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Rock Refuges Are Strongly Associated with Increased Urban Occupancy in the Western Fence Lizard, *Sceloporus occidentalis*

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Abstract: Urbanization has dramatically altered habitats for local species worldwide. While some species are unable to meet the challenges that these alterations bring, others are able to persist as long as a threshold for suitable habitat is met. For reptiles, a key feature for persistence in urban areas can be access to suitable refuges from predation, high temperatures, and/or other environmental challenges. We tested for effects of local and landscape variables affecting urban occupancy in the Western Fence Lizard, *Sceloporus occidentalis*, in transects across an urban–rural gradient, with a specific focus on the presence of rock, tree, and shrub refuges. We found that fence lizards were much more likely to be present in areas with more rock cover, and in parks or low-density residential areas. Occupancy was also positively related to canopy cover in the general vicinity, though negatively related to number of trees along the transects. Our results highlight the importance of assessing local habitat features to successfully predict the occupancy of reptile species in urban habitats, and present directions for future research with concrete conservation and management applications.

Keywords: urban ecology; reptile; Squamata; Phrynosomatidae; California

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1. Introduction

Anthropogenic environmental change is having global impacts on biodiversity through habitat loss and alteration, overharvesting, the spread of invasive species, pollutants, and climate change [1–4]. Urbanization, in particular, has numerous large-scale impacts on ecological processes [5,6]. Relative to species from nearby undeveloped environments, urban-dwelling species may experience challenges associated with increased habitat fragmentation and reduced connectivity between habitat patches, reduced vegetation and canopy cover, novel structures and substrates, altered types and patterns of predation, altered prey and water availability, changes in thermal environment, pollutants, novel stressors, and more [5,7–10]. Nevertheless, cities continue to support high levels of biodiversity, and can be important targets of conservation efforts [11,12].

Responses to urbanization may differ markedly within and between species, but understanding why and how species are able to persist in urban environments is critical as the world becomes increasingly urbanized [13]. In particular, there is urgent need for more studies that can inform management decisions by exploring the specific mechanisms that may foster increased community biodiversity and/or presence of individual species of management interest [11]. While an impressive amount of urban ecology research has been carried out in some taxonomic groups, and birds in particular [14–17], far less is known about reptiles, and how local environmental variables contribute to their persistence in suburban/urban areas.

Studies investigating the causal mechanisms affecting reptile occupancy are particularly urgent given the fact that reptiles, similar to other vertebrate groups, are showing widespread global declines [18–21]. Habitat loss and fragmentation is one of the most serious threats to reptile diversity [22]. Reptiles, especially species that are habitat specialists, may be particularly sensitive to habitat alteration due to relatively slow dispersal and recolonization rates [23,24]. Studies in lizards have suggested that they may be deterred by urban anthropogenic stressors such as noise [25], excess light [26,27], and vehicular traffic [28,29]. While a wide range of studies have begun to emerge on urban lizard morphology, reproduction, physiology, behavior, genetics, learning, and habitat occupancy [30–42], as well as several current reviews and meta-analyses [36,43–45], many more are needed to better understand the effects of urbanization and other anthropogenic land uses on reptiles.

Occupancy of lizards in urban areas has been shown to be influenced by habitat variables such as patch size, temperature and precipitation, vegetation type and structure, anthropogenic structures, and fire regime [41,46–52]. A key feature of reptile persistence in urban landscapes is access to suitable refuges. The presence of refuges can be critical for protection against predators and can provide needed relief from artificial lights or opportunities for thermoregulation, especially for ectotherms [26,27,53–55]. Urban landscapes can experience relatively rapid changes over the course of an individual's lifetime, challenging urban-dwellers to identify novel dangers and safe refuges in a dynamic environment [39].

A conspicuous reptile species in developed landscapes across the Western United States and Baja Mexico is the small Phrynosomatid Western Fence Lizard, *Sceloporus occidentalis* [56]. An ecological generalist, *S. occidentalis* is found in a variety of habitats in undeveloped areas, such as oak woodland, grasslands, chaparral, and coastal sage scrub [57,58]. *Sceloporus occidentalis* has also successfully colonized urban and suburban areas, and is commonly seen basking, defending territories, hunting insects, and interacting with mates in yards and city parks, on sidewalks, and on other anthropogenic structures such as fences and rock walls [37]. Past studies of *S. occidentalis* have shown behavioral and morphological differences between urban and rural populations [37,59,60]. However, there have been no studies of factors affecting *S. occidentalis* occupancy across an urban–rural gradient and the importance of refuges in light of its active lifestyle out in the open on both natural and built surfaces.

