Relative Habitat Use, Occupancy, and Species Richness of Bats Across the Gradient of Urbanization in an Arid Region

by

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A Thesis Presented in Partial Fulfillment
of the Requirements for the Degree
Master of Science

Approved November 2021 by the
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ARIZONA STATE UNIVERSITY

December 2021

ABSTRACT

Urbanization is a primary driver of ecological change and occurs across a gradient from low- to high- density development. Wildlife species can exhibit different responses to urbanization, with some species being more sensitive than others. Further, wildlife communities can exhibit varying patterns of species richness across the gradient of urbanization, where species richness can either decrease linearly or peak at intermediate levels of urbanization, consistent with the intermediate disturbance hypothesis (IDH). For chapter one, the objective was to evaluate the response of bats to urbanization across seasons. It was predicted that bat species would exhibit different responses to urbanization and that bats would increase use of urbanized areas in the summer season, where food and water resources were assumed to be greater. For chapter two, the objective was to evaluate species richness of bats across the gradient of urbanization in the summer season. Species richness of bats was predicted to either decrease linearly or peak at moderate levels of urban intensity. To test these hypotheses, 50 sites across the gradient of urbanization were sampled during four seasons using stationary acoustic bat monitors. Fourteen bat species were identified during 1000 nightly occasions. Consistent with chapter one predictions, bat species exhibited different responses to urbanization, with most bats being sensitive to urbanization. Counter to predictions, most bats did not appear to shift their response to urbanization across seasons. However, two bats (i.e., big brown bat and Yuma myotis) exhibited higher use of urbanized areas in the summer compared to other seasons. Consistent with chapter two predictions, species richness of bats decreased with increasing urban intensity. Results from this study demonstrate that most bats in the community were sensitive to urbanization, which is potentially related to species traits and has important conservation implications. First, it is likely important to maintain high-quality undeveloped habitat with low anthropogenic disturbance in wildland areas for species that are sensitive to urbanization and to maximize species richness. In addition, for bats that are tolerant of urbanization and to increase species richness in urbanized areas, it is likely important to preserve resources in urbanized areas and increase landscape connectivity.

DEDICATION

To Leo and Lucy.

ACKNOWLEDGMENTS

I would like to thank my advisor Dr. Jesse Lewis for his encouragement and expertise throughout the duration of this research project. I also appreciate the invaluable input provided by my other committee members: Dr. Marianne Moore and Dr. Steven Saul. A special thanks to Sally Wittlinger, Jeffery Haight, and Joe Dwyer for their assistance in the field, Angie McIntire, Dr. Marianne Moore, and Janet Tyburec for sharing their fundamental bat expertise, and Dr. Stevan Earl for his assistance in creating a database to manage my data. I also want to express appreciation to my family and friends for their support and patience throughout this arduous journey. Lastly, I want to thank the landowners who granted us access to their properties for our research, including Maricopa County Parks and Recreation Department, City of Phoenix Parks and Recreation – Natural Resources Division, Arizona Department of Transportation, Maricopa County Flood Control District, US Forest Service, Arizona State University campuses, Salt River Project, City of Phoenix, Glendale, Peoria, Scottsdale, and Chandler, and other private property owners across the Valley. This material is based upon work funded and supported by Arizona State University and the National Science Foundation under grant number DEB-1832016, Central Arizona-Phoenix Long-Term Ecological Research Program (CAP LTER).

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CHAPTER 1

HABITAT USE OF BATS AND OCCUPANCY OF BATS ACROSS THE GRADIENT OF URBANIZATION AND SEASONS

1. Abstract

Urbanization, occurring across a gradient from low- to high-density development, is a primary driver of landscape change that can affect biodiversity. Animals balance trade-offs in obtaining resources and avoiding anthropogenic disturbance across the gradient of urbanization to maximize their fitness. However, additional research is necessary to understand seasonal variations in how animals respond to urbanization, particularly in arid regions, where resource availability shifts drastically across seasons. Our objective was to evaluate the response of a suite of bat species to urbanization and whether species shift their response to urbanization across seasons. We predicted that the response of bats to urbanization would differ among species, with some species being more sensitive to urbanization than others. We also predicted that bat species would increase use of moderate and highly urbanized areas in the summer season, where food and water resources were assumed to be greater compared to wildland areas. To test these hypotheses, we used stationary acoustic bat monitors to sample 50 sites across the gradient of urbanization during four seasons. We identified 14 bat species during 1000 survey nights. Consistent with predictions, bat species exhibited different responses to urbanization, with some species more sensitive (i.e., big/pocketed free-tailed bat, canyon bat, hoary bat, silver-haired bat, western mastiff bat, western red bat, and 40 kHz Myotis) and other species more tolerant (i.e., California myotis, Mexican free-tailed bat and western yellow bat) of urbanization. Counter to predictions, most species (i.e., big/pocketed free-tailed bat, canyon bat, Mexican free-tailed bat, and western yellow bat) did not appear to shift their response to urbanization across seasons. However, consistent with predictions, two bat species (i.e., big brown bat and Yuma myotis) exhibited higher use of moderate and highly urbanized areas in the summer season compared to other seasons. Differences in the response of bats to urbanization among species was likely related to species traits (e.g., wing morphology, echolocation call metrics) and behavioral characteristics that influence a species' susceptibility to anthropogenic disturbances and ability to access available resources in urbanized areas. Ultimately, results from this study have management and conservation implications, as it is likely important to preserve resources in urbanized areas for bats that are more tolerant of urbanization and to maintain areas of undeveloped high-quality habitat with low anthropogenic disturbance in wildland areas for bats that are sensitive to urbanization.

2. Introduction

Habitat use involves trade-offs between maximizing the collection of resources (e.g., food, water) and minimizing the cost from abiotic, biotic, and anthropogenic factors that constrain use (e.g., landscape change, anthropogenic disturbances; (Gedir et al. 2020; Halpin 2000; Hoglander et al. 2015; Krausman 1999; Mysterud and Ims 1998). In addition, resources and costs can be dynamic. For example, although animals select for areas with food and water resources (Gedir et al. 2020; Hawkins, Porter, and Felizola

Diniz-Filho 2003; Hoglander et al. 2015; Marshal et al. 2006; McCain et al. 2018; Rehnus et al. 2016) these resources often vary seasonally, and wildlife populations can respond to resource fluctuations by spatially and temporally altering use of areas (Godvik et al. 2009; Hoglander et al. 2015; Wang et al. 2010; Zweifel-Schielly et al. 2009). It is unclear how trade-offs in habitat use change in space and time in many human-modified landscapes, especially in regions with dramatic shifts in resource availability across seasons.

Anthropogenic factors can create novel environments for animals, where each species responds differently to landscape modifications in order to balance trade-offs and maximize fitness. In particular, urbanization, occurring across a gradient from low- to high-density development, is a pervasive and expanding driver of landscape change that can affect biodiversity, where some species benefit and others are negatively impacted (Grimm et al. 2008; McDonald, Kareiva, and Forman 2008; McDonald, Marcotullio, and Güneralp 2013; McDonnell and Pickett 1990; Medley, McDonnell, and Pickett 1995; Savard, Clergeau, and Mennechez 2000; Seto, Parnell, and Elmqvist 2013). Compared to wildland areas, food and water resources can increase for some species at low to moderate levels of urban intensity (Falk 1976; McKinney 2002; Shochat et al. 2006). Areas with high levels of urbanization also can provide food and water resources, but these areas are typically characterized by greater amounts of impervious surfaces (e.g., houses, buildings, parking lots) and anthropogrenic disturbance, and may lack resources for some species (McKinney 2002, 2006; Shochat et al. 2006). Depending upon how wildlife responds to urbanization, species can be categorized into three guilds of urbanization: “Urbanization avoiders” reach their highest population densities in wildland areas, “urbanization adapters” peak in density at moderate levels of urbanization, and “urbanization exploiters” reach their highest densities in highly urbanized areas (Blair 1996; McKinney 2002). However, species’ use of urbanized areas can vary by season, possibly due to changing resources and resource availability in wildland areas (Fischer et al. 2015; Grimm et al. 2008; Krausman 1999).

Trade-offs in habitat use can be more pronounced in some regions, such as hot, arid environments (Gedir et al. 2020; Van de Ven, McKechnie, and Cunningham 2019), where climate differs significantly among seasons and seasonal precipitation can create large fluctuations in food and water availability (Noy-Meir 1973; Gedir et al. 2020; Van de Ven, McKechnie, and Cunningham 2019). Furthermore, urbanized environments in desert ecosystems can have higher plant productivity and more consistent water sources than the surrounding wildland areas in some seasons, such as during the hot and dry summer months (Brown, Valone, and Curtin 1997; Korine et al. 2015; Razgour, Korine, and Saltz 2010; Russo, Cistrone, and Jones 2012; Shochat et al. 2006). Habitat use along the gradient of urbanization in arid regions, therefore, involves seasonal trade-offs between obtaining available resources, such as food and water, and minimizing costs, such as anthropogenic disturbances (Acebes, Malo, and Traba 2013; Rubin et al. 2002). Varying resource availability across seasons in arid regions could produce dynamic patterns of habitat use along the gradient of urbanization, which is largely unknown for many important species groups.

Bats are a diverse group of species that play important roles in ecosystems around the world and can be sensitive to urbanization (Agosta 2002; Jones et al. 2009; Russo and Ancillotto 2015). In addition to urban intensity, habitat use of bat species is influenced by food and water availability and other anthropogenic disturbances (Barré et al. 2021; Conenna et al. 2019; Dalhoumi et al. 2018; Korine and Pinshow 2004; Russo and Ancillotto 2015; Saldaña-Vázquez and Munguía-Rosas 2013; Scanlon and Petit 2008; Schoeman 2016; Shapiro et al. 2020; Stone, Harris, and Jones 2015; C. Threlfall et al. 2011). Some bat species may select for areas with higher plant productivity and water availability, due to an increase in insect abundance and water resources, which might be especially important for bats in arid environments where water is a limiting resource during some seasons (Ancillotto et al. 2019; Korine et al. 2016; H. Li and Wilkins 2014; McCain 2007; Mendes et al. 2017; C. Threlfall et al. 2011). Although each bat species exhibits varying patterns of use along the urbanization gradient (Jung and Kalko 2011; Jung and Threlfall 2018; Russo and Ancillotto 2015; Schimpp, Li, and Kalcounis-Rueppell 2018; C.G. Threlfall, Law, and Banks 2012), it is unclear whether the response of bats to urbanization will remain consistent across seasons or change seasonally relative to varying resource availability.

The overall objective of this study was to evaluate how the response of bats to urbanization differed among a suite of bat species and whether species' responses to urbanization changed across seasons. This study was conducted in the Phoenix metropolitan area, which is one of the largest urbanized areas in the United States that continues to rapidly grow in population (Luck and Wu 2002; U.S. Census Bureau 2018;

Wu et al. 2011), and occurs in one of the hottest and driest climates in North America. In addition, this region of Arizona supports one of the highest diversities of bat species in the United States (Adams 2003; Arizona Game and Fish Department 2021). Our specific objectives were to test hypotheses evaluating (1) the relative habitat use and occupancy (hereafter collectively referred to as "use") for a suite of bat species across the gradient of urbanization, (2) whether the response of bats along the gradient of urbanization changed seasonally, and (3) whether bats exhibited stronger relationships with plant productivity and water in the summer season. We predicted that each bat species would exhibit varying population responses across the gradient of urbanization, with some bat species being more sensitive to urbanization and other species showing more tolerance to urbanization. We also expected some bat species to increase their use of moderate and highly urbanized areas during the summer season when we assumed that there were potentially greater food and water resources available in urbanized areas compared to wildland areas during this season. In addition, we predicted that bats across the gradient of urbanization would increase their use of areas with increased plant productivity and water in the summer season.

3. Methods

3.1 Study Area

The study area was located in the Phoenix metropolitan area, Arizona, USA, which exhibits a gradient of urbanization, from undeveloped wildland to highly urbanized areas (Figure 1.1). The region is one of the most urbanized areas in the United States, which continues to rapidly urbanize (Luck and Wu 2002; U.S. Census Bureau 2018; Wu et al. 2011). The Phoenix metropolitan area is in the northern Sonoran Desert and is characterized by a hot and dry climate with an average summer temperature of 30.8°C, an average winter temperature of 11.3°C, and an annual precipitation of around 180 mm (Buyantuyev, Wu, and Gries 2010; Wu et al. 2011). The climate supports desert and riparian vegetation including the saguaro cactus (*Carnegiea gigantea*), paloverde (*Parkinsonia spp.*), creosote bush (*Larrea tridentate*), Fremont cottonwood (*Populus fremontii*), and Arizona willow (*Salix arizonica*) (Buyantuyev, Wu, and Gries 2010; Grimm and Redman 2004). Throughout the valley, over 290 km of canals bring water from the Colorado, Salt, and Gila Rivers to residents, providing year-round water sources (Ellin 2010; Roach et al. 2008).

3.2 Sampling Design

We used 2010 National Agriculture Imagery Program (NAIP) imagery with 1x1 m resolution (X. Li 2015) to create an urban intensity layer, which was calculated as the proportion of urbanization (impervious surfaces) within a 1000 m radius buffer around each sampling location. Across the gradient of urbanization, we used a stratified random sampling design to select 10 sites in each of five strata of urban intensity ranging from undeveloped to highly developed (urban intensity ranges for the categories included 0-0.005, 0.006-0.17, 0.18-0.35, 0.36-0.53, and 0.54-0.81). Sites occurred below an elevation of 550 m to control for changes in temperature, topography, and vegetation, and were at least 1.5 km away from each other. We also avoided sampling areas associated with agriculture.

At each of the 50 sampling locations, one stationary, passive acoustic bat monitor was used to survey for five consecutive nights per season, from sunset to sunrise (Britzke, Gillam, and Murray 2013). All sites were surveyed during each of the four seasons in 2019: winter (January 7th – March 1st), spring (April 8th – May 31st), summer (July 8th – August 30th), and fall (October 7th – November 29th). The sites were divided into six groups, where each group contained eight or nine sites in proximity, that were surveyed in a random order every season. If a survey was not completed due to weather events, monitor malfunctions, or vandalism, then the site was resurveyed at the end of the season. Each site was surveyed using one SM4BAT- FS acoustic bat monitor with a vertically positioned SMM-U2 microphone (Wildlife Acoustics, Maynard, MA). To standardize the sampling of locations and reduce potential sampling bias, the microphone was placed 3 to 5 m off the ground, positioned within a potential bat flyway, and not within 15 m of water or large pavement surfaces, such as roads, to avoid sound interference (Britzke, Gillam, and Murray 2013; Weller and Zabel 2002). The microphone was also not directly below vegetation clutter, artificial light, or powerlines to avoid a possible behavior change, and thus an echolocation call change, in bats (Britzke, Gillam, and Murray 2013). Monitor settings were configured to maximize likelihood of capturing calls from bats in the Phoenix region, with call frequencies ranging from 8-60 kHz, and to filter out ambient noise as much as possible (Reichert et al. 2018).

3.3 Species Identification

To identify species, we used a combination of automated and manual identification of bat calls collected from the acoustic monitors, following the North American Bat Monitoring Program (NABat) guidelines (Reichert et al. 2018). First, all bat calls were imported into SonoBat 4.2.2 (SonoBat, Arcata, CA), where we used the software's automated process to remove noise files and identify species, with associated levels of confidence. Next, we manually identified bat calls by evaluating each call's characteristics and metrics. Only search-phase, or commuter, calls (i.e., calls produced while a bat navigates its environment) were used for manual identification because other call types, such as approach-phase calls or social calls, are less consistent and would have high overlap in call metrics among some species (Britzke, Gillam, and Murray 2013; Reichert et al. 2018). A species was considered to be confidently identified if the call metrics were within the typical ranges observed for that species and if there were at least five (three for rare or quiet species, such as *Eumops perotis*) consecutive search-phase call pulses with even inter-pulse intervals from one individual with no interference from another bat (Reichert et al. 2018). Using this process, a voucher file (i.e., one high quality, confidently identified recording per species per monitoring night; Reichert et al. 2018) was produced and used in analyses.

The expected regional pool of bat species for our study area depended on the geographic and elevation range of Arizona bat species during each season. Out of the 28 bat species recorded in Arizona, we expected 15 species to be present in the Phoenix metropolitan area, 11 of which were expected to be present year-round (Appendix A). It can be difficult to confidently, acoustically identify some species since multiple species can share similar call metrics. We therefore combined *Nyctinomops femorosaccus* and *Nyctinomops macrotis* calls into *Nyctinomops sp.,* as the species are acoustically indistinguishable from each other. In addition, myotis bat species that produce calls within the 35-45 kHz range (i.e., *Myotis auriculus, Myotis ciliolabrum, Myotis occultus, Myotis velifer* and *Myotis volans*) were classified as "40 kHz Myotis" due to high overlap in call characteristics (Corcoran and Conner 2012; Reichert et al. 2018). Calls classified as 40 kHz myotis species are most likely *Myotis velifer*, as the other species are either more likely to occur outside of the study area or are more likely to be found at higher elevations (Appendix A). However, we still classified these calls as "40 kHz Myotis" since some of the species more likely to be found at higher elevations could potentially travel through the study area.

3.4 Landscape and Environmental Variables

We evaluated three landscape variables that we expected to influence habitat use and occupancy probability: urbanization, plant productivity, and distance to water. The variable "urbanization" was measured at multiple scales and was defined as the proportion of urbanization (impervious surface) within a buffer (i.e., 125, 250, 500, 1000 and 2000 m radius) associated with a site (X. Li 2015). To evaluate non-linear relationships with urbanization, we also evaluated the quadratic relationship for urbanization. In addition, the variable "plant productivity" was defined as the normalized difference in vegetation index (NDVI) associated with a site, averaged across the duration of each season, and was measured at multiple scales (i.e., 125, 250, 500, 1000 and 2000 m radius buffers). Lastly, using Google Earth (Google, Mountain View, CA) and 2015 NAIP imagery (Zhang and Turner II 2020), we identified perennial water sources that were >7 m in length or width, including swimming pools (Hall et al. 2016; Nystrom and Bennett 2019; Razgour, Korine, and Saltz 2010). Using this information, we evaluated the variable “water”, which was the distance from each site to the nearest water source. It was hypothesized that plant productivity and water were important covariates to consider in part because it was assumed that insect abundance would be higher in areas with increased plant productivity (Haddad et al. 2001; Lightfoot and Whitford 1989; Siemann 1998) and increased water (Straka et al. 2020), which was particularly important for insectivorous bats. We considered evaluating a landscape heterogeneity metric “dissimilarity” (Farwell et al. 2020), but we excluded the covariate because it was highly correlated ($r > 0.60$) with other covariates across most scales.

For single-species single-season occupancy modeling, we evaluated two environmental variables that we expected to influence species detection probability: mintemp and moon. The variable “mintemp” was defined as the average minimum temperature across the five survey nights, or occasions, within a season (Caryl et al. 2016; Thornton et al. 2020). In addition, the variable “moon” was defined as the average percent lunar illumination at 23:00 hours (UTC-7) across the five occasions within a season (Allen et al. 2009; NASA 2019; Scanlon and Petit 2008). It was hypothesized that these variables would influence species detection because some bat species decrease activity when temperatures are low and lunar illumination is high (Erickson and West 2002; Saldaña-Vázquez and Munguía-Rosas 2013; Scanlon and Petit 2008). We predicted that detection probability of bats would exhibit a positive relationship with temperature during cooler seasons. Furthermore, we predicted that the response of bats to temperature would vary among species in the summer season, depending on the species' heat tolerance (Czenze et al. 2020). In addition, we predicted that the response of bats to lunar illumination would vary among species, potentially related to differences in species traits, such as foraging strategy (Saldaña-Vázquez and Munguía-Rosas 2013).

To aid in model convergence, all continuous variables were standardized by subtracting the sample mean and dividing by the standard deviation (Schielzeth 2010). We evaluated the correlation between all variables using a Pearson's correlation test and we did not include covariates that were highly correlated ($r > 0.60$) in the same model.

3.5 Statistical Analysis

For our analysis, we used detection/non-detection data, where a species was either detected (1) or not detected (0) during an occasion (e.g., night). There were a total of 5 occasions (i.e., nights) per site per season (winter, spring, summer, and fall).

We used two modeling approaches to evaluate (1) relative habitat use and (2) single-season occupancy in relation to landscape characteristics (MacKenzie et al. 2003; Royle and Nichols 2003). We used program R (R Development Core Team 2020) and the RMark package (Laake and Rexstad 2008) to evaluate models in Program MARK (White and Burnham 1999). First, we used Royle-Nichols (RN) models to evaluate heterogeneity in abundance (λ) across sites considering heterogeneity in detection probability (Royle and Nichols 2003). We followed the recommendation that RN models be used as a relative measure of intensity of habitat use for species with relatively large home ranges (Nakashima 2020), such as bats (Conenna et al. 2019; Klingbeil and Willig 2009). For RN models, we assumed the spatial distribution of animals across sites followed a Poisson distribution and that the probability of detecting a species at a site was related to the species-specific detection probability (r) and the number of visits, or animals, of the species at that site (Donovan 2007; Royle and Nichols 2003).

Second, we used single-species single-season occupancy models to estimate (a) occupancy probability (ψ; the probability that a site was occupied or used by the species) and (b) detection probability (p; the probability of detecting the species given that it was present at a site) (MacKenzie et al. 2017). It was assumed that populations were closed during a season (MacKenzie et al. 2017).

For both the RN and occupancy modeling model selection process, we determined the best scale (i.e., 125-2000 m radius buffer) for urbanization and plant productivity by evaluating which scale in univariate models was most supported based on Akaike Information Criteria corrected for small sample size (AICc; Anderson and Burnham 2004). To evaluate whether there was evidence of a non-linear relationship with urbanization, we compared model support for the linear and quadratic relationships for urbanization using AICc. In addition, we considered whether there was support for an interaction between urbanization and NDVI or water. The interaction term between urbanization and water was highly correlated with water and therefore the interaction term was not evaluated. Finally, using the best scales for each covariate, we evaluated all possible model combinations for each species and each season. We considered a variable as informative if it occurred in a model that outperformed the intercept-only model (i.e., model without covariates). We further identified a variable as an “uninformative parameter” if it did not sufficiently improve the log likelihood of models (Arnold 2010; Leroux 2019).

For the occupancy modeling model selection process, we first determined whether detection probability variables (i.e., mintemp or moon) informed detection probability for each species and each season. We compared a model with constant detection probability (p(.)) to a model where detection probability varied with mintemp (p(mintemp)), moon (p(moon)), and mintemp and moon (p(mintemp + moon)). If p(mintemp), p(moon), or p(mintemp+moon) were more supported than p(.) based on AICc, then the detection variable(s) was included in all subsequent models evaluating occupancy probability.

Using results from the RN and single-season single-species occupancy modeling, we classified bat species into “urbanization avoider”, “urbanization adapter”, and “urbanization exploiter” guilds based on where the species reached its highest relative habitat use or occupancy across the gradient of urbanization (Blair 1996). A bat was classified as an urbanization avoider if the species reached its highest relative habitat use or occupancy in wildland and low urbanization areas and exhibited a negative relationship with urbanization (Blair 1996; Callaghan et al. 2020). In contrast, a bat was classified as an urbanization exploiter if the species reached its highest relative habitat use or occupancy in areas of high urbanization and exhibited a positive relationship with urbanization (Blair 1996; Callaghan et al. 2020). Lastly, a bat was classified as an urbanization adapter if the species peaked in relative habitat use or occupancy in areas of intermediate urbanization and exhibited a unimodal, or quadratic, relationship with urbanization (Blair 1996). If a bat had too few detections to evaluate their response to urbanization using RN and occupancy models, but was only detected in wildland areas, then the species was considered a potential urbanization avoider. Any species that did not exhibit patterns consistent with the three urbanization categories were considered “unclassified”.

4. Results

Across our 50 sites during four seasons, we identified a total of 14 bat species during 1000 nightly occasions (Table 1.1). For most species, the greatest number of occasions (i.e., nightly sampling periods) that a species was detected occurred in the spring or summer season (Table 1.1). We obtained sufficient data to evaluate habitat use and occupancy of 14 species for at least one season, with 10 of these species allowing for comparisons across multiple seasons (Table 1.1).

4.1 Relative Habitat Use

4.1.1 Response to Urbanization

Habitat use estimated from Royle-Nichols (RN) models supported our hypothesis that some bat species would be more sensitive to urbanization than others (Figure 1.2; Appendix B-D). Some species (i.e., big/pocketed free tailed bat, canyon bat, hoary bat, silver-haired bat, western mastiff bat, western red bat, Yuma myotis, and 40 kHz Myotis) exhibited a negative relationship with urbanization in one or more seasons (Table 1.2;

Appendix B). In contrast, other species (i.e., big brown bat and Mexican free-tailed bat) exhibited a positive relationship with urbanization in one or more seasons (Table 1.2; Appendix B). Lastly, other bats (i.e., big brown bat, California myotis, western yellow bat, and Yuma myotis) exhibited their highest use of areas of intermediate urbanization (i.e., quadratic relationship) in one or more seasons (Table 1.2; Appendix B). Based on these results, bats were classified into the categories of urbanization avoider (i.e., big/pocketed free-tailed bat, canyon bat, hoary bat, silver-haired bat, western mastiff bat, western red bat, Yuma myotis, and 40 kHz Myotis), urbanization exploiter (i.e., big brown bat and Mexican free-tailed bat), and urbanization adapter (i.e., big brown bat, California myotis, western yellow bat, and Yuma myotis) (Table 1.3).

Estimates of habitat use from RN models also demonstrated that, counter to predictions, most bat species (i.e., big/pocketed free-tailed bat, canyon bat, Mexican free-tailed bat, western mastiff bat, and western yellow bat) did not appear to shift their response to urbanization across seasons (Table 1.2; Appendix B-D). However, some bat species did vary their response to urbanization across seasons (Figure 1.3; Table 1.2; Appendix B-D). For example, the big brown bat exhibited a quadratic relationship with urbanization during the spring season (i.e., urbanization adapter) and a positive relationship with urbanization in the summer season (i.e., urbanization exploiter) (Table 1.2 and 1.3; Appendix B), supporting our hypothesis that some bat species would increase habitat use of highly urbanized areas during the summer season. In addition, the Yuma myotis exhibited a quadratic relationship with urbanization in the spring and summer season (i.e., urbanization adapter) and a negative relationship with urbanization during the fall season (i.e., urbanization avoider) (Table 1.2 and 1.3; Appendix B).

