PATTERNS OF AMPHIBIAN AND REPTILE DISTRIBUTIONS ACROSS AN URBAN TO RURAL GRADIENT WITHIN THE SANTA MONICA MOUNTAINS NATIONAL RECREATION AREA

by

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(Under the Direction of John C. Maerz)

ABSTRACT

Urbanization is a process widely recognized for affecting the distribution and abundance of wildlife. Urbanization represents a syndrome of changes to the biophysical environment associated with increasing human population density; however, in ecological studies, urbanization is often treated as a qualitative, dichotomous landcover state (e.g., urban v. rural) or represented by a single covariate (e.g., area of impervious surface). This is potentially problematic when studying wildlife in urbanizing landscapes because wildlife will respond to the suite of specific changes to the biophysical environment that accompany increased human density. The objectives of my thesis were to analyze changes in habitat attributes in relation to human population density within the Santa Monica Mountains National Recreation Area and to relate patterns of amphibian and reptile distributions to specific environmental attributes or principal components of urbanizing habitats. I use four years of capture data from 79 pitfall arrays. Among our study sites, human population density was negatively correlated with protected area patch size, proximity to paved surfaces, human-made structures and artificial light sources. Models of reptile and amphibian occupancy and abundance generally did not include consistent urban attributes nor the composite index of urban attributes. For the most common lizard species, Western fence lizards (*Sceloporus occidentalis)* occupancy was positively correlated with human population density and slender salamander (*Batrachoseps spp.*) occupancy increased within greater proximity to human-made water sources. Occupancy of all other less common reptile species was related to vegetation and/or elevation, not directly related to the anthropogenic impacts of urbanization. Abundance model fit was generally poor; however, results suggest that abundance varied with vegetation among most herpetofaunal species. Our survival models generated similar results for Western fence lizards under count-based modeling approaches; however, both the count-based and capture-mark-recapture approaches may have generated inflated estimates due to low recapture rates and sampling design constraints.

INDEX WORDS: urban ecology, herpetology, population estimation, hierarchical models

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by

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BS, University of Maryland, 2014

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2019

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May 2019

DEDICATION

I dedicate this work and all the work that led up to its completion to my parents, my Grandparents, all my ancestors -known and unknown-, the maintenance, groundskeepers and facilities managers of the Forestry buildings (whose daily greetings and smiling faces mirrored my own in a department devoid of analogous representation) and to anyone who has ever claimed me as part of their village. This never would have happened without you.

-*- Thank you -*-

ACKNOWLEDGEMENTS

I thank everyone who had a hand in this research:

- ✓ My advisor and my committee members: Dr. Maerz, Dr. Irwin, and Dr. Delaney
- ✓ My academic funding supporters: UGA Graduate School's GRO assistantship and the National Science Foundation's Graduate Research Fellowship
- ✓ My collaborating institution in data collection: US National Park Service's Santa Monica Mountains National Recreation Area Inventory and Monitoring Program
- ✓ My shadow-support squad: i.e. the volunteers and interns stretching back to 2012 who assisted in collected the data I spent the past years laboring to analyze and all my fellow graduate students, worldwide, to be honest.
- ✓ My friends and family: my village knows who they are, because I can't help but remind them all the time; and if I were to list the entire troop, I'd need an additional thesis c;

hope she understands / i can't just change the weather

and i could be her biggest fan / please help me make it better

cause all i want to do is / chase your love

~Christopher Joseph Gallant III

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

For millennia, urban areas have been growing and spreading across the planet, shifting humanity from a diffuse, rural lifestyle to one of concentrated populations within heavily built environments (United Nations 2014). This transition in the way humans occupy the landscape precipitates great changes on natural systems including the loss or creation of habitat for wildlife (Holzer et al. 2017). In response to this changing dynamic, the field of urban wildlife ecology has grown to address these novel systems, though certain topics and taxa remain understudied (Magle et al. 2012). Urbanization and human development can alter or homogenize surrounding wildlife community composition (Devictor et al. 2007, Banville and Bateman 2012), by selecting against rare or endemic specialists and favoring nonnative or locally abundant generalist species. Urban landscapes can modify animal behaviors (Ditchkoff et al. 2006), which may in turn alter population dynamics (Murray and St. Clair 2015).

While there is consensus that urbanization is generally deleterious to most wildlife and beneficial to a select set of cosmopolitan species; there remains limited understanding of the factors that determine how wildlife respond to urbanization. This knowledge gap demands attention if we are to manage and conserve native species in expanding urban landscapes (Messmer 2009). One challenge to understanding urbanization effects on wildlife may be the varied ways researchers define or quantify “urban” in ecological contexts. Often, urban scientists delineate urban areas from natural, rural, or suburban areas using political boundaries or human population densities (Garden et al. 2007, Guderyahn et al. 2016, Braaker et al. 2017).

Alternatively, urban areas are delineated using a qualitative juxtaposition to rural areas (Banville and Bateman 2012, Sullivan et al. 2016), or delineated without any clear criteria at all (Dawson and Hostetler 2006). When researchers do attempt to measure the effects of quantitative urban attributes, they tend to focus on just a few dimensions associated with human development (e.g., land cover composition, van Rensburg 2009; impervious surfaces, Brady and Richardson 2017), but lack a more comprehensive evaluation of the multi-dimensional nature of urbanized areas. In reality, animals respond to the suite of biophysical changes associated with increased human density. By not studying suites of biophysical changes to habitats, we may often fail to identify the underlying mechanisms driving wildlife responses to urbanization.

The transdisciplinary field of urban ecology currently lacks a clear understanding of the complex relationships among dense human populations, biophysical attributes of urbanized habitats, and changes in wildlife behavior, life history, and abundance. In this thesis, I evaluate relationships between human population density and habitat attributes potentially important to reptiles and amphibians in the Santa Monica Mountains National Recreation Area (SAMO). Specifically, my objectives were to quantitatively link biophysical attributes potentially important to wildlife with human population density, and then relate those urban biophysical attributes or a composite index to patterns of amphibian and reptile occupancy, abundance, and survival. Ultimately, my goal is to develop ecologically derived descriptors of ‘urban’ that better reflect the complexities of such systems, to understand why urbanization can create varied and at times paradoxical responses among wildlife. Reptiles and amphibians are well-suited for such a study, as they are diverse, with varying habitat needs and life history strategies. However, previous urban herpetofaunal analyses are generally limited to a single taxon (Germaine and Wakeling 2001, Barrett and Price 2014, Sullivan et al. 2016), or focused on an isolated urban attribute such as roads (Andrews et al. 2008), artificial lighting (Perry et al. 2008), or vegetation and habitat structure (Garden et al. 2010). I am not aware of any published studies that simultaneously address a suite of species and habitat variables that characterize an urban syndrome.

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CHAPTER 2

PATTERNS OF AMPHIBIAN AND REPTILE OCCUPANCY AND ABUNDANCE ACROSS AN URBANIZING LANDSCAPE[1]

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[1] Herpetofaunal distribution patterns in an urban protected space, M.C. Miles, J.C. Maerz and K.S. Delaney. To be submitted to *Urban Ecosystems*.

Abstract

Defining ‘urban’ within an ecological lens has often been restricted to social and institutional identifiers such as ‘human population density’ that lack biological significance for the biota of ecosystems affected by urbanization. This is potentially problematic when studying wildlife in urbanizing landscapes because wildlife will respond to the suite of specific changes to the biophysical environment that accompany increased human density. The objectives of my thesis were to analyze changes in habitat attributes in relation to human population density within the Santa Monica Mountains National Recreation Area to relate patterns of herpetofaunal occupancy and abundance to specific environmental attributes or a principal-components index of urbanizing habitats. Among our 79 study sites, human population density was negatively correlated with habitat patch size, positively correlated with increased noise and proximity to human-made structures and artificial light sources. Counter to expectations, human population density was not correlated with distance to a road or human-made water source among our study sites; however, this was likely an artifact of selecting sites with road access for drift fence installation. Most models of reptile and amphibian occupancy and abundance did not directly correlate with a single urban attribute or the composite index of urban. Landcover and habitat, which described vegetation communities including some that are the result of human modification, were commonly important factors among reptile abundance models. Occupancy rates of the two most common lizard species, *Sceloporus occidentalis* and *Uta stansburiana*, were positively correlated with human population density and Slender salamander, *Batrachoseps spp.*, occupancy increased with greater proximity to human-made water sources. Occupancy of remaining, less common reptile species was related to vegetation, elevation, and/or proximity to known water sources and paved surfaces.

Introduction

More than half of the world's human population resides in urban areas, and expanding urbanization is expected to increase that to 66% of the human population by 2050 (United Nations 2014). Even though cities and suburbs are engineered specifically for people, plants and animals exist within all human developments; and currently, biologists and urban planners have a limited understanding of wildlife ecology within these built environments.

One potential reason for this limited understanding may be variation and inconsistencies among urban planners, social scientists, and biologists in their definitions for "urban" versus other land cover types (McEntyre et al. 2000). Social scientists and a few urban ecologists delineate urban areas from rural or suburban areas using political boundaries or human population densities (Garden et al. 2007, Guderyahn et al. 2016, Braaker et al. 2017). However, ecologists more commonly delineate urban areas using a qualitative juxtaposition to rural areas (Banville and Bateman 2012, Sullivan et al. 2016) or without any clear criteria at all (Dawson and Hostetler 2006). When researchers do attempt to quantify the effects of specific urban attributes, they tend to focus on just a few dimensions associated with human development (e.g., impervious surfaces, Brady and Richardson 2017; land cover composition, van Rensburg 2009), but lack a more comprehensive evaluation of the multi-dimensional nature of urbanized areas.

The suite of biophysical changes associated with urbanization is similar across urban centers worldwide (Parris 2014, McKinney 2002). For instance, as tracts of land are cleared and excavated for buildings and infrastructure, habitat loss leads to smaller, more fragmented habitat patches in urban areas with varying levels of disturbance (McGrath and Pickett 2011). Areas that are more recently or highly disturbed may have more compacted soils (Devigne et al. 2016) and impermeable surfaces that alter hydrologic regimes and increase pollutant dispersal. These modifications contribute to urban stream syndromes (Walsh et al. 2005) and are consistently associated with reduced biotic richness (Paul and Meyer 2001). Impermeable surfaces also contribute to climatic changes such as the urban heat-island effect (Kim 1992) and increased cloud cover, humidity, and incidences of thunderstorms (Changnon 2001). As people continue to populate urban areas, they alter pre-existing light (Longcore and Rich 2004) and noise regimes (McGregor et al. 2013) and contribute to changes in predator density (Ordeñana et al. 2010) and behavior (Murray and St. Clair 2015).

Wildlife respond to these changes in inconsistent and, at times, contradictory ways. Cities and other developed areas are often subject to biotic homogenization (McKinney 2006), a process that selects for urban-adaptable species. Urbanization often favors habitat or resource generalists (Jokimäki and Huhta 2000) and nonnative species (Devictor et al. 2007). In some cases, shifts in species interactions (e.g., loss of large carnivores) can create opportunities for rare or specialist species to thrive within urban landscapes (Sorace and Gustin 2009). Some studies suggest there can be greater species richness in suburban areas (Germaine and Wakeling 2001) as a result of increased habitat heterogeneity and productivity (though see McKinney 2002). These varied responses of wildlife within urbanizing landscapes illustrate the need for a greater mechanistic understanding of wildlife responses to the urbanization syndrome.

Anobjective of our study was to quantitatively link biophysical attributes potentially important to wildlife with human population density, which is the most common metric for classifying areas as urban. We then want to relate those urban biophysical states to patterns of amphibian and reptile occupancy and abundance. We contend that if we can develop ecologically derived descriptors of ‘urban’ that better reflect the complexities of such systems, we will better understand why urbanization can create varied and at times paradoxical responses among wildlife. Reptiles and amphibians are well-suited for such a study, as they are diverse, and have variable habitat needs and life history strategies. Previous urban herpetofaunal analyses are generally limited to a single taxon (Germaine and Wakeling 2001, Barrett and Price 2014, Sullivan et al. 2016), or focused on an isolated urban attribute such as roads (Andrews et al. 2008), artificial lighting (Perry et al. 2008), or vegetation and habitat structure (Garden et al. 2010), rather than addressing a suite of variables that characterize an urban syndrome.

Our study area was the Santa Monica Mountains National Recreation Area (SAMO). SAMO is an urban protected area partially within the megacity boundaries of Los Angeles, California and encompasses tracts of federal, state, local, and private land ownership (National Park Service 2015). SAMO contains a wide array of native reptile and amphibian species. The most recently published account of terrestrial herpetofaunal diversity in the region pre-dates much of the area's recent urbanization (de Lisle et al. 1986). A more recent assessment of freshwater herpetofauna in remnant watersheds of north Los Angeles concluded that streams in more developed watersheds often contain exotic crayfish and fish, and fewer native species; however, the most widespread native amphibian, the Pacific treefrog (*Hyla regilla)*, was not directly affected by urbanization but was less abundant in the presence of exotic crayfish (*Procambarus clarkia*) (Riley et al. 2005). To our knowledge, there have been no similar evaluations of terrestrial reptile and amphibian species responses to urbanization in the region. Here, we analyzed four years of trapping data to model patterns of occupancy and abundance among native herpetofauna as they relate to biophysical attributes and composite metrics of urbanization in SAMO’s protected areas.

Methods

Study site - The outermost boundaries of SAMO extend from Malibu and the Pacific coastline northwards into the base of the Simi Hills (Figure 2.1). Ventura County agricultural fields lie to the east and the city of Los Angeles lies to the west, creating a 60,000 ha perimeter surrounding equal parts public and privately-owned land. The region is characterized as a Mediterranean climate with cool wet winters and hot dry summers. The region is arid and experienced a prolonged drought during a portion of this study (Griffin and Anchukaitis 2014). Elevation peaks at 600 m allowing for pockets of development (Syphard et al. 2005) within a matrix of remnant sage-scrub habitat.

Site Selection and Pitfall Trap Arrays - In the early 2000s, SAMO ecologists installed a network of pitfall arrays and funnel snake traps at sites selected using a Generalized Random Tessellation Stratified (GRTS) approach based on ease of accessibility and stratified by habitat and landcover (Figure 2.1). The GRTS survey design used a spatially explicit algorithm to identify locations within the designated area that represent a holistic image of the landscape while maximizing statistical independence among sites (Stevens and Olsen 2004). These sites, and others, have been monitored since 2001 under the U.S National Park Service (NPS) Inventory and Monitoring Division (Busteed et al. 2006). In this analysis, we used 79 sites that were regularly sampled from October 2012 to August 2016 (Figure 2.1).

Pitfall arrays were T or Y-shaped structures of 30-cm tall nylon shade cloth. The three arms of the pitfall structure were 15 meters long with seven ~ 40-liter buckets buried flush with the surface of the surrounding soil, at the center of the array and at the midpoint and end of each arm. Approximately five times per year, pitfall traps were surveyed, in rotation, every eight weeks (primary periods) for four consecutive days (secondary periods) resulting in a robust sampling regime (Pollock 1982). For logistical reasons, all sites were not sampled concurrently, but rather in clusters of ~10 sites each. Trained technicians ran trapping periods and identified captured animals to species, determined sex when possible, and measured each animal from snout to the posterior of the vent. Measurements and observations were recorded in the field on tablets that synchronized nightly with a centralized database.

Urban Habitat Covariates - During the summer of 2016 at each pitfall trap array, we measured a suite of variables that previous research had identified as important drivers of amphibian and reptile occupancy and abundance. We measured the presence and distance to the nearest impervious surface (any anthropogenic non-porous ground cover such as cement), human-made water sources (sewer lines, drains, and other public structures containing water), built structures (anthropogenic structures including infrastructure support such as telephone poles and cell sites), and artificial light sources (i.e. from residential homes and streetlights) within a 200-500 m radius. We based this distance on estimates of maximum home range size for Side-blotched lizards (*Uta stansburiana*), which was one of our most common species (Palermo 2000). Additionally, we determined the dominant habitat type among the three vegetative compositions primarily found in the Mediterranean ecosystem (i.e. forest, shrub, and herb[aceous]), by extracting site-specific characteristics from SAMO-specific United States Geological Service GIS vegetation data (unpublished data 2018). These classifications are denoted by the phrases, ‘habitat’ or ‘habitat type’ throughout the analysis. We measured ambient noise volume at the pitfall array for 30 seconds using the Sound Meter Pro (v2.5) application on the Samsung Galaxy s7 Edge (program limited to measurements below 80dB). We used GIS to extract an additional suite of variables for each site including 2011 National Land Cover Database land use classification (Homer et al. 2015), 2010 United States Census tract population density and Euclidean distance to the nearest road (US Census Bureau TIGERLine 2012), and surface area of respective SAMO-protected green space from Bureau of Land Management servers. We used Google Earth mapping services to correct discrepancies between on-the-ground proximity estimates (Google Inc.) up to a maximum radius of 1000 meters and corrected inconsistencies between distance to impervious surfaces and roads (of which many were dirt or gravel) to create the attribute: distance to paved surfaces.

We used a Principal Components Analysis (PCA) to examine the relationships between human population density and habitat variables and to reduce the number of habitat variables into composite indices. This multivariate statistical technique extracts the most important information from a suite of inter-correlated quantitative variables and compresses the data set into a set of orthogonal composite variables [principal components] (Abdi & Williams 2010). Principal components are ranked by their importance as indicated by the proportion of the total 'inertia' for which this factor "explained." To interpret the components, we referenced the loadings associated with each represented urban attribute's contribution, in this way variables with minimal contributions translated to less influence in comprising the component. All variables were standardized prior to analysis, including the presences/proximity to urban features such as artificial light sources. If an urban feature was absent from the study site, a proxy distance of 1000 m was applied to indicate the feature existed outside of the 500 m inclusion radius. We conducted the PCA using the base statistical functions in the statistical program R (R Core Team 2016).