Through visual encounter surveys across an urban gradient, ranging from parks to low-density residential areas to high-density/commercial districts, we tested for effects of three potential refuge types—rock cover, shrub cover, and trees—on *S. occidentalis* occupancy that offer potential refuges from predators, high temperatures, artificial lights, and/or direct human impact. Lizards may find refuge under rocks or inside shrubs, or high up the trunk or under the canopy of trees. We predicted higher occupancy of lizards in areas with more available natural refuges, whether rock, shrub, or tree. We also controlled for potential effects of landscape variables that can serve as a proxy for both general degree of urban development (land type, canopy cover, imperviousness), proximity to potential source populations on undeveloped land (distance to the nearest stream, distance to the nearby National Forest), and environmental thermal extremes (average maximum temperature) in our analysis.

2. Materials and Methods

2.1. Study Area

In this study we observed occupancy of *Sceloporus occidentalis* across an urban–wild gradient in the city of Santa Barbara, CA (land area = ~51 km^2), USA, from 4 May–15 June 2020. Santa Barbara has an estimated population of 91,364 (~1800 persons/km^2) (https://www.census.gov/quickfacts/santabarbaracitycalifornia (accessed on 1 November 2021)) and is situated on a relatively narrow coastal plain that runs east–west, parallel between the Pacific Ocean and the Santa Ynez Mountains of the USDA Los Padres National Forest directly to the north of it. Santa Barbara's climate is classified as a warm-summer Mediterranean climate [61] and the natural landscape is dominated by chaparral and oak woodland ecosystems, although this natural landscape has decreased over the years due to urbanization and agricultural expansion [62]. The field work was conducted by two researchers, K.D. and S.W., during early summer, well after emergence from hibernation in February–March, but before eggs begin to hatch and hatchlings are abundant in July/August (A. Sparkman, pers. obs.). Other lizard species known to live in the Santa Barbara area include *Elgaria multicarinata* (southern alligator lizard), *Aspidoscelis tigris munda* (California whiptail), and *Uta stansburiana* (common side-blotched lizard). Western Fence Lizards are relatively easily distinguished because they are highly distinct from *E. multicarinata* and *A. tigris* in both morphology and behavior; while *U. stansburiana* is also a small Phrynosomatid lizard, they are easily differentiated with proper training via differences in color patterns and general morphology. No formal ethical approval was sought for this study, as it involved non-invasive observations of lizards in the field.

2.2. Field Sampling

We generated a grid with transect points at 1 km intervals ranging from the foothills to the coast across the entire city of Santa Barbara using QGIS 3.4.6-Madeira. There were 143 accessible sites that were visited from this grid; sites that were located on a water body, major highway, or other inaccessible location were excluded from our study. At each site, the researchers chose a safely traversable area as close as possible to the grid point where they could walk a roughly linear transect. Once an area was selected, the researchers walked a 5 m wide, 50 m long transect and conducted a visual encounter survey to document the presence or absence of *S. occidentalis*. Each transect was recorded as a track using Garmin eTrex 20× Handheld GPS. While conducting each survey, researchers walked slowly along the transect, careful not to exceed a width of 5 m, observing both sides thoroughly, including looking around rocks and under foliage. If a lizard was observed within transect boundaries, researchers marked it with a waypoint with the GPS. Transects were conducted between 8:30 a.m. and 5:30 p.m. Days/times with high wind speeds and/or very high or very low temperatures at which lizards would be unlikely to be active were avoided. The majority of transects were visited on three separate occasions separated by a week or more and at random with respect to time of day, although 19 of the 143 sites were visited only twice.

For each transect, three site-specific local landscape variables representing potential refuges—rock cover, shrub cover, and trees—were characterized in the field. For each of these variables, data were categorized into four levels: the presence of 0 instances of rocks/shrubs/trees would result in a characterization of "none", 1–3 instances were categorized as "limited", 4–6 instances were categorized as "several", and 7+ instances were categorized as "abundant". Only rocks (whether natural or human-altered) that provided potential refuge were counted, meaning there had to be a potential area for lizards to hide underneath the rock(s), between rocks, or in cracks in the rock(s).