4.1.2 Response to Plant Productivity and Distance to Water

In addition to urban intensity, habitat use of bats varied in relation to plant productivity and water (Table 1.2; Appendix B and E). Although variable, habitat use for some bats (i.e., big brown bat, California myotis, canyon bat, hoary bat, Mexican free-tailed bat, pallid bat, western mastiff bat, western red bat, western yellow bat, Yuma myotis, and 40 kHz Myotis) tended to exhibit a positive relationship with plant productivity across many seasons; however, some species (i.e., canyon bat, Mexican free-tailed bat, and silver-haired bat) exhibited a negative relationship with plant productivity in winter, spring, and fall (Table 1.2; Appendix B and E). In addition, there was variation in how bats responded to distance to water. Some bats (i.e., California myotis, Mexican free-tailed bat, western red bat, and western yellow bat) exhibited a negative relationship with distance to water across many seasons, indicating that habitat use decreased as distance to water increased (Table 1.2; Appendix E). In contrast, other bats (i.e., canyon bat and pallid bat) exhibited a positive relationship with distance to water (Table 1.2; Appendix E).

4.2 Occupancy

4.2.1 Response to Urbanization

Occupancy of bats ranged from 0.02 – 1.00 (Table 1.4), and results of occupancy models were similar to results of habitat use from RN models. Consistent with predictions, some bat species were more sensitive to urbanization than others (Appendix S6-S9).

Overall, counter to predictions, occupancy model results also demonstrated that most bats did not appear to shift their response to urbanization across seasons (Appendix F-I). However, consistent with predictions, the big brown bat exhibited a quadratic relationship with urbanization during the spring season (i.e., urbanization adapter) and a positive relationship with urbanization in the summer season (i.e., urbanization exploiter) (Table 1.3; Appendix F and G).

Although occupancy model results were similar to results of habitat use from RN models, there were a few differences. First, in the spring season, habitat use of the Yuma myotis exhibited a quadratic response to urbanization, while occupancy of the Yuma myotis exhibited a negative response to urbanization (Appendix B and F). In addition, in the fall season, habitat use of the Western yellow bat exhibited a quadratic response to urbanization, while occupancy of the Western yellow bat exhibited a positive response to urbanization (Appendix B and F).

4.2.2 Response to Plant Productivity and Distance to Water

In addition to urban intensity, occupancy of bats varied in relation to plant productivity and water (Appendix F, G and J). Occupancy for many bats (i.e., big brown bat, California myotis, canyon bat, hoary bat, western mastiff bat, western red bat, western yellow bat, Yuma myotis, and 40 kHz Myotis) exhibited a positive relationship with plant productivity across many seasons (Appendix G and J). In addition, there was variation in how bats responded to distance to water. Some bats (i.e., California myotis and western yellow bat) exhibited a negative relationship with distance to water in the spring and summer season, indicating that habitat use decreased as distance to water increased (Appendix G and J). In contrast, other bats (i.e., big/pocketed free-tailed bat and hoary bat) exhibited a positive relationship with distance to water in the winter, spring, and fall season (Appendix G and J).

4.2.3 Response to Temperature and Lunar Illumination

Detection probability in occupancy models of bat species ranged from 0.03 – 0.80 (Table 1.4) and was influenced by average minimum temperature and average lunar illumination for some species (Appendix F, G and J). Although variable, detection probability for many bats (i.e., big/pocketed free-tailed bat, canyon bat, Mexican free-tailed bat, western mastiff bat, and western yellow bat) tended to exhibit a positive relationship with temperature across many seasons; however, some species (i.e., big/pocketed free-tailed bat, canyon bat, hoary bat, Mexican free-tailed bat, and Yuma myotis) exhibited a negative relationship with temperature in the spring and summer season (Appendix G and J). Furthermore, consistent with predications, detection probability of some bats (i.e., big brown bat, California myotis, Mexican free-tailed bat, western yellow bat and Yuma myotis) exhibited a negative relationship with lunar illumination across all seasons the species was detected, whereas detection probability of other species (i.e., big/pocketed free-tailed bat, canyon bat, western red bat, and 40 kHz

Myotis) exhibited a positive relationship lunar illumination across all seasons the species was detected (Appendix G and J).

5. Discussion

Bats in our study exhibited varying responses to urbanization, where species likely balanced trade-offs in obtaining resources and avoiding anthropogenic disturbances across the gradient of urbanization. Based on how bats responded to urbanization, we classified bats into three guilds: urbanization avoider (i.e., big/pocketed free tailed bat, canyon bat, hoary bat, pallid bat, silver-haired bat, western mastiff bat, and 40 kHz Myotis), urbanization exploiter (i.e., Mexican free-tailed bat), and urbanization adapter (i.e., California myotis and western yellow bat). Differences in response of bats to urbanization among species was likely related to species traits and behavioral characteristics. For example, bats that avoided urbanized areas (i.e., urbanization avoiders) tended to be sensitive to human disturbance, specialized in roosting strategy, or potentially challenged to access available resources in urbanized areas due to traits such as weak flight and low mobility (Avila-Flores and Fenton 2005; Jung and Kalko 2011; Jung and Threlfall 2018). In contrast, bats that exploited resources in highly urbanized environments (i.e., urbanization exploiters) tended to be tolerant of anthropogenic disturbances, such as artificial lighting, and can access available resources with traits such as strong flight and high mobility (Avila-Flores and Fenton 2005; Jung and Kalko 2011; Jung and Threlfall 2018; Schoeman 2016). Further, bats that exhibited their highest use at intermediate levels of urbanization (i.e., urbanization adapters) tended to be flexible in roosting strategy and vary in flight strength and mobility (Adams 2003; Avila-Flores and Fenton 2005; Gehrt and Chelsvig 2004; Norberg and Rayner 1987; Schimpp, Li, and Kalcounis-Rueppell 2018). However, the big/pocketed free-tailed bat and western mastiff bat, which share many traits with urbanization exploiters, avoided urbanized areas. This was possibly due to the species' roosting requirements of high cliffs and complex rock features that are more widely available in wildland areas (Adams 2003; Arizona Game and Fish Department 2020; Remington 2006).

Due to dynamic resource availability across the gradient of urbanization, species might shift their response (i.e., urbanization category) to urbanization across seasons. Counter to our predictions, however, most bat species exhibited a consistent response to urbanization across seasons (i.e., did not shift their response to urbanization across seasons), even though some food and water resources were assumed to be greater in urbanized areas during the summer season. Thus, most bats in this study were consistent in how they used urbanization across seasons; potentially the cost of accessing resources in urbanized environments during the summer season did not outweigh the benefits. However, consistent with predictions, two bat species (i.e., big brown bat and Yuma myotis) shifted and increased their use of moderate and highly urbanized areas in the summer season compared to other seasons. The big brown bat was likely able to increase use of highly urbanized areas in the summer season due to traits that increase adaptability, such as a flexible roosting strategy, as well as traits that enable the species to access available resources, such as high mobility (Adams 2003; Avila-Flores and Fenton 2005; Gehrt and Chelsvig 2004; Norberg and Rayner 1987; Schimpp, Li, and Kalcounis-

Rueppell 2018). In addition, the Yuma myotis is closely associated with water and potentially increased use of moderately urbanized environments to access available water sources during the summer season (Adams 2003; Arizona Game and Fish Department 2020; Braun et al. 2015).

In addition to urban intensity, habitat use and occupancy of bats was influenced by plant productivity and water. We assumed that areas with increased plant productivity and water would exhibit increased food and water resources (Avila-Flores and Fenton 2005; Haddad et al. 2001; Lightfoot and Whitford 1989; Siemann 1998), and that those resources would be most abundant in urbanized areas during the hot and dry summer season, compared to wildland areas. Although some bat species (i.e., big brown bat, California myotis, canyon bat, pallid bat, western yellow bat, and 40 kHz Myotis) exhibited high use of areas with higher plant productivity during the summer season, it also appeared to be important to bats during other seasons that bats were active. Distance to water was not included in the top model for most bat species and seasons. However, it appeared to be an important variable for some bats during the summer season in particular. For example, the California myotis is often associated with water (Adams 2003; Arizona Game and Fish Department 2020), and this species used areas closer to water in the summer season.

For some bats, detection probability in occupancy models was influenced by average minimum temperature and average lunar illumination. Although many bat species (i.e., canyon bat, Mexican free-tailed bat, and western yellow bat) exhibited a positive relationship with temperature in the winter and fall season (Bender and Hartman

2015; Scanlon and Petit 2008), there were no consistent patterns during the spring and summer season, with some species (i.e., western mastiff bat and western yellow bat) exhibiting a positive relationship with temperature and other species (i.e., hoary bat, Mexican free-tailed bat, and Yuma myotis) exhibiting a negative relationship with temperature. During cooler seasons, bat activity can increases with warmer temperatures (Bender and Hartman 2015; Scanlon and Petit 2008; Meyer, Senulis, and Reinartz 2016), and some bats could potentially increase activity during cooler seasons in urbanized areas due to the urban heat island effect (Sachanowicz et al. 2019). Desert-adapted bat species can be tolerant of high temperatures, even during the summer (Bondarenco, Körtner, and Geiser 2014, 2016). However, our study demonstrated variation among species, which is potentially related to variation in heat tolerance among species (Bondarenco, Körtner, and Geiser 2013; Czenze et al. 2020). In addition, the influence of lunar illumination on the detection probability of bats was species-specific, with some species (i.e., big/pocketed free-tailed bat, canyon bat, western red bat, and 40 kHz Myotis) exhibiting a positive relationship with lunar illumination and other species (i.e., big brown bat, California myotis, Mexican free-tailed bat, western yellow bat and Yuma myotis) exhibiting a negative relationship with lunar illumination, also known as lunar phobia (Saldaña-Vázquez and Munguía-Rosas 2013). Lunar phobia (i.e., decreased activity during nights with increased moonlight) is potentially due to predation risk or prey availability, and reported to be exhibited by bats with certain traits, such as trawling insectivorous diet (i.e., diet of insects that fly close to or rest on water surfaces) and narrow-space foraging strategy (i.e., bats that tend to forage within dense vegetation or near the ground) (Lang et al. 2006; Saldaña-Vázquez and Munguía-Rosas 2013), which was consistent with some bats in our study, including a trawling insectivore (i.e., Yuma myotis) and a narrow-space forager (i.e., California myotis). However, some species (i.e., big/pocketed free-tailed bat, canyon bat, western red bat, and 40 kHz Myotis) exhibited a positive relationship with lunar illumination, demonstrating that there is wide variability in how bats respond to lunar illumination (Appel et al. 2017; Appel et al. 2019; Vásquez, Grez, and Rodríguez-San Pedro 2020). Although little research has evaluated increased bat activity during nights with increased moonlight, this could potentially result from changes in food resources or due to species interactions.

There are several considerations when interpreting the results of this study. First, there are limitations using acoustic bat monitoring. For example, some bat species are difficult to detect with acoustic monitors, such as bats that produce low intensity (i.e., "quiet") echolocation calls (i.e., California leaf-nosed bat, pallid bat, and Townsend's big-eared bat) (Reichert et al. 2018). Therefore, our methodology likely underestimated the occupancy and habitat use of the pallid bat and Townsend's big-eared bat and possibly contributed to not detecting the California leaf-nosed bat, which was known to occur in the study area (Adams 2003; Arizona Game and Fish Department 2020). Second, we assumed that areas with increased plant productivity and water exhibited increased insect abundance, which was the main food resource for the insectivorous bats in this study (Avila-Flores and Fenton 2005; Haddad et al. 2001; Lightfoot and Whitford 1989; Siemann 1998). However, insects can be influenced by a variety of factors along the gradient of urbanization that we were unable to measure in this study, such as artificial light, insect-plant associations, and other habitat considerations for insect species (Bolliger, Hennet, Wermelinger, Blum, et al. 2020; Bolliger, Hennet, Wermelinger, Bösch, et al. 2020; Jaganmohan, Vailshery, and Nagendra 2013; Rowse et al. 2016). Therefore, plant productivity might not be the best indicator of insect resources and additional landscape factors might better represent insect abundance and help explain bat use of areas. Furthermore, the availability of food resources in urbanized environments can depend on a bats' diet, where insect abundance across the gradient of urbanization may vary by species. Abundance of many prey species are negatively influenced by urbanization (Dar and Jamal 2021; Piano et al. 2020). However, abundance of some prey species can increase in urbanized areas, such as increased beetle and moth abundance in residential yards (Bang and Faeth 2011; Bates et al. 2014) or increased mosquito abundance around standing water (Rochlin et al. 2016; Wilke et al. 2019). Third, precipitation from monsoon rains during the summer season (July-August) could potentially influence bat use across the gradient of urbanization. During this study, the monsoon season exhibited below average precipitation, and was classified as one of the driest summers during the last 100 years (National Oceanic and Atmospheric Administration 2021). Thus, due to assumed limiting water and food resources, we would expect that bats might be more likely to increase their use of urbanized areas during the summer of this study, compared to years with above average summer precipitation when wildland areas would be expected to exhibit greater water resources. Lastly, we focused on two important population metrics to evaluate bat populations: relative habitat use and occupancy probability. However, there are other important metrics to consider for understanding bat use of urbanized environments, such as population density, activity patterns, species interactions, extinction and colonization, survival and reproduction of different age and sex classes, fitness, and competition (Gehrt and Chelsvig 2004; Lintott et al. 2016; Neece, Loeb, and Jachowski 2018; Patriquin et al. 2019; Rodríguez-Aguilar et al. 2017; Zuñiga-Palacios et al. 2021). For example, the Mexican free-tailed bat can exhibit high use in urbanized areas (Avila-Flores and Fenton 2005; Bredt and Uieda 1996; Krauel and LeBuhn 2016), and potentially exclude species that would otherwise be able to access available resources.

The trade-off between bats using resources within urbanized areas and avoiding anthropogenic disturbance has important implications for their management and conservation that is likely related to species-specific traits. For some species, the cost of urbanization appeared to outweigh the benefits of obtaining available resources in urbanized areas. For example, bats that avoided urbanized areas (i.e., canyon bat and 40 kHz Myotis) tended to be sensitive to anthropogenic disturbances or exhibit traits that make it difficult to access resources in urbanized environments, such as weak flight and low mobility (Avila-Flores and Fenton 2005; Jung and Kalko 2011; Jung and Threlfall 2018). In contrast, some bats appeared able to exploit resources in highly urbanized environments (i.e., Mexican free-tailed bat), and tend to be tolerant of anthropogenic disturbances and exhibit traits that allow them to access resources in highly urbanized environments, such as strong flight and high mobility (Avila-Flores and Fenton 2005; Jung and Kalko 2011; Jung and Threlfall 2018; Schoeman 2016). Further, bats that shift their response to urbanization across seasons (i.e., big brown bat) may exhibit traits that increase adaptability, such as flexibility in roosting strategy and edge-space foraging, as well as traits that enable the species to access resources in urbanized environments, such as high mobility (Adams 2003; Avila-Flores and Fenton 2005; Gehrt and Chelsvig 2004; Norberg and Rayner 1987; Schimpp, Li, and Kalcounis-Rueppell 2018). Ultimately, results from this study have important management and conservation implications for bats across the gradient of urbanization. For bats that exploit moderate to high levels of urbanization, outdoor parks, green-spaces, trees, water, and other landscape features may provide important resources to bats that enable them to use these areas (Dalhoumi et al. 2018; de Araújo and Bernard 2016; Johnson, Gates, and Ford 2008; Russo and Ancillotto 2015). For other bat species that tend to avoid urbanization and use wildland areas, it is likely important to maintain large areas of high-quality undeveloped habitat and with low anthropogenic disturbance in these areas (Ancillotto et al. 2019; Grindal, Morissette, and Brigham 1999; Korine et al. 2016).

Table 1.1: Total number of nightly occasions that 14 bat species were detected across 50 sites in the Phoenix metropolitan area, Arizona during four seasons (5 nightly occasions per season) in 2019. Bolded numbers indicate that sufficient data were available to evaluate Royle-Nichols (RN) models or single-species single-season occupancy models, for at least the intercept-only model.

	Total Number of Occasions Detected			
Bat Species	Winter	Spring	Summer	Fall
Big brown bat	0	**13**	**18**	0
Big/Pocketed free-tailed bat	**22**	**23**	**12**	**21**
California myotis	0	**16**	**40**	6
Canyon bat	**43**	**92**	**184**	**77**
Hoary bat	7	**16**	6	0
Mexican free-tailed bat	**157**	**188**	**160**	**120**
Pallid bat	0	**4**	**8**	0
Silver-haired bat	0	2	**3**	**8**
Townsend's big-eared bat	0	1	**3**	1
Western mastiff bat	6	**10**	**3**	**8**
Western red bat	**11**	**9**	3	**13**
Western yellow bat	**16**	**41**	**63**	**25**
Yuma myotis	**5**	**32**	**44**	**21**
40 kHz Myotis	0	**14**	**26**	0

Table 1.2: Habitat use (based on top Royle-Nichols (RN) model results) for 12 bat species in relation to urbanization (U), plant productivity (P), the interaction between U and P (UxP), and distance to water (W) in the Phoenix metropolitan area, AZ during four seasons in 2019. For each variable, we report the general relationship (positive = +; negative = -; or quadratic = Q) of the beta estimate and the most supported spatial scale (i.e., 125-2000 m radius buffers).

		U		P		UxP	W
Species	Season	Beta	Scale	Beta	Scale	Beta	Beta
Big brown bat	Spring	Q	250				
	Summer	+	500	+	125		
Big/pocketed free- tailed bat	Winter	-	1000				
	Spring	-	2000				
	Summer	-	1000				
	Fall	-	1000				
California myotis	Spring	Q	2000				
	Summer			+	2000		-
Canyon bat	Winter	-	1000	+	250		
	Spring	-	1000	-	125		
	Summer	-	2000				
	Fall	-	1000				+
Hoary bat	Spring	-	1000	+	2000		
Mexican free-tailed bat	Winter	+	125	-	125		
	Spring	+	500	+	2000		-
	Summer	+	2000				-
	Fall	+	500	-	500	+	
Pallid bat	Summer			+	2000		+
Silver-haired bat	Fall	-	500	-	2000	+	
Western mastiff bat	Spring			+	1000		
	Fall	-	1000	+	2000		
Western red bat	Winter	-	250				-
	Spring						
	Fall			+	500		
Western yellow bat	Winter	Q	500				
	Spring	Q	500	+	125		-
	Summer	Q	500				-
	Fall	Q	2000				
Yuma myotis	Spring	Q	500	+	2000		
	Summer	Q	2000	+	2000		
	Fall	-	250	+	2000		
40 kHz Myotis	Spring			+	2000		
	Summer	-	2000	+	2000	-	

Table 1.3: Urbanization guild classifications[1] for 14 bat species in the Phoenix metropolitan area, Arizona during four seasons in 2019 based on where the species reached its highest relative habitat use (based on top Royle-Nichols (RN) model results) or occupancy (based on single-species single-season occupancy model results) across the gradient of urbanization.

	Urbanization Guild[1]			
Bat Species	Winter	Spring	Summer	Fall
Big brown bat		Adapter	Exploiter	
Big/Pocketed free-tailed bat	Avoider	Avoider	Avoider	Avoider
California myotis		Adapter	Unclassified	
Canyon bat	Avoider	Avoider	Avoider	Avoider
Hoary bat		Avoider		
Mexican free-tailed bat	Exploiter	Exploiter	Exploiter	Exploiter
Pallid bat		*Avoider	*Avoider	
Silver-haired bat			Unclassified	Avoider
Townsend's big-eared bat			*Avoider	
Western mastiff bat		Unclassified	*Avoider	Avoider
Western red bat	Avoider	Unclassified		Unclassified
Western yellow bat	Adapter	Adapter	Adapter	Unclassified
Yuma myotis	Unclassified	Unclassified	Adapter	Avoider
40 kHz Myotis		Unclassified	Avoider	

[1] A bat was classified as an "urbanization avoider" if the species reached its highest relative habitat use or occupancy in wildland areas and exhibited a negative relationship with urbanization, an "urbanization exploiter" if the species reached its highest relative habitat use or occupancy in highly urbanized areas and exhibited a positive relationship with urbanization, and an "urbanization adapter" if the species reached its highest relative habitat use or occupancy in moderately urbanized areas and exhibited a quadratic relationship with urbanization. If a bat had too few detections to evaluate their response to urbanization using RN and occupancy modeling but was only detected in wildland areas, then the species was considered a potential urbanization avoider (indicated by an asterisk). Any other species that did not have sufficient data to evaluate their response to urbanization and any species that did not exhibit strong relationships with urbanization were considered "unclassified".

Table 1.4: Real estimates and standard errors (se) of occupancy probability (ψ) and detection probability (p) from the top model for 14 bat species across 50 sites in the Phoenix metropolitan area, Arizona during four seasons in 2019.

		ψ		p	
Species	Season	Estimate	se	Estimate	se
Big brown bat	Spring	0.27	0.16	0.12	0.06
	Summer	0.18	0.07	0.35	0.08
Big pocketed free-tailed bat	Winter	0.22	0.14	0.25	0.07
	Spring	0.52	0.15	0.21	0.05
	Summer	0.38	0.13	0.06	0.04
	Fall	0.25	0.10	0.29	0.07
California myotis	Spring	0.03	0.04	0.43	0.09
	Summer	0.34	0.10	0.40	0.06
Canyon bat	Winter	0.37	0.08	0.43	0.06
	Spring	0.62	0.08	0.62	0.05
	Summer	0.96	0.03	0.80	0.03
	Fall	0.57	0.08	0.56	0.04
Hoary bat	Spring	0.42	0.16	0.06	0.03
Mexican free-tailed bat	Winter	0.98	0.02	0.65	0.03
	Spring	1.00	0.00	0.77	0.03
	Summer	0.98	0.03	0.76	0.03
	Fall	0.96	0.04	0.50	0.04
Pallid bat	Spring	0.05	0.03	0.36	0.18
	Summer	0.09	0.04	0.36	0.12
Silver-haired bat	Summer	0.06	0.05	0.20	0.17
	Fall	0.48	0.42	0.07	0.06
Townsend’s big-eared bat	Summer	0.06	0.05	0.20	0.17
Western mastiff bat	Spring	0.02	0.02	0.48	0.12
	Summer	0.06	0.05	0.20	0.17
	Fall	0.13	0.07	0.24	0.11
Western red bat	Winter	0.61	0.35	0.06	0.04
	Spring	0.09	0.04	0.45	0.14
	Fall	0.23	0.10	0.20	0.08
Western yellow bat	Winter	0.83	0.28	0.03	0.02
	Spring	0.59	0.16	0.30	0.05
	Summer	0.83	0.09	0.31	0.04
	Fall	0.73	0.21	0.12	0.04
Yuma myotis	Winter	0.18	0.15	0.11	0.10
	Spring	0.50	0.13	0.20	0.05
	Summer	0.30	0.08	0.50	0.06
	Fall	0.39	0.14	0.20	0.06
40 kHz Myotis	Spring	0.25	0.11	0.17	0.06
	Summer	0.26	0.07	0.40	0.07

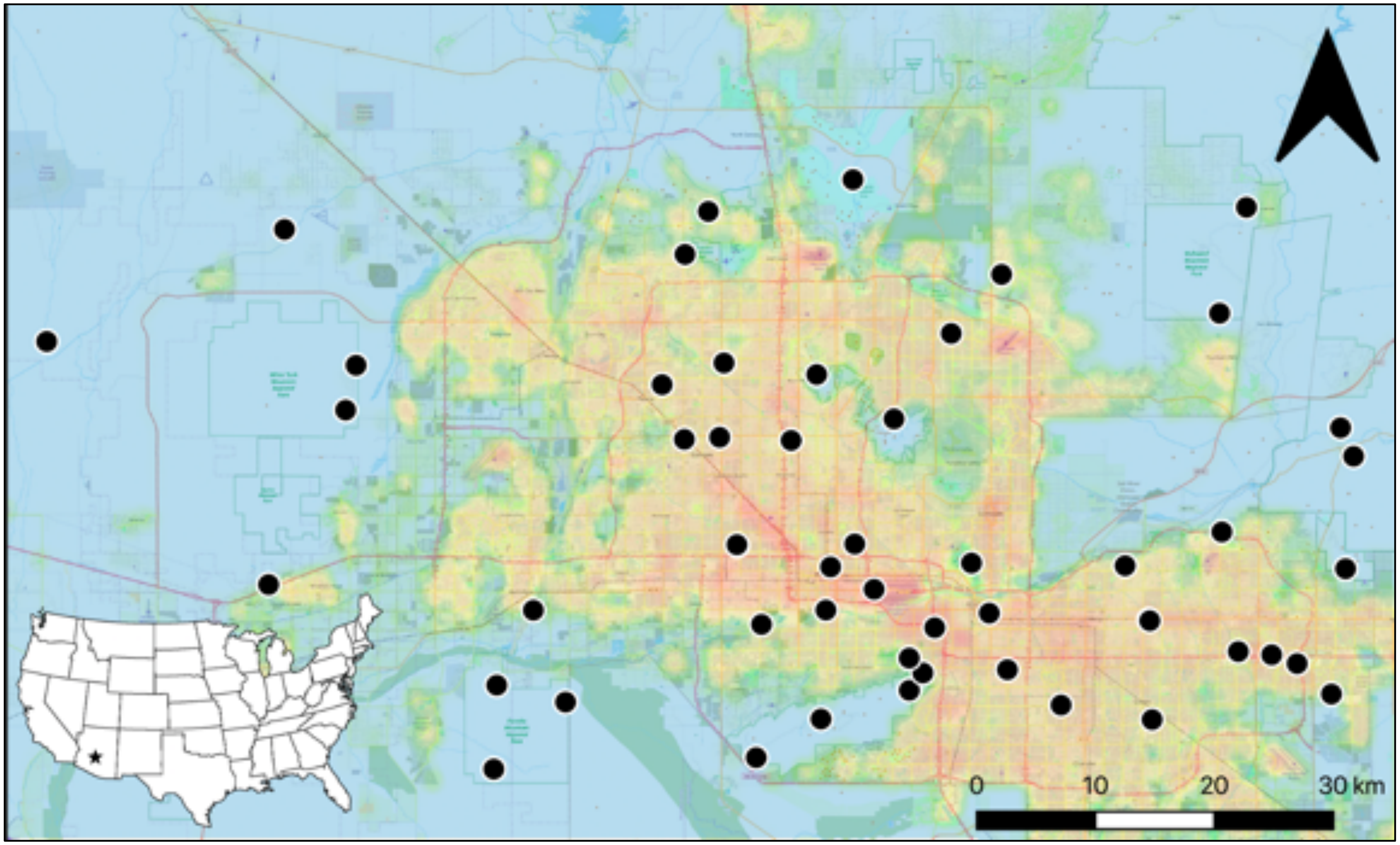

Figure 1.1: Fifty sampling locations (black circles) along the gradient of urban intensity from wildland areas (blue) to highly urbanized areas (red), in the Phoenix metropolitan area, Arizona.