Weather data - We compiled temperature data for each sampling event from individual HOBO loggers present at 20 sites and precipitation data from two central NPS affiliated Remote Automated Weather Stations (Watson et al. 2005). We fit linear models of average daily temperatures, recorded at each HOBO site during active trapping periods, to the average daily temperatures from a centrally located NPS weather station in Malibu Canyon. We then used the resultant functions to extrapolate average daily temperatures to supplement missing values in HOBO temperature data and estimate data at nearby sites (within 6 km of a site with HOBO data) when direct measurements of temperature were not available due to human error or equipment failure. Precipitation data was similar across the two weather stations, so we applied the recorded rainfall data of the eastern weather station to sites east of the Malibu Canyon ‘divide,’ and applied the western station values to those sites to the west. These values became observation-based weather covariates to estimate detection among sites.

Data Modeling - Imperfect detection and other stochastic processes prevent population distribution studies from comprehensively documenting every individual present in a given study area. Analysis with hierarchical models provides unbiased population estimates from a given sample by separating observed data into state and observation components (Kéry et al. 2009). The NPS Inventory and Monitoring protocol for SAMO is based on the structure of the Robust Design, dividing survey effort into primary and secondary sampling periods to satisfy the underlying assumptions associated with hierarchical occupancy and abundance models. Secondary sampling periods occur close to one another (i.e., on consecutive days of surveying) within each primary period (i.e., season, year, etc.) which are conceivably subject to changes in occupancy, abundance, etc. (Pollack 1982). Thus, the Robust Design is best suited for generating population parameter estimates as they relate to imperfect detection or other variables of interest.

Of all species captured over the survey period, only those with capture rates exceeding 0.1 per survey period were analyzed with hierarchical models (Pollock 1982). We analyzed detection/nondetection capture histories for SAMO's six most frequently captured herpetofauna species: Western fence lizards (*Sceloporus occidentalis,* SCOC), Side-blotched lizards (*Uta stansburiana,* UTST), Western skinks (*Plestiodon skiltonianus,* EUSK), Southern alligator lizards (*Elgaria multicarinata,* ELMU), Coastal whiptails (*Cnemidophorus tigris*, CNTI), and slender salamanders (*Batrachoseps spp.*, BANI) using multi-season occupancy modeling. The maximum likelihood-based approach uses species-based detection/non-detection capture histories to estimate four population parameters (detection probability (p), initial site occupancy (ψ), site colonization and site extinction) (MacKenzie et al. 2003). However, in the interest of this analysis, we only focused on covariate effects on the first two parameters and held the remaining two constant at respective mean values throughout the analysis. Similarly, we used an N-mixture abundance model based on maximum likelihood (Royle and Nichols 2003) to generate unbiased estimates of availability, abundance (N) and detection (p) for the same six species. As in the occupancy analysis, the remaining parameter (availability) remained constant at the mean throughout the N-mixture analysis.

We designed an identical suite of detection and initial occupancy/abundance candidate models for each species (see Table 2.1) and compared them using Akaike information criterion corrected for small sample sizes (AICc) (Burnham & Anderson 2002). Since we anticipated variable detection probabilities between sampling occasions for both occupancy and abundance models, we included time-varying weather covariates in the initial suite of detection models.

Candidate detection models were multivariable, comprised of additive and quadratic combinations of precipitation and temperature, in addition to an intercept-only null model in which all parameters were held constant. The configuration of weather variables included in the top detection model for each species, as determined by AICc, became the detection parameter configuration for the subsequent models directly manipulating occupancy [and abundance]. We used a systematic approach to arrive at a top multivariable model that was not overparameterized and identify the most salient urban attribute(s) influencing occupancy or abundance for each species analyzed, among the urban attributes studied. We used AICc to select the top univariate model, and then we added the factor from the next best univariate model that was also relatively non-collinear ($r < .65$). We used AICc to determine whether the addition of that second variable improved model performance. If the two-variable model outperformed the top univariate model, then it became our base model and we added the factor from the next best univariate model and again compared that model to the prior model using AICc. We repeated this process until either the addition of a variable did not meet the selected AICc criterion or the model had poor fit or singularities that indicated the model was over-parameterized for the data.

We estimated conditional occupancy or abundance with empirical Bayes methods and plotted these values along the gradient of observed values for those models within two ΔAICc of the lowest AICc model (Burnham & Anderson 2002). We conducted Chi-squared (X^2) Goodness of Fit tests with 100 simulations for the top performing model identified for each species, mapped the Bayesian site estimates, and reported model parameters for each respective species abundance and occupancy model as indicated by both methods**.** All analyses were conducted in the R package ‘unmarked’ (Fiske and Chandler 2011).

Results

General Capture Procedures - We analyzed pitfall trap data spanning 21 primary periods and 84 individual trapping occasions across 79 sites. In that time, we captured 4,518 individual reptile and amphibians comprising 25 different species (Table 2.2). The most frequently encountered reptile and amphibian species were the Western fence lizard (*Sceloprous occidentalis*; 1,836 captures) and slender salamander (*Batrachoseps spp.*; 839 captures), respectively. Altogether, total captures varied considerably between sites and among species, and there were sufficient captures to estimate occupancy and abundance for six species (see Table 2.2).

Weather Variables - The HOBO data loggers in SAMO provided temperature data for 1,632 of the 2,678 total site-days included in this study (excludes select trapping occasions when fire or severe weather prevented data collection). Since HOBO loggers were only present at 20 out of 79 sites, and not every active trapping occasion was successfully recorded by data loggers, linear models comparing average daily temperature between HOBO sites and the central NPS weather station were then used to predict average daily temperatures for the remaining trapping events (see Tables 2.3 and 2.4). Linear model parameters were positive across all sites, however the coefficient of determination (R^2) never exceeded 0.5, which suggested relative weak correspondence between HOBO loggers and the NPS weather station that may have limited the quality of our interpolated temperature data.

PCA of Urban Habitat Variables - The first two principal components accounted for 45.04% of the inertia among initial variables (PC1=24.4, PC2=16.5, Table 2.4). Principal component 1

(PC1) was largely a product of increasing human population density associated with smaller protected area patch size, increased noise and proximity to human-made lights, increased proximity to paved or otherwise impervious surfaces, and increased proximity to buildings (Table 2.5; Figure 2.2). Though larger protected areas and greater distances from human anthropogenic structures were important loadings on PC1 and negatively correlated with human population density, protected area size was weakly correlated (relatively orthogonal) with proximity to paved surfaces, buildings, and human-made light sources. Principal component 2 (PC2) was largely a product of increasing elevation and distance to anthropogenic water sources positively associated with decreasing area of protected space (Table 2.5; Figure 2.2).

Occupancy Models - Occupancy models estimated probability of detection and occupancy among species captured in the SAMO landscape. Among all studied species, detection models that included either linear or quadratic precipitation functions or quadratic temperature functions consistently performed better than null detection models (see Tables 2.6 and 2.7). Additionally, top detection models including temperature featured consistently positive beta values, suggesting that detection increased with increasing temperature among all taxa. Precipitation effects on detection were inconsistent across the studied species. Salamander detection was positively associated with precipitation; however, Western fence lizard detection was negatively correlated with precipitation.

Top occupancy models varied among species and did not consistently include similar relationships to urban attributes (Table 2.6). The top models for two taxa, Western fence lizards and Western skinks, were within 2 AICc of the null model and had low confidence in relationships to any parameters (Table 2.7 and 2.8). The top model of Western fence lizard occupancy predicted increasing occupancy and uncertainty with increasing human population density (Figure 2.3). The top model predicted Western skink occupancy was negatively correlated with elevation such that this species was predicted not to occupy sites above 33 meters in elevation (Figure 2.4); however, we caution that this model was within 2 AICc of the null model and goodness of fit was poor (Table 2.10). The top model for Coastal whiptail occupancy included elevation as the single parameter; however, despite no competing models and reasonable goodness of fit, the confidence interval for this model ranged between 0 and 1 across the entire range of elevation, suggesting that this model was poor at explaining the distribution of this species (Figure 2.5). We found reasonable predictive models for three species, all of which included urban attributes in the top model. Southern alligator lizard occupancy was best predicted by an additive model including site elevation, distance to water and surrounding vegetative habitat; however, we caution that the fit of this model was relatively poor. Slender salamander occupancy declined with increasing distance from a human-made water source, but also declined with increasing distance from a paved surface (Figure 2.6). Finally, Side-blotched lizard occupancy increased with human population density and declined with increasing distance from a paved surface (Figure 2.7).

Abundance Models – Across all species, the best models of capture probability included a quadratic relationship with temperature plus either a linear or quadratic relationship with precipitation (Tables 2.11 and 2.12). Additionally, the top abundance models for all species included the habitat type or landcover variables (Tables 2.13 and 2.14). Western fence lizard abundance was higher in developed, grass, and shrub habitats compared to forested habitats, and among grass and shrub habitats, fence lizard abundance was negatively correlated with elevation

(Figure 2.8). Within developed habitats and shrublands, predicted fence lizard abundance was consistently high regardless of elevation. Southern alligator lizard abundance was greater in forested and herbaceous habitats compared to shrub habitats, and declined with increasing distance from human-built structures and elevation (Figure 2.9). Side-blotched lizard abundance was greater in herbaceous and shrub habitat compared to forested habitat, but among all habitat types, increased with increasing size of the protected area (Figure 2.10). Coastal whiptail abundance was significantly higher in shrub habitats compared to forest or herbaceous habitat, was positively correlated with protected area size, and was negatively correlated with distance from a human-made light source (Figure 2.11). Western skink abundance was highest in herbaceous habitats compared to forest or shrub habitats, and within all three habitat types was negatively correlated with PC 1, indicating that skink abundance declined with increasing distance from paved areas, human-built structures, human-made light sources, and larger protected areas (Figure 2.12). Slender salamander abundance was greater in forested habitats and mixed forest or developed landcover classes. Noise volume was a factor in the top model of salamander abundance, but the standardized coefficient was relatively small compared to the importance of vegetation and landcover and the relationship to noise volume was not consistent among habitat types (see coefficients Figure 2.13). Therefore, the inclusion of noise in the top model may represent a spurious association.

Discussion

The results of this study demonstrate that, among the five most common reptile species and the most common terrestrial amphibian species, there were no consistent relationships between occupancy or abundance and specific attributes associated with urbanization. Different species showed no correlation, negative correlations, and positive correlations to urban attributes, and several species showed positive and negative correlations to different attributes of urbanization. Occupancy of three species appeared unrelated to any urbanization attributes, though we caution that we could not identify any robust model to predict occupancy for those species. Skink abundance was positively correlated with the principal component that integrated multiple urban attributes including proximity to paved areas, human-built structures, human-made light sources, and smaller protected areas. Three species showed positive relationships to some urban attributes but negative response to others. Side-blotched lizard occupancy increased with proximity to paved surfaces and human population density and Coastal whiptail abundance increased with proximity to human-made light sources; however, the abundances of both species declined with reductions in protected area size. Southern alligator lizard occupancy was weakly associated with proximity to human-made water sources, but Southern alligator lizard abundance increased with proximity to human-built structures. Some species also demonstrated paradoxical responses to urban attributes within the same landscape. For example, Slender salamander occupancy increased with proximity to human-made water sources in addition to proximity to paved surfaces. That human-made water sources might increase salamander occupancy is intuitive, as these animals are highly sensitive to moisture. Like other salamanders in the family Plethodontidae (Feder 1983), *Batrachoseps* are sensitive to water loss, and their abundance should be positively related to wetter soils. Many *Batraschoseps* species are more common in riparian habitats adjacent to small streams (Brode and Bury 1984, Guderyahn et al. 2010). However, salamanders and other amphibians are also susceptible to increased mortality from polluted runoff associated with roadways and urban drainage (Barrett and Price 2014). Collectively, our results are consistent with other studies that show varied effects of urbanization on native wildlife, in which some species may benefit or be unaffected by increasing human density and the associated changes to the environment (Prange & Ghert 2004).

A clear relationship that emerged from our analysis was the importance of landcover and dominant vegetation on the abundance of all six of the most common reptile and amphibian species. Vegetation structure was already known to influence the composition and abundance of lizard communities in the arid ecosystems of the western U.S. and Mexico (Germano and Lawhead 1986; Schorr et al. 2011). Vegetation affects thermal environments, refuge from predators, prey availability, and movement of lizards (Bozanich and Feldman 2015). Generally, heterogeneous vegetation increases lizard diversity, while more homogenous vegetation is associated with reduced diversity favoring some species over others (Peterson and Whitford 1987; Menke 2003). Though changes in vegetation type are not considered a specifically ‘urban’ attribute, it is important to recognize that most vegetation change with these arid ecosystems is the direct result of human activities including the introduction of grazing livestock, altered fire regimes, and the introduction of nonnative plant species that typically promote more homogenous vegetation (Syphard et al. 2018). For example, in California, historic grass cover would have been dominated by native bunch grasses that are interspersed with open patches of bare ground. However, California’s grasslands are currently dominated nonnative annual grasses (Keeley 2003) that have a different phenology and form dense fields atypical of historic vegetation structure. Centuries of human occupation within the chaparral landscape of southern Californian converted acres of natural shrub and sage scrub habitat into agricultural lands by the early twentieth century, followed by urban and residential over the latter half of the twentieth century (Syphard et al. 2018).

Studies in both field and laboratory settings have identified possible mechanisms of habitat avoidance, reduced performance, or reduced abundance among lizards because of nonnative grass invasion (Newbold 2005; Valentine et al. 2006; Rieder et al. 2010). However, we found that the presence of herbaceous vegetation, such as grass, was associated with increased abundance of four of five lizard species. We note that our methods do not allow us to distinguish between invasive cheatgrass, ornamental lawn grass, other herbaceous cover, and native bunch grass; the latter of which is associated with increased lizard species richness (Menke 2003). Other studies have documented positive relationships between nonnative grasses and herpetofauna (as reviewed in Martin and Murray 2011), including studies that report positive relationships between grass cover and Side-blotched lizards specifically (Castellano and Valone 2006). It is possible that urbanization can have some positive effects on lizard species by promoting more open habitat (Twinkle 1967, Pike et al. 2011) that, in urban areas, is more likely to have herbaceous cover. Despite its effects on movement, grass invasions may also indirectly benefit some lizard species via its effects on competition or predation risk (Castellano and Valone 2006; Schorr et al. 2011). The mechanisms driving the positive association we identified between lizard abundance, herbaceous habitats, and how vegetation structure is related to urbanization warrant future attention as it may lead to specific habitat management recommendations.

A key finding of this study relates to the metrics commonly used to distinguish urban from rural localities for ecological study. Much of the literature published on urban ecology references human population density, often as communicated by federal institutions like the U.S. census bureau, to delineate urban areas from the less developed spaces surrounding them (McEntyre 2000). Our principal components analysis indicated that ‘urban’, as represented by the density of people associated within an area, was not clearly, linearly associated with typical ‘urban’ habitat variables within SAMO, nor were all typical urban attributes strongly correlated with one another. For example, we found a negative correlation between population density and the size of a protected area, which fits the convention that greater human densities leave fewer, smaller, more fragment protected spaces for wildlife. However, we found relatively orthogonal relationships between the size of a protected area (degree of fragmentation) and other anthropogenic habitat attributes such as the distance to paved surfaces such as roads and driveways, built structures, and artificial light sources. In addition, some urban attributes such as proximity to anthropogenic water sources were roughly orthogonal to other distinctly anthropogenic urban attributes such as proximity to buildings, anthropogenic light sources, and paved surfaces. This illustrates that a single classification or metric of ‘urban’ is unlikely to capture the complexity of changes to animal environments within an urbanizing landscape.

Importantly, as a measure of ‘urban’, human population density was not a strong predictor of occupancy or abundance for our focal reptile and amphibian species. Human population density was included in the top model for predicting Side-blotched lizard occupancy (Walkup et al. 2017). The relationships between human population density and Side-blotched lizard occupancy was positive, which contradicts the prevailing narrative of reduced native wildlife diversity in areas of high human density (Chace and Walsh 2006), however it aligns with the findings of Riley et al. (2005) that the most widespread native amphibian in SAMO’s urban streams was unaffected by the direct effects of urbanization.

As mentioned previously, other research efforts in the Santa Monica Mountains have focused on amphibian responses to urbanization, specifically within aquatic or riparian systems (Riley et al. 2005). Though slender salamanders are terrestrial, we found a positive correlation between salamander occupancy and proximity to an anthropogenic water source such as sewer pipes and drains. This result also illustrates that some anthropogenic modifications to landscapes, such as the creation of novel water sources, can create habitat attractive to and potentially suitable for wildlife such as amphibians. We caution that anthropogenic water sources are not necessarily 'healthy' habitats for amphibians. Anthropogenic water sources can be ecological traps by exposing wildlife to harmful invasive species, pollutants, and pathogens (Riley et al. 2005; Ruiz et al. 2010). Weinsten (2009) found that the waterborne amphibian pathogen, *Batrachochytrium dedrobatidis*, is established among terrestrial *Batrachoseps* populations in California where it can cause mortality, though populations where the disease is present appear to be stable.

We note that the suite of urban attributes we analyzed was not exhaustive. We attempted to measure other relevant urban habitat attributes including soil compaction, presence of ornamental vegetation, and urban heat index; however, we were not successful in rigorously quantifying these attributes. These attributes may be important predictors that could be examined in future studies. The age of developed areas and disturbance histories of the remnant protected green spaces may also be important determinants of reptile and amphibian occupancy and abundance that we did not consider in this study (Ramalho and Hobbs 2011). Finally, we cannot ignore that some responses of reptiles and amphibians to urbanization will be mediated indirectly through effects on other taxa including predators and prey. For example, recent research on wind farms showed that built infrastructure reduced the presence of higher level predators such as birds of prey, which in turn was linked to an increased abundance of lizards and small vertebrates (Thaker et al. 2018). Urbanization is frequently, though not exclusively, associated with reductions in top predator communities and the release of mesopredator populations (Prange and Gerht 2004; Sorace and Gustin 2008; Magle et al. 2014).

Limitations of our study include the poor correspondence between temperature data from HOBO loggers and weather station data that was used to interpolate weather data for some capture periods. Given the importance of those weather variables in our detection models, poor quality weather covariates may have reduced model performance. In the absence of direct measurements of weather, we propose that future re-analysis of our data could evaluate the use of interpolated weather data from sources such as Daymet (https://daymet.ornl.gov) or PRISM (http://www.prism.oregonstate.edu).

