2_1 = 0.016$, $P = 0.901$).

As expected, time had an effect on lizard body temperature, with lizards being warmer post-trial compared to pre-trial ($\chi^2_1 = 20.1341$, $P < 0.001$). However, trial type did not affect lizard body temperature ($\chi^2_2 = 0.031$, $P = 0.985$). Interestingly, lizards from urban areas were consistently warmer than nonurban lizards ($\chi^2_1 = 4.9202$, $P = 0.027$; Supplementary Fig. S2).

DISCUSSION

Our study aimed to determine whether urbanization influences western fence lizards' responses to potential competitors, both

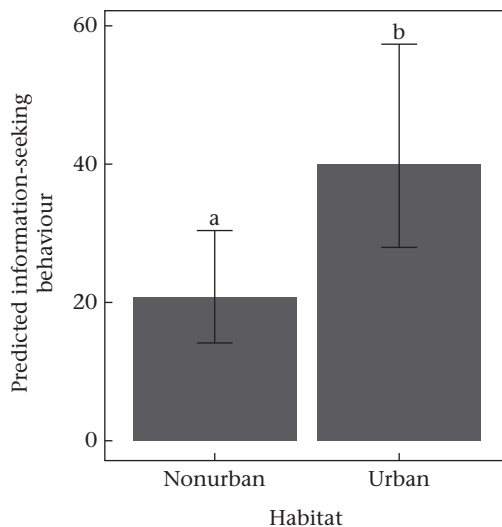


Figure 3. Effect of urbanization on predicted lizard information-seeking behaviours (with 95% confidence levels). Lizards from urban areas were predicted to exhibit more information-seeking behaviours than those from nonurban areas. Lower-case letters above bars represent statistically significant differences.

conspecific and novel heterospecific lizards. Overall, we found that urbanization had no effect on competitor-induced stress, display behaviour or aggressive behaviour, but urbanization did affect information-seeking behaviours, with urban lizards exhibiting more tongue flicking and head scanning than nonurban lizards. Although we found minimal effects of urbanization on responses to competitors, visual displays or aggression, CORT, and time spent basking were significantly impacted by the type of competitor encountered (heterospecific versus conspecific), suggesting that fence lizards maintain responses to competitors across different environments despite the habitat alterations that come with urbanization. Notably, although time spent basking decreased in the presence of a novel heterospecific lizard, decreased basking did not appear to affect thermoregulatory performance under the conditions tested, as body temperatures did not differ among trial types. The change in time spent using the basking site may suggest that fence lizards exhibit a displacement response to introduced competitors or novel stimuli. However, other explanations could lead to this finding, and these are discussed below.

Western fence lizards basked less during heterospecific trials than during conspecific or control trials. The basking site was a limited resource within the arena, creating potential for direct or indirect competition. Basking is vital for temperature maintenance and physiological performance in fence lizards, affecting their reproduction and survival (Adolph & Porter, 1993; McGinnis, 1966). Cold body temperatures in lizards can result in slow or sluggish movements (Bennett, 1990). Fence lizards placed into the arenas were at lower body temperatures than what the species generally prefers, suggesting a motivation to utilize the basking site to achieve preferred body temperatures. Indeed, lizards exhibited an increase in body temperature from pre- to post-trial. We found reduced usage of the basking site in the presence of a novel heterospecific competitor. However, this did not translate to lower body temperatures in the heterospecific trials as predicted lizard body temperatures did not significantly differ among trial types. The fence lizards could have gained temperature by other thermoregulatory tactics, such as staying near the basking area but not directly on the basking perch. This would still suggest a shift in microhabitat use and/or thermoregulatory behaviour in the presence of a heterospecific competitor or novel stimulus. We did not take the temperature of stimulus lizards, which could have potentially impacted our results by affecting their motivation to use the basking site.