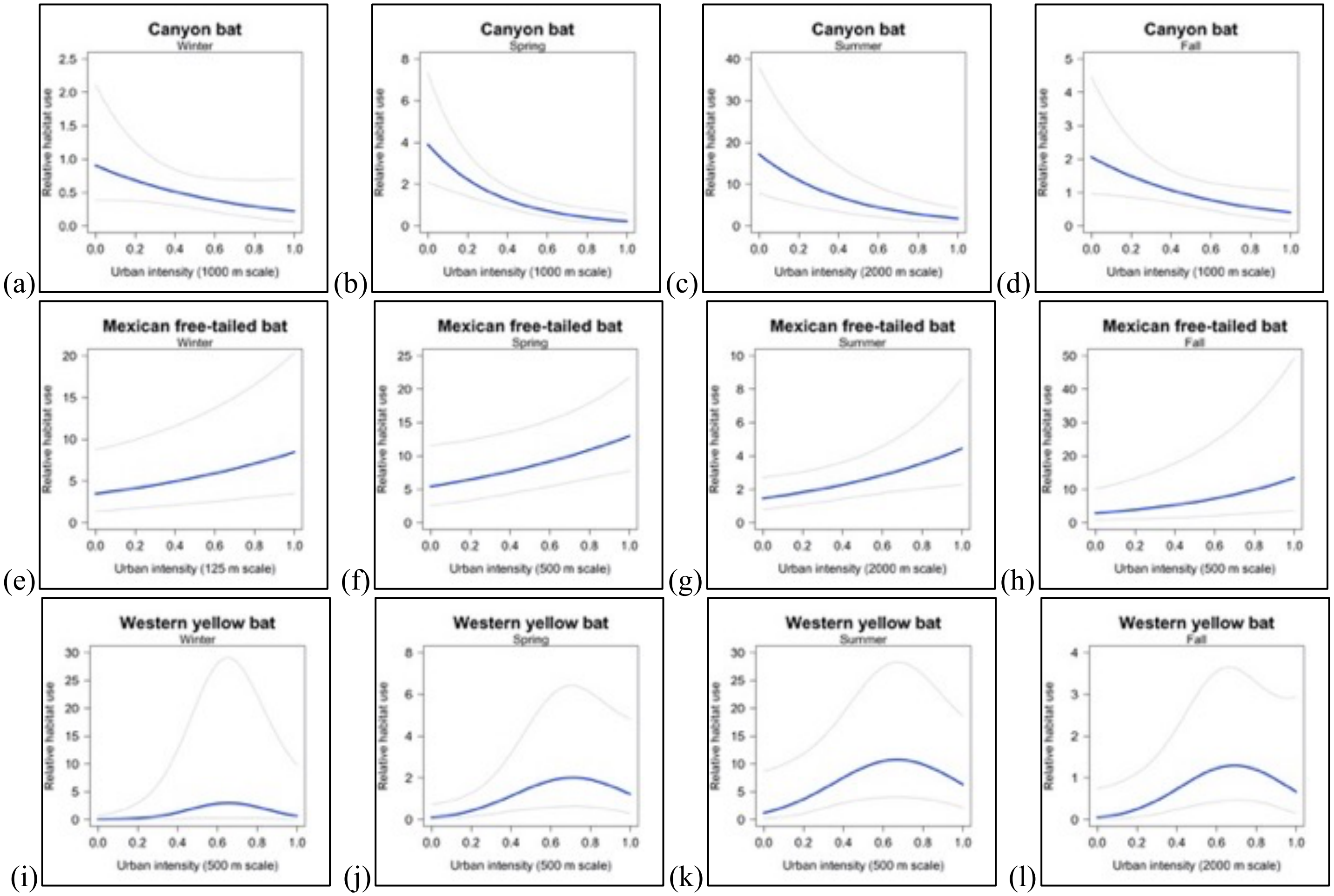

Figure 1.2: Several bat species exhibited consistent relationships with urbanization across seasons. Predicted relative habitat use (with associated 95% confidence intervals) based on Royle-Nichols (RN) models across the gradient of urbanization (from low to high urban intensity) for the canyon bat (i.e., urbanization avoider) in the (a) winter, (b) spring, (c) summer, and (d) fall, the Mexican free-tailed bat (i.e., urbanization exploiter) in the (e) winter, (f) spring, (g) summer, and (h) fall, and the western yellow bat (i.e., urbanization adapter) in the (i) winter, (j) spring, (k) summer, (l) and fall season. Note that the y-axes are on different scales.

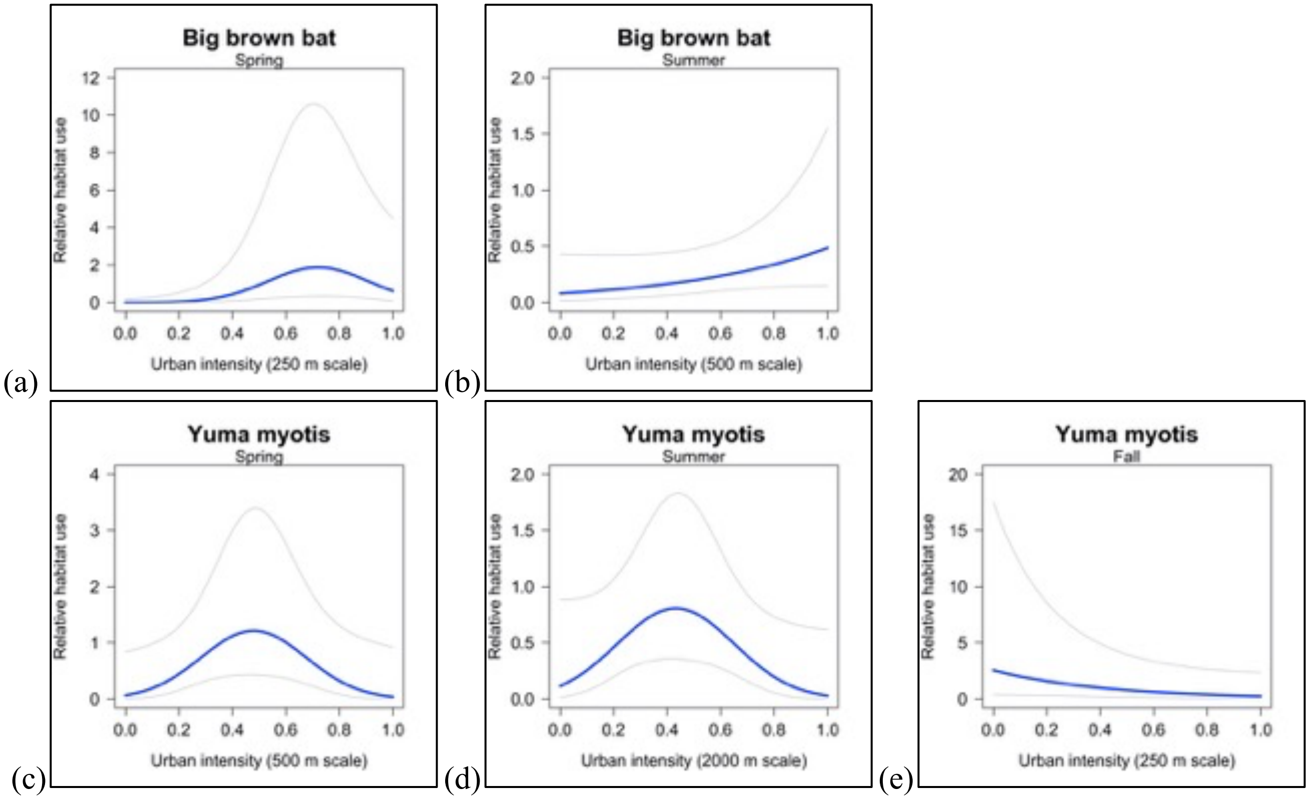

Figure 1.3: Some bat species shifted their response to urbanization (i.e., urbanization category) across seasons. Predicted relative habitat use (with associated 95% confidence intervals) based on Royle-Nichols (RN) models across the gradient of urbanization (from low to high urban intensity) for the big brown bat in the (a) spring (i.e., urbanization adapter) and (b) summer (i.e., urbanization exploiter), and the Yuma myotis in the (c) spring (i.e., urbanization adapter), (d) summer (i.e., urbanization adapter), (e) and fall (i.e., urbanization avoider) season. Note that the y-axes are on different scales.

CHAPTER 2

SPECIES RICHNESS OF BATS DECLINES ACROSS THE GRADIENT OF URBANIZATION IN AN ARID REGION

1. Abstract

Wildlife communities exhibit varying patterns of species richness across environmental gradients and respond to a diversity of landscape and anthropogenic factors. In particular, urbanization is a rapidly growing driver of ecological change and occurs across a gradient of intensity from low- to high-density development. Species richness (the number of species present) can potentially exhibit varying patterns across the gradient of urbanization, where species richness can either decrease linearly or peak at intermediate levels of urbanization, consistent with the intermediate disturbance hypothesis (IDH). However, additional research is necessary to understand patterns of species richness across the gradient of urbanization for many important species groups, particularly in understudied regions, such as arid environments. Our objectives were to evaluate species richness of bats (1) along the gradient of urbanization and (2) in response to plant productivity and distance to water. We predicted that species richness of bats would decrease with increased urban intensity if high levels of urbanization had an overall negative effect on the bat community. In contrast, we predicted that species richness of bats would peak at intermediate levels of urbanization, consistent with the IDH, if moderate levels of urbanization provided resources that bats were able to exploit. We also predicted that the bat community would exhibit a positive relationship with plant productivity and a negative relationship with distance to water. To test these hypotheses, we used stationary acoustic bat monitors to sample 50 sites along the gradient of urbanization in the Phoenix metropolitan area in the summer season. We identified a total of 14 bat species during 250 survey nights. Consistent with predictions, species richness of bats decreased with increasing urban intensity, indicating that high levels of urbanization had a negative effect on most bats in the community. In addition, species richness of bats exhibited a negative relationship with distance to water, indicating that species richness was increased in areas closer to water. However, counter to predictions, species richness of bats did not appear to exhibit a strong relationship with plant productivity. These results have important management and conservation implications for the bat community. To increase species richness of bats in urbanized areas, it is likely important to maintain food and water resources in urbanized areas and to increase landscape connectivity from wildland areas to urbanized areas. To maximize species richness of bats in wildland areas, it is likely important to maintain high-quality undeveloped habitat for bats that are sensitive to urbanization.

2. Introduction

The number of species that occur in an area (i.e., species richness) varies across environmental gradients (Mayor et al. 2015; McDonnell and Hahs 2008; McKinney 2008), and is a fundamental community characteristic that responds to a diversity of landscape and anthropogenic factors (Chiba 2007; Currie, Francis, and Kerr 1999; Hawkins et al. 2003; Stein, Gerstner, and Kreft 2014; Udy et al. 2021). In particular, urbanization is a rapidly growing driver of ecological change (McDonald, Kareiva, and Forman 2008; Seto, Parnell, and Elmqvist 2013; Grimm et al. 2008), which can directly and indirectly modify the landscape through land conversion and human activities (Grimm et al. 2008; Seto, Parnell, and Elmqvist 2013) and strongly influence plant and animal populations and communities (McDonald, Kareiva, and Forman 2008; McKinney 2002, 2008). However, the effect of urbanization on biodiversity varies across the gradient of urbanization, from undeveloped wildlands to low-density development to high-density urbanized areas (McDonnell and Pickett 1990; McKinney 2002). Across this gradient, urbanization can create novel patterns of wildlife communities, with species demonstrating positive or negative population effects in response to varying levels of urbanization (Angold et al. 2006; Grimm et al. 2008).

For wildlife communities, species richness can exhibit varying patterns across the gradient of urbanization and in relation to other environmental factors. For example, species richness for vertebrates and invertebrates can peak in wildland areas and decrease with increasing levels of urbanization (Cavia, Cueto, and Suárez 2009; Chace and Walsh 2006; McKinney 2006, 2008; Piano et al. 2020), indicating that urbanization can have an overall negative effect on species richness. In contrast, species richness (i.e., as reported for birds, small mammals, invertebrates, and plants) can peak at intermediate levels of urbanization, where environmental heterogeneity is assumed to be the highest, which is consistent with the intermediate disturbance hypothesis (IDH) (Blair and Launer 1997; Connell 1978; Grimm et al. 2008; McKinney 2008; Racey and Euler 1982). In addition, landscape characteristics, such as plant productivity and water, can have a positive effect on species richness (Hawkins et al. 2003; Koh, Lee, and Lin 2006; Lisón and Calvo 2011). Regional climate can also influence species richness. For example, species richness in some arid regions can decrease with increasing intensity of some disturbance types, in contrast to the hump-shaped pattern consistent with the IDH in more mesic areas (Gao and Carmel 2020).Ultimately, some important and understudied species groups potentially can exploit anthropogenic resources in unique climatic regions, which provides an opportunity to test hypotheses of how species richness varies across ecological gradients in novel environments.

Bats are a highly diverse group of mammals that play important roles in ecosystems around the world (Agosta 2002; Jones et al. 2009; Russo and Ancillotto 2015) and exhibit a wide range of responses to urbanization. Urbanization can have positive or negative effects on bats, which can influence their populations and use of urbanized areas. In temperate, tropical, and grassland systems, species richness of bats tends to decrease as urbanization increases (Avila-Flores and Fenton 2005; Coleman and Barclay 2011; Hourigan, Johnson, and Robson 2006; Jung and Kalko 2011; Kurta and Teramino 1992). Across other ecological gradients, species richness of bats can exhibit a positive relationship with plant productivity and water availability (Korine et al. 2015; Laverty and Berger 2021; Lisón and Calvo 2011). However, in arid regions climate differs significantly among seasons and variable precipitation can create large fluctuations in food and water availability (Gedir et al. 2020; Noy-Meir 1973; Van de Ven, McKechnie, and Cunningham 2019). Furthermore, urbanized environments in desert regions can have higher plant productivity and more consistent water sources than the surrounding wildland areas in some seasons, such as during the hot and dry summer months (Brown, Valone, and Curtin 1997; Korine et al. 2015; Razgour, Korine, and Saltz 2010; Russo, Cistrone, and Jones 2012; Shochat et al. 2006). Therefore, conditions in arid regions could produce novel patterns of species richness along the gradient of urbanization.

Arid ecosystems can exhibit strong contrasts in resource availability among wildland, low, moderate, and highly urbanized areas, which can potentially shape bat communities in novel ways. Bats can be particularly affected by food and water availability in arid regions, but availability of these resources can be strongly altered by human development (Bazelman 2016; Korine et al. 2015; Korine et al. 2016; Loumassine et al. 2020; Razgour, Korine, and Saltz 2010; Russo, Cistrone, and Jones 2012). Urbanized areas in arid regions can potentially have a positive effect on some bat species by increasing water availability through human-made bodies of water that are often more permanent than natural water sources (Korine et al. 2015; Razgour, Korine, and Saltz 2010; Russo, Cistrone, and Jones 2012). In addition, an increase in water availability in urbanized areas can increase vegetation productivity and foraging opportunities (Korine et al. 2015; Razgour, Korine, and Saltz 2010; Shochat et al. 2006; Straka et al. 2020). Therefore, some bat species might exhibit increased populations in urbanized environments to use these limiting resources. Although species richness of bats can decrease along the urbanization gradient (Avila-Flores and Fenton 2005; Coleman and Barclay 2011; Hourigan, Johnson, and Robson 2006; Jung and Kalko 2011; Kurta and Teramino 1992), it is unclear how patterns of species richness vary across the gradient of urbanization in an arid region, where there is expected to be increased food and water resources in urbanized areas.

The overall objective of this study was to evaluate how species richness of bats responded to the gradient of urbanization in an arid environment in relation to urban intensity, plant productivity, and distance to water. This study was conducted in the southwestern United States, which is one of the hottest and driest regions in North America and also supports the highest number of bat species on the continent (Ammerman, Hice, and Schmidly 2012; Arizona Game and Fish Department 2021; Frey, MacDonald, and Cook 2006).In addition, the Phoenix metropolitan area is one of the largest urbanized regions in the US and continues to expand (U.S. Census Bureau 2018). The specific objectives of our study were to (1) test hypotheses of how species richness of bats varied across the gradient of urbanization and (2) evaluate the response of the bat community to other landscape variables, plant productivity and distance to water. If high levels of urbanization had an overall negative effect on the bat community, we predicted that species richness of bats would decrease with increased urban intensity. In contrast, if moderate levels of urbanization provided resources that bats could exploit, we predicted that species richness of bats would peak at intermediate levels of urbanization, as consistent with the intermediate disturbance hypothesis. Overall, it was predicted that species richness of bats would exhibit a positive relationship with plant productivity and negative relationship with distance to water, due to assumed increased food (i.e., insects) and water resources in these areas.

3. Methods

3.1 Study Area

The study area was located in the Phoenix metropolitan area, Arizona, USA, which exhibits a gradient of urbanization, from undeveloped wildland to highly urbanized areas (Figure 1.1). The region is one of the most urbanized areas in the United States, which continues to rapidly urbanize (Luck and Wu 2002; U.S. Census Bureau 2018; Wu et al. 2011). The Phoenix metropolitan area is in the northern Sonoran Desert and is characterized by a hot and dry climate with an average summer temperature of 30.8°C, an average winter temperature of 11.3°C, and an annual precipitation of around 180 mm (Buyantuyev, Wu, and Gries 2010; Wu et al. 2011). The climate supports desert and riparian vegetation including the saguaro cactus (*Carnegiea gigantea*), paloverde (*Parkinsonia spp.*), creosote bush (*Larrea tridentate*), Fremont cottonwood (*Populus fremontii*), and Arizona willow (*Salix arizonica*) (Buyantuyev, Wu, and Gries 2010; Grimm and Redman 2004). Throughout the valley, over 290 km of canals bring water from the Colorado, Salt, and Gila Rivers to residents, providing year-round water sources (Ellin 2010; Roach et al. 2008).

3.2 Sampling Design

We used 2010 National Agriculture Imagery Program (NAIP) imagery with 1x1 m resolution (X. Li 2015) to create an urban intensity layer, which was calculated as the proportion of urbanization (impervious surfaces) within a 1000 m radius buffer around each sampling location. Across the gradient of urbanization, we used a stratified random sampling design to select 10 sites in each of five strata of urban intensity ranging from undeveloped to highly developed (urban intensity ranges for the categories included 0-0.005, 0.006-0.17, 0.18-0.35, 0.36-0.53, and 0.54-0.81). Sites occurred below an elevation of 550 m to control for changes in temperature, topography, and vegetation, and were at least 1.5 km away from each other. We also avoided sampling areas associated with agriculture.

At each of the 50 sampling locations, one stationary, passive acoustic bat monitor was used to survey for five consecutive nights per season, from sunset to sunrise (Britzke, Gillam, and Murray 2013). All sites were surveyed during each of the four seasons in 2019: winter (January 7th – March 1st), spring (April 8th – May 31st), summer (July 8th – August 30th), and fall (October 7th – November 29th). The sites were divided into six groups, where each group contained eight or nine sites in proximity, that were surveyed in a random order every season. If a survey was not completed due to weather events, monitor malfunctions, or vandalism, then the site was resurveyed at the end of the season. Each site was surveyed using one SM4BAT- FS acoustic bat monitor with a vertically positioned SMM-U2 microphone (Wildlife Acoustics, Maynard, MA). To standardize the sampling of locations and reduce potential sampling bias, the microphone was placed 3 to 5 m off the ground, positioned within a potential bat flyway, and not within 15 m of water or large pavement surfaces, such as roads, to avoid sound interference (Britzke, Gillam, and Murray 2013; Weller and Zabel 2002). The microphone was also not directly below vegetation clutter, artificial light, or powerlines to avoid a possible behavior change, and thus an echolocation call change, in bats (Britzke, Gillam, and Murray 2013).

Monitor settings were configured to maximize likelihood of capturing calls from bats in the Phoenix region, with call frequencies ranging from 8-60 kHz, and to filter out ambient noise as much as possible (Reichert et al. 2018).

3.3 Species Identification

To identify species, we used a combination of automated and manual identification of bat calls collected from the acoustic monitors, following the North American Bat Monitoring Program (NABat) guidelines (Reichert et al. 2018). First, all bat calls were imported into SonoBat 4.2.2 (SonoBat, Arcata, CA), where we used the software’s automated process to remove noise files and identify species, with associated levels of confidence. Next, we manually identified bat calls by evaluating each call’s characteristics and metrics. Only search-phase, or commuter, calls (i.e., calls produced while a bat navigates its environment) were used for manual identification because other call types, such as approach-phase calls or social calls, are less consistent and would have high overlap in call metrics among some species (Britzke, Gillam, and Murray 2013; Reichert et al. 2018). A species was considered to be confidently identified if the call metrics were within the typical ranges observed for that species and if there were at least five (three for rare or quiet species, such as *Eumops perotis*) consecutive search-phase call pulses with even inter-pulse intervals from one individual with no interference from another bat (Reichert et al. 2018). Positively identified bat call were considered independent if they occurred >15 minutes apart. Using this process, a voucher file (i.e., one high quality, confidently identified recording per species per monitoring night; Reichert et al. 2018) was produced and used in analyses.

The expected regional pool of bat species for our study area depended on the geographic and elevation range of Arizona bat species during each season. Out of the 28 bat species recorded in Arizona, we expected 15 species to be present in the Phoenix metropolitan area, 11 of which were expected to be present year-round (Appendix A). It can be difficult to confidently, acoustically identify some species since multiple species can share similar call metrics. We therefore combined *Nyctinomops femorosaccus* and *Nyctinomops macrotis* calls into *Nyctinomops sp.,* as the species are acoustically indistinguishable from each other. In addition, myotis bat species that produce calls within the 35-45 kHz range (i.e., *Myotis auriculus, Myotis ciliolabrum, Myotis occultus, Myotis velifer* and *Myotis volans*) were classified as "40 kHz Myotis" due to high overlap in call characteristics (Corcoran and Conner 2012; Reichert et al. 2018). Calls classified as 40 kHz myotis species are most likely *Myotis velifer*, as the other species are either more likely to occur outside of the study area or are more likely to be found at higher elevations (Appendix A). However, we still classified these calls as "40 kHz Myotis" since some of the species more likely to be found at higher elevations could potentially travel through the study area.

3.4 Environmental and Landscape Variables

We evaluated two environmental variables that we expected to influence species detection probability: mintemp and moon. The variable "mintemp" was defined as the average minimum temperature across the five survey nights, or occasions (Caryl et al. 2016; Thornton et al. 2020). In addition, the variable “moon” was defined as the average percent lunar illumination at 23:00 hours (UTC-7) averaged across the five occasions (Allen et al. 2009; NASA 2019; Scanlon and Petit 2008) It was hypothesized that these variables would influence species detection because bat species vary in their response to temperature and lunar illumination, with some species more sensitive to heat and high lunar illumination, and other species more tolerant of heat and high lunar illumination (Erickson and West 2002; Saldaña-Vázquez and Munguía-Rosas 2013; Scanlon and Petit 2008). We predicted that the bat community would either exhibit no relationship with temperature or a negative relationship with temperature during the summer season. In addition, if most species exhibit lunar phobia, then we expect the bat community to exhibit a negative relationship with lunar illumination.

In addition, we evaluated three landscape variables that we expected to influence the occupancy of each species, and thus species richness: urbanization, plant productivity, and distance to water. The variable “urbanization” was measured at multiple scales and was defined as the proportion of urbanization (impervious surface) within a buffer (i.e., 125, 250, 500, 1000 and 2000 m radius) associated with a site (X. Li 2015). To evaluate non-linear relationships with urbanization, we also evaluated the quadratic relationship for urbanization. In addition, the variable “plant productivity” was defined as the normalized difference in vegetation index (NDVI) associated with a site, averaged across the summer season, and was measured at multiple scales (i.e., 125, 250, 500, 1000 and 2000 m radius buffers). Lastly, using Google Earth (Google, Mountain View, CA) and

2015 NAIP imagery (Zhang and Turner II 2020), we identified perennial water sources that were >7 m in length or width, including swimming pools (Hall et al. 2016; Nystrom and Bennett 2019; Razgour, Korine, and Saltz 2010). Using this information, we evaluated the variable “water”, which was the distance from each site to the nearest water source. It was hypothesized that plant productivity and water were important covariates to consider in part because it was assumed that insect abundance would be higher in areas with increased plant productivity (Haddad et al. 2001; Lightfoot and Whitford 1989; Siemann 1998) and increased water (Straka et al. 2020) which is particularly important for insectivorous bats. We considered evaluating a landscape heterogeneity metric “dissimilarity” (Farwell et al. 2020), but we excluded the covariate because it was highly correlated ($r > 0.60$) with other covariates across most scales.

To aid in model convergence, all continuous variables were standardized by subtracting the sample mean and dividing by the standard deviation (Schielzeth 2010). We evaluated the correlation between all variables using a Pearson’s correlation test and we did not include covariates that were highly correlated ($r > 0.60$) in the same model.

3.5 Statistical Analysis

For our analysis, we used detection/non-detection data, where a species was either detected (1) or not detected (0) during an occasion (e.g., night). There were a total of 5 occasions (i.e., nights) per site during the summer season.

We used a Dorazio-Royle (DR) multispecies occupancy community model with data augmentation to estimate (a) occupancy probability (ψ; the probability that a site was occupied or used by the species), and (b) detection probability (p; the probability of detecting the species given that it was present at a site) and (c) species richness (Nsite; species richness at a site) (Dorazio and Royle 2005; Kery and Royle 2015). The DR community model is a hierarchical model that treats species-specific parameters as random effects (Kery and Royle 2015). We included 4 augmented species (Kery and Royle 2015) to account for the 18 species (i.e., 15 expected species and 3 rare species; Appendix A) that could potentially be in the study area (Adams 2003; Arizona Game and Fish Department 2020; Bat Conservation International 2021). Rare species included the Allen's lappeted bat, silver-haired bat, and spotted bat, which are believed to either potentially occur in the study area or be infrequent visitors based on landscape characteristics, broad-scale range maps, or historical records (Adams 2003, Arizona Game and Fish Department 2020). We evaluated models using the JAGS program (Plummer 2003) and jagsUI package (Kellner, Kellner, and System Requirements 2021) in program R (R Development Core Team 2020).