We derived estimates of landscape characteristics over a 0.02 km^2 area surrounding each transect using QGIS and publicly available GIS layers of tree canopy (NLCD 2016), urban imperviousness (NLCD 2019), California streams (CDFW 2018), USDA Los Padres National Forest regional boundary (USDA 2015), and the average maximum temperature (°C) for each month (WorldClim 2.1, 2017). The NLCD percent tree canopy layer is a 30 m raster geospatial dataset that contains percent tree canopy estimates, as a continuous variable, for each pixel across all land covers and types and are generated by the United States Forest Service. The MRLC Urban Imperviousness layer is a raster dataset that provides the average percentage of anthropogenic-created impervious surface (i.e., impenetrable to rain, such as asphalt or concrete) for each pixel. The CDFW California Streams layer has high-resolution, measured polyline features representing entire streams for the state of California. The USDA Forest Service Regional Boundaries layer is a dataset that shows the boundaries of lands administered by the Forest Service. Note that the Los Padres National Forest is an expansive area of undeveloped land bordering the entire northern reaches of Santa Barbara (with the southern end being entirely ocean, and the eastern and western edges continuous with other urban communities), making it the most significant potential natural source population in the region. The WorldClim layer has a spatial resolution of 2.5 min and shows the average maximum temperature (°C) from 1970–2000 for each pixel in the study area each month observations took place. While we did not collect weather data during each survey, we found that the temperatures from WorldClim were strongly correlated ($p < 0.0001$) to current temperatures from 65 Weather Underground weather stations distributed across Santa Barbara, suggesting that the historical data can serve as a robust proxy for average temperatures at transect sites during our study period. We classified land type into four categories based on a combination of ground observations and reference to zoning data from the city of Santa Barbara: park, low-density residential, high-density residential, and commercial.

2.3. Statistical Analysis

To investigate factors influencing occupancy for *S. occidentalis*, occupancy and detection probability were examined using single-season, single-species occupancy models [63] in the program PRESENCE [64]. Within the occupancy models, variables were divided into two categories: (1) survey covariates that may affect probability of detection (p) when searching for lizards and (2) habitat covariates (both local and landscape-level) for predicting the probability of occupancy (ψ) that may differ among sites but are constant between surveys.

We ran models with each detection variable (researcher, time of day, and day of year) with ψ held constant. As none of these models were superior to the null model with constant p (ΔAICc > 3), we used constant p for the detection probability for all subsequent occupancy models. To examine occupancy, we first ran a series of models for each 4-level refuge variable (rock cover, shrub cover, and tree cover), contrasting each level with the remaining three levels (e.g., none coded as "0", and limited/several/abundant coded as "1", etc.). As these preliminary models suggested that the none/limited and several/abundant levels were behaving in a similar manner, for the sake of simplicity we conducted all final model comparisons with 2-level refuge variables, with none/limited coded as "0" and several/abundant coded as "1". A similar process was followed with respect to land type, such that we conducted all final models with a 2-level land type variable, with park/low-density residential coded as "0", and commercial/high-density residential coded as "1".

Subsequently, we ran all possible combinations of both local and landscape variables: rock cover, shrub cover, tree cover, land type, percent canopy cover, percent imperviousness, distance to nearest stream, distance to nearest forest boundary, and monthly average maximum temperature—with two main exceptions. First, imperviousness and canopy cover were never included in the same model, as these two variables were highly correlated ($r = -0.67$). Second, land type was not included in the same models as imperviousness, canopy, distance to nearest stream, distance to forest, as these variables differed significantly between land types. The best-fitting models were selected as the ones with the lowest AICc scores, with a ΔAICc < 3. Odds ratios were calculated for each categorical variable in the top model.

3. Results

We conducted three *S. occidentalis* surveys at 143 sites, with the exception of 19 transect sites being visited only twice, for a total of 410 surveys completed across an urban/wild gradient across the city of Santa Barbara. Lizards were observed at least once in 89/143 sites, resulting in a naïve occupancy of 0.62 across all habitats (Figure 1). The null model with constant p model had $\psi = 0.77 \pm 0.06$ (SE), suggesting that imperfect detection should be accounted for when analyzing occupancy.