Our results indicate a behavioural shift that may help us understand the displacement of western fence lizards by Italian wall lizards in California. Exploitation competition occurs when one competitor reduces the availability of a shared resource for another competitor, and over time, this can have negative impacts on the less competitive species (Holdridge et al., 2016; Rosa et al., 2023). Exploitation competition has been found in other *Podarcis* lizard species, where invasive Italian wall lizards displaced native congeners from a food resource through exploitation (Damas-Moreira et al., 2020). Invasive species can have higher levels of aggression, boldness and exploration compared to native species (Chapple et al., 2011; Weis, 2010), and these characteristics may contribute to the displacement of natives. To fully address whether Italian wall lizard behaviour influenced our results, it would be ideal for future studies to record behaviour of both the stimulus and the focal lizards. Alternatively, western fence lizards could have been responding to the novelty of the Italian wall lizards, as they were not collected from areas where they occur with Italian wall lizards. Lizards are known to alter thermoregulatory behaviour in response to perceived risk and novel stimuli (Chabaud et al., 2023), so this could also explain our findings. Future studies could attempt to disentangle effects of novel stimuli from heterospecific

competitors. Aside from novelty, Italian wall lizards are a larger species than western fence lizards, so our findings could also reflect a response to the size difference of the heterospecific (Rusch & Angilletta, 2017). There was no significant difference in time spent basking between conspecific and control trials, suggesting that the lizards utilized the basking site in the same way when alone and in the presence of a conspecific competitor. Together, these patterns support the idea that reduced use of the basking site in heterospecific trials reflects either a response to novelty, body size or indirect competition, rather than direct competitive displacement.

Western fence lizards displayed more during conspecific trials than during control and heterospecific trials, and they were more aggressive (biting and quickly approaching the stimulus) during conspecific compared to heterospecific trials. Territorial behaviours are well studied in *Sceloporus* lizards (Carpenter, 1978; Cooper & Burns, 1987; Haenel et al., 2003; Rothblum & Janssen, 1978), and western fence lizards commonly use headbobs and push-ups during conspecific interactions (Carpenter, 1978). Aggressive behaviour such as biting, chases and approaches have also been observed between western fence lizards but seem to be less frequent than push-ups and headbobs, which may be due to aggressive behaviours being more energetically costly (Sheldahl & Martins, 2000). How display and aggressive behaviours are used in heterospecific interactions has not been well studied. Direct competition between *Sceloporus* lizards and heterospecifics may be negligible and may only be important when food resources are limited (Dunham, 1980; Paterson et al., 2018). Our study suggests that these behaviours are not common in heterospecific interactions, and there may be other behaviours used when communicating with heterospecifics, such as scent marking (Font et al., 2012). However, we did find that western fence lizards displayed more during heterospecific trials than during control trials, so heterospecific encounters triggered a significant display response, albeit at much lower rates than during conspecific trials, and it is unclear whether this would be ecologically significant.

Fence lizards were also more stressed (had higher CORT) when paired with a conspecific competitor compared to when paired with a heterospecific competitor. This finding, along with our behavioural results, suggest that conspecifics elicit higher behavioural and physiological responses than novel heterospecifics. Although blood samples were not taken before each trial, baseline CORT from samples taken upon capture showed no difference between urban and nonurban lizards (results in Putman et al., 2025). Because the wall lizards were completely novel to fence lizards, they may not have recognized them as a potential competitor or threat. However, western fence lizards do not seem to be aggressive towards familiar native heterospecific species, such as side-blotched lizards and sagebrush lizards, *Sceloporus graciosus*, and this may be due to differences in microhabitat preferences (Zani, 2023).

Surprisingly, we found no effect of urbanization on how lizards responded to potential competitors, which was the primary goal of this research. This is surprising because we had well-supported expectations based on how urbanization alters species diversity and the habitat use of urban dwellers. Prior work has found lizard population densities to be higher in urban areas compared to rural areas, and these differences are often associated with higher levels of territorial displays, aggression and/or wounding rates (from conspecific interactions) (Baxter-Gilbert & Whiting, 2019; Stroud et al., 2019). A recent study also found urban lizards to be more social and tolerant of conspecifics than nonurban lizards (Maune et al., 2025). Similarly, striped field mice, *Apodemus agrarius*, are more tolerant of conspecifics in urban areas and are not as likely to avoid interactions with conspecifics, behavioural responses