Another limitation of our study was not using time varying models despite that fact that the data was collected over multiple seasons and years. We did not include time varying models in our analysis to minimize the computational effort of our candidate models. Reptile and amphibian communities are dynamic and persistent urban wildlife populations have been known to maintain higher turnover rates than their rural analogues (Padilla and Rodewald 2014). By not allowing occupancy or abundance to change and holding non-target parameters such as colonization and extinction or availability constant, we may have inflated occupancy and abundance estimates and reduced our ability to detect the effects of specific attributes.

In conclusion, though social lexicon delineates urban according to human population density, our study demonstrates that while some wildlife habitat attributes associated with urbanization are correlated with human population density, the relationships between human population density and other aspects of wildlife habitat may not be strongly correlated. Moreover, the impact of urbanization on native reptile and amphibian communities varies among species and may result from a combination of the direct effects of human modification in addition to the indirect effects mediated by other organisms responding to the urban landscape. Therefore, it may be inappropriate to use an over-simplified “urban” land classification to address how and why wildlife respond to urbanization.

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Tables

Table 2.1. The candidate model set begins with occasion-based weather covariates (‘Precip’ refers to precipitation and ‘Temp’ refers to temperature) related to the detection parameter; the candidate models. Next, the target parameter (i.e., occupancy or abundance) is modeled with respect to individual site-based urban attributes. The ‘Abbreviations’ column indicates urban attribute abbreviations; the ‘Number’ column provides labels for detection candidate models that appear in other tables and figures.

Number	**Detection**	**Abundance or Occupancy**	**Abbreviations**
1	~1	~1	null
2	~Temp	~Habitat	Habitat
3	~Precip	~Landcover	Landcover
4	~Precip+Temp	~Distance to Paved Surface	PavedDist
5	~Temp^2	~Human Population Density	PopD
6	~Precip^2	~Ambient Volume	Volume
7	~Temp^2 + Precip	~Elevation	Elev.m
8	~Precip^2 + Temp	~Surface Area of Protected Area	Area.acr
9	~Temp^2 + Precip^2	~Distance to Buildings	Buildt.
		~Distance to Artificial Light	Lights.
		~Distance to Anthropocentric Water	Water.
		~Principal Component 1	PC1
		~Principal Component 2	PC2

Table 2.2. Total number of captures by species for all 79 pitfall arrays actively surveyed in the SAMO terrestrial monitoring program from November 2012 to May 2016. Species codes were used to abbreviate identified herpetofauna, those denoted by an asterisk (*) are listed as California species of special concern. Taxa totals include mortalities that were found in traps but not identified to the species.

Species Code	**Latin Name**	**Common Name**	**Sum Captures**
Amphibians			**1028**
BANI	*Batrachoseps nigriventris*	Black-bellied slender salamander	839
BUBO	*Anaxyrus boreas halophilus*	California toad	121
ENES	*Ensatina eschscholtzii eschscholtzii*	Monterey Ensatina	16
HYRE	*Pseudacris regilla*	Pacific treefrog	50
TATO	*Taricha torosa*	California newt	1
ANLU	*Aneides lugubris*	Arboreal salamander	1
Reptiles			**3490**
Lizards			**3323**
SCOC	*Sceloporus occidentalis*	Western fence lizard	1799
UTST	*Uta stansburiana*	Side-blotched lizard	731
EUSK	*Plestiodon skiltonianus*	Western skink	377
CNTI*	*Cnemidophorus tigris*	Coastal whiptail*	167
ELMU	*Elgaria multicarinata*	Southern alligator lizard	198
PHCO*	*Phrynosoma blainvilli*	Blainville's horned lizard*	22
ANPU	*Anniella pulchra*	California legless lizard	3
Snakes			**167**
LAGE	*Lampropeltis californiae*	California kingsnake	32
DIPU*	*Diadophis punctatus modestus*	San Bernardino ringneck snake*	28
MALA	*Coluber lateralis lateralis*	California striped racer	28
PICA	*Pituophis catenifer annectens*	San Diego gopher snake	26
CRVI	*Crotalus oreganus helleri*	Southern Pacific rattlesnake	24
MAFL	*Coluber flagellum piceus*	Red coachwhip	8
HYTO	*Hypsiglena ochrorhyncha klauberi*	San Diego nightsnake	7
TAPL	*Tantilla planiceps*	California black-headed snake	7
COCO	*Coluber constrictor Mormon*	Western yellow-bellied racer	3
LEHU	*Rena humilis humilis*	Southern threadsnake	2
SAHE*	*Salvadora hexalepis virgultea*	Coast patch-nosed snake*	1
THHA*	*Thamnophis hammondii*	Two striped garter snake*	1

Table 2.3. Correlations between average daily temperature values recorded by HOBO data-loggers and the NPS weather station during trapping occasion from 2012-2016 that were used to interpolate missing temperature data from study sites within 6 km of a HOBO station.

Hobo Site	Slope	Intercept	R^2	Sites Applied
1	0.6390	30.1641	0.4165	2, 10
4	0.6865	26.6045	0.4239	62, 63
15	0.5443	36.7909	0.3931	9, 11, 17
29	0.4935	39.1832	0.3757	23, 27, 28
52	0.4133	40.3322	0.1426	106, 107, 111, 112
55	0.6186	27.6470	0.3821	56, 59, 113
67	0.6847	26.1014	0.3863	66
71	0.5306	33.5921	0.2775	21, 68, 69, 70, 71, 72
74	0.6662	29.4430	0.4858	73, 75
77	0.7337	24.1116	0.4571	76, 77, 78, 79, 80, 81
83	0.5017	38.7976	0.4725	82
88	0.5017	38.7976	0.4986	84, 85, 86, 87, 88
91	0.4605	40.0560	0.3887	89, 90, 91, 92, 93
96	0.5030	39.3062	0.4654	94, 95, 96, 97, 98, 101
99	0.3438	47.4414	0.1915	n/a
102	0.3278	47.4740	0.1177	42
105	0.4030	40.8253	0.1694	49, 100, 103, 105
109	0.4504	43.2141	0.2942	104, 108, 109, 110
117	0.6304	29.6818	0.5035	114, 115, 116, 118
120	0.6079	30.8412	0.4612	119, 121

Table 2.4. Summary statistics for temperatures recorded in the Santa Monica Mountains during the survey period from November 2012 to May 2016. 20 HOBO data loggers were deployed to actively record temperature during trapping occasions, though human error, equipment failures, and extreme weather events resulted in missed occasions for select sites.

HOBO Site	Min (°F)	Mean (°F)	Median (°F)	Max (°F)	Standard Deviation	No. of Survey Days HOBO Recorded Data
1	55.61	69.66	70.79	89.64	8.94	135
4	53.83	69.23	70.36	85.81	6.82	129
15	59.73	70.46	71.00	89.89	5.62	113
29	57.02	71.04	71.79	82.39	5.42	104
52	46.19	66.05	69.63	79.26	7.58	156
55	37.49	66.27	68.80	85.67	8.07	143
67	51.15	69.00	70.44	91.54	7.11	135
71	52.25	67.08	69.23	83.35	6.91	126
74	47.15	71.08	71.09	93.96	7.78	143
77	42.54	70.00	70.33	93.11	8.86	143
83	55.66	70.49	71.28	82.39	5.22	131
88	58.74	71.20	71.84	84.35	5.37	131
91	56.07	69.15	70.69	79.56	5.29	131
96	57.33	71.06	71.76	81.38	5.35	105
99	51.74	68.82	70.54	81.48	5.62	138
102	52.07	67.67	69.60	78.85	5.75	157
105	47.47	65.83	68.14	75.38	6.76	157
109	57.61	71.26	71.81	80.32	4.91	105
117	44.67	68.63	69.88	83.37	7.37	143
120	42.68	68.70	70.09	83.23	7.46	134

Table 2.5. Principal component analysis (PCA) of human population density and urban habitat covariates. Above: Standard deviation associated and the proportion of the variance explained by each individual principal component. Urban attributes driving variation for the first four components are denoted in bold. Below: The loading contributions of each individual urban attribute towards the composition of each individual principal component.

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**
Volume	**-0.310**	0.033	**-0.693**	0.187	-0.234	-0.049	0.388	0.424
PopD	**-0.413**	-0.173	-0.165	**0.522**	0.399	0.356	-0.077	-0.456
Elev.m	-0.003	**-0.699**	0.193	0.118	-0.556	-0.073	0.283	-0.259
Area.acr	**0.427**	**0.401**	-0.244	-0.072	-0.245	0.395	0.354	-0.500
Water.	0.031	**-0.480**	**-0.322**	**-0.680**	0.324	0.308	0.041	0.010
Buildt.	**0.398**	-0.143	**-0.384**	0.128	0.303	-0.691	0.004	-0.297
Lights.	**0.445**	-0.165	0.249	0.341	0.396	0.220	0.483	0.398
PavedDist	**0.440**	-0.204	-0.287	0.280	-0.252	0.297	-0.635	0.221

	PC1	**PC2**	**PC3**	**PC4**	**PC5**	**PC6**	**PC7**	**PC8**
Standard Deviation	1.5211	1.1354	1.0839	0.9635	0.8985	0.8153	0.7093	0.5644
Proportion of Variance	0.2892	0.1611	0.1469	0.1160	0.1009	0.0831	0.0629	0.0398
Cumulative Variance	0.2892	0.4504	0.5972	0.7133	0.8142	0.8973	0.9602	1.0000

Table 2.6. Detection (p) model selection table for each reptile and amphibian species using Akaike's Information Criterion (AICc). Species codes can be found in Table 2.2. Displayed is the top model and any additional models that were within two ΔAICc of the top model.

Species Code	Model Number	Covariates in Model	ΔAICc
SCOC	**9**	Temp^2+Precip^2	0.00
	7	Temp^2+Precip	0.72
UTST	**5**	Temp^2	0.00
	7	Temp^2+Precip	0.43
	9	Temp^2+Precip^2	1.99
BANI	**4**	Precip+Temp	0.00
	7	Temp^2+Precip	0.07
	3	Precip	1.36
CNTI	**5**	Temp^2	0.00
	2	Temp	1.58
	7	Temp^2+Precip	1.99
EUSK	**7**	Temp^2+Precip	0.00
	9	Temp^2+Precip^2	1.88
ELMU	**7**	Temp^2+Precip	0.00
	5	Temp^2	0.97
	9	Temp^2+Precip^2	1.86

Table 2.7. Coefficients (Beta) and standard errors (SE) for probability of detection (p) of top occupancy models for each study species as a function of temperature and precipitation.

Species Code	Covariates	Beta	SE	Lower CI	Upper CI
SCOC	(Intercept)	-0.6573	0.0527	-0.76059	-0.554008
	Temp	0.3372	0.081	0.17844	0.49596
	I(Temp^2)	-0.0271	0.00673	-0.04029	-0.013909
	Precip	-0.4713	0.1448	-0.75511	-0.187492
	I(Precip^2)	0.0241	0.01211	0.000364	0.047836
UTST	(Intercept)	-0.953	0.0958	-1.14077	-0.765232
	Temp	0.639	0.1254	0.393216	0.884784
	I(Temp^2)	-0.265	0.164	-0.58644	0.05644
BANI	(Intercept)	-0.441	0.1292	-0.69423	-0.187768
	Precip	0.205	0.0707	0.066428	0.343572
	Temp	0.183	0.1267	-0.06533	0.431332
CNTI	(Intercept)	-2.144	0.165	-2.4674	-1.8206
	Temp	0.982	0.224	0.54296	1.42104
	I(Temp^2)	-0.206	0.321	-0.83516	0.42316
EUSK	(Intercept)	-1.444	0.171	-1.77916	-1.10884
	Temp	0.458	0.164	0.13656	0.77944
	I(Temp^2)	-0.244	0.204	-0.64384	0.15584
	Precip	-1.403	0.786	-2.94356	0.13756
ELMU	(Intercept)	-2.417	0.183	-2.77568	-2.05832
	Temp	0.267	0.189	-0.10344	0.63744
	I(Temp^2)	-0.385	0.241	-0.85736	0.08736
	Precip	-0.255	0.196	-0.63916	0.12916

Table 2.8. Occupancy (ψ) model selection for each reptile and amphibian species using Akaike's Information Criterion (AICc). Species codes can be found in Table 2.2. Presented are the top model and all other models within two ΔAICc of the top model.

Species Code	**Covariates in Model**	**AICc**	**ΔAICc**
SCOC	~PopD	5902.59	0
	~PopD+Water.	5903.91	1.32
	~1	5904.19	1.6
	~PopD+Volume	5904.54	1.95
UTST	~DomVeg+ Population+ Area	3708.76	0
BANI	~Water.+PavedDist	1536.07	0
	~Water.	1537.62	1.55
CNTI	~Elev.m	1123.31	0
EUSK	~Elev.m,	2217.54	0
	~Elev.m+Buildt.,	2218.02	0.48
	~Elev.m+PopD,	2218.26	0.72
	~Buildt.,	2218.8	1.26
	~Buildt.+PopD,	2218.9	1.35
	~PopD,	2218.96	1.41
	~1,	2219.39	1.85
ELMU	~DomVeg+Elev.m+Water.	1436.43	0
	~DomVeg+Elev.m+PopD	1438.27	1.84

Table 2.9. Coefficients (Beta) and standard errors (SE) for top probability of occurrence (ψ) models of amphibian and reptile species as a function of urban attributes (each row within a species corresponds to the covariates or intercept of that species' top model, as determined by AICc). Species codes can be found in Table 2.2.

Species Code	Covariates in Model	Beta	SE	loweCI	upperCI
SCOC	(Intercept)	0.11	0.31	-0.49	0.70
	PopD	0.58	0.38	-0.16	1.31
UTST	(Intercept)	-16.242	570.773	-1134.96	1102.47
	PopD	0.839	0.368	0.12	1.56
	Dominant Veg. herbs	15.478	570.773	-1103.24	1134.19
	Dominant Veg. shrub	14.52	570.773	-1104.20	1133.24
	PavedDist	0.731	0.415	-0.08	1.54
BANI	(Intercept)	-2.70	0.68	-4.03	-1.36
	Distance to Water	-0.73	0.31	-1.33	-0.12
	PavedDist	-1.16	0.78	-2.69	0.37
CNTI	(Intercept)	-42.50	57.80	-155.79	70.79
	Elevation	44.30	60.30	-73.89	162.49
EUSK	(Intercept)	-2.95	0.91	-4.73	-1.17
	Elevation	-1.48	0.84	-3.12	0.16
ELMU	(Intercept)	41.3	40.2	-37.49	120.09
	Dominant Veg. herbs	17.3	281.9	-535.22	569.82
	Dominant Veg. shrub	-75.3	73	-218.38	67.78
	Elevation	-28	28.6	-84.06	28.06
	Distance to Water	23.1	83.9	-141.34	187.54

Table 2.10. Goodness-of-Fit table for top occupancy models among amphibian and reptile species. The final column [Pr(t_B>t0)] indicates the p-value estimated by 100-iteration Chi-squared goodness of fit test (specifically, the probability that the observed Chi-squared statistic is less than the simulated bootstrap sample statistics); ** denotes P > 0.05 such that we fail to reject the null hypothesis and conclude that the model fit is adequate. t0 = Original statistic computed from data and fitted model. t_B = Vector of 100 bootstrapped sample statistics. Species code abbreviations are available in Table 2.2.

Species Code	**t0**	**Pr(t_B>t0)**
SCOC	5226	0.366**
UTST	5758	0.941**
BANI	6248	0.455**
CNTI	5154	0.941**
EUSK	6394	0.010
ELMU	5571	0.891**

Table 2.11. N-mixture detection (p) model selection table for amphibian and reptile species using Akaike's Information Criterion (AIC). Species codes can be found in Table 2.2. The top model and any additional models within two ΔAIC of the top model are presented.

Species Code	**Covariates in Model**	**AICc**	**ΔAICc**
SCOC	Temp^2+Precip^2	8097.38	0.00
	Precip^2+Temp	8099.44	2.06
UTST	Precip^2+Temp	3841.43	0.00
	Temp^2	3841.79	0.36
	Temp^2+Precip^2	3843.23	1.80
BANI	Precip^2+Temp	5122.87	0.00
CNTI	Temp^2+Precip^2	1338.57	0.00
EUSK	Precip^2+Temp	2601.68	0.00
	Temp^2+Precip^2	2603.49	1.81
ELMU	Precip^2+Temp	1704.01	0.00
	Temp^2	1704.45	0.43
	Precip	1705.33	1.32

Table 2.12. Coefficients (Beta) and standard errors (SE) for probability of detection (p) as a function of temperature and precipitation by species for top abundance models. Species codes can be found in Table 2.2.

Species Code	Covariate	Beta	SE	Lower CI	Upper CI
SCOC	(Intercept)	-1.55	0.08	-1.71	-1.39
	Temp	0.40	0.07	0.27	0.53
	I(Temp^2)	-0.03	0.01	-0.05	-0.02
	Precip	-0.46	0.12	-0.70	-0.22
	I(Precip^2)	0.02	0.01	0.00	0.04
UTST	(Intercept)	-1.46	0.11	-1.68	-1.24
	Temp	0.56	0.11	0.35	0.78
	I(Temp^2)	-0.33	0.15	-0.61	-0.04
	Precip	-0.09	0.06	-0.21	0.03
BANI	(Intercept)	-1.45	0.09	-1.63	-1.49
	Temp	-0.73	0.12	-0.96	-0.49
	I(Temp^2)	0.06	0.01	0.04	0.08
	Precip	0.17	0.03	0.10	0.24
CNTI	(Intercept)	-2.91	0.60	-3.21	-1.73
	Temp	0.76	0.23	0.31	1.22
	I(Temp^2)	-0.10	0.11	-0.31	0.10
	Precip	-5.95	3.77	-13.34	1.44

	I(Precip^2)	0.92	0.56	-0.17	2.01
EUSK	(Intercept)	-1.89	0.19	-1.52	-2.26
	Temp	0.28	0.14	0.00	0.56
	I(Temp^2)	-0.32	0.18	-0.67	0.03
	Precip	-1.67	0.82	-3.27	-0.07
ELMU	(Intercept)	-2.18	0.22	-1.75	-2.61
	Temp	0.316	0.187	-0.07	0.67
	I(Temp^2)	-0.279	0.238	-0.70	0.25
	Precip	-0.221	0.187	-0.60	0.14

Table 2.13. Model selection results for multivariate N-mixture models of amphibian and reptile abundance using Akaike's Information Criterion (AICc). The top models (lowest AICc) are reported for each species in addition to those within two ΔAICc of the top model.