Researcher, day of the year, and time of day did not influence p, and thus were not considered further. The top 10 models predicting occupancy are presented in Table 1. The four variables consistently occurring in the top model and/or all models with ΔAICc < 3 from the top model were rock cover, land type, transect-level tree cover, and canopy cover. Shrub cover also appeared in three of the top ten models, but did not appear to improve model fit. Distance to the nearest forest boundary, distance to the nearest stream, percent imperviousness, and the average maximum temperature did not appear in any of the top models explaining lizard occupancy.

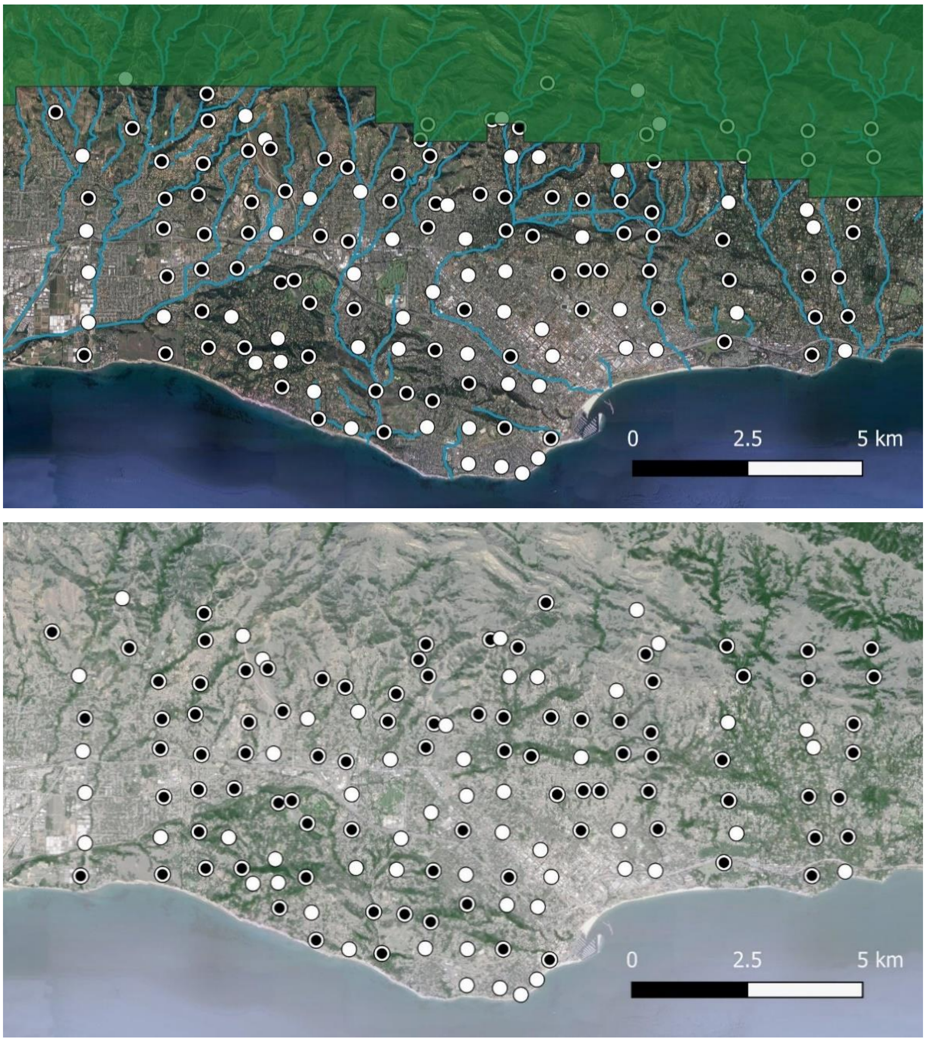

Figure 1. Locations of *S. occidentalis* survey transects. Open circles indicate transects where lizards were not observed on any visit, whereas circles with black centers indicate transects where lizards were observed on at least one visit. The upper map shows the boundary of the Los Padres National Forest (green), as well as streams across the study area (blue). The lower map shows the distribution of canopy cover across the study area, with the dark to light green gradient reflecting a continuum of high to low canopy cover.