hypothesized to result from high conspecific densities in urban areas (Łopucki et al., 2021). In our study, western fence lizard density was higher in urban areas (see Supplementary Material), corroborating these prior studies, and although this could suggest more intense or frequent conspecific interactions, we did not find significant effects of urbanization on responses to competitors (in behaviours or CORT). Urban western fence lizards were as aggressive as nonurban lizards when paired with an unfamiliar competitor and their CORT concentrations were equally elevated. Thus, we failed to find evidence for urban lizards being more responsive to conspecifics than nonurban lizards. It is possible that increased population densities in urban areas may translate to smaller territories that are maintained with similar levels of aggression and visual displays as those in nonurban habitats. Even though urban and nonurban areas differ in the types of basking substrate (i.e. availability in natural or human-made materials) (Grimm et al., 2008), perhaps the availability of such resources was similar between our selected sites. If we had chosen a different resource such as food, it may have elicited different responses between habitat types (Uyeda et al., 2015). For future study, it may also be interesting to allow the focal lizards to form a territory within the arena, which may influence their responses to competitors (Maune et al., 2025). Urban and nonurban populations were also close enough for gene flow to occur, and this could prevent differentiation of phenotypes if traits are under strong genetic control (García-Ramos & Kirkpatrick, 1997; Lenormand, 2002).

Urbanization affected two responses in our study: information-seeking behaviours and body temperature. Lizards from urban areas showed significantly more head scans and tongue flicks compared to lizards from nonurban areas. This suggests that urban animals may be more aware of their surroundings or may need to gather information more often. Behaviours related to information gathering can benefit animals in areas that may be unpredictable, or if information is patchy (Arvidsson & Matthysen, 2016; Stephens, 1987), characteristics of many urban environments (Parker & Nilon, 2008; Prange et al., 2004). Thus, urban lizards may rely on these behaviours more than lizards from nonurban areas. Our research laboratory has also found that urban areas may be a high-risk environment for lizards, as urban lizards stay closer to refuge and have higher rates of tail loss compared to nonurban lizards (Putman et al., 2021, 2024; Álvarez-Ruiz et al., 2023). This could potentially explain why urban lizards exhibited more information-seeking behaviours when we introduced them to the novel arena (i.e. because they need to assess risk more often). This behavioural response could be part of a behavioural syndrome associated with variation in exploratory and antipredator behaviours due to urbanization (Batabyal et al., 2017; Sol et al., 2013). Urban areas differ from nonurban areas in many ways such as in resources, impervious surface cover, temperature and pollution (Chapman et al., 2017; Giery et al., 2025; Murena, 2004; Putman et al., 2019), and these variables could potentially affect foraging, movement and other behaviours, which may have downstream effects on information gathering behaviours. We did not find a difference in body temperature across trial types despite basking differences, but we did find that lizards from urban areas achieved warmer body temperatures than lizards from nonurban areas (in pretrial and post-trial measurements). Urban lizards could have higher body temperatures than nonurban lizards due to urban heat-island effects (Campbell-Staton et al., 2020; Thawley et al., 2019). Our results may suggest a preference for higher body temperatures in urban lizards, but this would need to be tested experimentally.

In conclusion, we did not find an effect of urbanization on lizards' responses to potential competitors, even though urban areas

had higher population densities of fence lizards. Both urban and nonurban lizards exhibited more visual displays, higher aggression and elevated CORT in response to a conspecific competitor compared to a novel heterospecific competitor. Urbanization impacted the information-seeking behaviours of lizards, a response that could be associated with the need to assess more risks in urban areas, and urbanization impacted body temperature, which may be associated with different thermal environments between urban and nonurban habitats. Lizards basked less during heterospecific trials, demonstrating a potential for exploitation competition between these species or a response to novelty. Yet, displacement from the basking site was not associated with negative effects on thermoregulation. Overall, our study contributes to gaps of knowledge on how human-induced environmental changes, like urbanization, affect species interactions and offers paths to better understand mechanisms of displacement of native species by introduced competitors.

Author Contributions

Emily R. Urquidi: Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Breanna J. Putman:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization.

Data Availability

Data and R code are available as Supplementary Material.

Declaration of Interest

The authors declare no competing interests.

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Supplementary Material

Supplementary material associated with this article is available at <https://doi.org/10.1016/j.anbehav.2026.123602>.

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