Species Code	Abundance Formula	AICc	ΔAICc
SCOC	Elevation + Landcover	8043.21	0
UTST	Dominant Veg.+ PopD + Area.acr	3708.76	0
BANI	Dominant Veg.+ Landcover + Volume	4712.82	0
CNTI	Dominant Veg.+ Area.acr + Lights.	1295.07	0
	Dominant Veg.+ Area.acr	1295.14	0.071
	Dominant Veg.+ Area.acr + PopD	1296.21	1.137
	Dominant Veg.+ Area.acr + PavedDist	1296.83	1.76
EUSK	Dominant Veg.+ PC1	2540.08	0
ELMU	Dominant Veg.+ Elevation + Buildt.	1673.67	0

Table 2.14. Coefficients (Beta) and standard errors (SE) for covariates in top multivariate abundance models of specific amphibian and reptile species.

Species Code	Covariate	Beta	SE	loweCI	upperCI
SCOC	(Intercept)	2.00	0.15	1.69	2.30
	Elevation	-0.375	0.053	-0.48	-0.27
	Landcover. Grasslands	-0.406	0.202	-0.80	-0.01
	Landcover. Mixed Forest	-0.915	0.383	-1.67	-0.16
	Landcover. Shrub/Scrub	0.227	0.126	-0.02	0.47
UTST	(Intercept)	-0.809	0.3543	-1.50	-0.11
	Dominant Veg. herbs	2.233	0.3744	1.50	2.97
	Dominant Veg. shrub	1.763	0.3602	1.06	2.47
	PopD	0.61	0.0566	0.50	0.72
	Area.acr	0.763	0.0965	0.57	0.95
BANI	(Intercept)	3.78	0.1119	3.56	4.00
	Dominant Veg. herbs	-1.434	0.1704	-1.77	-1.10
	Dominant Veg. shrub	-2.056	0.1565	-2.36	-1.75
	Landcover. Grasslands	-2.726	0.4587	-3.63	-1.83
	Landcover. Mixed Forest	-1.071	0.3227	-1.70	-0.44
	Landcover. Shrub Scrub	-1.317	0.1228	-1.56	-1.08
	Volume	-0.219	0.0537	-0.32	-0.11
CNTI	(Intercept)	-0.962	0.432	-1.81	-0.12
	Dominant Veg. herbs	-0.558	0.71	-1.95	0.83
	Dominant Veg. shrub	1.568	0.428	0.73	2.41
	Area.acr	0.514	0.141	0.24	0.79
	Lights.	-0.222	0.149	-0.51	0.07
EUSK	(Intercept)	1.059	0.2411	0.59	1.53
	Dominant Veg. herbs	0.833	0.2121	0.42	1.25
	Dominant Veg. shrub	-0.815	0.2529	-1.31	-0.32
	PC1	-0.179	0.0774	-0.33	-0.03
ELMU	(Intercept)	1.293	0.3251	0.66	1.93
	Dominant Veg. herbs	0.236	0.2332	-0.22	0.69
	Dominant Veg. shrub	-0.586	0.2515	-1.08	-0.09
	Elevation	-0.414	0.1126	-0.63	-0.19
	Buildt.	-0.315	0.0938	-0.50	-0.13

Table 2.15. Chi-Square goodness-of-fit results for top multivariate abundance models of amphibian and reptile species. The final column indicates the p-value estimated by Chi-squared goodness of fit test (specifically, the probability that the observed Chi-squared statistic is less than the simulated bootstrap sample statistics); ** denotes P > 0.05 such that we fail to reject the null hypothesis and conclude that the model fit is adequate. t0 = Original statistic computed from data and fitted model. t_B = Vector of 100 bootstrapped sample statistics. Species abbreviations are available in Table 2.1.

Species Code	t0	Pr(t_B>t0)
UTST	8721.00	0.00
BANI	26392.00	0.00
CNTI	7794.00	0.01
EUSK	7566.00	0.01
ELMU	7794.00	0.01

Figures

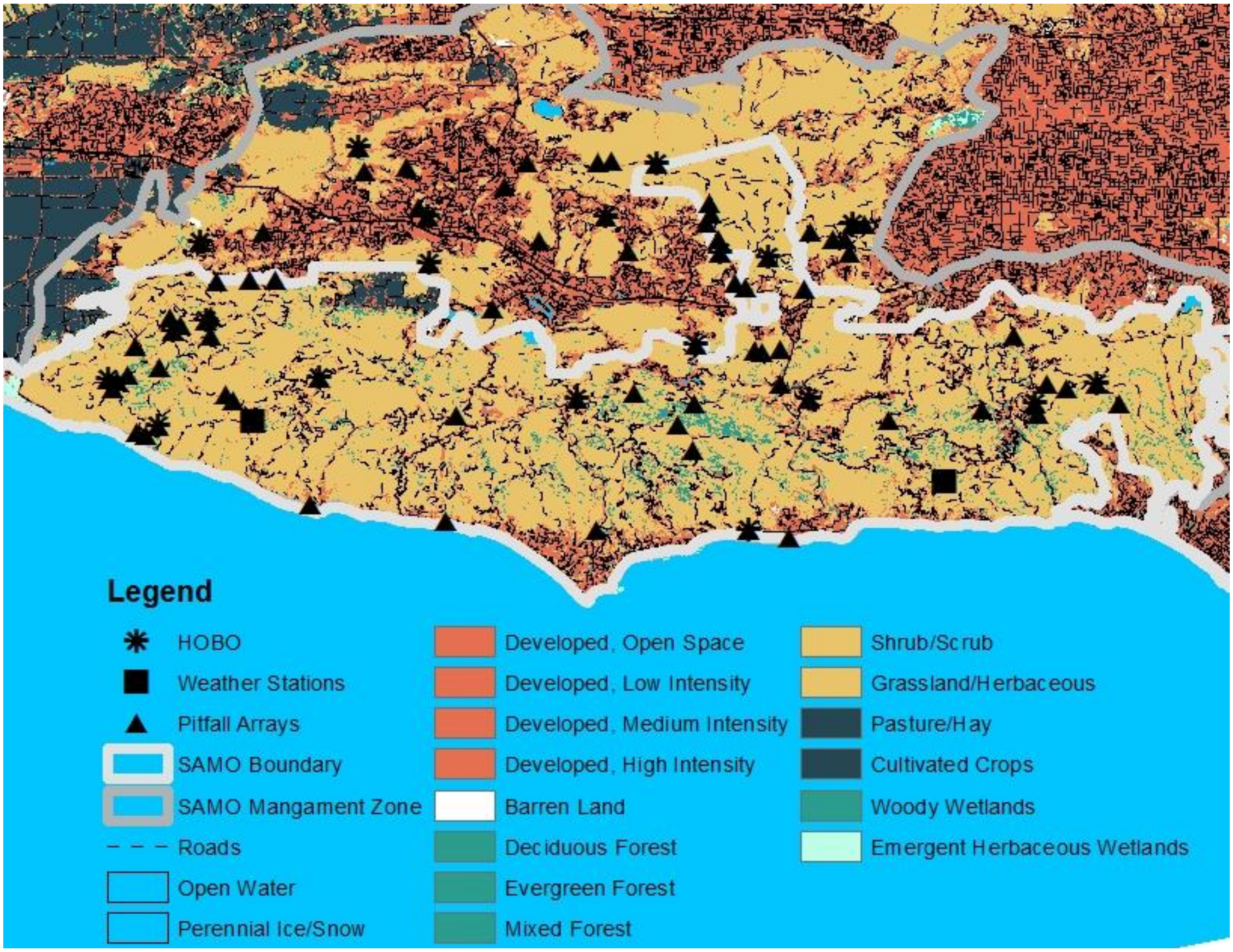


Figure 2.1. Map of study sites in the Santa Monica Mountains National Recreation Area showing landcover and the locations of the 79 pitfall array sites and HOBO temperature loggers.

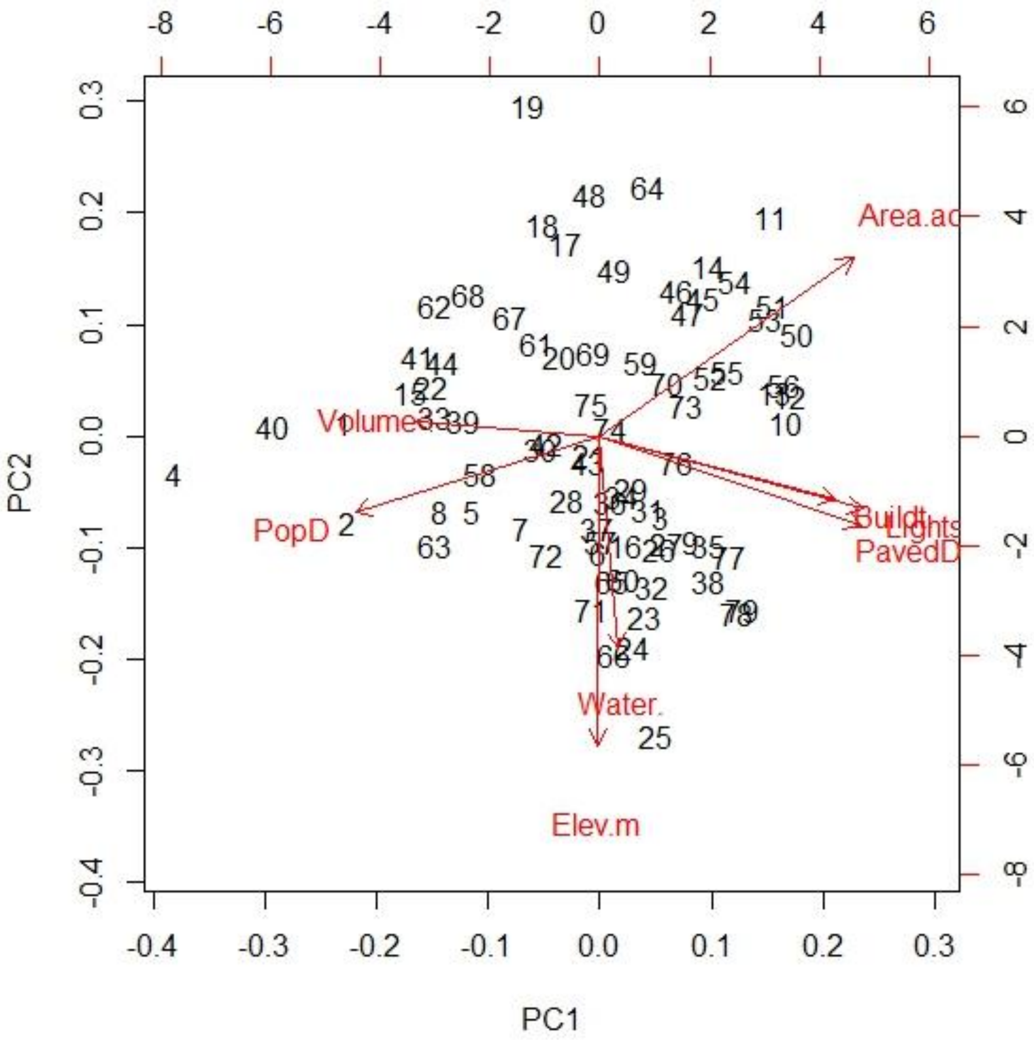


Figure 2.2. Standardized biplot of the first two principal components describing the variation among urban attributes at the 79 pitfall array sites in SAMO. PC1 was largely a product of increasing human population density associated with smaller protected area patch size, increased noise and proximity to human-made lights, increased proximity to paved or otherwise impervious surfaces, and increased proximity to buildings. PC2 was largely a product of increasing elevation and distance to anthropogenic water sources positively associated with decreasing area of protected space. Each numbered label corresponds to a separate pitfall array study site and each vector labeled in red corresponds to an abbreviation of each urban attribute.

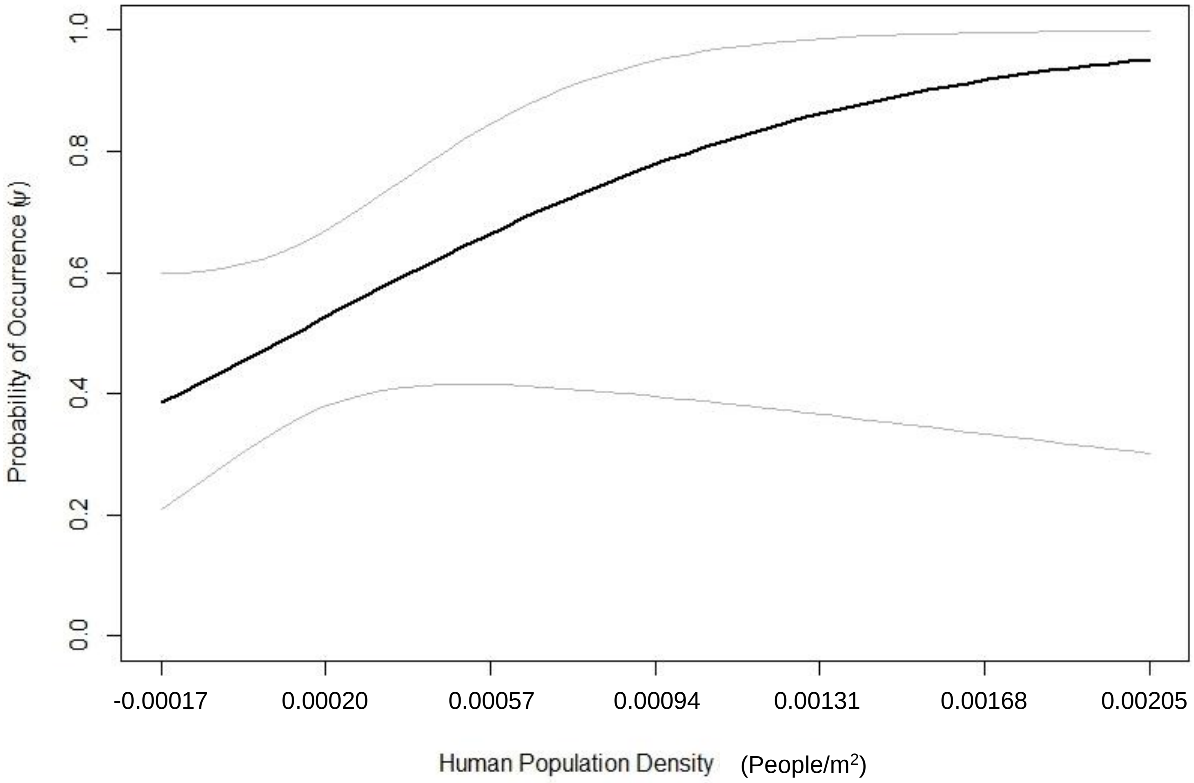
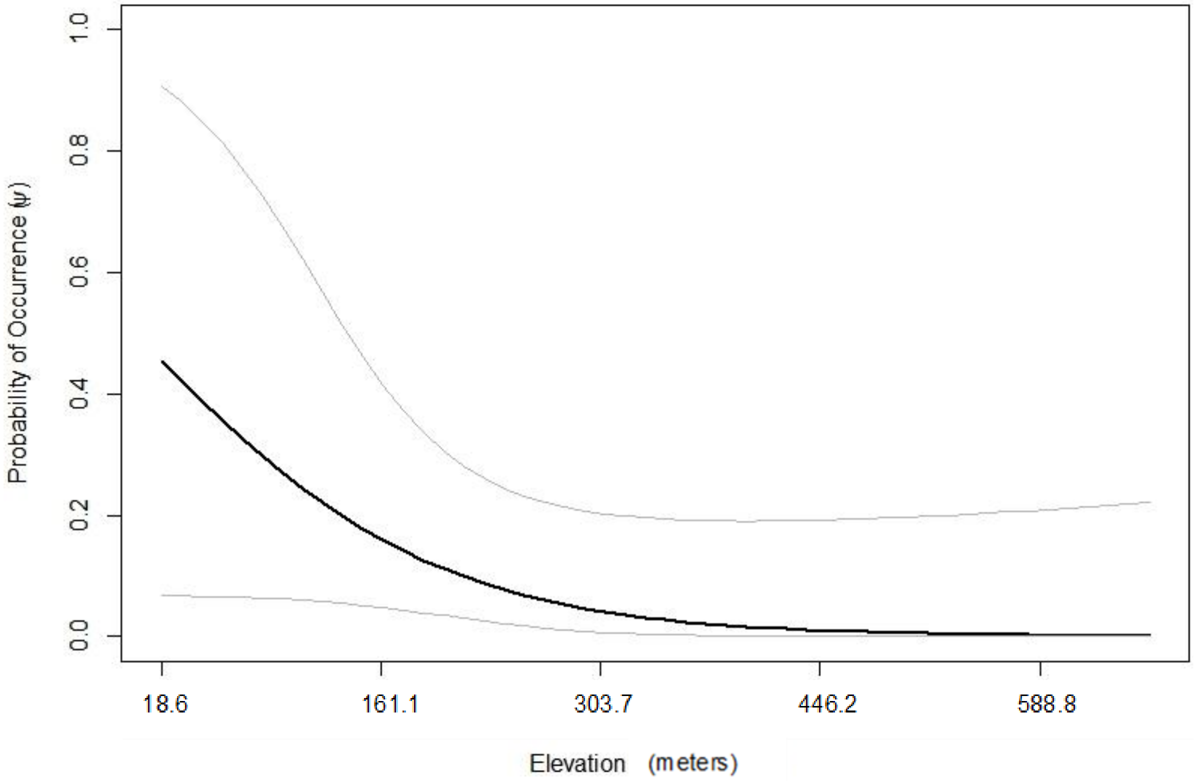


Figure 2.3. Probability of occupancy for Western fence lizards (*Sceloporus occidentalis)* as a function of human population density (people/m^2) among the 79 SAMO study sites. The black line represents the predicted relationship and the gray lines represent 95% confidence intervals.