Table 1. Top 10 models for *S. occidentalis* occupancy across the urban–rural gradient in Santa Barbara, California. AICc values, change in AICc values relative to the top model, and AIC weights (ω are shown. Data are also provided on the null model with no covariates.

Model	AICc	ΔAICc	ω
1 rock cover + tree cover + land type	511.05	0	0.2124
2 rock cover + land type	511.34	0.29	0.1838
3 rock cover + tree cover + canopy cover	512.29	1.24	0.1143
4 rock cover + shrub cover + tree cover + land type	512.3	1.25	0.1137
5 rock cover + shrub cover + land type	512.67	1.62	0.0945
6 rock cover + canopy cover	513.23	2.18	0.0714
7 rock cover + tree cover	513.54	2.49	0.0612
8 rock cover + shrub cover + tree cover + canopy cover	513.75	2.7	0.0551
9 rock cover	513.76	2.71	0.0548
10 tree cover + canopy cover	514.54	3.49	0.0371
1 group, constant p (null model)	520.58	9.53	0.0018

The top occupancy model included three variables: rock cover (none/limited vs. several/abundant), tree cover (none/limited vs. several/abundant), and land type (park/low-density residential vs. commercial/high density residential) (Table 1). The average ψ of sites where rock cover was none/limited was 0.62 ± 0.01 (SE), whereas ψ was 0.90 ± 0.01 (SE) where rock cover was characterized as several/abundant. Odds ratios indicate that with several/abundant rocks, the odds of lizards being present was 5.15 (95% CI: 1.14, 23.24) times higher than without several or abundant rocks (Figure 2). In contrast, the average ψ of sites where tree cover was none/limited was 0.83 ± 0.03 (SE), whereas ψ was 0.69 ± 0.02 (SE) where trees were characterized as several/abundant (Figure 2). Odds ratios indicate that several/abundant trees decreased the odds of lizards being present 2.48 (95% CI: 0.67, 9.14) times. The average ψ of sites where land type was characterized as park/low-density residential was 0.82 ± 0.02 (SE), whereas ψ was 0.57 ± 0.03 (SE) at commercial/high-density residential sites. The odds of lizards being present at park/low-density residential sites was 3.18 (95% CI: 1.03, 9.80) times higher than in commercial/high density land types.

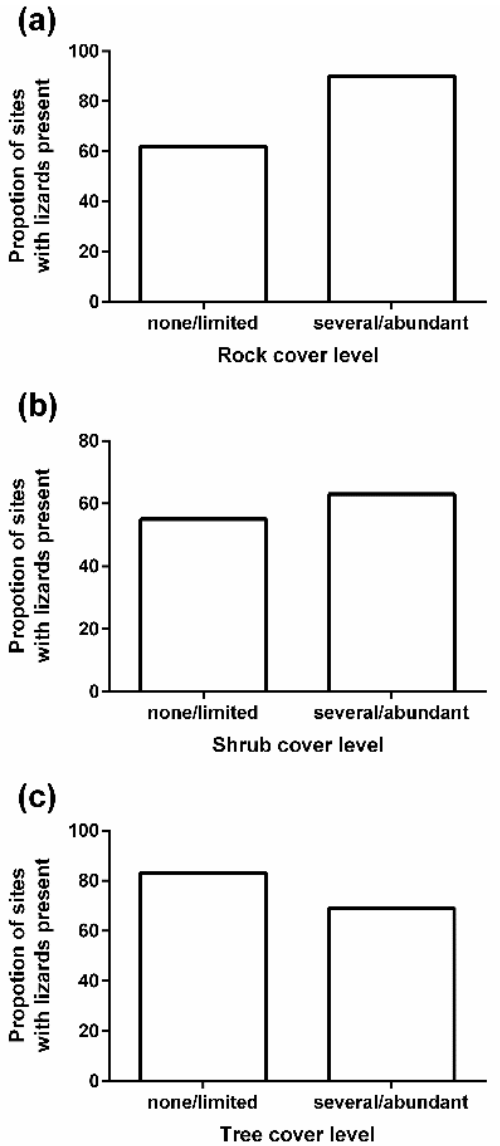

Figure 2. Proportion of sites with lizards present with respect to (**a**) rock cover, (**b**) shrub cover, and (**c**) transect-level tree cover. Only rock cover and tree cover appeared in the top models.