For our model selection process, we first determined whether detection covariates (i.e., mintemp or moon) informed detection probability. We compared a model with constant detection probability (p(.)) to a model where detection probability varied with mintemp (p(mintemp)), moon (p(moon)), and mintemp and moon (p(mintemp + moon)). If p(mintemp), p(moon), or p(mintemp+moon) were more supported than p(.) based on the Deviance Information Criterion (DIC; Spiegehalter et al. 2014), then the detection variable(s) was included in all subsequent models. Next, we determined the best scale (i.e., 125-2000 m radius buffer) for urbanization and plant productivity by evaluating which scale in univariate models was most supported based on DIC. To evaluate whether there was evidence of a non-linear relationship with urbanization, we compared model support for the linear and quadratic relationships for urbanization using DIC. Finally, using the best scales for each covariate, we evaluated all possible model combinations. We considered a variable as informative if it occurred in a model that outperformed the intercept-only model (i.e., model without covariates).

4. Results

Across our 50 sites during the summer season, we identified a total of 14 bat species during 250 nightly occasions, where the number of occasions bats were detected ranged from 3 to 184 (Table 1.1).

Dorazio-Royle (DR) community occupancy model results supported our hypothesis that species richness of bats would decline across the gradient of urbanization (Table 2.1; Figure 2.2; Appendix K). The bat community exhibited a negative relationship with urbanization (β = -1.35, se = 0.65), and urbanization was included in the top three models (Table 2.1; Figure 2.2).

In addition to urban intensity, the bat community was influenced by distance to water, but not plant productivity (Table 2.1). Consistent with predictions, the bat community exhibited a negative relationship with distance to water (β = -0.90, se = 0.36), indicating that species richness increased in areas closer to water (Table 2.1; Figure 2.3). However, counter to predictions, the bat community did not appear to be strongly influenced by plant productivity (Table 2.1). Plant productivity did not occur in the top model, and the bat community did not exhibit a strong relationship with plant productivity (β = -0.33, se = 0.30) in the topmost model in which the variable occurred (Table 2.1).

DR community model results demonstrated that minimum temperature and lunar illumination had some effect on the detection probability of bats (Table 2.1). Minimum temperature and lunar illumination appeared to be important detection probability variables, where models including those variables outperformed the intercept model. However, counter to predictions, there were no strong relationships between the bat community and minimum temperature (β = 0.16, se = 0.22) or lunar illumination (β = -0.19, se = 0.23), potentially due to different responses to the detection variables among species in the summer season (Chapter 1; Table 2.1).

5. Discussion

The bat community in our study exhibited a declining pattern of species richness across the gradient of urbanization, which is consistent with increasing urbanization exhibiting an overall negative effect on species richness of bats (Cavia, Cueto, and Suárez 2009; Chace and Walsh 2006; McKinney 2006, 2008; Piano et al. 2020). The declining pattern of species richness of bats was consistent with other research in the study area demonstrating that most bats (i.e., big/pocketed free tailed bat, canyon bat, hoary bat, pallid bat, silver-haired bat, western mastiff bat, and 40 kHz Myotis) were associated with wildland areas and low levels of urbanization, with only a few bats (i.e., big brown bat, Mexican free-tailed bat, western yellow bat, and Yuma myotis) exhibiting high use of areas of moderate and high levels of urbanization (Chapter 1). The negative effect of urbanization on species richness of bats is likely related to species traits, where most bats in the community tended to be sensitive to anthropogenic disturbances or have traits (i.e., weak flight and low mobility) that decrease the bats' ability to access available resources in urbanized areas (Avila-Flores and Fenton 2005; Jung and Kalko 2011; Jung and Threlfall 2018).

Further, counter to predictions, species richness of bats did not peak at moderate levels of urban intensity, as predicted by the intermediate disturbance hypothesis (IDH), even though important resources (i.e., food and water) and environmental heterogeneity were assumed to be greater in moderately urbanized areas compared to wildland areas (Blair and Launer 1997; Connell 1978; Grimm et al. 2008; McKinney 2008). Further, in arid regions, urbanized areas can have greater plant productivity and water availability compared to wildland areas, particularly in the hot and dry summer season (Brown, Valone, and Curtin 1997; Faeth et al. 2005; Korine et al. 2015; Razgour, Korine, and Saltz 2010; Russo, Cistrone, and Jones 2012; Shochat et al. 2006). However, species richness may tend to decline across some disturbance gradients in more arid regions, opposed to exhibiting a hump shaped pattern in more mesic regions (Gao and Carmel 2020). Therefore, species richness of bats, and potentially other vertebrates, could be more likely to decrease across the gradient of urbanization in arid environments, despite limited resources in wildland areas and increased resources in urbanized environments during the hot and dry summer season.

In addition to urbanization, species richness of bats exhibited a negative relationship with increasing distance to water, demonstrating that species richness of bats was increased in areas closer to water. This is consistent with our expectations, as water can be an important resource for desert bat communities (Ancillotto et al. 2019; Korine et al. 2016; H. Li and Wilkins 2014; McCain 2007; Mendes et al. 2017; C. Threlfall et al. 2011) and to positively influence species richness of bats (Hawkins et al. 2003; Lisón and Calvo 2011). Counter to predictions, however, species richness of bats did not appear to be influenced by plant productivity. This was potentially due to differences in responses of bats to plant productivity among species in the summer season (Chapter 1), or due to plant productivity not being an effective proxy for food resources (i.e., insect abundance; Bollinger et al. 2020a, 2020b; Jaganmohan, Vailshery, and Nagendra 2013; Rowse et al. 2016).

There are several considerations when interpreting the results of this study. First, species richness was likely underestimated in wildland areas. For example, the rare species (i.e., Allen's lappeted bat, spotted bat, and silver-haired bat) that potentially occurred in our study area also tended to be associated with wildland areas (Appendix A; Adams 2003, Arizona Game and Fish Department 2020). Further, some bat species are difficult to detect with acoustic monitors, such as bats that produce low intensity (i.e., "quiet") echolocation calls (i.e., Allen's lappeted bat, California leaf-nosed bat, pallid bat, spotted bat, and Townsend's big-eared bat) (Reichert et al. 2018). Additionally, the Allen's lappeted bat, pallid bat, spotted bat and Townsend's big-eared bat tended to associate more with wildland areas than more urbanized areas (Adams 2003, Arizona

Game and Fish Department 2020). Second, our study focused on the summer season, when the most bat species and detections occurred in the study area (Chapter 1, Table 1.1) and when resource availability was expected to exhibit the greatest differences between wildland and urbanized areas (Brown et al. 1997, Shochat 2006, Razgour et al. 2010, Russo et al. 2012, Korine et al. 2015). However, bat species occurred in the study area during other seasons (Chapter 1, Table 1.1), where it is possible that species richness of bats would exhibit an even stronger negative relationship with urbanization compared to the summer season, as bats are expected to exhibit their highest use of urbanized areas in the summer season (Korine et al. 2015; Razgour, Korine, and Saltz 2010; Shochat et al. 2006; Straka et al. 2020). However, species richness of bats could potentially increase in urbanized areas in cooler seasons, where temperatures are expected to be higher compared to wildland areas (Golden 2004; Grimm et al. 2008), which could potentially increase bat activity. Further, species richness could also potentially be relatively high in urbanized areas during the spring and fall seasons due to an increase in migratory species moving through the area (Cryan 2003). Third, precipitation from monsoon rains during the summer season (July-August) could potentially influence species richness across the gradient of urbanization. During this study, the monsoon season exhibited below average precipitation, and was classified as one of the driest summers during the last 100 years (National Oceanic and Atmospheric Administration 2021). Thus, due to assumed limiting water and food resources, we would expect that bats might be more likely to increase their use of urbanized areas during the summer of this study, compared to years with above average summer precipitation when wildland areas would be expected to exhibit greater water resources. Lastly, there are other community factors we were unable to measure that could influence species richness of bats across the gradient of urbanization, such as competition, species-interactions, and predator-prey relationships (Fox and Fox 2000; Sandom et al. 2013; Shurin and Allen 2001). For example, the Mexican free-tailed bat can exhibit high use in urbanized areas (Avila-Flores and Fenton 2005; Bredt and Uieda 1996; Krauel and LeBuhn 2016), potentially competing with and excluding some species that could access available resources in urbanized areas, which could ultimately reduce species richness.

Consistent with other regions, species richness of bats declined across the gradient of urbanization in an arid region (Avila-Flores and Fenton 2005; Coleman and Barclay 2011; Hourigan, Johnson, and Robson 2006; Jung and Kalko 2011; Kurta and Teramino 1992),. This may be due to the majority of bats in the community being sensitive to anthropogenic disturbances and expressing traits that decrease their ability to access resources in urbanized areas. Therefore, the cost of urbanization appears to outweigh the benefits of bats obtaining resources in urbanized environments, even in an arid region where food and water resources can potentially be limiting in wildland areas during the hot and dry summer season. Ultimately, these results have important management and conservation implications. To increase species richness in urbanized areas, it is likely important to maintain food and water resources in urbanized areas (Ancillotto et al. 2019; de Araújo and Bernard 2016; Lepczyk et al. 2017) and landscape connectivity between wildland and urbanized areas, such as by maintaining flyways with low anthropogenic disturbance (i.e., light and noise pollution, human activity, and road density) (Bazelman 2016; Berthinussen and Altringham 2012; Bunkley et al. 2015; Frey-Ehrenbold et al. 2013; Haddock et al. 2019; Hale et al. 2012; Russo and Ancillotto 2015; Schaub, Ostwald, and Siemers 2008). In addition, to maximize species richness in wildland areas, large areas of high-quality undeveloped habitat with low anthropogenic disturbance and water sources should be preserved (Collas et al. 2017; Johnson, Gates, and Ford 2008; Krauel and LeBuhn 2016).

Table 2.1: Dorazio-Royle (DR) community occupancy model results for the bat community in the Phoenix metropolitan area, Arizona in the summer of 2019. Parameters include detection probability (p) and occupancy probability (psi). Models include the intercept-only model (p(.) psi (.)) and the variables include detection probability variables minimum seasonal temperature (T) and average percent moon illumination (M), and occupancy variables include urbanization (U), plant productivity (P), and distance to water (W). The most supported spatial scale (i.e., 125- 2000 m radius buffers) for urbanization and plant productivity follows the associated variable in the model description. Model results include the number of terms in the model (K), DIC value, delta DIC (ΔDIC), and community-average beta estimates for each variable, followed by the associated standard error (se).

					p								psi
					T		M		U		P		W
Model	K	DIC	ΔDIC	β	se	β	se	β	se	β	se	β	se
p(T + M) psi(U.1000 + W)	6	1655.79	0.00	0.16	0.22	-0.19	0.23	-1.35	0.65			-0.90	0.36
p(T + M) psi(U.1000 + P.125 + W)	7	1659.21	3.42	0.17	0.21	-0.23	0.23	-1.27	0.68	-0.33	0.30	-0.03	3.13
p(T + M) psi(U.1000)	5	1676.71	20.92	0.15	0.21	-0.28	0.25	-1.01	0.67				
p(T + M) psi(.)	4	1691.95	36.16	0.06	0.20	-0.05	0.21						
p(T + M) psi(W)	5	1699.68	43.89	0.09	0.20	-0.01	0.20					-0.43	0.33
p(T + M) psi(P.125)	5	1705.57	49.78	0.08	0.19	-0.09	0.20			0.51	0.18		
p(T + M) psi(P.125 + W)	6	1718.54	62.75	0.12	0.20	-0.03	0.20			0.05	0.23	-0.41	0.34
p(T + M) psi(U.1000 + P.125)	6	1723.67	67.88	0.16	0.21	-0.29	0.25	-1.07	0.72	0.25	0.28		
p(.) psi(.)	2	1770.34	114.55										

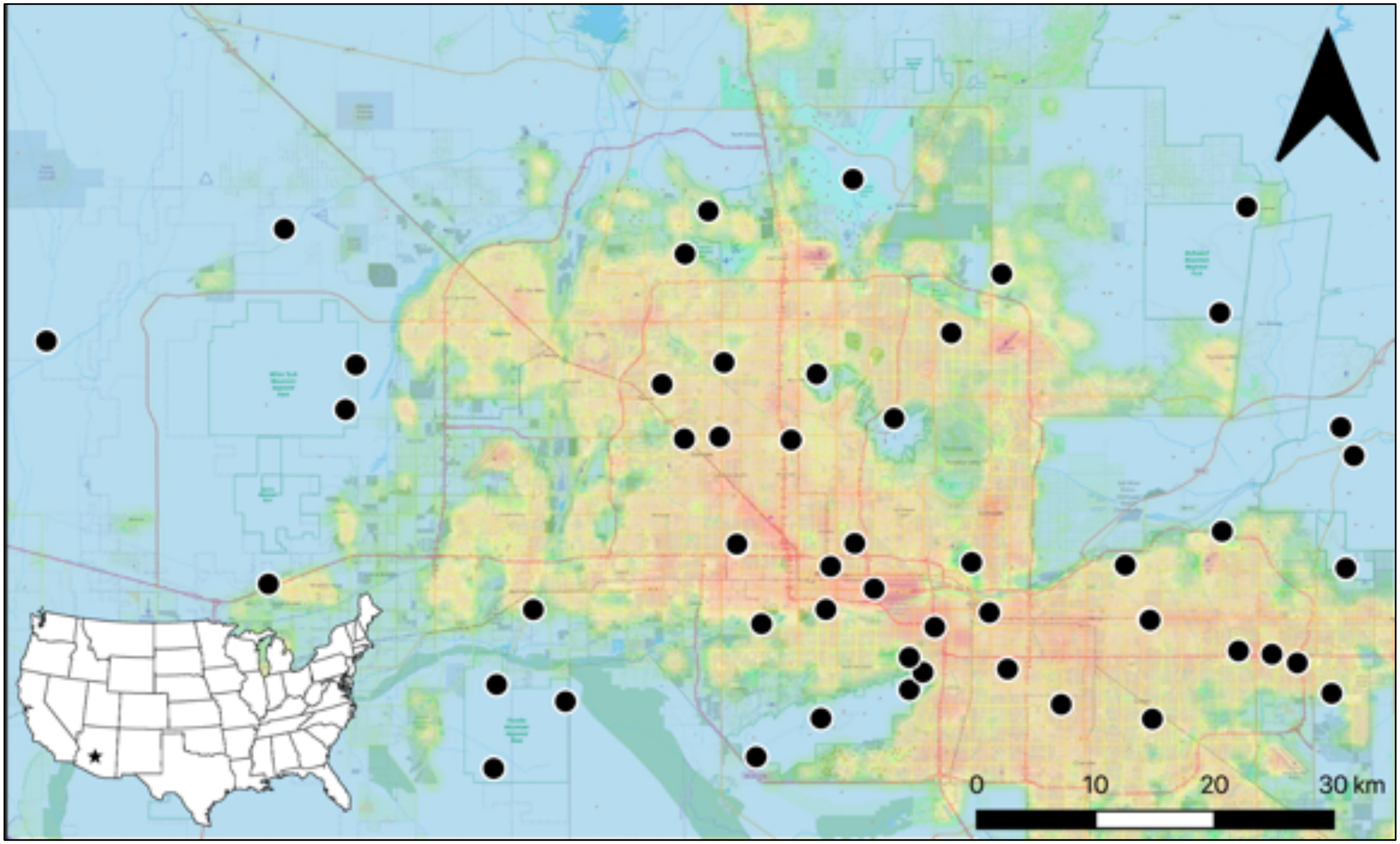

Figure 2.1: Fifty sampling locations (black circles) along the gradient of urban intensity from wildland areas (blue) to highly urbanized areas (red), in the Phoenix metropolitan area, Arizona.

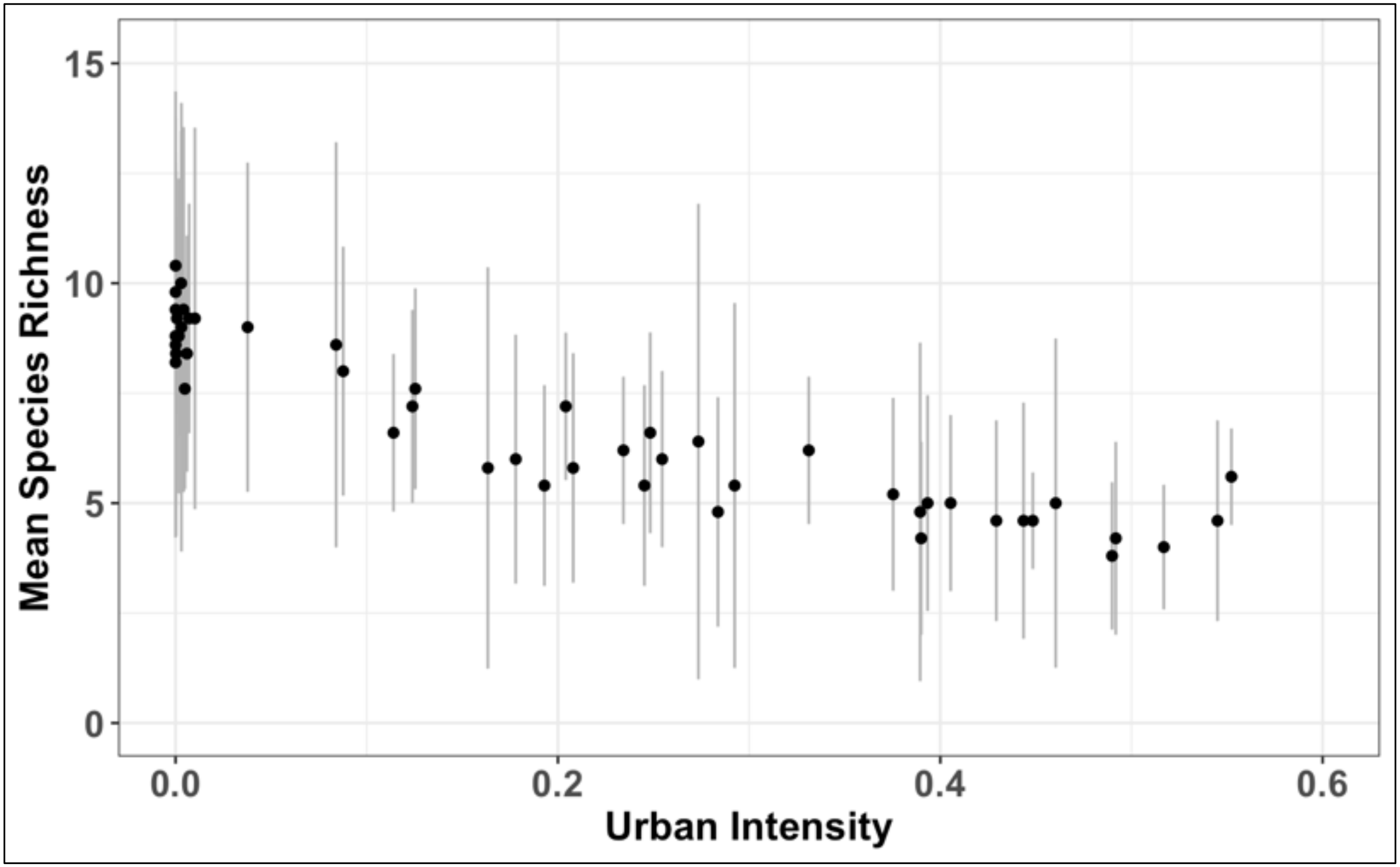

Figure 2.2: Predicted species richness of bats decreases along the gradient of urbanization (based on the top Dorazio-Royle (DR) community model) in the Phoenix metropolitan area, Arizona in the summer of 2019. The error bars represent 95% confidence intervals.

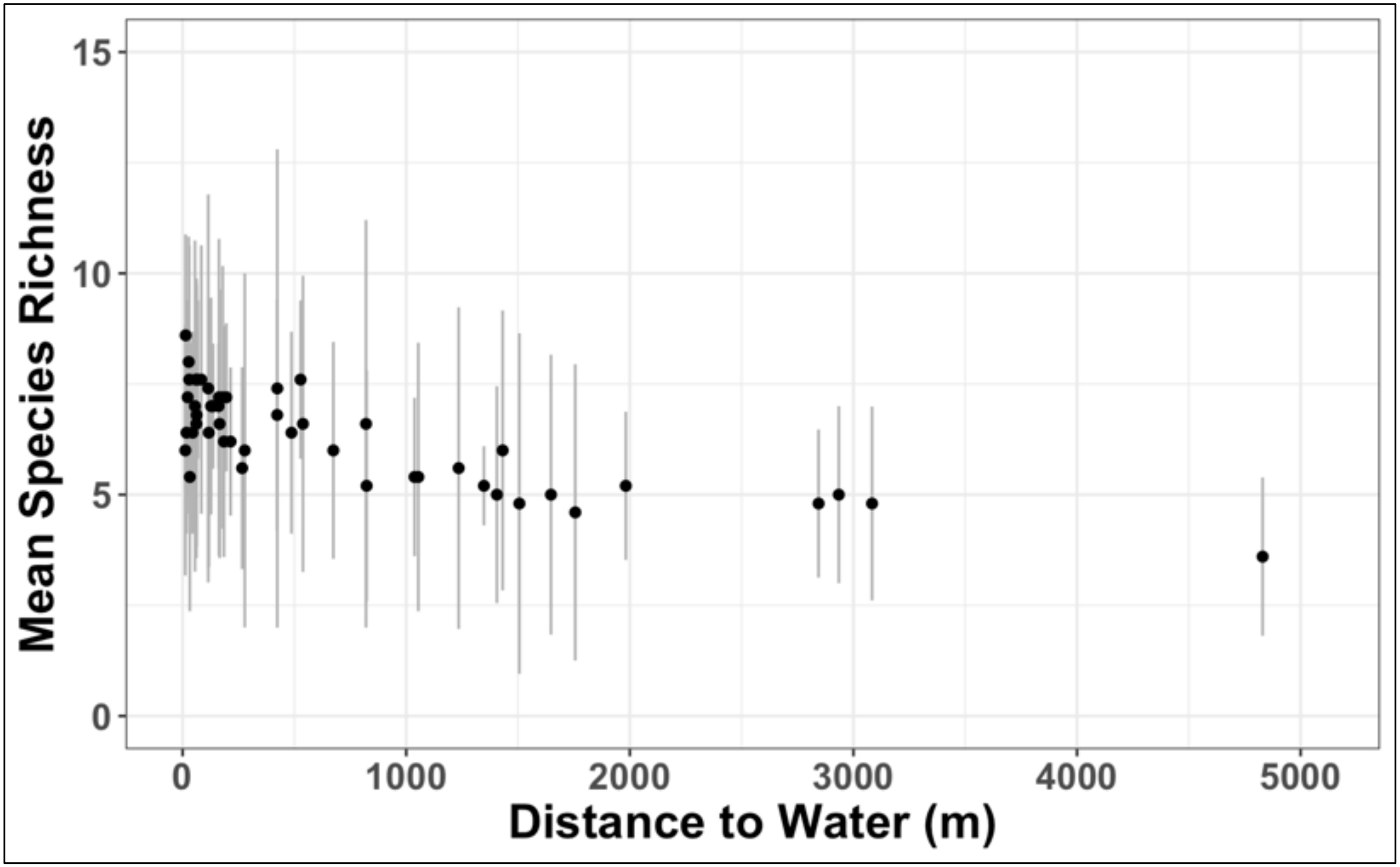

Figure 2.3: Predicted species richness of bats decreases with increasing distance to water (based on the top Dorazio-Royle (DR) community model) in the Phoenix metropolitan area, Arizona in the summer of 2019. The error bars represent 95% confidence intervals.

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APPENDIX A

LIST OF BAT SPECIES EXPECTED TO OCCUR IN THE STUDY AREA

Appendix A: List of known bat species in Arizona and whether they were expected to occur in the Phoenix metropolitan area based on published species information, including the seasons in which bat species were expected to occur in Arizona based on records and known migratory patterns, whether species were expected to occur in the study area between 280-550 m elevation, and whether species were considered rare in the study area. Species information was compiled from Adams (2003), Arizona Game and Fish Department (2020), Bat Conservation International (2021), Cryan (2003), and local bat experts (Dr. Marianne Moore, Arizona State University; Angie McIntire, Arizona Game and Fish Department; Janet Tyburec, Bat Survey Solutions)

Bat Species	Seasons Expected in Arizona	Range/Elevation in Study Area	Rare in Study Area
Allen's big-eared bat *Idionycteris phyllotis*	Year-round	Yes	Yes
Arizona myotis *Myotis occultus*	Year-round	No	No
Big brown bat *Eptesicus fuscus*	Year-round	Yes	No
Big free-tailed bat *Nyctinomops macrotis*	-	Yes	No
California leaf-nosed bat *Macrotus californicus*	Year-round	Yes	No
California myotis *Myotis californicus*	Year-round	Yes	No
Canyon bat *Parastrellus hesperus*	Year-round	Yes	No
Cave myotis *Myotis velifer*	Year-round	Yes	No
Fringed myotis *Myotis thysanodes*	Year-round	No	No
Ghost-faced bat *Mormoops megalophylla*	-	No	-
Hoary bat *Lasiurus cinereus*	Spr-Sum-Fall	Yes	No
Lesser long-nosed bat *Leptonycteris yerbabuenae*	Spr-Sum-Fall	No	-

Long-legged myotis *Myotis volans*	Year-round	No	No
Mexican free-tailed bat *Tadarida brasiliensis*	Year-round	Yes	No
Mexican long-tongued bat *Choeronycteris mexicana*	Winter	No	-
Pallid bat *Antrozous pallidus*	Year-round	Yes	No
Pocketed free-tailed bat *Nyctinomops femorosaccus*	-	Yes	No
Silver-haired bat *Lasionycteris noctivagans*	Spr-Sum	Yes	Yes
Small-footed myotis *Myotis ciliolabrum*	Year-round	No	-
Southwestern myotis *Myotis auriculus*	Spr-Sum	No	-
Spotted bat *Euderma maculatum*	Year-round	Yes	Yes
Townsend’s big-eared bat *Corynorhinus townsendii*	Year-round	Yes	No
Underwood’s mastiff bat *Eumops underwoodi*	Year-round	No	-
Western long-eared myotis *Myotis evotis*	Year-round	No	-
Western mastiff bat *Eumops perotis*	Year-round	Yes	No
Western red bat *Lasiurus blossevillii*	Spr-Sum	Yes	No
Western yellow bat *Lasiurus xanthinus*	Year-round	Yes	No
Yuma myotis *Myotis yumanensis*	Year-round	Yes	No

APPENDIX B

ROYLE-NICHOLS MODEL RESULTS

Appendix B: Results of habitat use based on Royle-Nichols (RN) models for 14 bat species in the Phoenix metropolitan area, Arizona during four seasons in 2019. Species include the big brown bat (Table B1), the big/pocketed free-tailed bat (Table B2), the California myotis (Table B3), the canyon bat (Table B4), the hoary bat (Table B5), the Mexican free-tailed bat (Table B6), the pallid bat (Table B7), the silver-haired bat (Table B8), the Townsend's big-eared bat (Table B9), the western mastiff bat (Table B10), the western red bat (Table B11), the western yellow bat (Table B12), the Yuma myotis (Table B13) and the 40 kHz Myotis (Table B14). Parameters include species specific detection probability (r) and relative habitat use (Lambda). Models include the intercept-only model (r(.) Lambda (.)) and the variables include urbanization (U), quadratic relationship for urbanization (UQ), plant productivity (P), the interaction between urbanization and plant productivity (UxP), the interaction between quadratic urbanization and plant productivity (UQxP), and distance to water (W). The most supported spatial scale (i.e., 125- 2000 m radius buffers) of urbanization and plant productivity follows the associated variable in the model description. Result tables include the number of terms in the model (K), AICc value, delta AICc (ΔAICc), model weight (wt), and beta estimates for each variable, followed by the associated standard error (se).