Western Skink Occupancy by Elevation

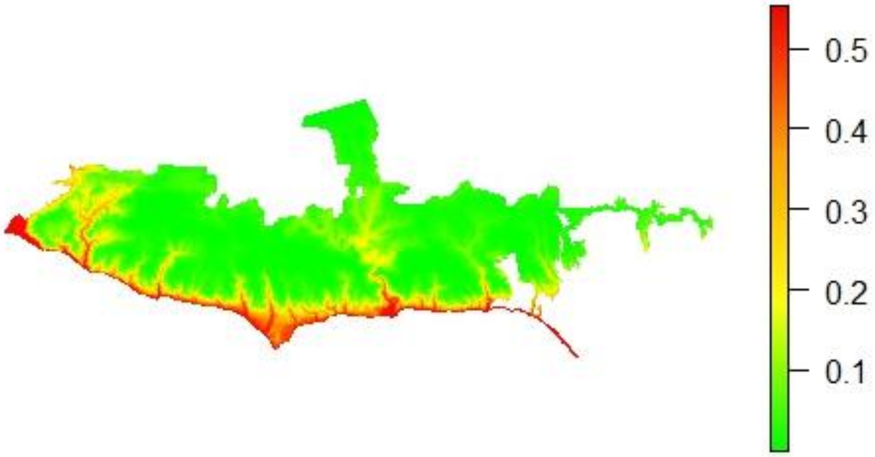


Figure 2.4. (Above) Probability of occupancy for Western skinks (*Plestiodon skiltonianus)* as a function of elevation (m) among SAMO study sites. The black line represents the predicted relationship and the gray lines represent 95% confidence intervals. (Below) Heatmap of Western skink occupancy within SAMO management boundary.

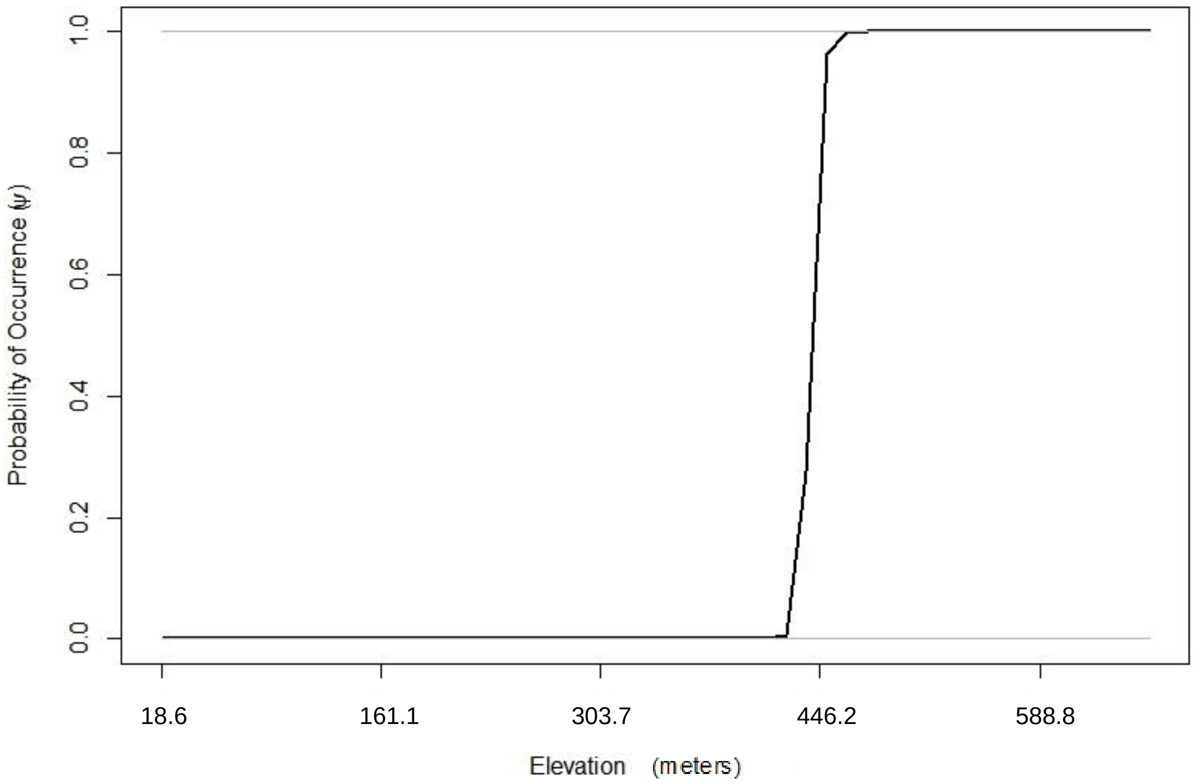


Figure 2.5. Probability of occupancy for Coastal whiptails (*Cnemidophorus tigris)* as a function of elevation (m) among the 79 SAMO study sites. The black line represents the predicted relationship and the gray lines represent 95% confidence intervals.

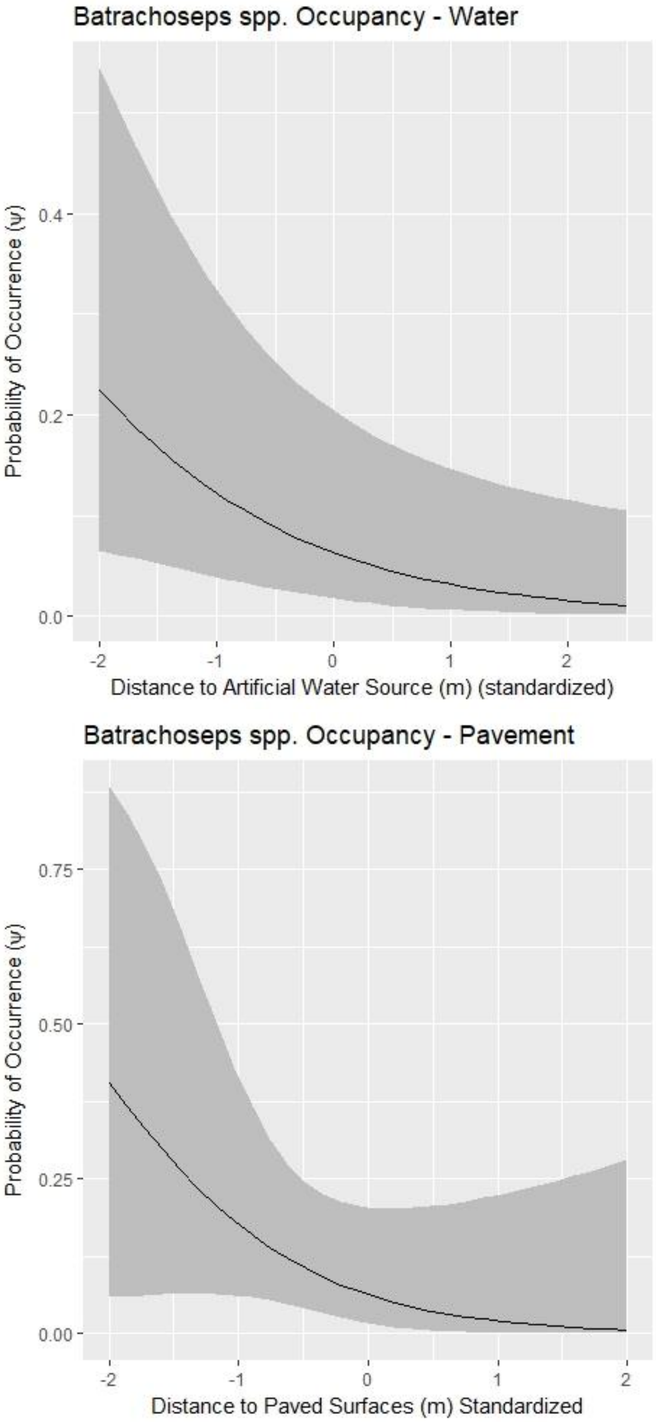


Figure 2.6. Probability of occupancy for the slender salamander (*Batrachoseps spp.)* as a function of distance to anthropogenic water (Top) and paved surfaces (Bottom) observed among the 79 SAMO study sites. The black line represents the predicted relationship and the gray shading represents a 95% confidence interval.

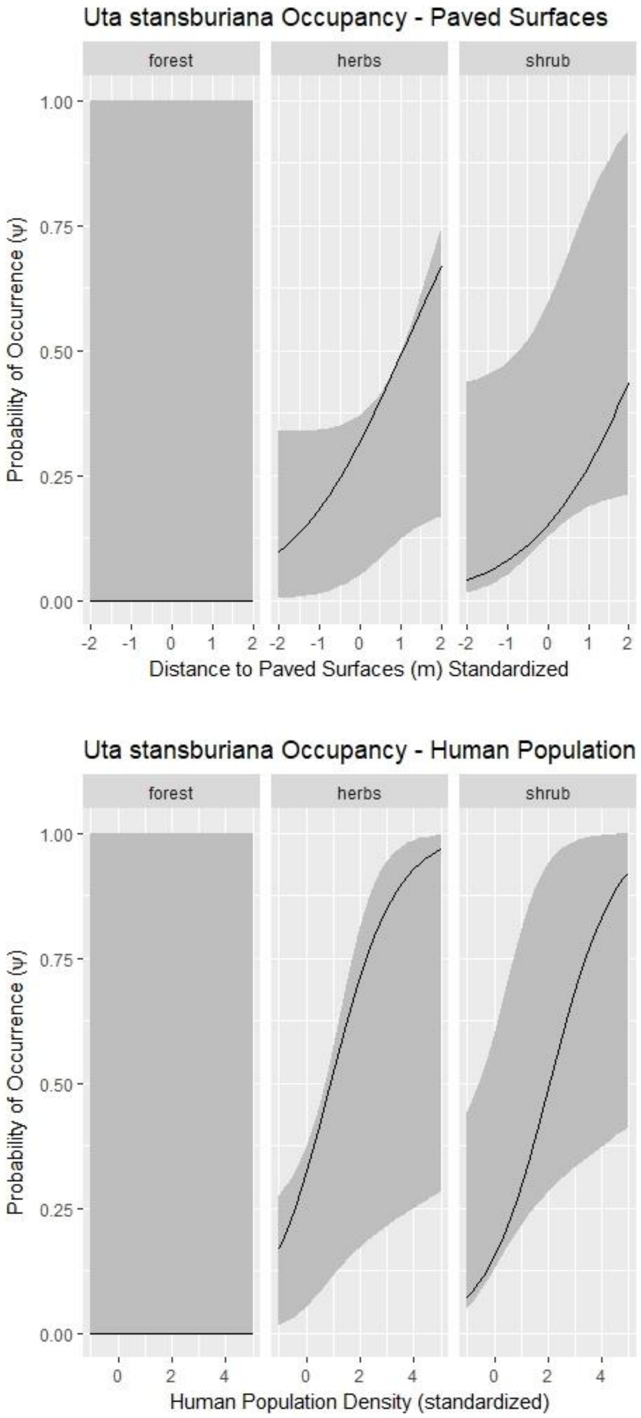


Figure 2.7. Probability of occupancy for Side-blotched lizards (*Uta stansburiana)* as a function of habitat type and distance to paved surfaces (Top) or human population density (people/m^2) (Bottom) among the 79 SAMO study sites. The black line represents the predicted relationship and the gray shaded areas represent 95% confidence intervals.

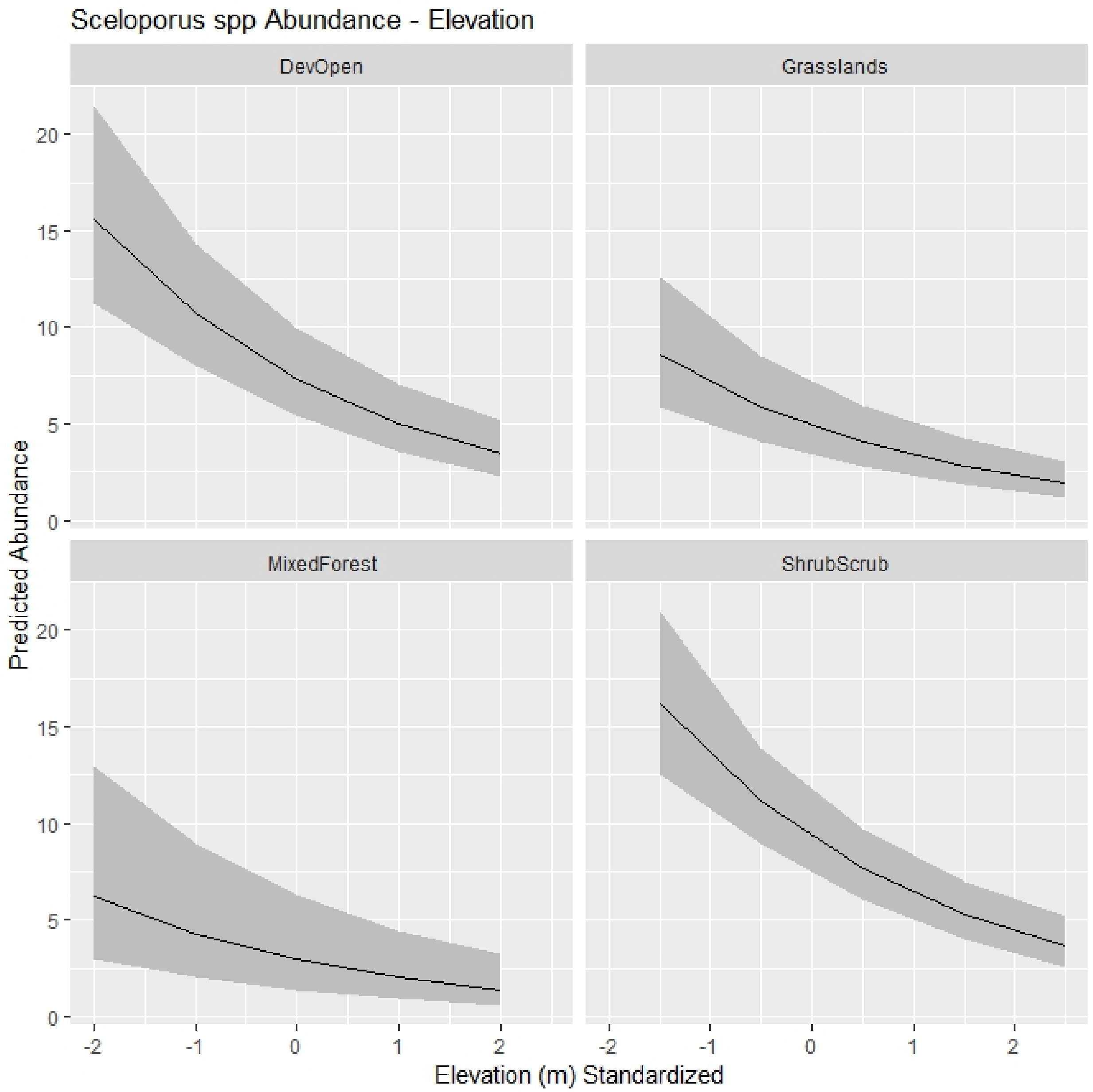


Figure 2.8. Estimated abundance of Western fence lizards (*Sceloporus occidentalis*) as a function of the four NLCD landcover types and site elevation. Shaded areas indicate 95% confidence intervals.

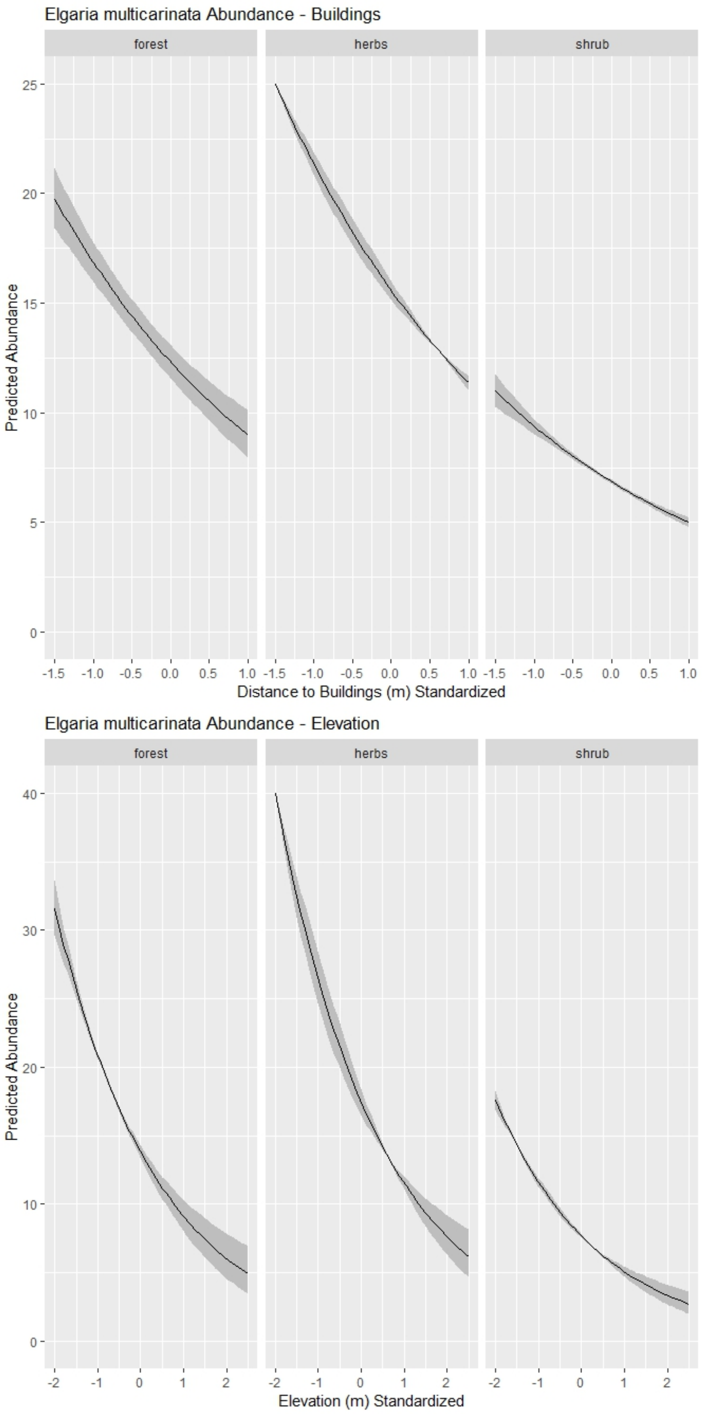


Figure 2.9. Estimated abundance of Southern alligator lizards (*Elgaria multicarinata*) as a function of dominant vegetation (habitat) type in addition to distance to buildings (Top) and site elevation (Bottom). Black lines represent top model predictions and shaded areas indicate 95% confidence intervals.