The third-best model was equivalent to the top model, and includes canopy cover instead of the land type variable featured in the top two models (note that we did not combine these highly-related variables in the same models), indicating a positive relationship between percent canopy cover and lizard occupancy ($\beta = 2.75 \pm 1.71$ (SE); Figure 3).

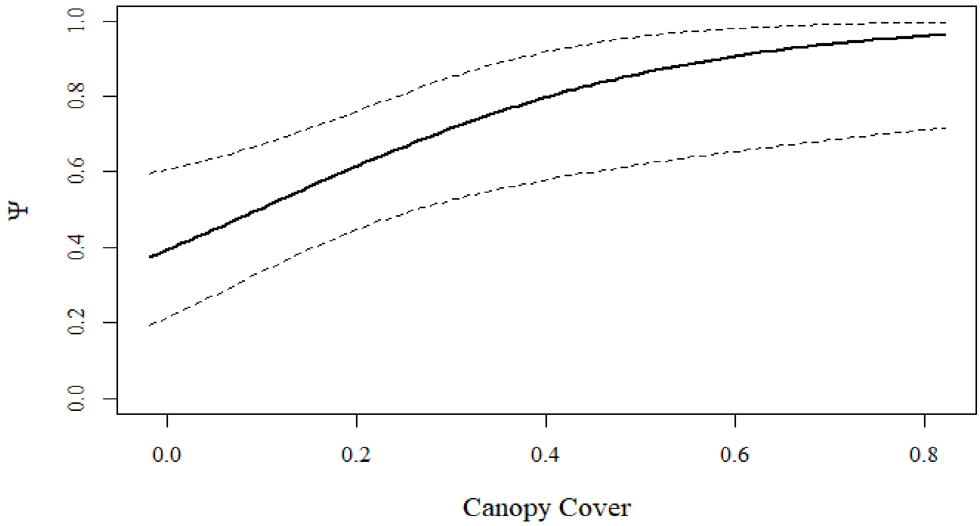

Figure 3. Probability of occupancy with increasing percent canopy cover in the area surrounding the *S. occidentalis* survey transects.

4. Discussion

Urbanization can have powerful consequences for occupancy of urban species, both through increasing fragmentation and decreasing connectivity, and through alterations in local habitat variables—whether an increase in hazards, or a reduction in access to key habitat requirements [5,8]. Some studies have indicated that lizard populations can be highly sensitive to habitat fragmentation and rely on connectivity to undeveloped land to persist [41,55,65–67], while other work suggests that small, generalist species may be able to persist in small patches if the habitat is of sufficient quality [48,68]. While we could not test for effects of patch size per se, as our study did not feature a patch-based design, we found no significant relationship in fence lizard occupancy related to the distance between our study transects and undeveloped land along the Los Padres National Forest boundary or the nearest stream. Rather, consistent with other studies investigating lizard persistence in small patches, our findings suggest that local habitat features may be the most important factors determining fence lizard occupancy in urban areas. We found that rock cover is strongly associated with fence lizard presence, and that land type and tree cover (at two spatial scales) may also be key features determining urban occupancy of *S. occidentalis*.

In our study, sites with more than four (several/abundant) potential rock refuges over the 50 m transects increased lizard occupancy rates from 62% to 90% on average relative to sites with fewer than four potential rock refuges (none/limited), suggesting that this habitat feature alone may be a powerful determinant of lizard persistence in and/or colonization of urban areas (Figure 1). Rock cover can be critical because rocks can offer both refuge from predators as well as opportunities for thermoregulation in the same location [53–55]. Interestingly, one recent study also found that urban lizards are highly dependent on rough, rocky substrates in both urban and rural areas for sheltered sleep sites and shielding them from night light [27]. Fence lizards may be reliant on rock refuges for any and all of these reasons, which further behavioral studies could examine.