Table B1: RN model results for the big brown bat in the spring and summer season.

						U		UQ		P		UxP		UQxP		W	
Season	Model	K	AICc	ΔAICc	wt	β	se	β	se	β	se	β	se	β	se	β	se
Spring	r(.) Lambda(U.250 + UQ.250)	4	95.12	0.00	0.35	1.84	0.67	-1.22	0.54								
	r(.) Lambda(U.250 + UQ.250 + P.2000)	5	95.64	0.52	0.27	1.77	0.64	-1.09	0.53	0.47	0.34						
	r(.) Lambda(U.250 + UQ.250 + W)	5	96.94	1.82	0.14	2.24	0.87	-1.51	0.69							0.45	0.51
	r(.) Lambda(U.250 + UQ.250 + P.2000 + W)	6	97.17	2.05	0.13	2.30	0.87	-1.41	0.66	0.52	0.35					0.60	0.52
	r(.) Lambda(.)	2	100.31	5.19	0.03												
	r(.) Lambda(U.250 + UQ.250 + P.2000 + UxP + UQxP)	7	100.34	5.22	0.03	2.01	0.79	-1.30	0.64	0.29	0.45	-0.34	0.69	0.54	0.76		
	r(.) Lambda(P.2000)	3	100.94	5.82	0.02					0.43	0.34						
	r(.) Lambda(W)	3	101.17	6.05	0.02											-0.54	0.54
	r(.) Lambda(U.250 + UQ.250 + P.2000 + UxP + UQxP + W)	8	101.81	6.69	0.01	2.73	1.08	-1.73	0.80	0.29	0.50	-0.46	0.70	0.69	0.85	0.74	0.58
	r(.) Lambda(P.2000 + W)	4	102.02	6.90	0.01					0.41	0.33					-0.53	0.54
Summer	r(.) Lambda(P.125)	3	105.86	0.00	0.29					0.56	0.20						
	r(.) Lambda(U.500 + P.125)	4	105.95	0.09	0.28	0.53	0.34			0.63	0.21						
	r(.) Lambda(P.125 + W)	4	107.68	1.83	0.12					0.50	0.21					-0.36	0.54
	r(.) Lambda(U.500 + P.125 + UxP)	5	108.25	2.40	0.09	0.52	0.34			0.63	0.21	0.11	0.26				
	r(.) Lambda(U.500 + P.125 + W)	5	108.42	2.56	0.08	0.52	0.38			0.62	0.24					-0.03	0.55
	r(.) Lambda(.)	2	109.54	3.68	0.05												
	r(.) Lambda(W)	3	109.88	4.02	0.04											-0.68	0.60
	r(.) Lambda(U.500)	3	110.74	4.88	0.03	0.32	0.30										
	r(.) Lambda(U.500 + P.125 + UxP + W)	6	110.83	4.98	0.02	0.50	0.38			0.62	0.23	0.11	0.26			-0.05	0.56
	r(.) Lambda(U.500 + W)	4	112.00	6.15	0.01	0.18	0.35									-0.56	0.63

Table B2: RN model results for the big/pocketed free-tailed bat in the winter, spring, summer and fall season.

						U		P		UxP		W	
Season	Model	K	AICc	ΔAICc	wt	β	se	β	se	β	se	β	se
Winter	r(.) Lambda(U.1000)	3	123.09	0.00	0.72	-1.85	0.62						
	r(.) Lambda(U.1000 + W)	4	125.00	1.91	0.28	-1.65	0.67					0.16	0.22
	r(.) Lambda(W)	3	133.14	10.05	0.00							0.57	0.16
	r(.) Lambda(P.250 + W)	4	134.12	11.02	0.00			0.31	0.27			0.51	0.19
	r(.) Lambda(P.250)	3	137.36	14.26	0.00			0.55	0.26				
	r(.) Lambda(.)	2	139.76	16.67	0.00								
Spring	r(.) Lambda(U.2000)	3	134.06	0.00	0.31	-1.09	0.39						
	r(.) Lambda(U.2000 + P.2000 + UxP)	5	134.91	0.85	0.20	-1.13	0.42	0.05	0.33	-0.49	0.25		
	r(.) Lambda(U.2000 + P.2000)	4	135.10	1.04	0.18	-1.08	0.40	0.36	0.30				
	r(.) Lambda(U.2000 + W)	4	135.69	1.62	0.14	-1.35	0.51					-0.26	0.32
	r(.) Lambda(U.2000 + P.2000 + UxP + W)	6	136.83	2.76	0.08	-1.39	0.53	-0.07	0.37	-0.55	0.27	-0.26	0.33
	r(.) Lambda(U.2000 + P.2000 + W)	5	137.15	3.08	0.07	-1.29	0.52	0.31	0.31			-0.20	0.32
	r(.) Lambda(P.2000 + W)	4	142.09	8.02	0.01			0.52	0.31			0.36	0.21
	r(.) Lambda(.)	2	142.21	8.15	0.01								
	r(.) Lambda(P.2000)	3	142.21	8.15	0.01			0.45	0.30				
	r(.) Lambda(W)	3	142.54	8.48	0.00							0.30	0.20
Summer	r(.) Lambda(U.1000)	3	81.05	0.00	0.43	-2.67	1.27						
	r(.) Lambda(U.1000 + P.1000)	4	82.14	1.09	0.25	-2.91	1.24	0.60	0.45				
	r(.) Lambda(U.1000 + W)	4	83.41	2.36	0.13	-2.73	1.39					-0.04	0.38
	r(.) Lambda(U.1000 + P.1000 + UxP)	5	84.32	3.27	0.08	-2.56	1.21	0.15	0.94	-0.54	0.96		
	r(.) Lambda(U.1000 + P.1000 + W)	5	84.57	3.52	0.07	-2.85	1.27	0.65	0.51			0.08	0.39
	r(.) Lambda(U.1000 + P.1000 + UxP + W)	6	86.77	5.72	0.02	-2.38	1.23	0.20	0.85	-0.60	0.86	0.16	0.40
	r(.) Lambda(W)	3	90.82	9.77	0.00							0.56	0.22
	r(.) Lambda(P.1000 + W)	4	92.26	11.21	0.00			0.40	0.40			0.62	0.23
	r(.) Lambda(.)	2	93.00	11.95	0.00								
	r(.) Lambda(P.1000)	3	94.94	13.89	0.00			0.20	0.34				
Fall	r(.) Lambda(U.1000)	3	110.05	0.00	0.53	-2.42	0.95						
	r(.) Lambda(U.1000 + W)	4	112.41	2.36	0.16	-2.39	1.02					0.02	0.25
	r(.) Lambda(U.1000 + P.1000)	4	112.41	2.37	0.16	-2.42	0.95	0.00	0.31				
	r(.) Lambda(U.1000 + P.1000 +UxP)	5	113.99	3.95	0.07	-2.69	1.18	-0.72	0.73	-0.74	0.66		
	r(.) Lambda(U.1000 + P.1000 + W)	5	114.88	4.84	0.05	-2.39	1.03	0.01	0.33			0.02	0.26
	r(.) Lambda(U.1000 + P.1000 + UxP + W)	6	116.58	6.53	0.02	-2.67	1.27	-0.71	0.77	-0.73	0.67	0.01	0.27
	r(.) Lambda(W)	3	122.96	12.91	0.00							0.50	0.18
	r(.) Lambda(P.1000 +W)	4	123.98	13.93	0.00			0.37	0.32			0.57	0.20
	r(.) Lambda(.)	2	126.45	16.41	0.00								
	r(.) Lambda(P.1000)	3	128.33	18.29	0.00			0.18	0.29				

Table B3: RN model results for the California myotis in the spring and summer season.

						U		UQ		P		W	
Season	Model	K	AICc	ΔAICc	wt	*β*	se	*β*	se	*β*	se	*β*	se
Spring	r(.) Lambda(U.2000 + UQ.2000)	4	83.97	0.00	0.42	-0.61	0.94	-2.98	1.25				
	r(.) Lambda(U.2000 + UQ.2000 + P.2000)	5	84.60	0.63	0.31	-0.76	1.02	-3.04	1.3	0.51	0.39		
	r(.) Lambda(U.2000 + UQ.2000 + W)	5	86.17	2.20	0.14	-0.79	0.98	-2.76	1.34			-0.51	1.07
	r(.) Lambda(U.2000 + UQ.2000 + P.2000 + W)	6	87.18	3.22	0.08	-0.75	1.08	-3.08	1.47	0.52	0.42	0.05	1.1
	r(.) Lambda(P.2000)	3	91.13	7.16	0.01					0.63	0.39		
	r(.) Lambda(P.2000 + W)	4	91.22	7.25	0.01					0.58	0.38	-0.99	0.85
	r(.) Lambda(W)	3	91.24	7.28	0.01							-1.07	0.88
	r(.) Lambda(.)	2	91.64	7.67	0.01								
Summer	r(.) Lambda(P.2000 + W)	4	177.50	0.00	0.49					0.56	0.22	-1.02	0.56
	r(.) Lambda(U.500 + UQ.500 + P.2000 + W)	6	180.09	2.59	0.13	-0.02	0.42	-0.44	0.43	0.46	0.22	-0.95	0.68
	r(.) Lambda(U.500 + UQ.500 + P.2000)	5	180.27	2.77	0.12	0.46	0.32	-0.82	0.41	0.51	0.23		
	r(.) Lambda(P.2000)	3	180.85	3.36	0.09					0.77	0.23		
	r(.) Lambda(W)	3	181.39	3.89	0.07							-1.37	0.61
	r(.) Lambda(U.500 + UQ.500 + W)	5	181.79	4.29	0.06	0.04	0.43	-0.63	0.46			-1.14	0.73
	r(.) Lambda(U.500 + UQ.500)	4	183.01	5.51	0.03	0.61	0.32	-1.17	0.42				
	r(.) Lambda(.)	2	189.13	11.63	0.00								

Table B4: RN model results for the canyon bat in the winter, spring, summer and fall season.

						U		P		UxP		W	
Season	Model	K	AICc	ΔAICc	wt	β	se	β	se	β	se	β	se
Winter	r(.) Lambda(P.250)	3	180.96	0.00	0.32			0.44	0.24				
	r(.) Lambda(U.1000)	3	181.47	0.51	0.24	-0.42	0.26						
	r(.) Lambda(.)	2	182.04	1.08	0.18								
	r(.) Lambda(P.250 + W)	4	183.22	2.26	0.10			0.48	0.27			-0.08	0.25
	r(.) Lambda(U.1000 + W)	4	183.61	2.64	0.08	-0.50	0.32					-0.12	0.26
	r(.) Lambda(W)	3	184.00	3.03	0.07							0.12	0.20
Spring	r(.) Lambda(U.1000 + P.125)	4	232.37	0.00	0.31	-0.83	0.21	-0.43	0.22				
	r(.) Lambda(U.1000 + P.125 + W)	5	233.07	0.71	0.22	-0.68	0.23	-0.41	0.23			0.23	0.17
	r(.) Lambda(U.1000 + W)	4	233.99	1.62	0.14	-0.59	0.23					0.28	0.17
	r(.) Lambda(U.1000)	3	234.06	1.69	0.13	-0.78	0.20						
	r(.) Lambda(U.1000 + P.125 + UxP)	5	234.39	2.03	0.11	-0.80	0.18	-0.41	0.16	0.17	0.15		
	r(.) Lambda(U.1000 + P.125 + UxP + W)	6	235.01	2.64	0.08	-0.64	0.23	-0.40	0.22	0.20	0.24	0.25	0.18
	r(.) Lambda(W)	3	239.47	7.11	0.01							0.55	0.15
	r(.) Lambda(P.125 + W)	4	240.72	8.35	0.00			-0.20	0.19			0.54	0.16
	r(.) Lambda(.)	2	249.57	17.21	0.00								
	r(.) Lambda(P.125)	3	249.90	17.53	0.00			-0.24	0.18				
Summer	r(.) Lambda(U.2000)	3	235.02	0.00	0.48	-0.66	0.12						
	r(.) Lambda(U.2000 + W)	4	236.77	1.75	0.20	-0.74	0.16					-0.11	0.14
	r(.) Lambda(U.2000 + P.500)	4	237.22	2.19	0.16	-0.66	0.12	0.05	0.12				
	r(.) Lambda(U.2000 + P.500 + UxP)	5	238.60	3.58	0.08	-0.69	0.12	0.10	0.13	-0.19	0.18		
	r(.) Lambda(U.2000 + P.500 + W)	5	239.22	4.20	0.06	-0.73	0.15	0.02	0.12			-0.10	0.13
	r(.) Lambda(U.2000 + P.500 + UxP + W)	6	240.70	5.68	0.03	-0.76	0.16	0.07	0.13	-0.20	0.19	-0.10	0.15
	r(.) Lambda(P.500 + W)	4	258.26	23.23	0.00			0.21	0.12			0.40	0.13
	r(.) Lambda(W)	3	259.14	24.11	0.00							0.34	0.13
	r(.) Lambda(.)	2	264.53	29.51	0.00								
	r(.) Lambda(P.500)	3	265.61	30.58	0.00			0.12	0.11				
Fall	r(.) Lambda(U.1000 + W)	4	239.95	0.00	0.26	-0.48	0.22					0.26	0.14
	r(.) Lambda(U.1000)	3	240.39	0.44	0.21	-0.65	0.21						
	r(.) Lambda(U.1000 + P.2000)	4	240.49	0.53	0.20	-0.69	0.20	-0.26	0.17				
	r(.) Lambda(U.1000 + P.2000 + W)	5	241.54	1.58	0.12	-0.55	0.23	-0.17	0.18			0.20	0.16
	r(.) Lambda(U.1000 + P.2000 + UxP)	5	242.52	2.57	0.07	-0.65	0.21	-0.21	0.20	0.13	0.20		
	r(.) Lambda(W)	3	242.65	2.70	0.07							0.42	0.12
	r(.) Lambda(U.1000 + P.2000 + UxP + W)	6	243.72	3.77	0.04	-0.52	0.24	-0.14	0.20	0.11	0.19	0.19	0.15
	r(.) Lambda(P.2000 + W)	4	245.02	5.07	0.02			0.01	0.17			0.42	0.12
	r(.) Lambda(.)	2	249.41	9.46	0.00								
	r(.) Lambda(P.2000)	3	251.10	11.15	0.00			-0.13	0.17				

Table B5: RN model results for the hoary bat in the spring season.

						U		P		W	
Season	Model	K	AICc	ΔAICc	wt	*β*	se	*β*	se	*β*	se
Spring	r(.) Lambda(U.1000 + P.2000)	4	107.50	0.00	0.48	-0.92	0.43	0.82	0.31		
	r(.) Lambda(U.1000 + P.2000 + W)	5	109.97	2.47	0.14	-0.90	0.49	0.83	0.34	0.02	0.35
	r(.) Lambda(P.2000)	3	110.49	2.99	0.11			0.75	0.35		
	r(.) Lambda(U.1000)	3	110.52	3.02	0.11	-0.79	0.41				
	r(.) Lambda(P.2000 + W)	4	111.30	3.80	0.07			0.91	0.38	0.37	0.26
	r(.) Lambda(U.1000 + W)	4	112.48	4.98	0.04	-0.97	0.52			-0.23	0.39
	r(.) Lambda(.)	2	112.73	5.23	0.04						
	r(.) Lambda(W)	3	114.54	7.04	0.01					0.19	0.26

Table B6: RN model results for the Mexican free-tailed bat in the winter, spring, summer and fall season.

						U		P		UxP		W	
Season	Model	K	AICc	ΔAICc	wt	β	se	β	se	β	se	β	se
Winter	r(.) Lambda(P.125)	3	318.92	0.00	0.54			-0.30	0.10				
	r(.) Lambda(U.125)	3	321.03	2.11	0.19	0.26	0.10						
	r(.) Lambda(P.125 + W)	4	321.27	2.36	0.17			-0.30	0.11			0.01	0.12
	r(.) Lambda(U.125 + W)	4	323.22	4.31	0.06	0.25	0.10					-0.05	0.12
	r(.) Lambda(.)	2	325.19	6.28	0.02								
	r(.) Lambda(W)	3	326.15	7.24	0.01							-0.14	0.12
Spring	r(.) Lambda(U.500 + P.2000 + W)	5	246.30	0.00	0.58	0.36	0.12	0.27	0.11			-0.30	0.13
	r(.) Lambda(U.500 + P.2000 + UxP + W)	6	248.86	2.56	0.16	0.37	0.12	0.27	0.11	0.02	0.11	-0.29	0.13
	r(.) Lambda(U.500 + P.2000)	4	249.44	3.14	0.12	0.53	0.11	0.32	0.11				
	r(.) Lambda(U.500 + W)	4	250.79	4.49	0.06	0.28	0.11					-0.33	0.13
	r(.) Lambda(U.500 + P.2000 + UxP)	5	251.54	5.24	0.04	0.54	0.11	0.31	0.11	0.07	0.12		
	r(.) Lambda(P.2000 + W)	4	253.17	6.88	0.02			0.21	0.09			-0.51	0.11
	r(.) Lambda(W)	3	254.75	8.46	0.01							-0.49	0.13
	r(.) Lambda(U.500)	3	255.91	9.62	0.00	0.43	0.10						
	r(.) Lambda(P.2000)	3	270.69	24.40	0.00			0.19	0.11				
	r(.) Lambda(.)	2	271.19	24.90	0.00								
Summer	r(.) Lambda(U.2000 + W)	4	255.32	0.00	0.31	0.33	0.13					-0.37	0.20
	r(.) Lambda(U.2000 + P.125 + W)	5	255.84	0.51	0.24	0.35	0.14	0.18	0.12			-0.30	0.20
	r(.) Lambda(U.2000 + P.125)	4	256.09	0.76	0.21	0.45	0.12	0.24	0.12				
	r(.) Lambda(U.2000)	3	257.37	2.05	0.11	0.44	0.11						
	r(.) Lambda(W)	3	258.21	2.89	0.07							-0.60	0.20
	r(.) Lambda(P.125 + W)	4	259.15	3.83	0.05			0.16	0.13			-0.54	0.20
	r(.) Lambda(P.125)	3	266.59	11.26	0.00			0.29	0.14				
	r(.) Lambda(.)	2	268.37	13.05	0.00								
Fall	r(.) Lambda(U.500 + P.500 + UxP)	5	324.38	0.00	0.72	0.45	0.13	-0.34	0.15	0.46	0.16		
	r(.) Lambda(U.500 + P.500 + UxP + W)	6	326.87	2.48	0.21	0.43	0.15	-0.35	0.15	0.46	0.16	-0.04	0.13
	r(.) Lambda(U.500 + P.500)	4	331.49	7.11	0.02	0.24	0.11	-0.22	0.13				
	r(.) Lambda(U.500)	3	332.07	7.69	0.02	0.32	0.11						
	r(.) Lambda(P.500 + W)	4	332.90	8.52	0.01			-0.35	0.13			-0.22	0.14
	r(.) Lambda(P.500)	3	333.34	8.96	0.01			-0.33	0.13				
	r(.) Lambda(U.500 + P.500 + W)	5	333.45	9.07	0.01	0.19	0.14	-0.26	0.14			-0.11	0.15
	r(.) Lambda(U.500 + W)	4	334.43	10.05	0.00	0.32	0.12					0.01	0.14
	r(.) Lambda(.)	2	337.68	13.30	0.00								
	r(.) Lambda(W)	3	338.59	14.21	0.00							-0.15	0.14

Table B7: RN model results for the Pallid bat in the spring and summer season. Note that there were no model results for landscape variables of the pallid bat in the spring season because there were too few detections to reliably evaluate relationships.

						P		W	
Season	Model	K	AICc	ΔAICc	wt	*β*	se	*β*	se
Spring	r(.) Lambda(.)	2	34.13	0.00	1.00				
Summer	r(.) Lambda(P.2000 + W)	4	55.48	0.00	0.55	1.72	0.79	1.00	0.51
	r(.) Lambda(P.2000)	3	57.17	1.70	0.24	0.94	0.50		
	r(.) Lambda(.)	2	58.36	2.88	0.13				
	r(.) Lambda(W)	3	59.39	3.91	0.08			0.41	0.33

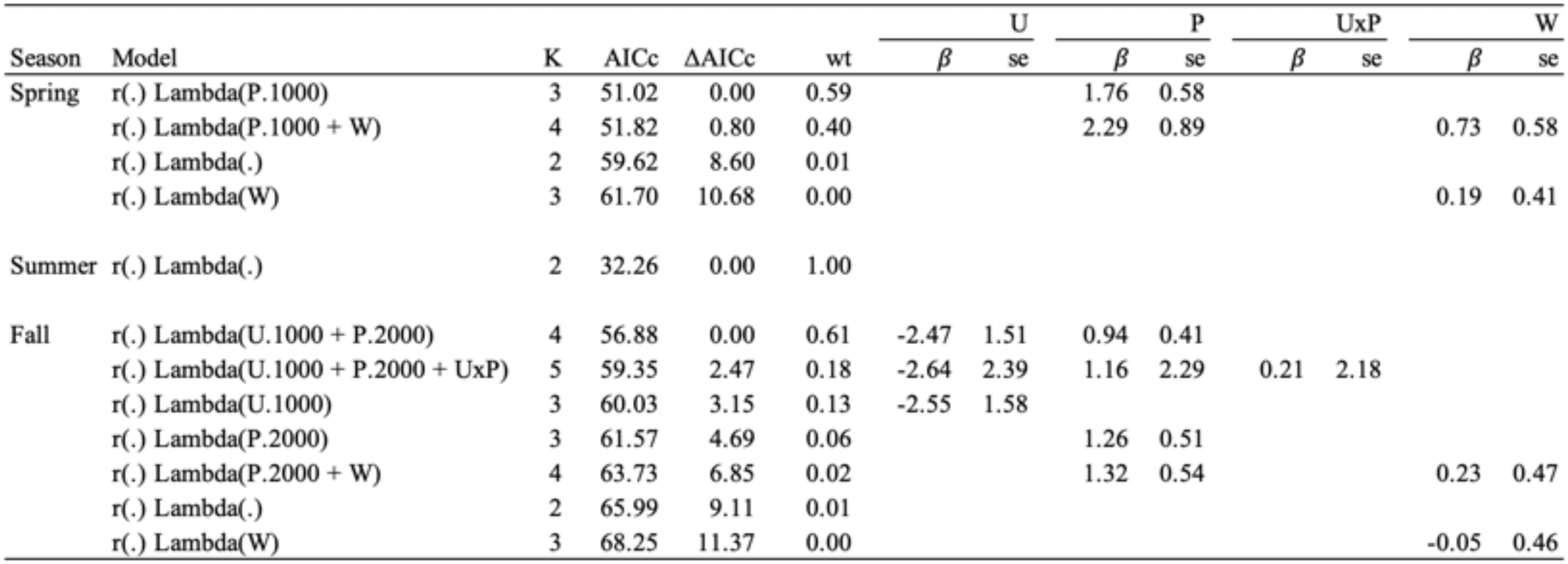
Table B8: RN model results for the silver-haired bat in the summer and fall season. Note that there were no model results for landscape variables of the silver-haired bat in the summer season because there were too few detections to reliably evaluate relationships.

						U		P		UxP		W	
Season	Model	K	AICc	ΔAICc	wt	*β*	se	*β*	se	*β*	se	*β*	se
Summer	r(.) Lambda(.)	2	32.26	0.00	1.00								
Fall	r(.) Lambda(P.2000)	3	74.14	0.00	0.15			-0.58	0.34				
	r(.) Lambda(U.500 + P.2000 + UxP)	5	74.17	0.03	0.15	-0.16	0.50	-0.57	0.60	1.02	0.81		
	r(.) Lambda(U.500 + P.2000)	4	74.43	0.29	0.13	-0.60	0.46	-0.71	0.40				
	r(.) Lambda(U.500 + P.2000 + UxP + W)	6	74.43	0.29	0.13	-0.53	0.63	-0.55	0.59	1.28	0.96	-0.77	0.62
	r(.) Lambda(U.500 + P.2000 + W)	5	74.47	0.33	0.12	-0.95	0.55	-0.88	0.42			-0.77	0.59
	r(.) Lambda(.)	2	74.60	0.46	0.12								
	r(.) Lambda(U.500)	3	75.45	1.31	0.08	-0.51	0.47						
	r(.) Lambda(P.2000 + W)	4	76.03	1.89	0.06			-0.65	0.36			-0.30	0.49
	r(.) Lambda(U.500 + W)	4	76.80	2.66	0.04	-0.79	0.58					-0.49	0.55
	r(.) Lambda(W)	3	76.80	2.66	0.04							-0.10	0.41

Table B9: RN model results for the Townsend's big-eared bat in the summer season. Note that there were no model results for landscape variables of the Townsend's big-eared bat in the summer season because there were too few detections to reliably evaluate relationships.