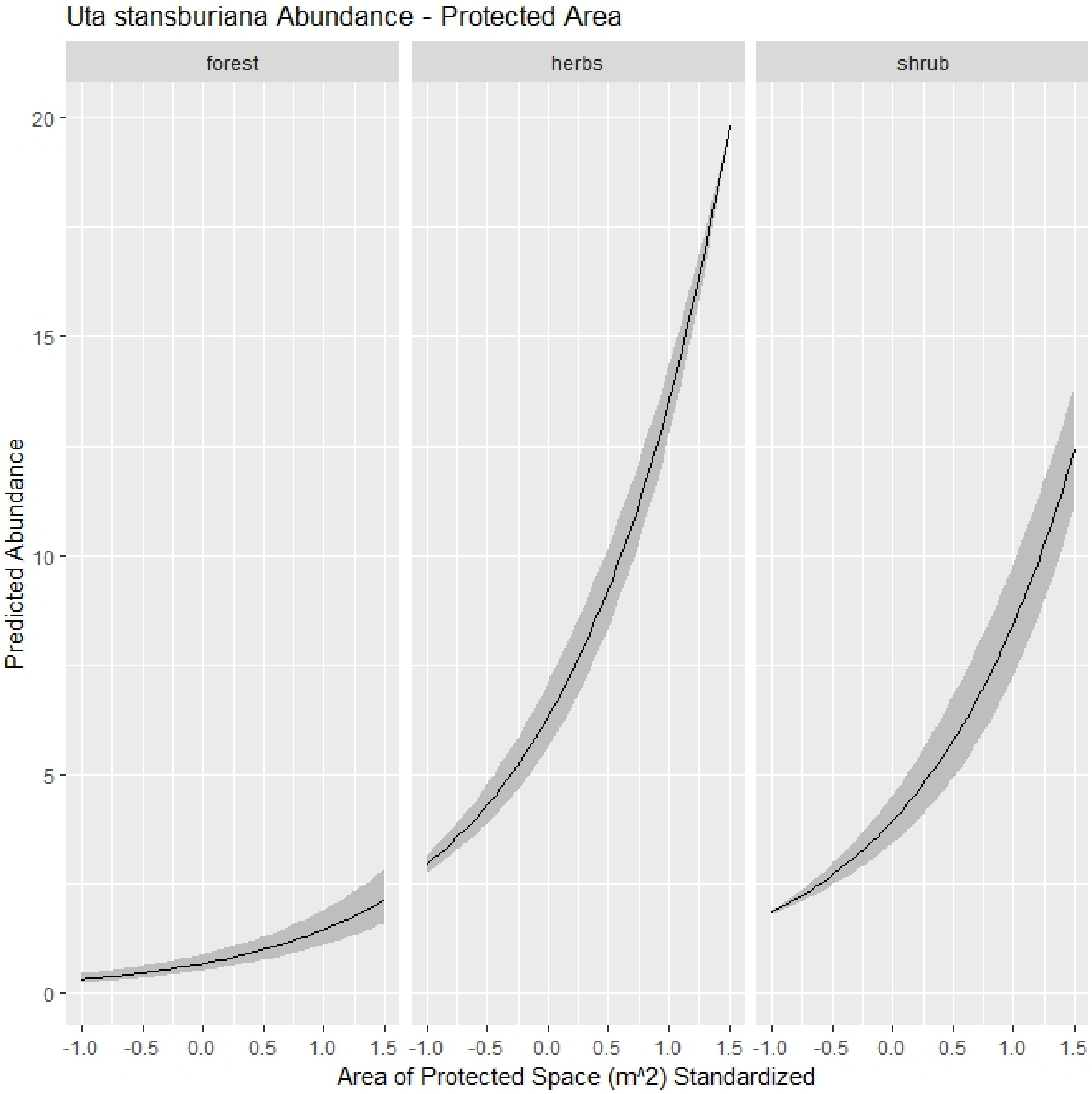


Figure 2.10. Estimated abundance of Side-blotched lizards (*Uta stansburiana*) as a function of the dominant habitat type in addition to surface area of protected space (m^2). Shaded areas indicate 95% confidence interval.

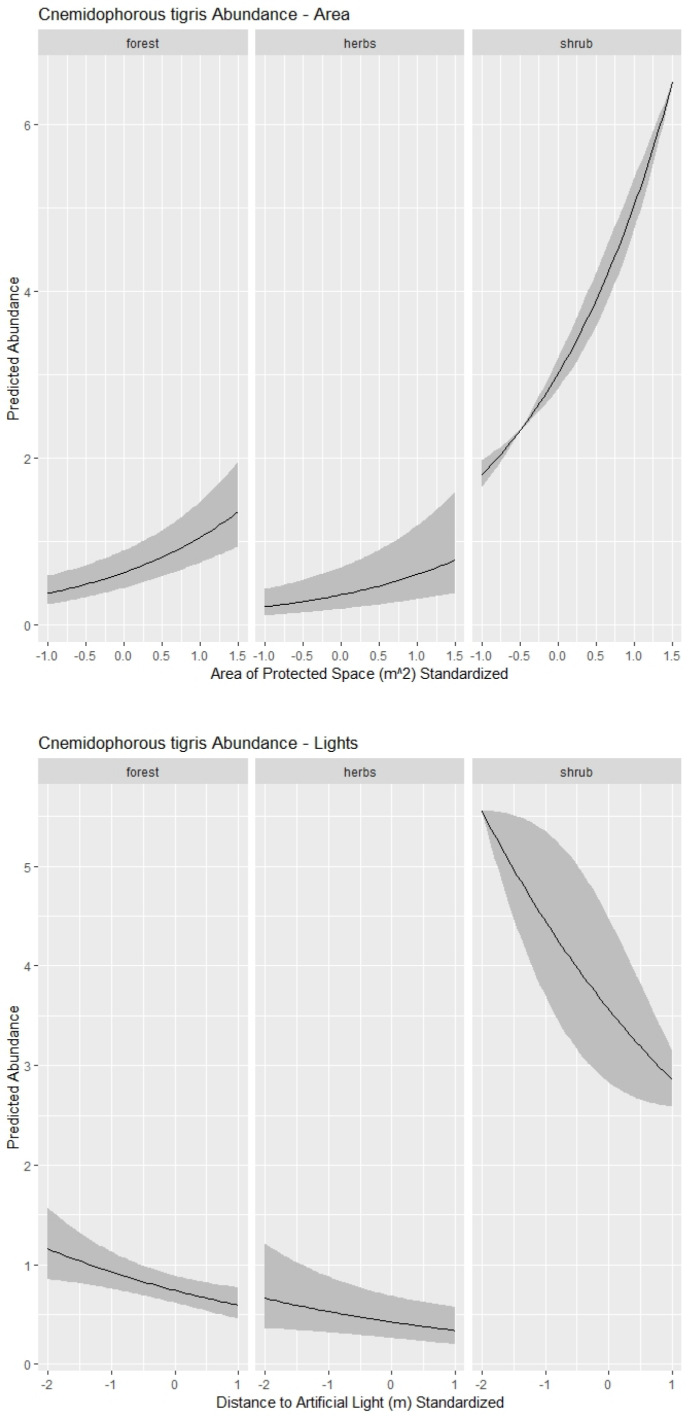


Figure 2.11. Estimated abundance of Coastal whiptail lizards (*Cnemidophorous tigris*) as a function of dominant vegetation (habitat) type in addition to the surface area of the protected space in which a study site is located (Left) and the proximity to artificial lighting (Right). Shaded areas indicate 95% confidence intervals.

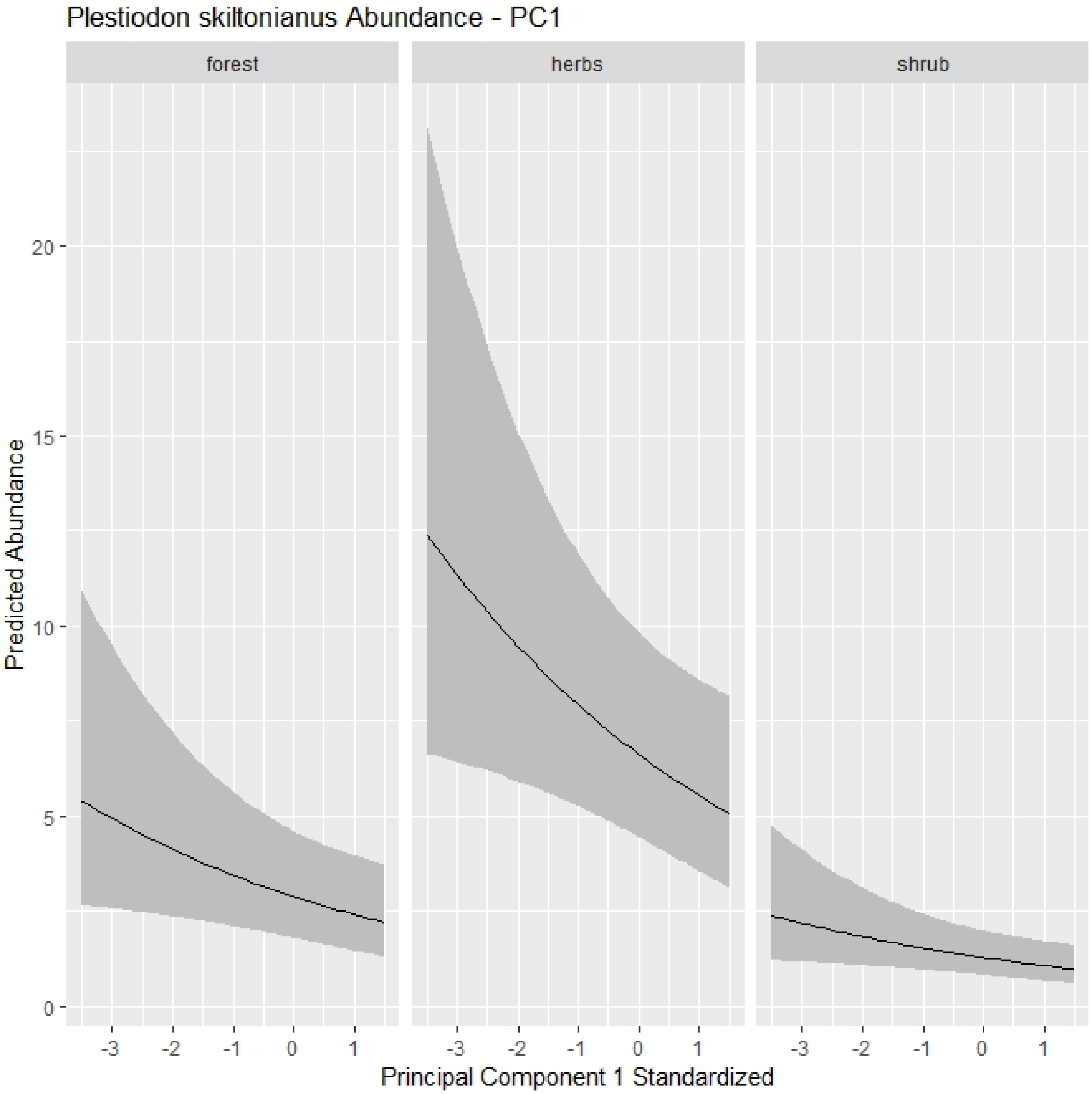


Figure 2.12. Estimated abundance of Western skinks (*Plestiodon skiltonianus*) as a function of dominant vegetation (habitat) type in addition to the first principal component. Shaded areas indicate 95% confidence intervals

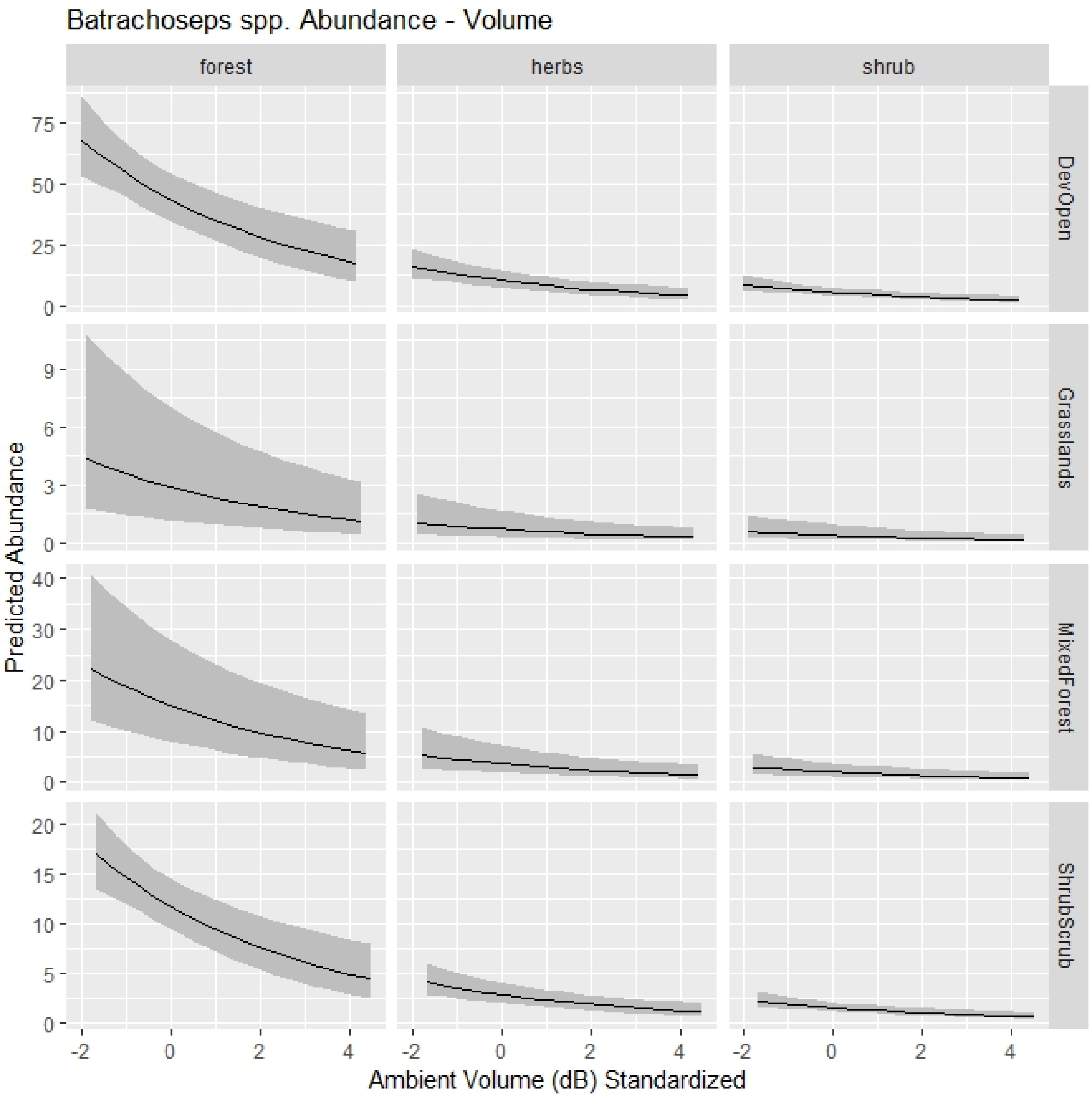


Figure 2.13. Estimated abundance of slender salamanders (*Batrachoseps spp.*) as a function of ambient volume in addition to dominant habitat type (Top) or landcover type (Right). Shaded areas indicate 95% confidence intervals.

CHAPTER 3

ESTIMATING SURVIVAL OF TWO LIZARD SPECIES WITHIN AN URBANIZING LANDSCAPE[2]

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[2] Herpetofaunal distribution patterns in an urban protected space, M.C. Miles, J.C. Maerz and K.S. Delaney. To be submitted to *Urban Ecosystems*.

Abstract

Urbanization is an anthropogenic phenomenon with a myriad of effects on native wildlife that we still do not fully understand. Estimates of proximate changes in behavior or vital rates (e.g., survival, fecundity) can aid in understanding why wildlife distributions and abundances do or do not respond to anthropogenic landscape change. We used capture-mark-recapture and unmarked, count-based estimates, to model relationships between attributes of urbanizing landscapes and apparent survival of two common reptile species in the Santa Monica Mountains National Recreation Area in Thousand Oaks (SAMO), CA. For Western fence lizards (*Sceloporous occidentalis*), *N-mixture* models of repeated counts identified relationships between habitat attributes and survival that were similar to prior models of habitat and abundance. In contrast, because of low recapture rates and sparse data, capture-recapture models generated non-informative estimates of survival among Side-blotched lizards. These results illustrate the complexities associated with quantifying lizard survival within an urban landscape.

Introduction

The rapid pace of urbanization presents new challenges for ecosystems and resident wildlife (McKinney 2002). Cities, towns, and other developed spaces have recently expanded to cover approximately 3% of Earth’s terrestrial surface area (Liu et al. 2014) and include more than half the world’s human population (United Nations 2014). These shifts in land use can displace native wildlife species and select for nonnative or generalist species (McKinney 2006; van Rensburg 2009), resulting in significant changes to community composition. For example, in the prior chapter (Chapter 2), we demonstrated that changes in habitat composition or landcover related to urbanization have different effects on occupancy and abundance patterns of common lizard species. The two most common species, Western fence lizards (*Sceloporus occidentalis*) and Side-blotched lizards (*Uta stansburiana*), showed different responses to urban habitat characteristics. Western fence lizard abundance declined with increasing elevation and were most abundant in open canopy landcover types such as open developed spaces and shrub/scrub, whereas Side-blotched lizard abundance increased in larger patches of protected space and both occupancy and abundance declined in forested habitat types (Chapter 2). The mechanisms underlying these species-specific responses to local habitat changes are not known.