While rock cover was in all of our top models, land type and canopy cover (which are highly associated, and therefore not included in the same models) were also present in the top models. Probability of lizard occupancy went up from 57% on average in commercial/high-density residential areas to 82% in park/low-density residential areas—a pattern that is easily discernible when lizard presence/absence at transects is mapped

(Figure 1). Commercial/high-density residential areas may be associated with increased noise, artificial light, vehicular traffic, foot traffic, domestic animals, environmental temperatures, and ground imperviousness, as well as reduced canopy cover [5,8]. In our study, neither percent imperviousness nor maximum environmental temperature were important in any of the top models, which is perhaps not surprising, given that even for urban lizards in Phoenix, Arizona, a city with a high urban heat island effect, thermal patterns have not yet impacted lizard distribution and relative abundance at larger scales [69]. Nevertheless, it is possible that the other aspects of more intensively developed areas listed here could be playing a role in affecting habitat suitability for lizards.

Given that canopy cover did independently show a marked positive effect on occupancy when included in models with rock cover (Figure 3), the effect of land type may be at least partially attributable to the suitable "patches" of undeveloped land even in residential areas, which may reduce the intensity of other aspects of highly-developed areas that reduce habitat suitability. Indeed, this is consistent with studies in other lizard species suggesting that small pockets of vegetation, including residential gardens, are highly important for the persistence of lizard populations. For instance, studies suggest that Tennent's leaf-nosed lizards (*Ceratophora tennentii*) are affected by shade, humidity, and density of perches in microhabitat pockets [70]; blue-tongued lizards (*Tiliqua scincoides*) use corridors of dense vegetation to move between retreat sites and actively avoided crossing roads [71]; and common skinks (*Oligosoma nigriplantare polychrome*) are more likely to be present in untidy gardens [55].

While canopy cover over the general vicinity of the transects was positively related to occupancy, several of our top models included local tree cover on the transect itself. Interestingly, transect-level tree cover showed a weak negative effect on lizard occupancy. On average, sites with more than four trees (several/abundant) had 69% occupancy, whereas sites with fewer than four trees (none/limited) had 83% occupancy (Figure 2c). This is perhaps surprising given that fence lizard presence has been associated with proximity to trees and shrubs in undeveloped areas [72]. However, other research in fence lizards shows remarkably habitat generalism, with populations in some areas being highly arboreal, and populations in other areas being primarily out in the open [57,58]. Our finding that there was a negative association between lizard occupancy and higher numbers of trees at the transect level suggests that in some cases other refuges could be sufficient, and basking areas out from under the shade of trees are at more of a premium in this system.

Surprisingly, shrub cover did not appear to be highly influential in our study (Figure 2b), regardless of the fact that these lizards can frequently be observed fleeing into low-growing vegetation (A. Sparkman, pers. obs.), and have been associated with proximity to shrubs in the wild [72]. However, this finding may be impacted by the fact that the majority of transects (80%) had "abundant" (more than seven) shrubs present. Thus, it is possible that there may be synergistic effects of shrub presence/absence and rock cover abundance that we were unable to detect in this study; future work could more directly target sites with different levels of shrub cover, to definitively determine whether or not its absence is detrimental to lizard urban occupancy.

While we focused primarily on "natural" features affecting lizard occupancy, study of two co-occurring *Anolis* species has demonstrated that they utilized different parts of urban habitats, one using more "natural" portions of the urban environment and the other using more anthropogenic structures [38]. Future work in fence lizards could also explore use of incidental anthropogenic refuges such as crevices in walls and fences, refuse piles, or other artificial cover in urban areas, and whether these are used more/less in the absence of natural refuges. Furthermore, the strong correlation between rock cover and fence lizard occupancy in our study suggests that an experimental framework could be useful in establishing to what degree artificial construction of rock refuges could foster expansion of fence lizards within residential areas. Different degrees of transect-level tree cover in the immediate area and canopy cover in the general vicinity could also be factored into the experimental design.

Our study is limited in that we focus on a single species in a particular location over one time period; nevertheless, it is a clear demonstration of how fine-scale examination of a particular locale can provide illuminating natural history insights into species occupancy. We provide evidence that clearly-defined habitat features can strongly impact fence lizard occupancy on an urban landscape, in a manner that opens up several avenues for investigation of how to maintain and perhaps even extend their presence in developed areas. Our work demonstrates how the study of local habitat variables can shed light on specific mechanisms affecting occupancy of individual species, and generates robust information for effective reptile conservation and management in urban areas.

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