Season	Model	K	AICc	ΔAICc	wt
Summer	r(.) Lambda(.)	2	32.26	0.00	1.00

Table B10: RN model results for the western mastiff bat in the spring, summer and fall season. Note that there were no model results for landscape variables of the western mastiff bat in the summer season because there were too few detections to reliably evaluate relationships.



						U		P		UxP		W	
Season	Model	K	AICc	ΔAICc	wt	β	se	β	se	β	se	β	se
Spring	r(.) Lambda(P.1000)	3	51.02	0.00	0.59			1.76	0.58				
	r(.) Lambda(P.1000 + W)	4	51.82	0.80	0.40			2.29	0.89			0.73	0.58
	r(.) Lambda(.)	2	59.62	8.60	0.01								
	r(.) Lambda(W)	3	61.70	10.68	0.00							0.19	0.41
Summer	r(.) Lambda(.)	2	32.26	0.00	1.00								
Fall	r(.) Lambda(U.1000 + P.2000)	4	56.88	0.00	0.61	-2.47	1.51	0.94	0.41				
	r(.) Lambda(U.1000 + P.2000 + UxP)	5	59.35	2.47	0.18	-2.64	2.39	1.16	2.29	0.21	2.18		
	r(.) Lambda(U.1000)	3	60.03	3.15	0.13	-2.55	1.58						
	r(.) Lambda(P.2000)	3	61.57	4.69	0.06			1.26	0.51				
	r(.) Lambda(P.2000 + W)	4	63.73	6.85	0.02			1.32	0.54			0.23	0.47
	r(.) Lambda(.)	2	65.99	9.11	0.01								
	r(.) Lambda(W)	3	68.25	11.37	0.00							-0.05	0.46

Table B11: RN model results for the western red bat in the winter, spring and fall season.

						U		UQ		P		W	
Season	Model	K	AICc	ΔAICc	wt	β	se	β	se	β	se	β	se
Winter	r(.) Lambda(Urb250 + W)	4	86.36	0.00	0.87	-1.74	0.82					-1.91	1.00
	r(.) Lambda(Urb250)	3	92.44	6.08	0.04	-0.80	0.56						
	r(.) Lambda(W)	3	92.44	6.09	0.04							-1.02	0.80
	r(.) Lambda(.)	2	93.25	6.90	0.03								
	r(.) Lambda(P.2000)	3	94.35	7.99	0.02					0.42	0.39		
Spring	r(.) Lambda(.)	2	58.68	0.00	1.00								
Fall	r(.) Lambda(P.500)	3	96.57	0.00	0.43					0.66	0.22		
	r(.) Lambda(U.250 + UQ.250 + P.500)	5	98.50	1.92	0.17	0.04	0.63	-1.42	1.09	0.56	0.24		
	r(.) Lambda(P.500 + W)	4	98.67	2.10	0.15					0.62	0.23	-0.23	0.47
	r(.) Lambda(U.250 + UQ.250)	4	100.15	3.57	0.07	0.00	0.64	-1.56	1.01				
	r(.) Lambda(.)	2	100.31	3.73	0.07								
	r(.) Lambda(U.250 + UQ.250 + P.500 + W)	6	101.04	4.47	0.05	-0.04	0.71	-1.33	1.16	0.54	0.26	-0.11	0.54
	r(.) Lambda(W)	3	101.59	5.01	0.04							-0.43	0.51
	r(.) Lambda(U.250 + UQ.250 + W)	5	102.03	5.45	0.03	-0.29	0.73	-1.19	1.07			-0.42	0.61

Table B12: RN model results for the western yellow bat in the winter, spring, summer and fall season.

						U		UQ		P		W	
Season	Model	K	AICc	ΔAICc	wt	β	se	β	se	β	se	β	se
Winter	r(.) Lambda(U.500 + UQ.500)	4	115.41	0.00	0.59	1.15	0.48	-1.09	0.46				
	r(.) Lambda(U.500 + UQ.500 + W)	5	117.87	2.46	0.17	1.20	0.63	-1.13	0.56			0.07	0.57
	r(.) Lambda(W)	3	118.74	3.33	0.11							-0.87	0.58
	r(.) Lambda(.)	2	120.14	4.74	0.06								
	r(.) Lambda(P.2000)	3	120.91	5.50	0.04					-0.36	0.30		
	r(.) Lambda(P.2000 + W)	4	121.01	5.61	0.04					-0.11	0.37	-0.79	0.64
Spring	r(.) Lambda(P.125 + W)	4	199.97	0.00	0.38					0.38	0.07	-0.71	0.33
	r(.) Lambda(U.500 + UQ.500 + P.125)	5	200.40	0.43	0.30	0.74	0.29	-0.51	0.27	0.46	0.15		
	r(.) Lambda(P.125)	3	202.37	2.40	0.11					0.49	0.15		
	r(.) Lambda(U.500 + UQ.500 + P.125 + W)	6	202.45	2.48	0.11	0.57	0.37	-0.41	0.30	0.42	0.15	-0.29	0.42
	r(.) Lambda(W)	3	203.49	3.52	0.06							-0.88	0.42
	r(.) Lambda(U.500 + UQ.500)	4	206.17	6.20	0.02	0.67	0.29	-0.63	0.28				
	r(.) Lambda(U.500 + UQ.500 + W)	5	206.59	6.62	0.01	0.32	0.38	-0.38	0.31			-0.60	0.48
	r(.) Lambda(.)	2	208.33	8.36	0.01								
Summer	r(.) Lambda(U.500 + UQ.500 + W)	5	268.81	0.00	0.26	0.49	0.19	-0.42	0.16			-0.46	0.22
	r(.) Lambda(U.500 + UQ.500)	4	269.06	0.24	0.23	0.77	0.20	-0.61	0.18				
	r(.) Lambda(W)	3	269.08	0.26	0.22							-0.88	0.28
	r(.) Lambda(U.500 + UQ.500 + P.2000)	5	270.47	1.65	0.11	0.74	0.20	-0.55	0.19	0.14	0.14		
	r(.) Lambda(P.2000 + W)	4	270.81	2.00	0.09					0.11	0.14	-0.83	0.28
	r(.) Lambda(U.500 + UQ.500 + P.2000 + W)	6	270.99	2.17	0.09	0.49	0.25	-0.41	0.20	0.09	0.14	-0.41	0.31
	r(.) Lambda(P.2000)	3	281.02	12.20	0.00					0.28	0.16		
	r(.) Lambda(.)	2	281.84	13.03	0.00								
Fall	r(.) Lambda(U.2000 + UQ.2000)	4	157.37	0.00	0.34	0.76	0.37	-0.59	0.33				
	r(.) Lambda(W)	3	158.65	1.27	0.18							-0.68	0.46
	r(.) Lambda(U.2000 + UQ.2000 + P.125)	5	159.55	2.18	0.11	0.73	0.37	-0.56	0.34	0.11	0.20		
	r(.) Lambda(.)	2	159.78	2.40	0.10								
	r(.) Lambda(U.2000 + UQ.2000 + W)	5	159.79	2.41	0.10	0.84	0.38	-0.65	0.27			0.13	0.47
	r(.) Lambda(P.125 + W)	4	160.60	3.23	0.07					0.14	0.21	-0.61	0.46
	r(.) Lambda(P.125)	3	160.74	3.37	0.06					0.25	0.21		
	r(.) Lambda(U.2000 + UQ.2000 + P.125 + W)	6	162.02	4.65	0.03	0.85	0.51	-0.64	0.41	0.13	0.21	0.19	0.51

Table B13: RN model results for the Yuma myotis in the winter, spring, summer and fall season. Note that there were no model results for landscape variables of the Yuma myotis in the winter season because there were too few detections to reliably evaluate relationships.

						U		UQ		P		UxP		W	
Season	Model	K	AICc	ΔAICc	wt	β	se	β	se	β	se	β	se	β	se
Winter	r(.) Lambda(.)	2	51.19	0.00	1.00										
Spring	r(.) Lambda(U.500 + UQ.500 + P.2000)	5	166.48	0.00	0.32	-0.16	0.37	-1.11	0.54	0.55	0.27				
	r(.) Lambda(U.500 + UQ.500 + P.2000 + W)	6	167.39	0.91	0.20	-0.48	0.42	-0.76	0.56	0.54	0.26			-0.54	0.46
	r(.) Lambda(U.500 + UQ.500)	4	167.96	1.48	0.15	-0.08	0.37	-1.20	0.54						
	r(.) Lambda(U.500 + UQ.500 + W)	5	168.71	2.23	0.10	-0.45	0.45	-0.79	0.59					-0.57	0.49
	r(.) Lambda(P.2000)	3	168.85	2.37	0.10					0.65	0.29				
	r(.) Lambda(P.2000 + W)	4	169.51	3.03	0.07					0.63	0.28			-0.40	0.34
	r(.) Lambda(.)	2	171.39	4.92	0.03										
	r(.) Lambda(W)	3	171.70	5.23	0.02									-0.43	0.36
Summer	r(.) Lambda(P.2000)	3	167.09	0.00	0.34					1.01	0.23				
	r(.) Lambda(U.2000 + UQ.2000 + P.2000)	5	167.38	0.30	0.30	-0.41	0.38	-0.90	0.47	0.84	0.26				
	r(.) Lambda(P.2000 + W)	4	168.46	1.37	0.17					0.90	0.25			-0.34	0.38
	r(.) Lambda(U.2000 + UQ.2000 + P.2000 + W	6	168.47	1.38	0.17	-0.67	0.40	-0.63	0.49	0.76	0.26			-0.61	0.55
	r(.) Lambda(U.2000 + UQ.2000 + W)	5	173.97	6.88	0.01	-0.70	0.41	-0.77	0.48					-1.11	0.69
	r(.) Lambda(U.2000 + UQ.2000)	4	175.18	8.09	0.01	-0.20	0.35	-1.24	0.44						
	r(.) Lambda(W)	3	179.11	12.03	0.00									-0.78	0.45
	r(.) Lambda(.)	2	181.78	14.69	0.00										
Fall	r(.) Lambda(U.250 + P.2000)	4	141.43	0.00	0.28	-0.70	0.40			0.47	0.26				
	r(.) Lambda(U.250)	3	142.46	1.03	0.17	-0.76	0.40								
	r(.) Lambda(P.2000)	3	143.15	1.72	0.12					0.58	0.27				
	r(.) Lambda(U.250 + W)	4	143.18	1.75	0.11	-0.99	0.46							-0.37	0.32
	r(.) Lambda(U.250 + P.2000 + W)	5	143.29	1.86	0.11	-0.85	0.47			0.41	0.27			-0.24	0.32
	r(.) Lambda(U.250 + P.2000 + UxP)	5	143.55	2.12	0.10	-0.81	0.49			0.68	0.46	0.34	0.61		
	r(.) Lambda(P.2000 + W)	4	145.43	4.00	0.04					0.60	0.28			0.08	0.26
	r(.) Lambda(U.250 + P.2000 + UxP + W)	6	145.47	4.04	0.04	-0.99	0.55			0.63	0.46	0.37	0.62	-0.25	0.32
	r(.) Lambda(.)	2	145.48	4.05	0.04										
	r(.) Lambda(W)	3	147.73	6.30	0.01									-0.03	0.26

Table B14: RN model results for the 40 kHz Myotis in the spring and summer season.

						U		P		UxP		W	
Season	Model	K	AICc	ΔAICc	wt	β	se	β	se	β	se	β	se
Spring	r(.) Lambda(P.2000)	3	97.34	0.00	0.30			0.95	0.37				
	r(.) Lambda(U.2000 + P.2000)	4	98.44	1.10	0.17	-0.46	0.42	0.80	0.38				
	r(.) Lambda(U.2000 + P.2000 + W)	5	99.02	1.68	0.13	-0.95	0.57	0.59	0.39			-0.69	0.56
	r(.) Lambda(U.2000 + W)	4	99.09	1.76	0.12	-1.34	0.55					-0.95	0.59
	r(.) Lambda(P.2000 + W)	4	99.61	2.27	0.10			0.94	0.37			-0.12	0.40
	r(.) Lambda(U.2000)	3	100.64	3.30	0.06	-0.71	0.40						
	r(.) Lambda(U.2000 + P.2000 + UxP)	5	100.91	3.58	0.05	-0.47	0.49	0.80	0.46	0.02	0.46		
	r(.) Lambda(U.2000 + P.2000 + UxP + W)	6	101.56	4.23	0.04	-1.02	0.66	0.66	0.48	0.11	0.50	-0.71	0.57
	r(.) Lambda(.)	2	102.19	4.85	0.03								
	r(.) Lambda(W)	3	104.31	6.98	0.01							-0.13	0.37
Summer	r(.) Lambda(U.2000 + P.2000 + UxP)	5	133.81	0.00	0.28	-0.82	0.33	0.58	0.29	-0.53	0.24		
	r(.) Lambda(U.2000 + P.2000)	4	134.49	0.67	0.20	-0.79	0.38	0.54	0.32				
	r(.) Lambda(U.2000)	3	134.98	1.16	0.16	-0.66	0.33						
	r(.) Lambda(U.2000 + P.2000 + UxP + W)	6	136.36	2.54	0.08	-0.88	0.43	0.55	0.33	-0.53	0.25	-0.08	0.36
	r(.) Lambda(U.2000 + P.2000 + W)	5	136.89	3.08	0.06	-0.87	0.48	0.52	0.33			-0.09	0.34
	r(.) Lambda(U.2000 + W)	4	136.91	3.09	0.06	-0.84	0.44					-0.21	0.33
	r(.) Lambda(P.2000)	3	137.13	3.31	0.05			0.43	0.28				
	r(.) Lambda(.)	2	137.21	3.39	0.05								
	r(.) Lambda(P.2000 + W)	4	137.85	4.03	0.04			0.56	0.31			0.32	0.23
	r(.) Lambda(W)	3	138.80	4.98	0.02							0.20	0.22

APPENDIX C

PREDICTED RELATIVE HABITAT USE ACROSS THE GRADIENT OF URBANIZATION

Appendix C: Predicted relative habitat use (with associated 95% confidence intervals) based on the top Royle-Nichols (RN) models (with associated 95% confidence intervals) across the gradient of urbanization for 9 bat species in the Phoenix metropolitan area, Arizona during four seasons in 2019. Species include the big brown bat (Figure C1), the big/pocketed free-tailed bat (Figure C2), the California myotis (Figure C3), the canyon bat (Figure C4), the Mexican free-tailed bat (Figure C5), the western mastiff bat (Figure C6), the western yellow bat (Figure C7), the Yuma myotis (Figure C8) and the 40 kHz Myotis (Figure C9). Note that the y-axes are on different scales.

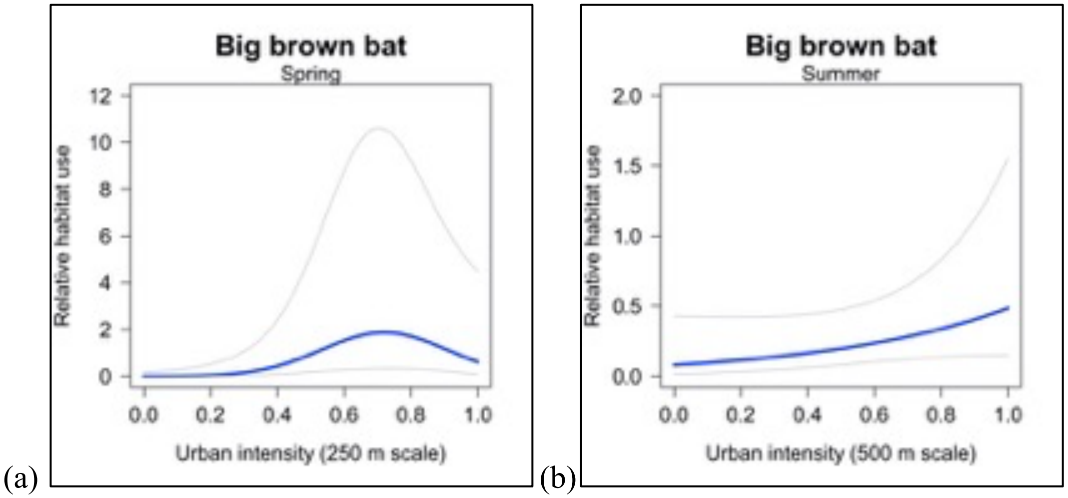


Figure C1: Predicted relative habitat use (based on RN models) across the gradient of urbanization shifted across seasons for the big brown bat in the (a) spring (i.e., urbanization adapter) and (b) summer (i.e., urbanization exploiter) season.

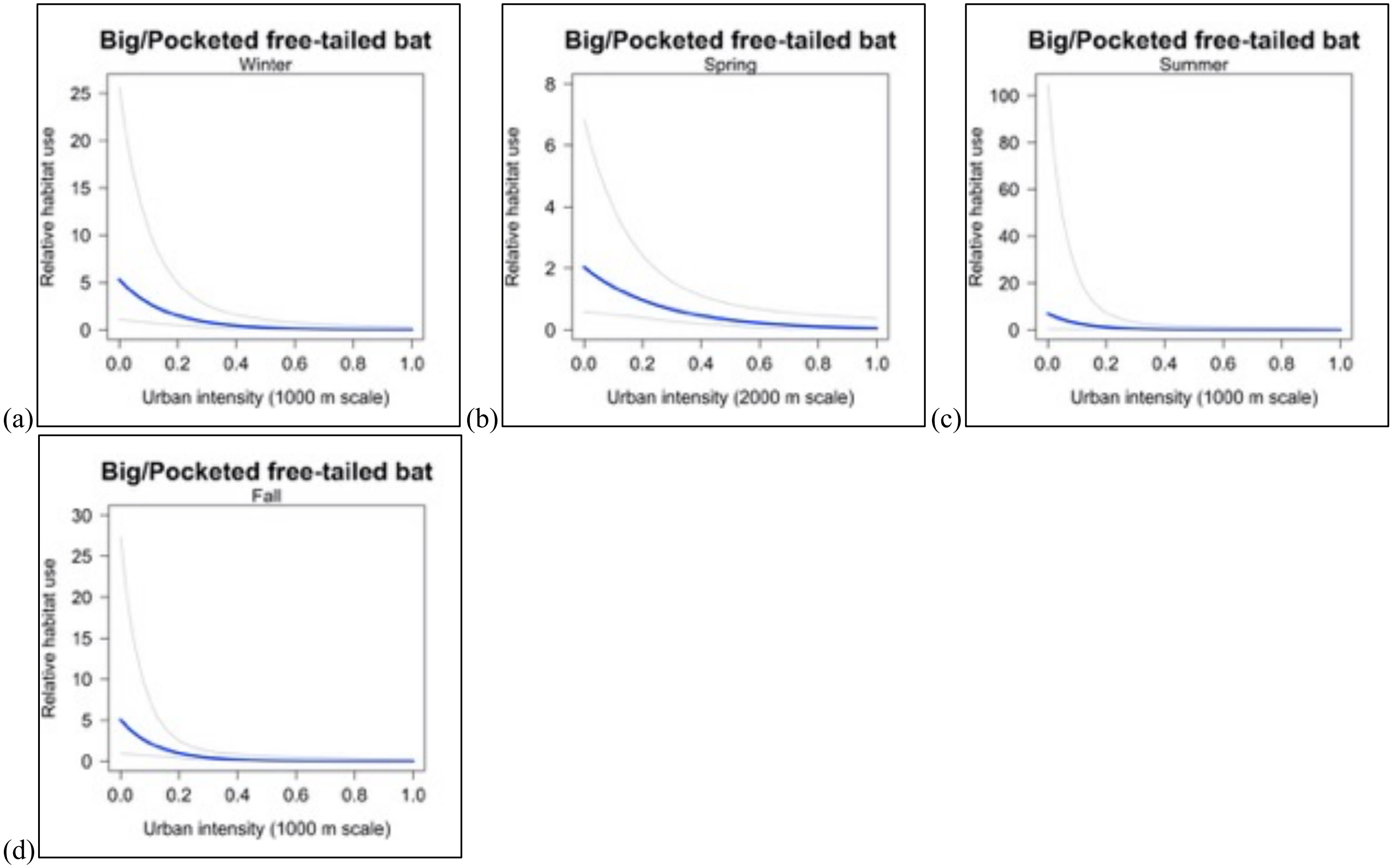


Figure C2: Predicted relative habitat use (based on RN models) across the gradient of urbanization was consistent across all four seasons for the big/pocketed free-tailed bat (i.e., urbanization avoider) in the (a) winter, (b) spring, (c) summer, and (d) fall season.

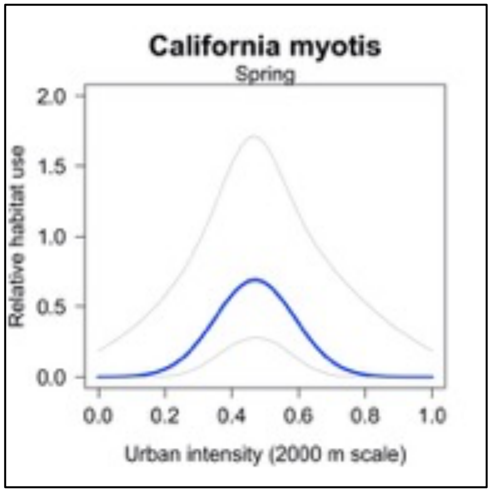


Figure C3: Predicted relative habitat use (based on RN models) across the gradient of urbanization for the California myotis (i.e., urbanization adapter) in the spring season.

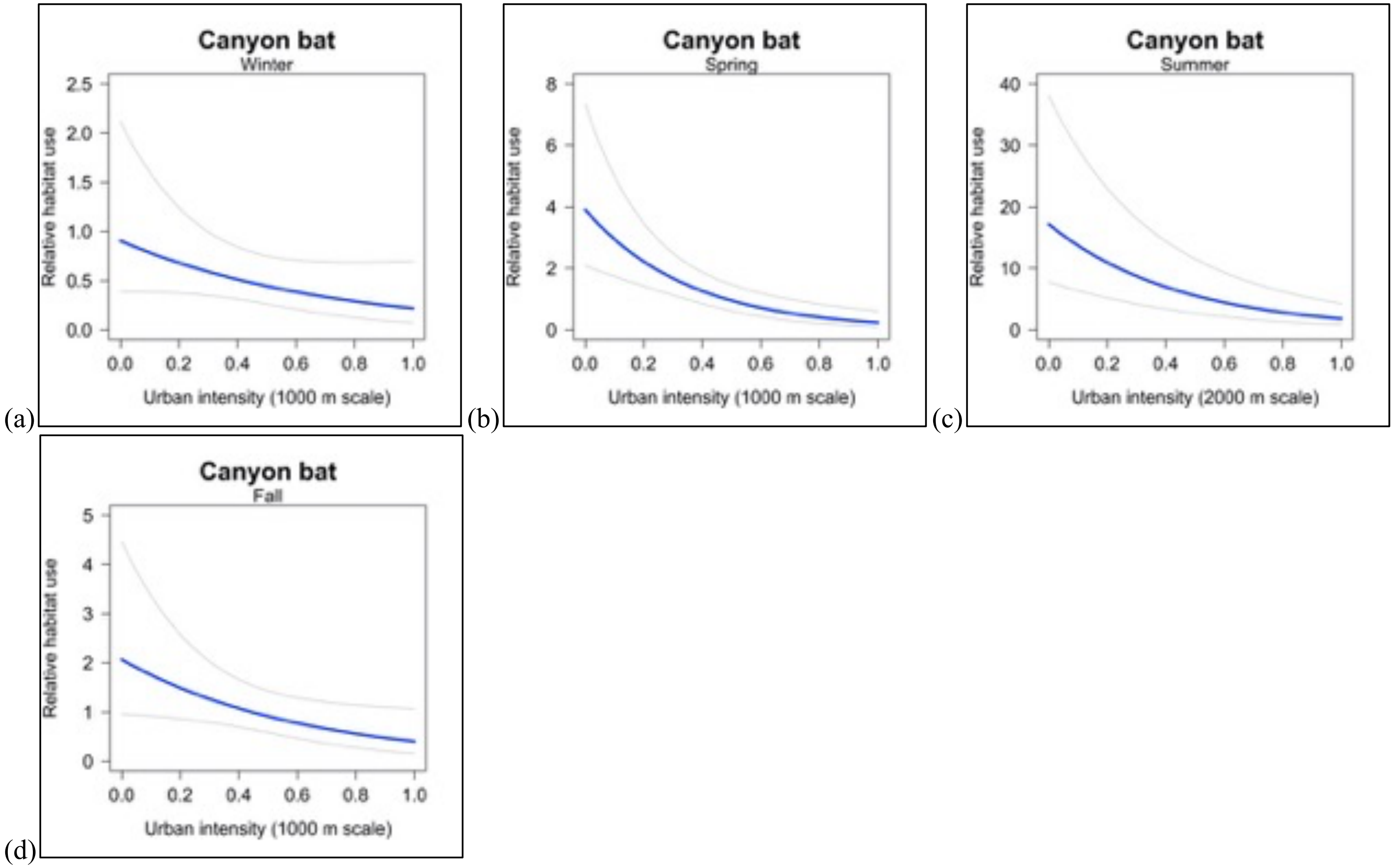


Figure C4: Predicted relative habitat use (based on RN models) across the gradient of urbanization was consistent across all four seasons for the canyon bat (i.e., urbanization avoider) in the (a) winter, (b) spring, (c) summer, and (d) fall season.