Estimates of proximate changes in behavior or vital rates (e.g., survival, fecundity) can aid in understanding why wildlife distributions and abundances do or do not respond to anthropogenic landscape change (Ditchkoff et al. 2006; Sullivan et al. 2016). To estimate changes in vital rates, investigators often rely on specific survey methods and associated models (Conroy and Carroll 2011) but encounter new challenges within human-dominated spaces and with urban-tolerant populations. Urban wildlife exhibit behavior modifications that may not be suited to traditional trapping or capture methods, including changes to foraging and antipredator behaviors (Aviles-Rodrigues 2015) and the use of artificial substrates (Kolbe et al. 2016). The disciplinary standard for attaining vital rate estimates of imperfectly detected populations is capture-mark-recapture (CMR). CMR requires robust datasets with sufficient recapture rates to generate reasonable estimates, which can be prohibitively expensive in terms of time and effort, especially when attempting to conduct studies over large spatial scales or numbers of sites (Royle and Nichols 2003). Alternatively, multistate, “unmarked” N-mixture models might yield comparable vital rate estimates using count data (Zipkin et al. 2014) and represent a less resource intensive approach to traditional CMR. However, a tradeoff in the calculation of N-mixture models allows for greater flexibility at the expense of the robustness of parameter estimates. N-mixture models may overestimate or entirely fail to generate estimates when assumptions are violated (e.g., incomplete site closure due to temporary emigration [via burrows]). Indeed, insufficient individual detection rates contribute to greater uncertainty in N-mixture model parameter estimation, reducing their overall capacity to detect trends (Ward et al. 2017).

Here, we compare estimates of apparent survival (hereafter survival) between CMR and N-mixture models for Western fence lizards and Side-blotched lizards, the two most commonly encountered lizard species in the Santa Monica Mountains National Recreation Area (SAMO) (see Chapter 2). We identify similarities between species survival estimates, and contrast relationships between lizard survival and site-based urban attributes. Based on results from previous modelling efforts, we hypothesize that the factors impacting survival rates will be similar to those urban attributes driving species abundance for both commonly captured lizard species.

Methods

Study Area - The Santa Monica Mountains National Recreation Area (SAMO) is a system of federal, state, and local protected areas centered around the Santa Monica Mountains within the Greater Los Angeles Metropolitan Area. The outermost boundaries of SAMO extend from Malibu and the Pacific coastline northwards into the base of the Simi Hills. Ventura County agricultural fields lie to the east and the city of Los Angeles lies to the west, creating a 60,000 ha perimeter surrounding equal parts public and privately-owned land. Ecologists have monitored terrestrial species at this park for the last four years with an extensive network of pitfall trap arrays, yet, the most recent published account of local terrestrial herpetofaunal diversity pre-dates much of the area's recent urbanization (de Lisle et al. 1986). The area is characterized by cool wet winters and hot dry summers, although southern California is particularly arid and experienced a prolonged drought during the years of this study (Griffin and Anchukaitis 2014). Elevation peaks at 600 m allowing for pockets of development within a matrix of remnant sage-scrub habitat.

Study species - Western fence lizards and Side-blotched lizards are common, small-bodied lizards found throughout the western United States. Western fence lizards are a climbing species found on low-lying structures or perches from which they disembark to feed on the ground (Pianka 1986). They are the most commonly captured reptile or amphibian in the Santa Monica Mountains (Miles, Chapter 2). Side-blotched lizards are a ground dwelling species common to open arid and semi-arid habitats such as the grasslands, coastal scrub, and chaparral found in SAMO (Palermo 2000). Male and female Side-blotched lizards defend home ranges that can vary from 400 to 800 m^2.

Site Selection and Pitfall Trap Arrays - SAMO ecologists designed a network of pitfall arrays and funnel snake traps using a Generalized Random Tessellation Stratified (GRTS) approach for selecting study sites in the early 2000s, based on ease of accessibility and stratified by habitat and landcover (Figures 2.1 and 2.2). The GRTS survey design used a spatially explicit algorithm to identify locations in an area that represent a holistic image of the landscape while maintaining statistical independence among sites (Stevens and Olsen 2004). These sites, and others, have been monitored since 2001 under the NPS Inventory and Monitoring Division (Busteed et al. 2006). In this analysis, we used 79 sites that were regularly sampled from November 2013 to May 2015 (Figure 2.1). Sites were divided into eight regions of roughly 10 sites each, and technicians conducted trapping for four consecutive days (secondary surveying periods) within a pair of regions. Pairs of regions were rotated every two weeks, such that regions were not revisited for a minimum of 40 days (primary periods) though the actual duration between trapping periods varied over the study period.

Pitfall arrays were T or Y-shaped structures of 30-cm wide nylon shade cloth. The three arms of the pitfall structure were 15 meters long with seven ~40-liter buckets buried flush with the surface of the surrounding soil, at the center of the array and at the midpoint and end of each arm. Approximately five times per year, pitfall traps were surveyed, in rotation, every eight weeks (primary periods) for four consecutive days (secondary periods) resulting in a robust sampling regime (Pollock 1982). Trained technicians ran trapping periods and identified captured animals to species, determined sex when possible, and measured each animal from snout to the posterior of the vent. Lizards were marked with unique toe clips before release. Measurements and observations were recorded in the field on tablets that synchronized nightly with a database that maintained up-to-date toe clip records.

Urban Habitat Covariates - During the summer of 2016 at each pitfall trap array, we measured a suite of variables that previous research had identified as important drivers of amphibian and reptile occupancy and abundance. We measured the presence and distance to the nearest impervious surface (any anthropogenic non-porous ground cover such as cement), human-made water sources (sewer lines, drains, and other public structures containing water), built structures (anthropogenic structures including infrastructure support such as telephone poles and cell sites), and artificial light sources (from residential homes and streetlights) within a 200-500 m radius. We based this distance on estimates of maximum home range size for Side-blotched lizards (*Uta stansburiana*), which was one of our most common species (Palermo 2000). Additionally, we determined the dominant habitat type among the three vegetative compositions primarily found in the Mediterranean ecosystem (i.e. forest, shrub, and herb[aceous]), by extracting site-specific characteristics from SAMO-specific United States Geological Service GIS vegetation data (unpublished data 2018). These classifications are denoted by the phrases, ‘habitat’ or ‘habitat type’ throughout the analysis. We measured ambient noise volume at the pitfall array for 30 seconds using the Sound Meter Pro (v2.5) application on the Samsung Galaxy s7 Edge (program limited to measurements below 80dB). We used GIS to extract an additional suite of variables for each site including 2011 National Land Cover Database land use classification (Homer et al. 2015), 2010 United States Census tract population density and Euclidean distance to the nearest road (US Census Bureau TIGERLine 2012), and surface area of respective SAMO-protected green space from Bureau of Land Management servers. We used Google Earth mapping services to correct discrepancies between on-the-ground proximity estimates (Google Inc.) up to a maximum radius of 1000 meters and corrected inconsistencies between distance to impervious surfaces and roads (of which many were dirt or gravel) to create the attribute: distance to paved surfaces.

We used a Principal Components Analysis (PCA) to examine the relationships between human population density and habitat variables and to reduce the number of habitat variables into composite indices. This multivariate statistical technique extracts the most important information from a suite of inter-correlated quantitative variables and compresses the data set into a set of orthogonal composite variables [principal components] (Abdi & Williams 2010). Principal components are ranked by their importance as indicated by the proportion of the total ‘inertia’ for which this factor “explained.” To interpret the components, we referenced the loadings associated with each represented urban attribute’s contribution, in this way variables with minimal contributions translated to less influence in comprising the component. All variables were standardized prior to analysis, including the presences/proximity to urban features such as artificial light sources. If an urban feature was absent from the study site, a proxy distance of 1000 m was applied to indicate the feature existed outside of the 500 m inclusion radius. We conducted the PCA using the base statistical functions in the statistical program R (R Core Team 2016).

Weather data - We compiled temperature data for each sampling event from individual HOBO loggers present at 20 sites and precipitation data from two central NPS affiliated Remote Automated Weather Stations (Watson et al. 2005). We fit linear models of average daily temperatures, recorded at each HOBO site during active trapping periods, to the average daily temperatures from a centrally located NPS weather station in Malibu Canyon. We then used the resultant functions to extrapolate average daily temperatures to supplement missing values in HOBO temperature data and estimate data at nearby sites (within 6 km of a site with HOBO data) when direct measurements of temperature were not available due to human error or equipment failure. Precipitation data was similar across the two weather stations, so we applied the recorded rainfall data of the eastern weather station to sites east of the Malibu Canyon 'divide,' and applied the western station values to those sites to the west. These values became observation-based weather covariates to estimate detection among sites.

Data Modeling - The NPS Inventory and Monitoring protocol for SAMO is based on the structure of the Robust Design (Pollock 1982), dividing survey effort into primary and secondary sampling periods to satisfy the underlying assumptions associated with hierarchical demographic models. “Closed” secondary sampling periods occur close to one another (i.e. on consecutive days of surveying) within each primary period (Pollack 1982). The periods between primary periods (i.e. the roughly five-week season between re-sampling events) are assumed to be “open” to demographic change. Thus, the Robust Design is well-suited for generating estimates of imperfect detection and temporary emigration needed to generate unbiased estimates of survival.

Raw data for individually marked animals was re-formatted into consecutive capture histories for 14 primary periods of four-day secondary sampling periods, beginning in November 2013 and ending in May of 2015. The maximum likelihood-based (Kendall et al. 1995) approach uses individual-based detection/non-detection capture histories to estimate five parameters (detection probability (p), survival (S), recapture probability, and two movement parameters). However, for our analyses, we only manipulated the first two parameters and held the remainder constant at the estimated global mean value. As a second approach to estimating survival, raw capture data was reformatted into a count matrix of pitfall array sites by trapping occasions for each species. The N-mixture approach uses these repeated counts to estimate four parameters: detection probability (p), survival (ω), abundance and recruitment (Dail & Madsen 2011), though again the latter two were held constant in our analyses.

We designed an identical suite of candidate models for both species (see Table 3.1) and compared them using Akaike information criterion corrected for small sample sizes (AICc) (Burnham & Anderson 2002). Since we anticipated variable detection probabilities between sampling occasions, we included time-varying weather covariates in the initial suite of detection models. These models included additive and quadratic combinations of precipitation and temperature, in addition to a null model in which all parameters were held constant. To relate the environmental conditions of the urban gradient to patterns survival, we then generated a model set with the best detection covariates identified for each species, and allocated each individual urban attribute and the two, composite metrics (PC1 & PC2) to a separate candidate model such that the survival parameter (*S* for CMR models and ω for count-based models) only ever varied as a function of a single variable. We used AICc to select the top univariate model, and then added a second, relatively non-collinear ($r < .65$) variable to determine whether the addition of that variable improved model performance by AICc and model fit. If a two variable model outperformed the top univariate model, that became our base model and we tested whether the addition of a third covariate improved model performance. We repeated this process until either the addition of a variable did not meet the selected AICc criterion or the model had poor fit or singularities that indicated the model was over-parameterized.

Again, we estimated conditional apparent survival with empirical Bayes methods and plotted these values along the gradient of observed values for the lowest AICc model (Burnham & Anderson). We reported model parameters for both species survival models as indicated by both methods for all models within 2 ΔAICc of the lowest model. All CMR estimation and analyses were conducted in the R package MARK (Laake 2013) and all count-based estimations and analyses were conducted with the pcountOpen function in the R package ‘unmarked’ (Fiske and Chandler 2011).

Results

A full summary of the PCA and weather regression results is available in Chapter 2. In short, Principal component 1 (PC1) was largely a product of increasing human population density associated with smaller protected area patch size, increased noise and proximity to human-made lights, increased proximity to paved or otherwise impervious surfaces, and increased proximity to buildings. Though larger protected areas and greater distances from human anthropogenic structures were important loadings on PC1 and negatively correlated with human population density, protected area size was weakly correlated with proximity to paved surfaces, buildings, and human-made light sources. Principal component 2 (PC2) was largely a product of increasing elevation and distance to anthropogenic water sources positively associated with decreasing area of protected space. Temperature regression fit between HOBO data loggers and central weather station was poor (Chapter 2).

Among the 79 array sites and 21 primary periods, we had 1,799 captures of 1,493 individual Western fence lizards and 731 captures of 582 individual Side-blotched lizards. Observation-based weather covariates improved the performance of CMR detection models for Western fence lizards only (Table 3.1). The top competing capture probability models for fence lizards included a quadratic relationship with temperature combined with a quadratic relationship with precipitation. The top model for Western fence lizard survival included the additive combination of distance to paved surfaces and size of protected area, such that annual survival increased with proximity to a paved surface and with increased protected area size (Figure 3.1). In contrast, the “unmarked” N-mixture detection model for Western fence lizards included a quadratic relationship with temperature and a quadratic relationship with precipitation. The top “unmarked” model estimates of Western fence lizard survival varied as a function of landcover classification and included a negative correlation with elevation that varied over observed landcover types (Figure 3.2). At the lowest elevation, estimated survival was highest and similar among all habitat types but declined more steeply with increasing elevation within mixed forest habitats.

Due to low numbers of individual recaptures, we were unable to generate reliable survival estimates for Side-blotched lizards using the capture-recapture analysis in Program Mark. For the N-mixture analyses, the top detection models for Side-blotched lizards included a quadratic relationship with temperature and a linear relationship with precipitation (Table 3.1). The top "unmarked" survival model for Side-blotched lizards included a weak positive relationship with human population density in addition to a slightly stronger positive relationship with site elevation (Figure 3.3). Both unmarked and rMark estimates of apparent survival probability are high reaching or approaching 1 (i.e. complete survival), with varying degrees of confidence.

Discussion

Our results appear to suggest that survival rates of the two most common lizard species respond differently to habitat changes associated with urbanization; however, we found no correspondence between covariates of capture-recapture and unmarked-estimates for one species, and little correspondence between covariate relationships with survival estimates and earlier models of lizard occupancy or abundance. In our prior analyses, we found that Western fence lizard occupancy was positively correlated with human population density, and abundance estimates declined with elevation and were lowest in mixed forest habitat. In contrast, our CMR estimates suggest that fence lizard survival increased with the size of protected area and with increasing proximity to paved surfaces. Therefore, there is no correspondence between the factors that we identified as affecting fence lizard survival and those driving occupancy or abundance. However, the predicted decline in survival with increasing distance from paved surfaces seems surprising considering the prevalence of road-based mortalities among reptiles, as documented in the literature (reviewed in Andrews et al. 2008). We did find that unmarked estimates of fence lizard survival declined with elevation and in mixed forest land cover, which is consistent with prior abundance models, but these models are not independent. This level of precision within relationships identified through ‘unmarked’ analysis may stem from the limitations and overparameterizations inherent to N-mixture modelling when applied to sparse datasets (Barker et al. 2018).

We were unable to estimate survival rates of Side-blotched lizards because of very poor recapture rates. The limited numbers of recaptures were often widely spaced by as many as six or seven primary periods (~1 year). The maximum likelihood model framework of Program Mark is ill-suited to resolving survival estimates when individuals survive long durations while having infrequent captures. Essentially, the pattern of limited recaptures results in a high probability that an individual is estimated to be alive but undetected. It is also possible that those later recaptures were misidentified, leading to data that are unresolvable. We do not know of any published estimates of Side-blotched lizard survival, so we cannot determine whether survival over multiple years (e.g., > 4 years) is common. If mortality rates over 2-3 years are high, then it is unlikely that CMR efforts with low capture probabilities will yield reasonable estimates of Side-blotched lizard survival needed to inform patterns within SAMO or management actions. Our model suggests that Side-blotched lizard ~9-week survival increased with increasing human population density, and declined with increasing elevation; however, neither of these covariates were associated with Side-blotched lizard occupancy or abundance. Overall, this leaves us with low confidence in our current ability to explain Side-blotched lizard survival and relate that to patterns of abundance across SAMO sites. We suggest that development of new models or reevaluation of the value of CMR should be considered for future work. Assuming limited misidentification, it is possible that a Bayesian framework would yield more reliable model estimates (Rankin et al. 2016); however, we caution that the low recapture rate would still likely yield high uncertainty around survival estimates and associated covariates. One means to improve efficiency may be the development of an integrative population modeling framework (Zipkin & Saunders 2018) that uses repeated count data from a large array of sites with capture recapture efforts concentrated at a subset of sites. Such a data collection and modeling framework could prove more utilitarian and reduce labor associated with ongoing monitoring.

Our objectives were to compare two approaches of varying data collection intensity for estimating common lizard survival and to relate patterns of survival to previously modeled patterns of occupancy and abundance. Though labor intensive, capture-mark-recapture is the gold standard for survival estimation; however, despite high numbers of captures, CMR using the maximum likelihood framework of Program Mark was only able to estimate survival for one of the two most common lizard species in SAMO. Low capture probabilities leading to few, highly interspersed recaptures yielded unreliable estimates of survival and associated covariates. Because of their high abundance and secretive habits, low capture probabilities despite high numbers of individual captures is a common characteristic of reptile and amphibian capture-recapture data. Therefore, the problems that we encountered for the second most common lizard species in SAMO are likely to be common for most species of amphibian and reptile in the region. Alternatively, we were able to generate “unmarked” estimates for both species; however, for the one species where we could use both CMR and unmarked approaches, estimated annual survival – while comparable – were not explained by similar model covariates. The lack of correspondence between covariates and survival estimates using the two approaches leaves little confidence in the “unmarked” models as adequate for estimating how lizard vital rates vary as a function of urbanization.