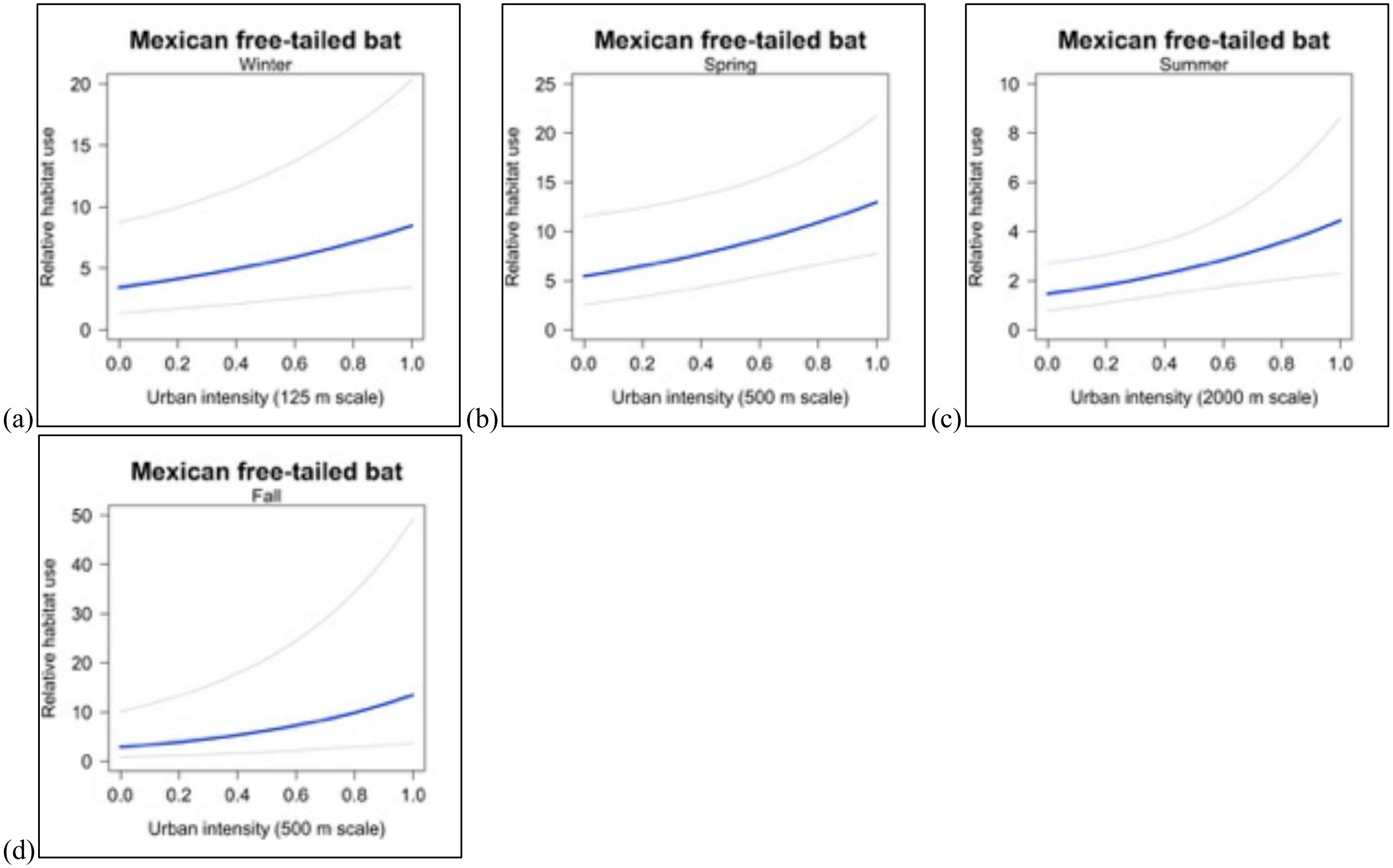


Figure C5: Predicted relative habitat use (based on RN models) across the gradient of urbanization was consistent across all four seasons for the Mexican free-tailed bat (i.e., urbanization exploiter) in the (a) winter, (b) spring, (c) summer, and (d) fall season.

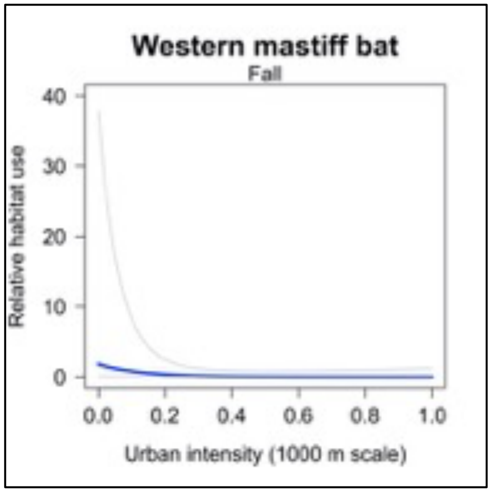


Figure C6: Predicted relative habitat use (based on RN models) across the gradient of urbanization for the western mastiff bat (i.e., urbanization avoider) in the fall season.

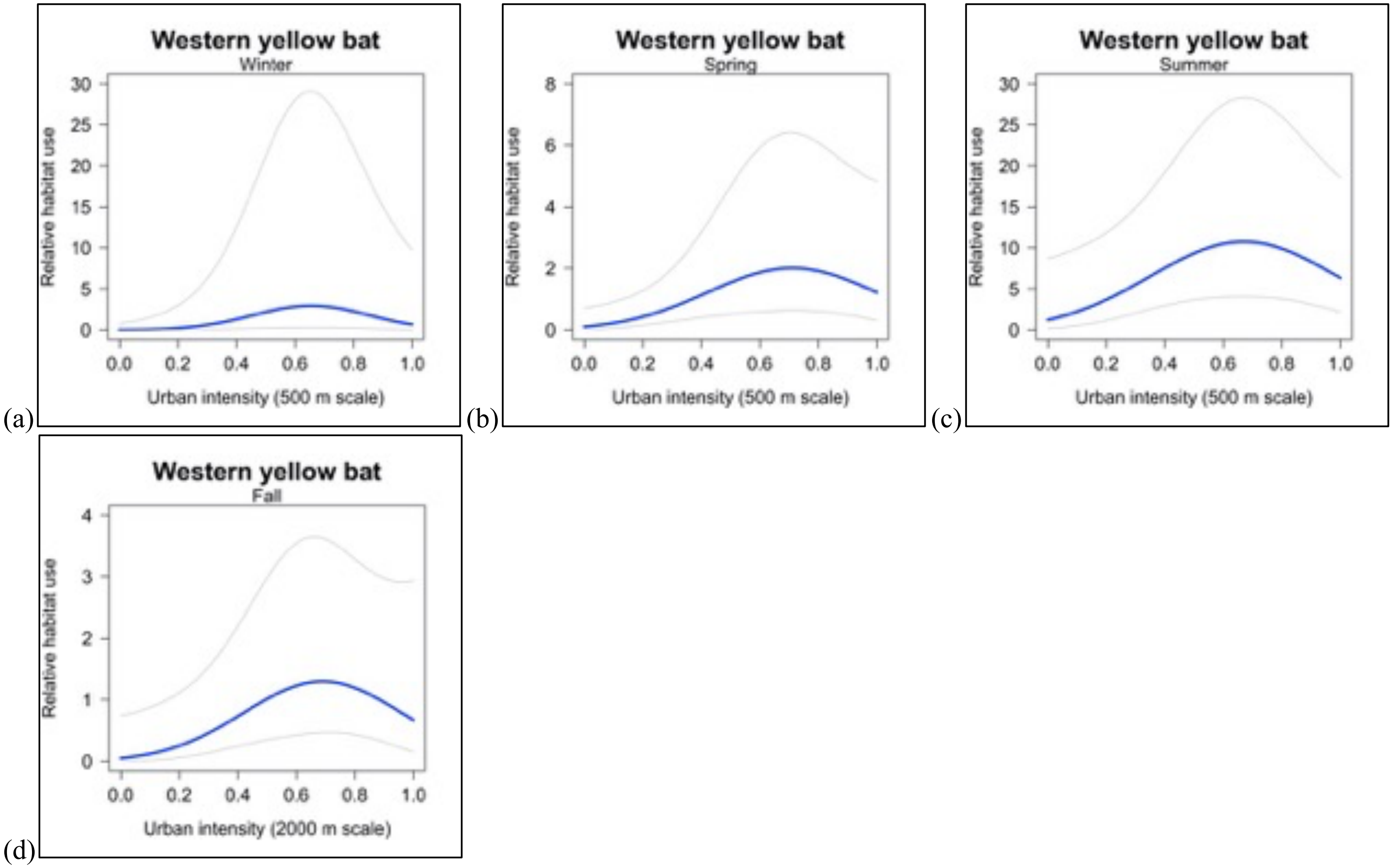


Figure C7: Predicted relative habitat use (based on RN models) across the gradient of urbanization was consistent across all four seasons for the western yellow bat (i.e., urbanization adapter) in the (a) winter, (b) spring, (c) summer, and (d) fall season.

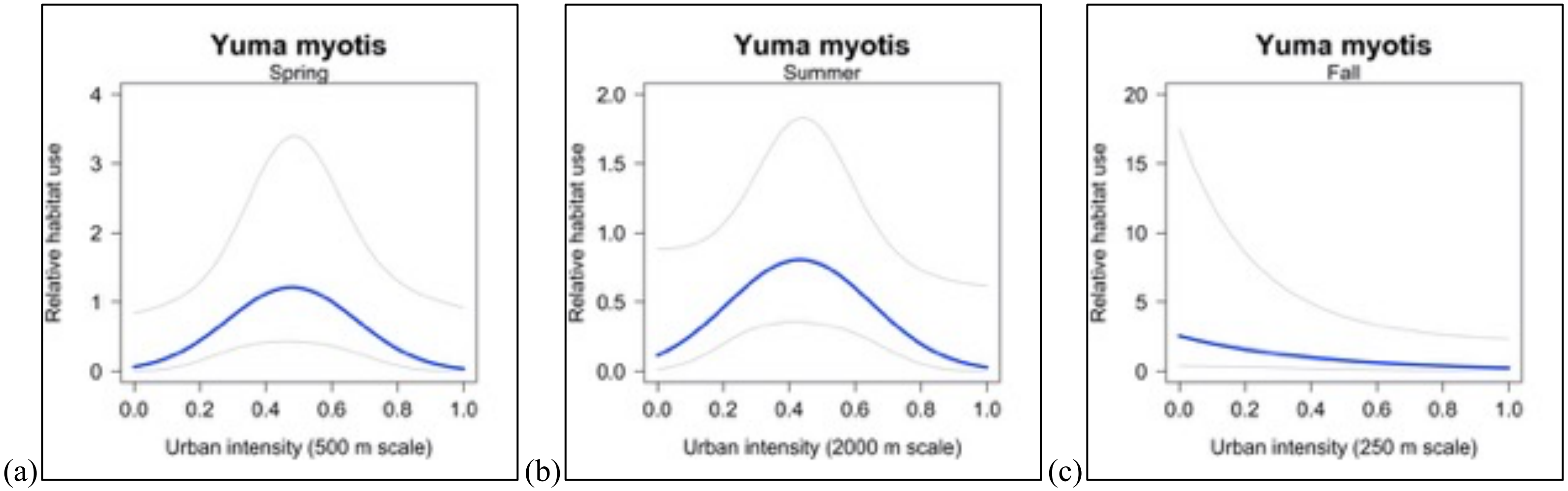


Figure C8: Predicted relative habitat use (based on RN models) across the gradient of urbanization shifted across seasons for the Yuma myotis in the (a) spring (i.e., urbanization adapter), (b) summer (i.e., urbanization adapter), and (c) fall (i.e., urbanization avoider) season.

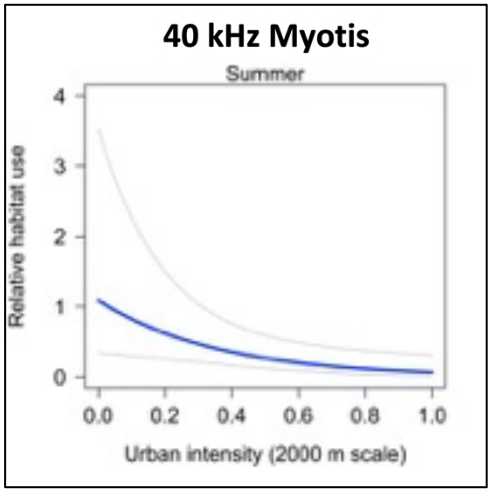
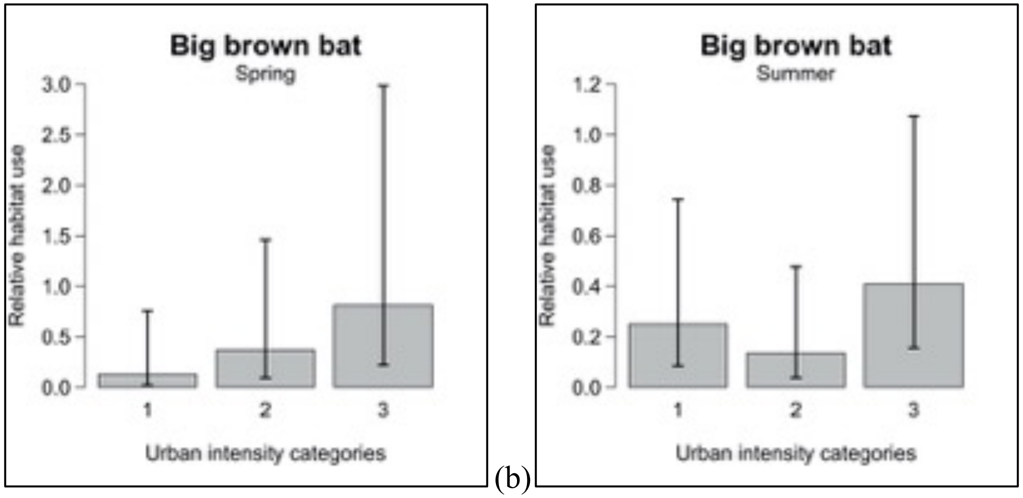


Figure C9: Predicted relative habitat use (based on RN models) across the gradient of urbanization for the 40 kHz Myotis (i.e., urbanization avoider) in the summer season.

APPENDIX D

RELATIVE HABITAT USE ACROSS URBAN INTENSITY CATEGORIES

Appendix D: Estimates of relative habitat use based on Royle-Nichols (RN) models across three categories of urban intensity at a 1000 m scale (low (0-0.01), moderate (0.02-0.30), and high urban intensity (0.31-0.61)) for 14 bat species in the Phoenix metropolitan area, Arizona during four seasons in 2019. Species include the big brown bat (Figure D1), the big/pocketed free-tailed bat (Figure D2), the California myotis (Figure D3), the canyon bat (Figure D4), the hoary bat (Figure D5), the Mexican free-tailed bat (Figure D6), the pallid bat (Figure D7), the silver-haired bat (Figure D8), the Townsend's big-eared bat (Figure D9), the western mastiff bat (Figure D10), the western red bat (Figure D11), the western yellow bat (Figure D12), the Yuma myotis (Figure D13) and the 40kHz myotis (Figure D14). The error bars represent 95% confidence intervals. Note that the y-axes are on different scales.



(a) (b)

Figure D1: Relative habitat use (based on RN models) across urban intensity categories for the big brown bat in the (a) spring and (b) summer season.

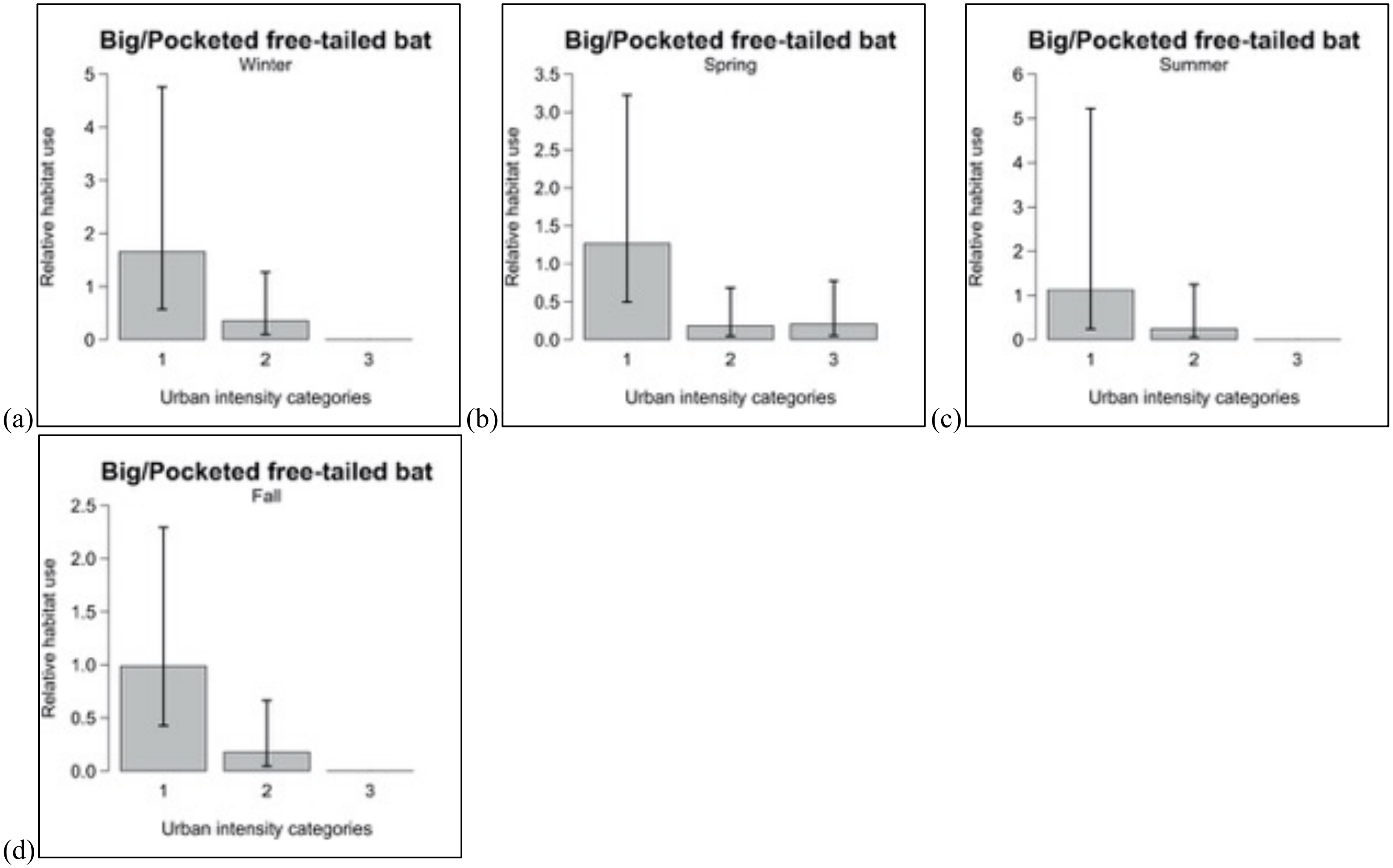
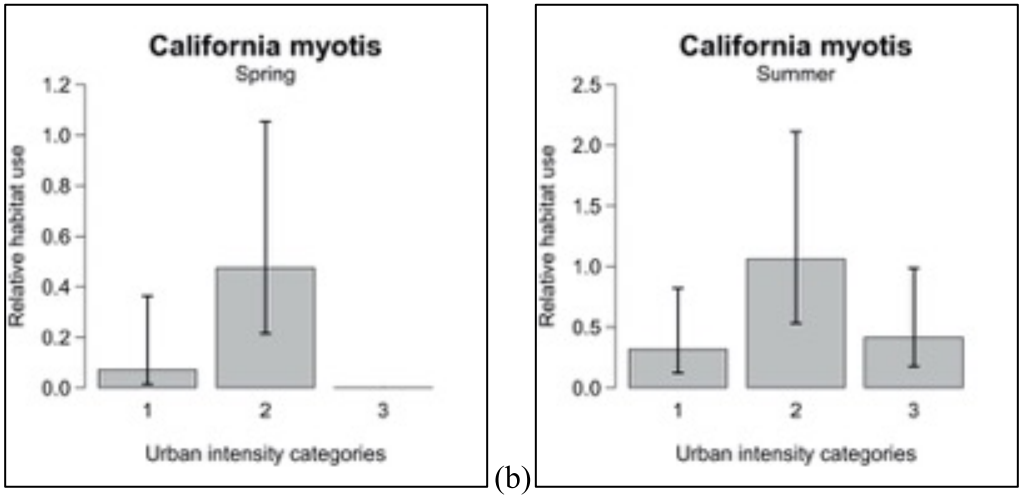
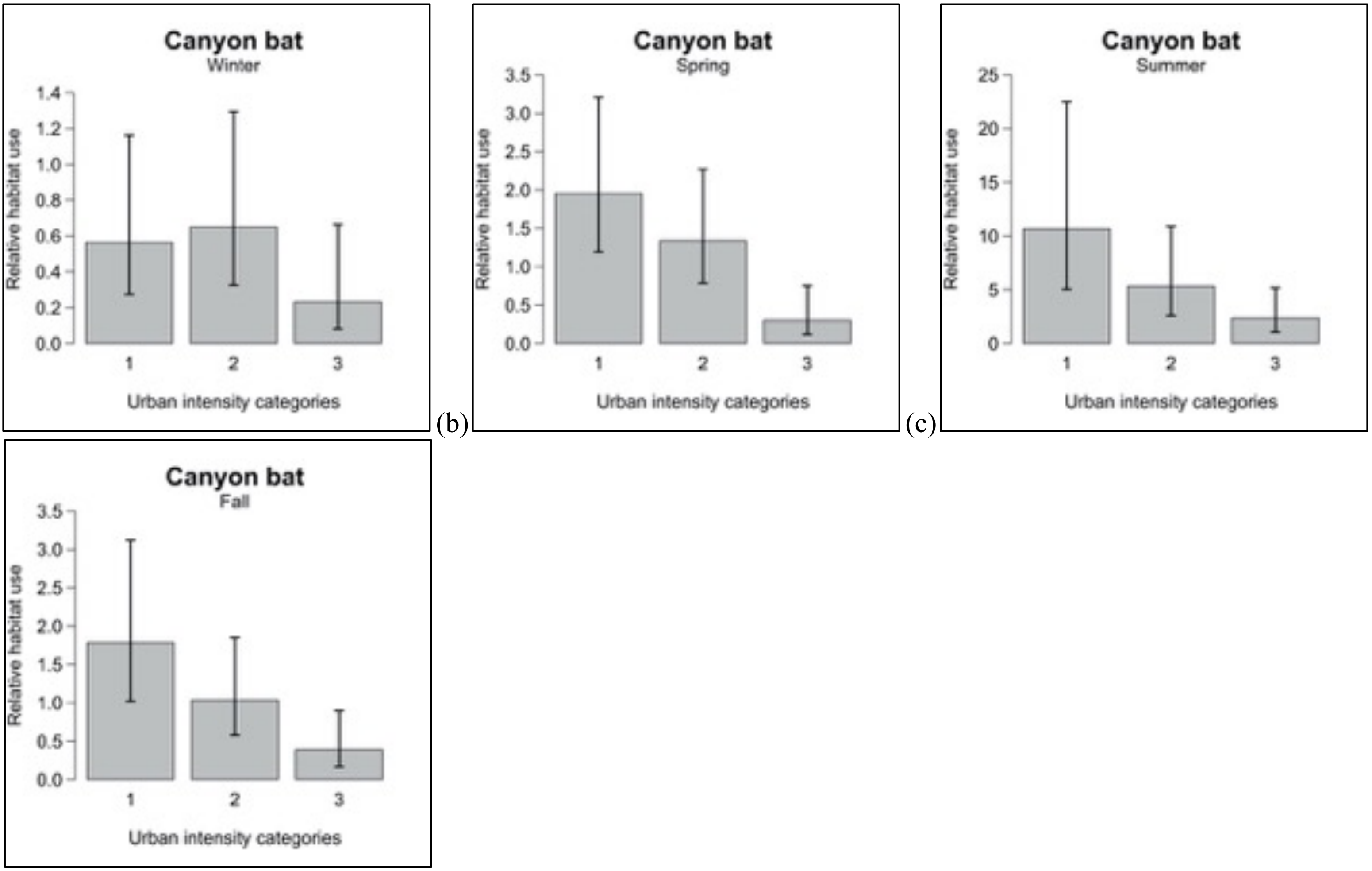


Figure D2: Relative habitat use (based on RN models) across urban intensity categories for the big/pocketed free-tailed bat in the (a) winter, (b) spring, (c) summer, and (d) fall season.



(a) (b)

Figure D3: Relative habitat use (based on RN models) across urban intensity categories for the California myotis in the (a) spring and (b) summer season.



(a) (b) (c) (d)

Figure D4: Relative habitat use (based on RN models) across urban intensity categories for the canyon bat in the (a) winter, (b) spring, (c) summer, and (d) fall season.

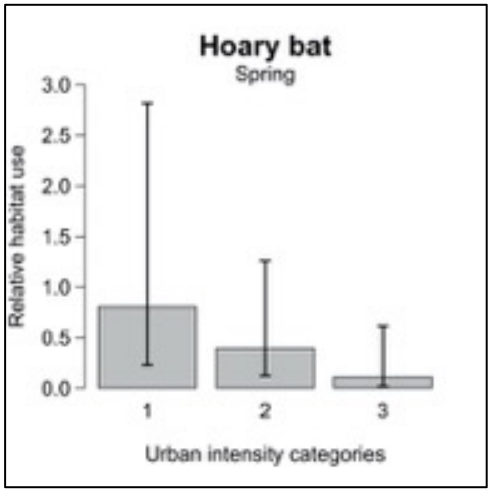


Figure D5: Relative habitat use (based on RN models) across urban intensity categories for the hoary bat in the spring season.