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Tables

Table 3.1 Survival model selection tables in ‘MARK’ for Western fence lizards (SCOC) and Side-blotched lizards (UTST) using Akaike’s information criterion corrected for small sample sizes (AICc). Above are model comparisons varying detection probability (p) and below are model comparisons for the survival parameter (S). For each represented species, the table includes the AIC value, difference in AIC value from the identified top model (ΔAIC), and the weighted value (weight), for the following models: the identified top model (denoted in bold) and whichever additional models are within two ΔAIC of the top model, possibly including the null model if no others were comparable by AIC. Gammas (movement parameters) and f0 (recapture probability) were held constant at mean values.

Species	**Capture probability/detection models**	**AICc**	**ΔAIC**	**weight**
SCOC	**S(~1)Gamma''(~1)Gamma'(~1)p(~temp^2+precip^2)c(~1)f0(~1)**	3790.47	0.00	0.87
UTST	**S(.), Gamma''(.)Gamma'(.), c(.), f0(.), p(.)**	1986.33	0.00	0.78

Species	**State models**	**AICc**	**ΔAIC**	**weight**
SCOC	**S(~paved+area)Gamma''(~1)Gamma'(~1)p(~(temp+I(temp^2)+precip+I(precip^2))) c(~1)f0(~1)**	3774.80	0.00	0.45
	S(~paved+area+pop)Gamma''(~1)Gamma'(~1)p(~(temp+I(temp^2)+precip+I(precip^2))) c(~1)f0(~1)	3775.51	0.71	0.32
UTST	**S(~herbs+shrub+water)Gamma''(~1)Gamma'(~1)p(~1)c(~1)f0(~1)**	1814.50	0	0.98

Table 3.2 Survival beta estimates from 'MARK' (above) and 'unmarked' (below) for Western fence lizard (SCOC) and Side-blotched lizard (UTST) top models. Model estimates (Beta) and respective standard error values (SE) are presented on the scale of log-link.

MARK

Species	Model(Cov)	Beta	SE	lowerCI	upperCI
SCOC	S:(Intercept)	3.87	0.05	3.77	3.96
	S:paved	-0.26	0.06	-0.38	-0.14
	S:area	0.12	0.05	0.01	0.22

unmarked

Species	Model(Cov)	Beta	SE	lowerCI	upperCI
SCOC	(Intercept)	4.06	0.20	3.67	4.44
	Elev.m	-0.46	0.06	-0.57	-0.35
	LandcoverGrasslands	-0.52	0.20	-0.92	-0.12
	LandcoverMixedForest	-1.14	0.34	-1.81	-0.46
	LandcoverShrubScrub	0.27	0.14	0.00	0.54
UTST	(Intercept)	5.56	0.29	4.99	6.13
	Elev.m	-0.78	0.14	-1.06	-0.51
	PopD	0.21	0.09	0.02	0.39

Table 3.3 Survival model selection tables in ‘unmarked’ for Western fence lizards (SCOC) and Side-blotched lizards (UTST) using Akaike’s Information Criterion corrected for small sample sizes (AICc). Above are model comparisons varying detection probability (p) and below are model comparisons for the survival parameter (omega). For each represented species, the table includes the number of parameters estimated, the AICc value, difference in AIC value from the identified top model (ΔAICc), and the cumulative weight (Cumulative weight), for the following models: the identified top model (denoted in bold) and whichever additional models are within two ΔAIC of the top model, possibly including the null model if no others were comparable by AIC. Lambda (abundance) and gamma (recruitment) were held constant at the mean value throughout analysis. Top models are denoted in bold.

Species	**Detection models**	**AICc**	**ΔAIC**	**Cumulative weight**
SCOC	**lambda(.), gamma(.), omega(.), p(Temp^2+Precip^2)**	8426.67	0	0.67
	lambda(.), gamma(.), omega(.), p(Precip^2+Temp)	8428.12	1.45	1
UTST	**lambda(.), gamma(.), omega(.), p(Temp^2)**	4354.24	0	0.53
	lambda(.), gamma(.), omega(.), p(Precip^2+Temp)	4355.1	0.86	0.87

Species	**State models**	**AICc**	**ΔAIC**	**Cumulative weight**
SCOC	**lambda(.), gamma(.), omega(Elevation+Landcover), p(Temp^2+Precip^2)**	5329.9	0	0.55
	lambda(.), gamma(.), omega(Elevation+Landcover+Area of Protected Space), p(Temp^2+Precip^2)	5331.62	1.73	0.79
	lambda(.), gamma(.), omega(Elevation+Landcover+Distance to Water), p(Temp^2+Precip^2)	5331.81	1.92	1
UTST	**lambda(.), gamma(.), omega(Elevation+Human Population Density), p(Temp^2)**	2888.96	0	1

Figures

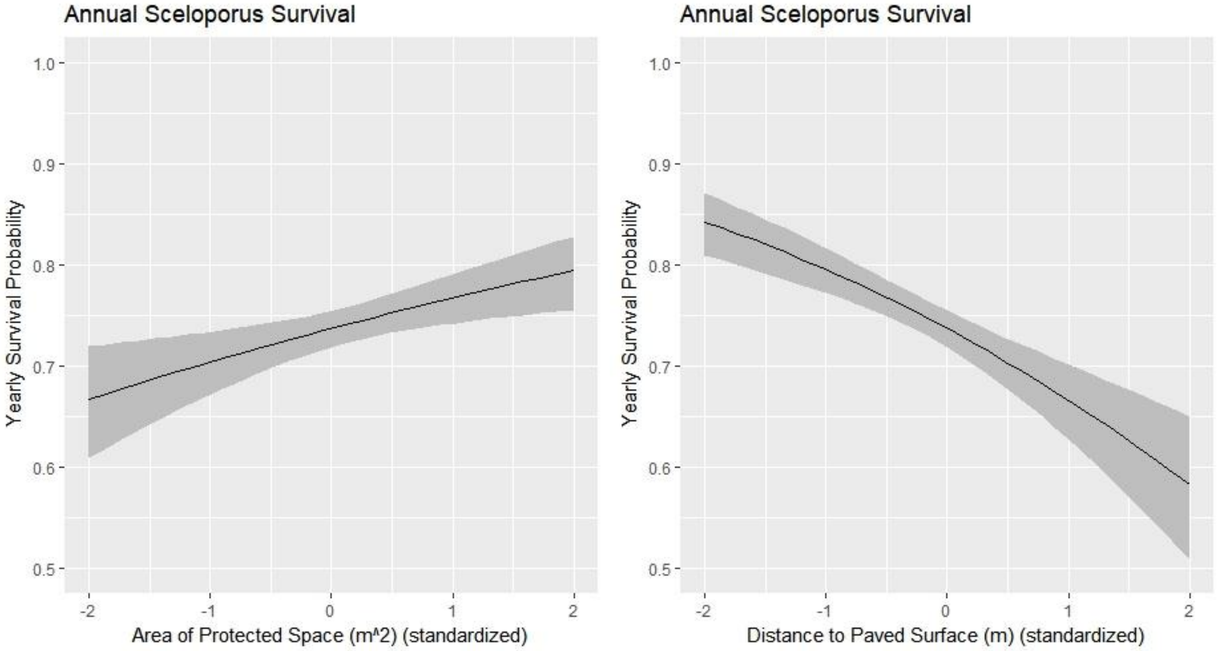

Figure 3.1 Estimated annual survival based on capture-mark-recapture of *Sceloporus occidentalis* as a function of standardized protected area size (left) and distance to paved surfaces (right). The black line represents the predicted relationship and the gray shading represent 95% confidence intervals.

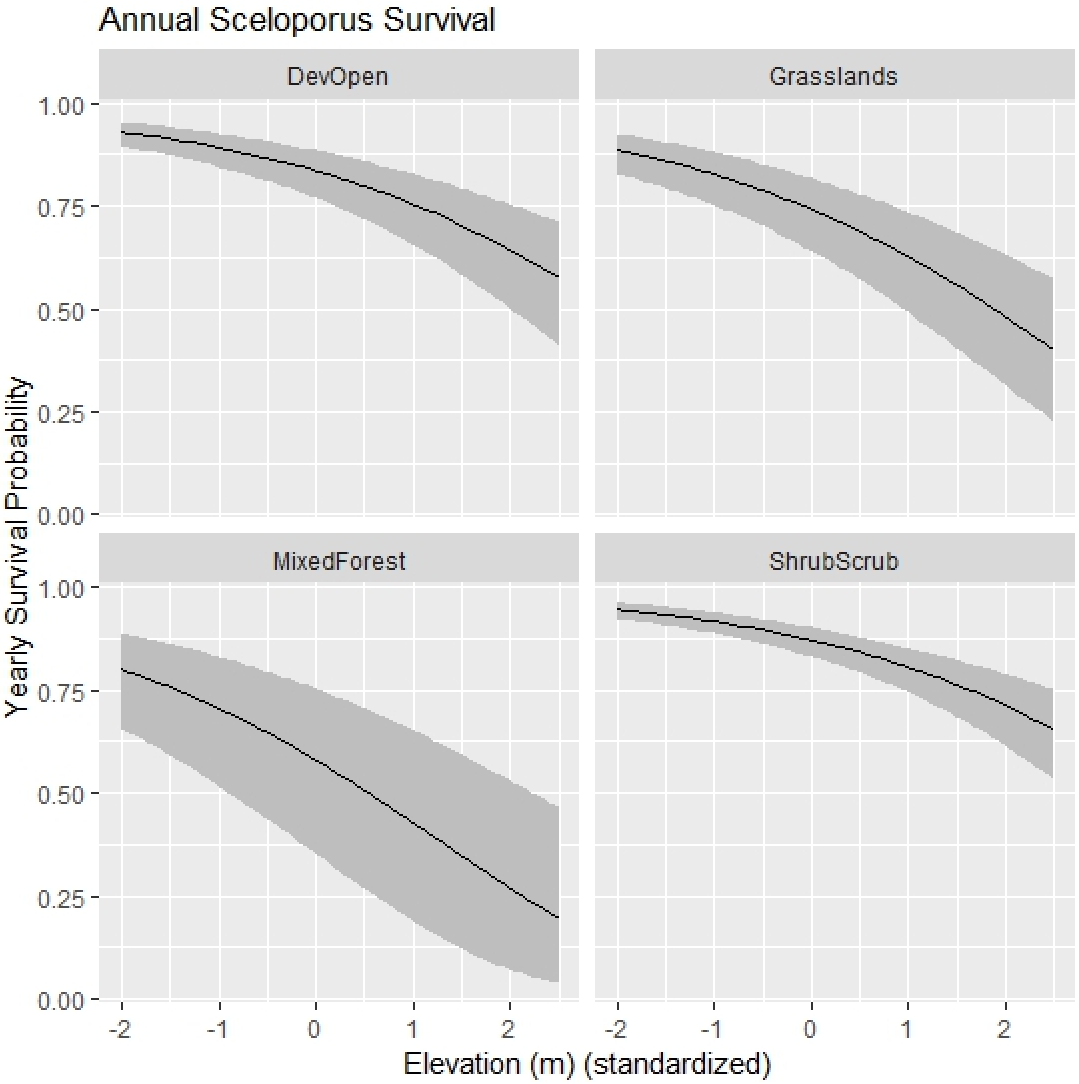

Figure 3.2. Estimated annual survival based on “unmarked” N-mixture model of *Sceloporus occidentalis* counts as a function of standardized elevation and landcover classification. The black line represents the predicted relationship and the gray shaded areas represent 95% confidence intervals.

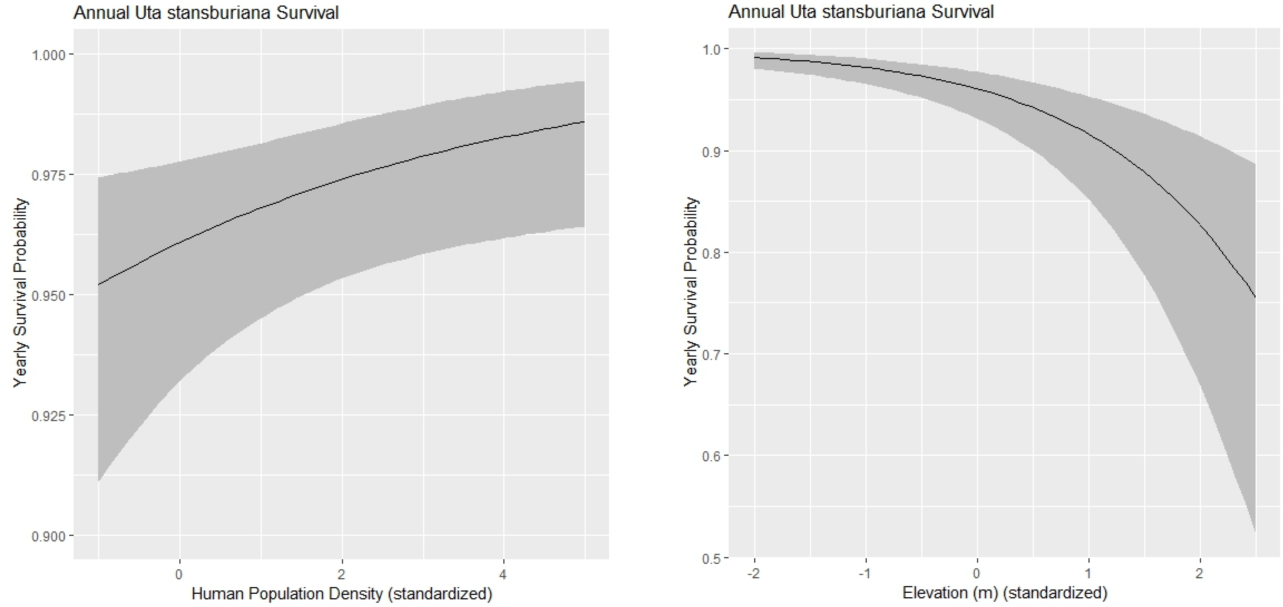

Figure 3.3. Estimated annual survival based on “unmarked” N-mixture model of *Uta stansburiana* survival as a function of standardized human population density (left panel) and site elevation (right panel). Gray shading represent 95% confidence intervals around predicted estimates.

CHAPTER 4

CONCLUSION

In this thesis, I evaluated relationships between human population density and habitat attributes potentially important to reptiles and amphibians in the Santa Monica Mountains National Recreation Area (SAMO). I demonstrated that ‘urban’, as represented by the density of people within an area, was not clearly associated with typical ‘urban’ environmental attributes within SAMO. I did find negative correlations between population density and the size of surrounding protected areas, which fit the convention that greater human densities leave fewer, smaller, more fragmented protected spaces for wildlife. I also found noise was positively correlated with human population density and both were negatively correlated with the distance to anthropogenic features such as paved surfaces, buildings, and artificial light sources. However, the most predictive attributes studied included the categorical vegetative habitat and landcover types and site elevation. One or more of these three attributes appeared in all but three of the top models for species occupancy, abundance or survival.

Overall, most native herpetofauna did not share consistent occupancy or abundance patterns in relation to specific measures or composite indices of urban habitat attributes within the Santa Monica Mountains protected areas. However, for the most common amphibian species, proximity to human-made water sources was positively correlated with occupancy, and for the two most common lizard species, Western fence lizards and Side-blotched lizards, occupancy increased with increasing human population density. Additionally, abundance and survival of Western fence lizards, the most common lizard species, decreased with increasing site elevation and varied across the three vegetative habitat types. These results demonstrate that some species within the same urban landscape may respond negatively to urban habitat attributes not strongly correlated with human population density, and that species may vary in their sensitivity to urban habitat change.

Our analysis and inferential capacity were constrained by insufficient recaptures of marked animals and low detection rates of urban herpetofauna, generally. Further work concerning urban herpetofauna distributions and vital rates would benefit from the application of integrated population models and Bayesian modeling techniques. Specifically, future efforts could attempt to address the barriers to parameter estimation posed by rare or cryptic species with insufficient recapture rates. Integrated population models provide a framework for mitigating sparse or fragmentary data by combining different types of demographic data/models to understand underlying ecological and demographic responses to environmental variation. Likewise, Bayesian methods incorporate prior information and specialized inferences to improve model performance for small sample sizes with similar if not greater precision than achieved through frequentist statistical methods.

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Appendix A. Additional summary statistics for urban attributes and precipitation. A1 depicts the number of site classified as each habitat and landcover type. Vegetative habitat type (top row) was characterized by the dominant plant taxa present in discrete patches of varying size as identified by the United State Geological Survey. Landcover type (left column) was extracted from National Land Cover Database raster data (Homer et al. 2015) at a constant 30 m spatial resolution derived from Landsat Thematic Mapper imagery. A2 depicts unstandardized summary statistics for all numeric urban attributes. Abbreviation key can be found in Table 2.3. A3 depicts the summary statistics for precipitation recorded at weather stations on the east and west sides of SAMO over the full length of the study period (SAMO underwent a severe drought).

A1

Array Sites	forest	herbs	shrub	Total Sites
DevOpen	2	5	7	14
Grasslands	1	6	2	9
MixedForest	1		1	2
ShrubScrub	15	9	30	54
Total Sites	19	20	40	79

A2

Urban Attribute (abbreviation)	Urban Attribute (full)	Units	Minimum	Mean	Median	Standard Deviation	Maximum
Volume	Ambient Volume	Decibels	20.00	34.96	33.00	8.95	76.00
PopD	Human Population Density	Persons per squared-meter	3.92E-06	2.02E-04	4.05E-05	3.70E-04	1.97E-03
Elev.m	Site Elevation	Meters	33.79	303.67	289.46	142.55	632.97
Area.acr	Protected Space Surface Area	Acres	12.11	5254.82	2195.07	5694.15	13893.77
Water.	Proximity to Anthropogenic Water Source	Meters	8.00	459.28	500.00	131.73	500.00
Buildt.	Proximity to Buildings	Meters	15.00	340.38	500.00	211.75	500.00
Lights.	Proximity to Artificial Light Source	Meters	40.00	425.82	500.00	161.11	500.00
PavedDist	Proximity to Paved Surfaces	Meters	30.00	395.21	234.31	358.74	1000.00
PC1	Principal Component 1	N/A	-5.14	0.00	0.18	1.52	2.40
PC2	Principal Component 2	N/A	-2.71	0.00	0.07	1.14	2.98

A3

Precipitation (in.)	East	West
Min	0.00	0.00
Mean	0.03	0.03
Median	0.00	0.00
Max	2.44	2.97