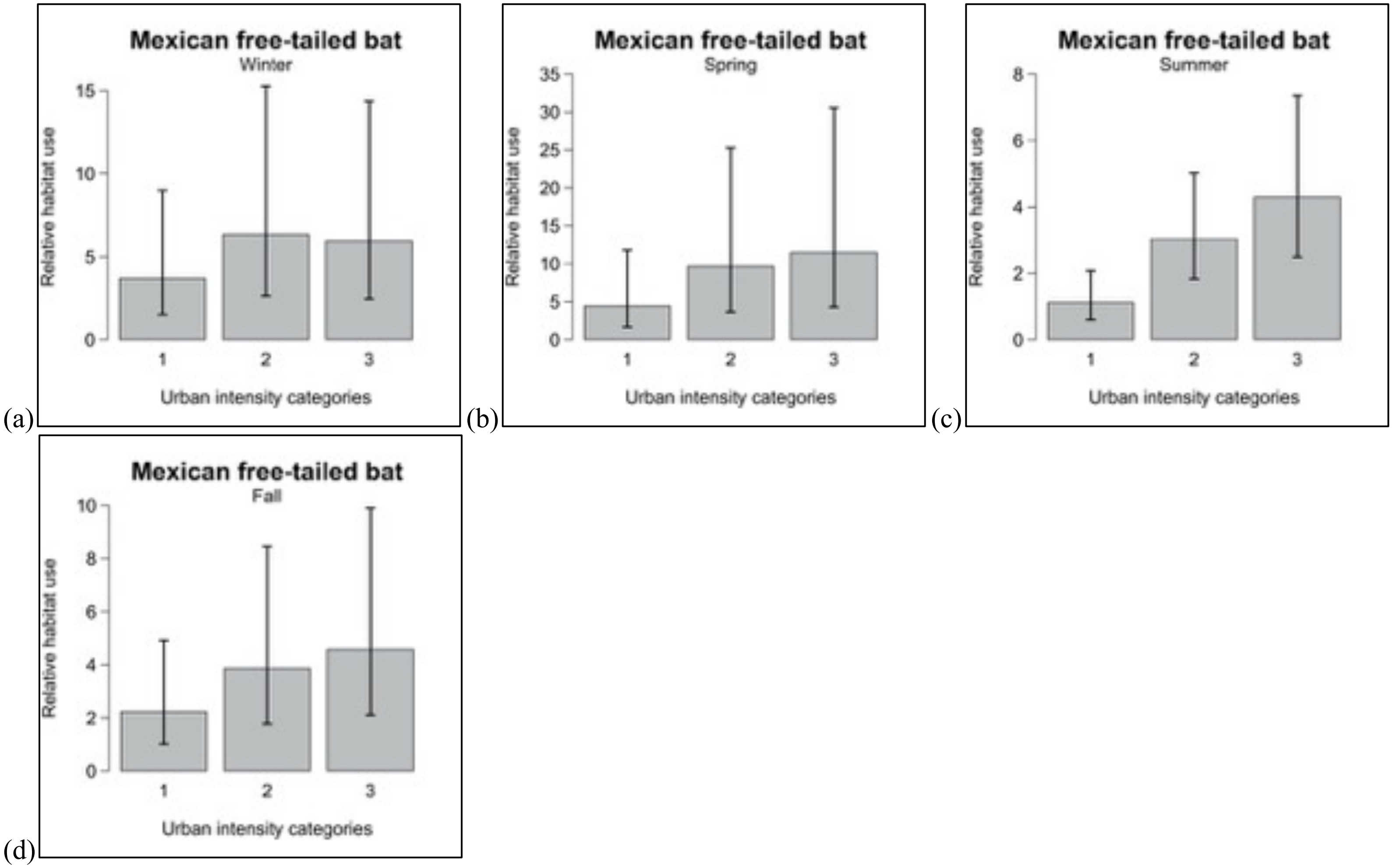
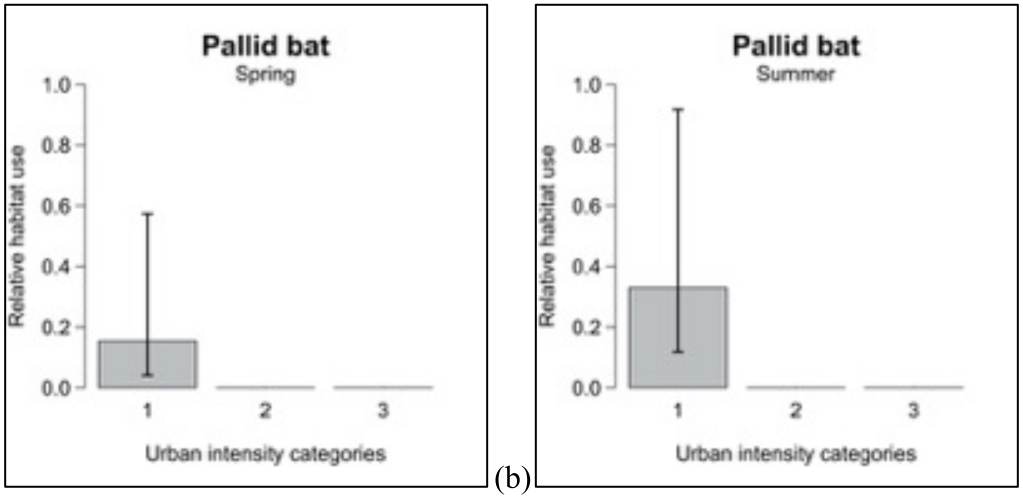
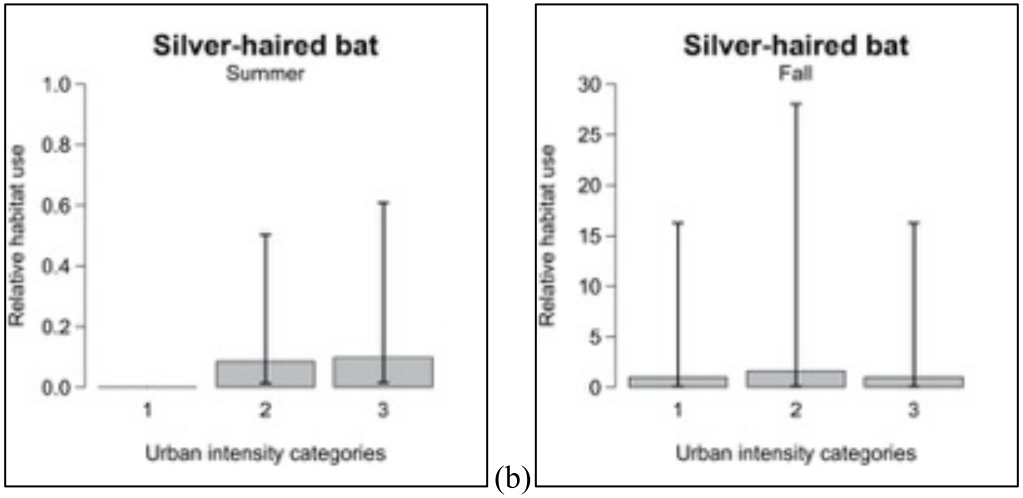


Figure D6: Relative habitat use (based on RN models) across urban intensity categories for the Mexican free-tailed bat in the (a) winter, (b) spring, (c) summer, and (d) fall season.



(a) (b)

Figure D7: Relative habitat use (based on RN models) across urban intensity categories for the pallid bat in the (a) spring and (b) summer season.



(a) (b)

Figure D8: Relative habitat use (based on RN models) across urban intensity categories for the silver-haired bat in the (a) summer and (b) fall season.

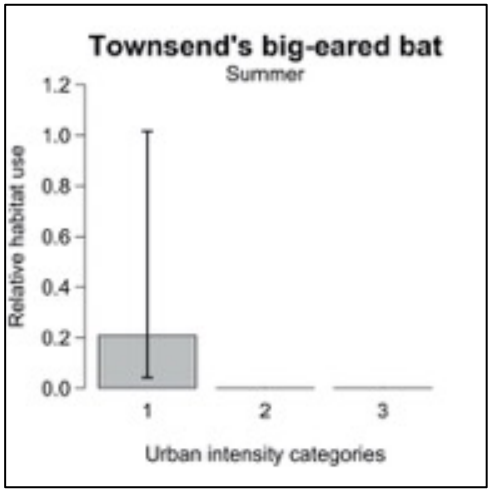


Figure D9: Relative habitat use (based on RN models) across urban intensity categories for the Townsend's big-eared bat in the summer.

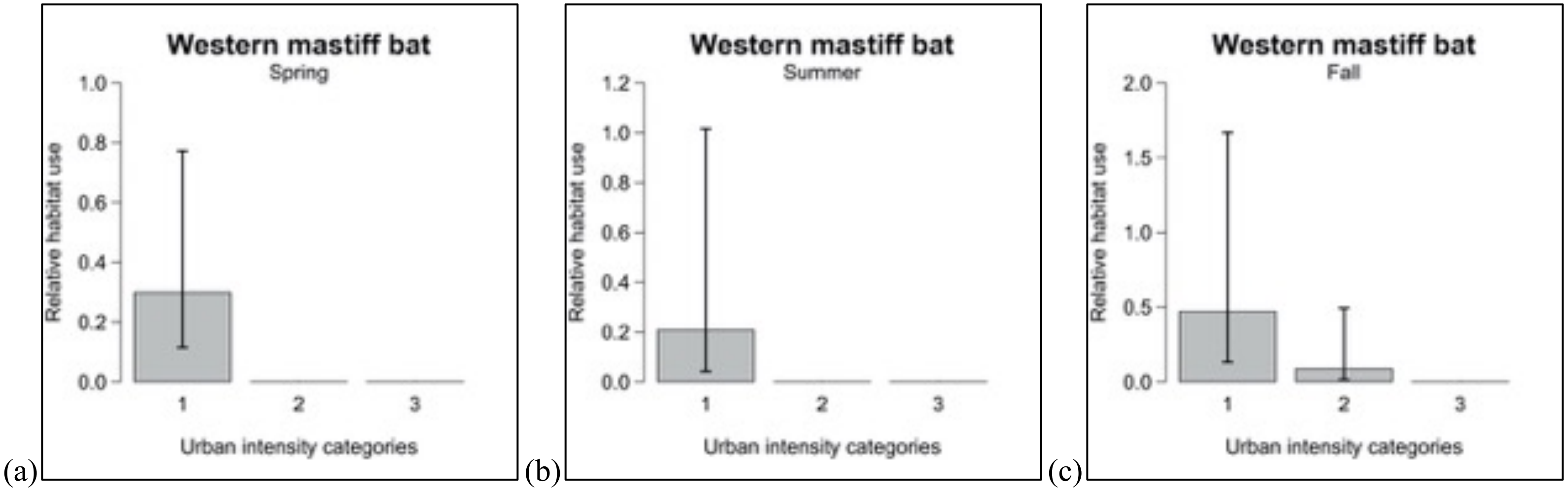


Figure D10: Relative habitat use (based on RN models) across urban intensity categories for the western mastiff bat in the (a) spring, (b) summer, and (c) fall season.

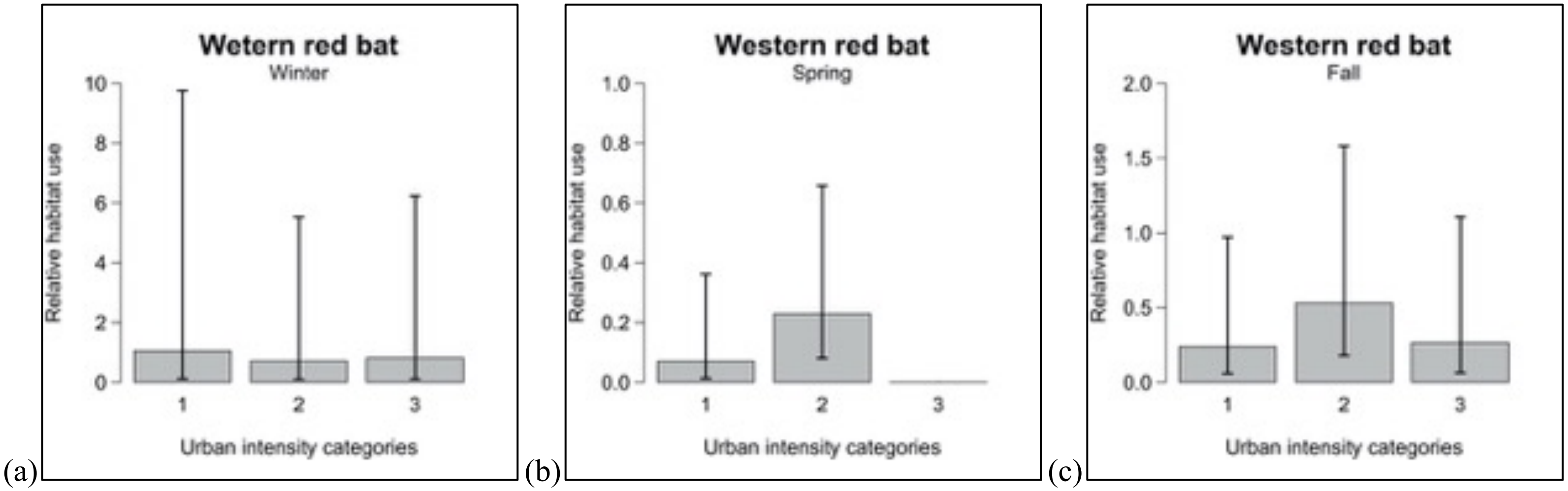


Figure D11: Relative habitat use (based on RN models) across urban intensity categories for the western red bat in the (a) winter, (b) spring, and (c) summer season.

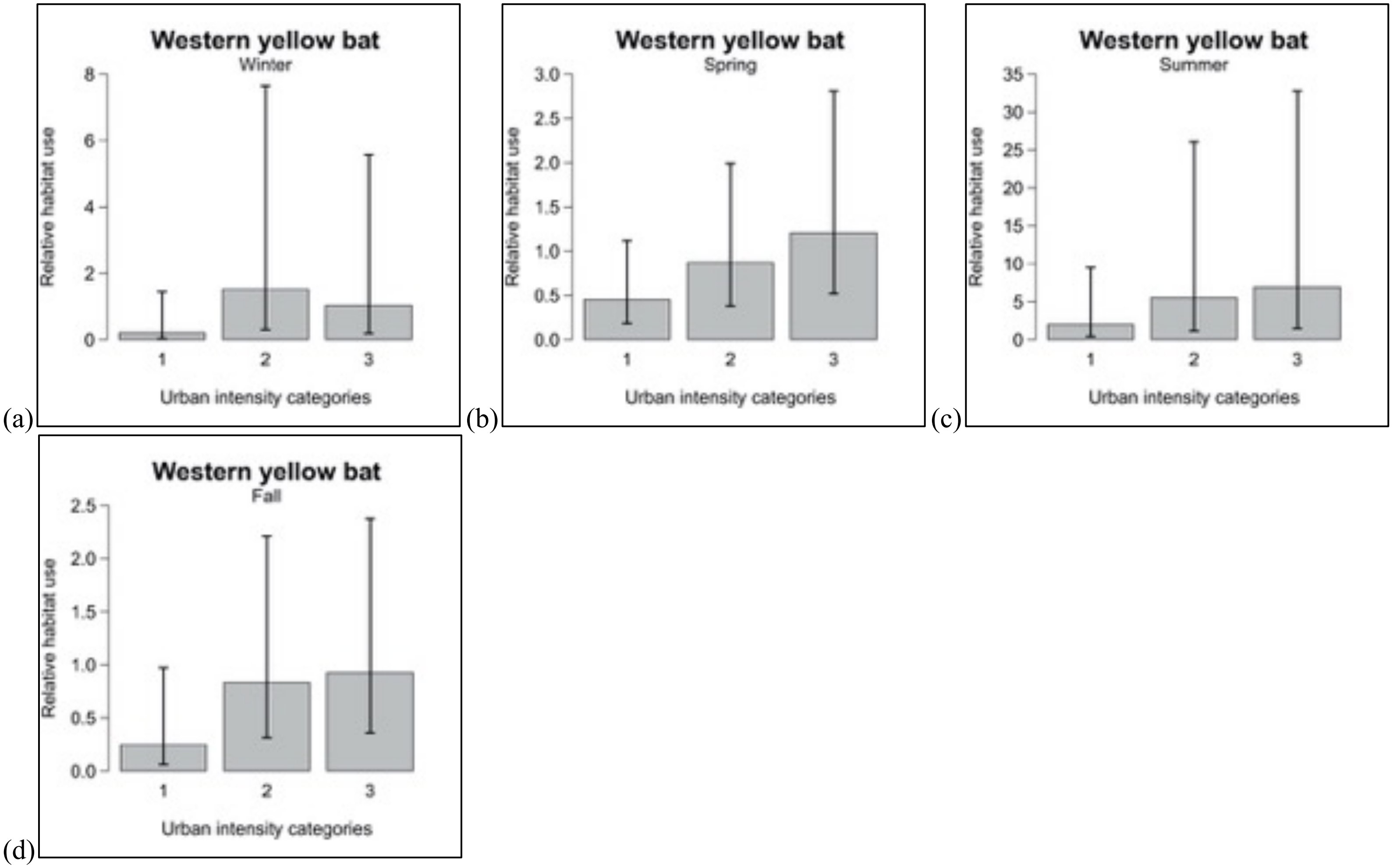


Figure D12: Relative habitat use (based on RN models) across urban intensity categories for the western yellow bat in the (a) winter, (b) spring, (c) summer, and (d) fall season.

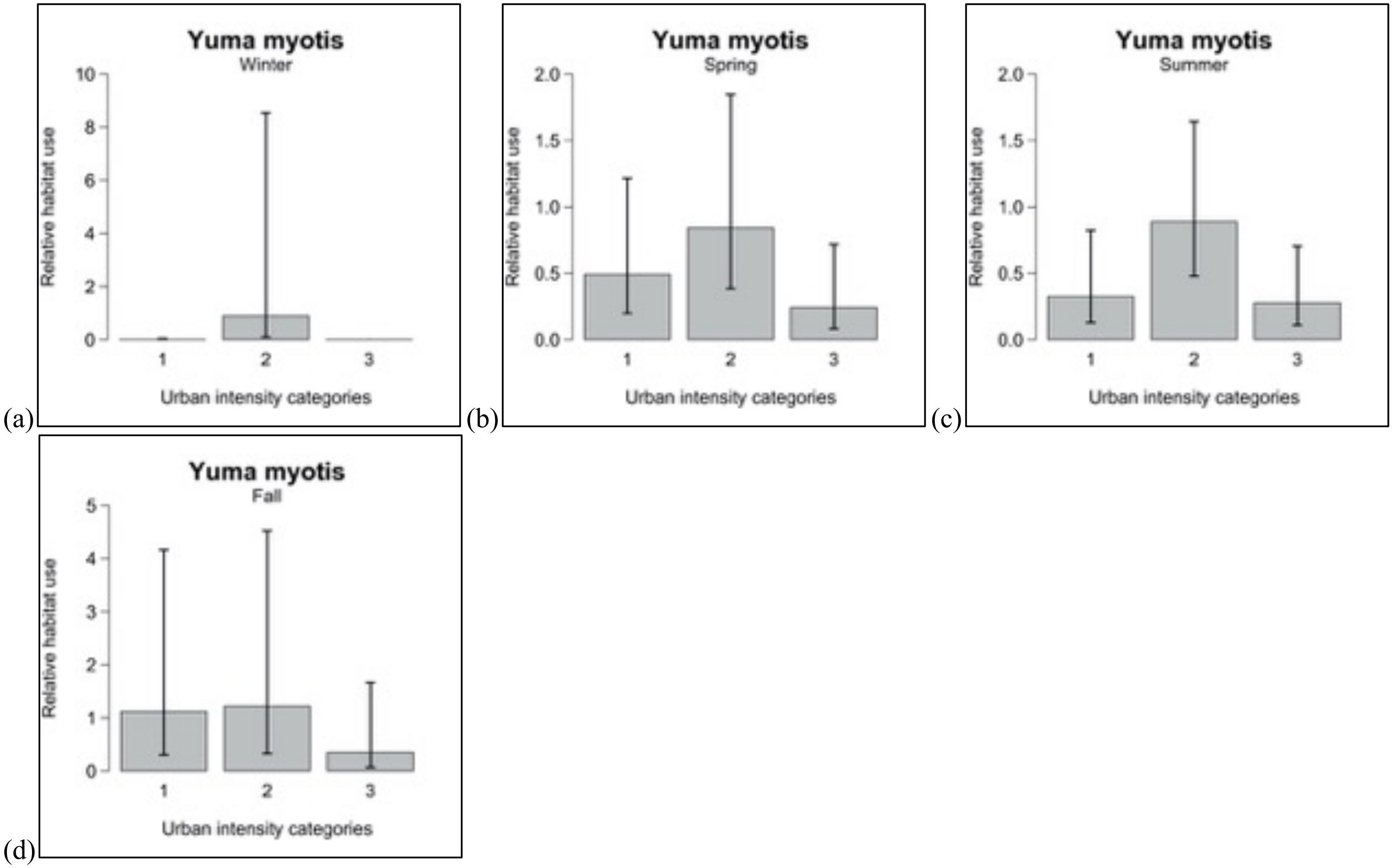


Figure D13: Relative habitat use (based on RN models) across urban intensity categories for the Yuma myotis in the (a) winter, (b) spring, (c) summer, and (d) fall season.

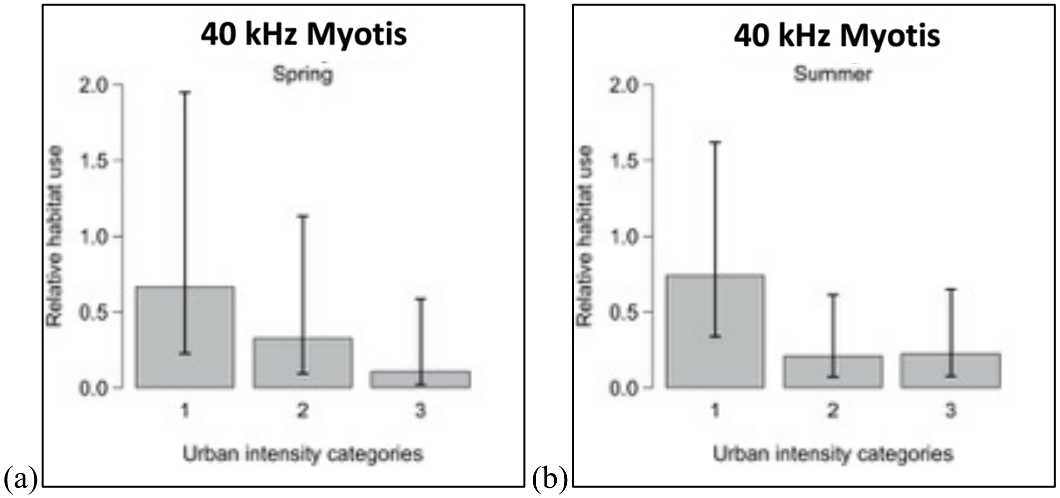
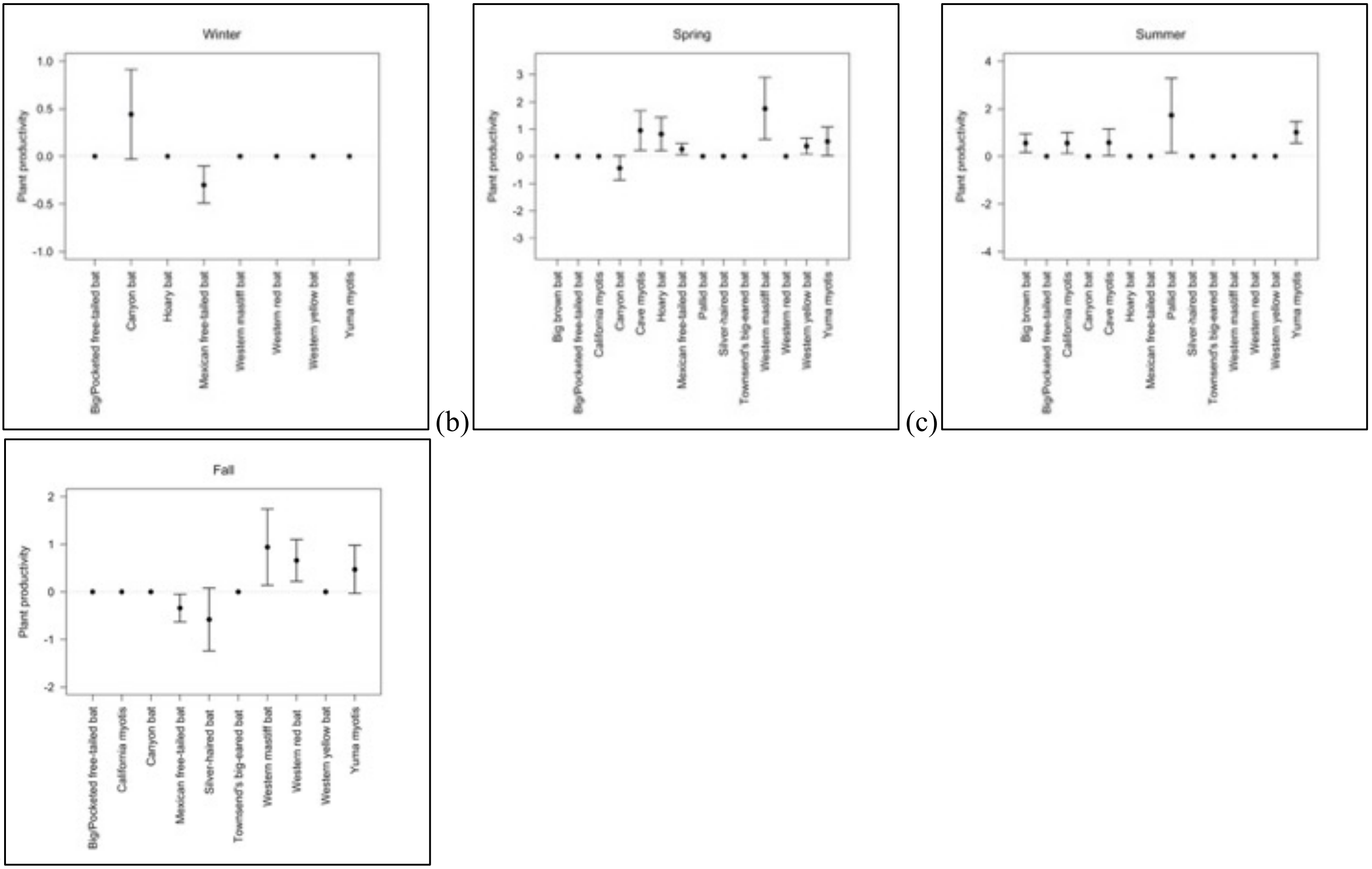


Figure D14: Relative habitat use (based on RN models) across urban intensity categories for the 40 kHz Myotis in the (a) spring and (b) summer season.

APPENDIX E

SPECIES RELATIONSHIPS WITH LANDSCAPE VARIABLES ACROSS SEASONS BASED ON ROYLE-NICHOLS MODELS

Appendix E: Summary of how habitat use of bats (based on the top Royle-Nichols (RN) models) varied in relation to the variables plant productivity (Figure E1) and distance to water (Figure E2) among 14 species and four seasons in the Phoenix metropolitan area, Arizona in 2019. The error bars represent 95% confidence intervals. Note the y-axes are on different scales.



(a) (b) (c) (d)

Figure E1: Bat species' relationships (based on RN models) with the variable "plant productivity" in the (a) winter, (b) spring, (c) summer and (d) fall season.

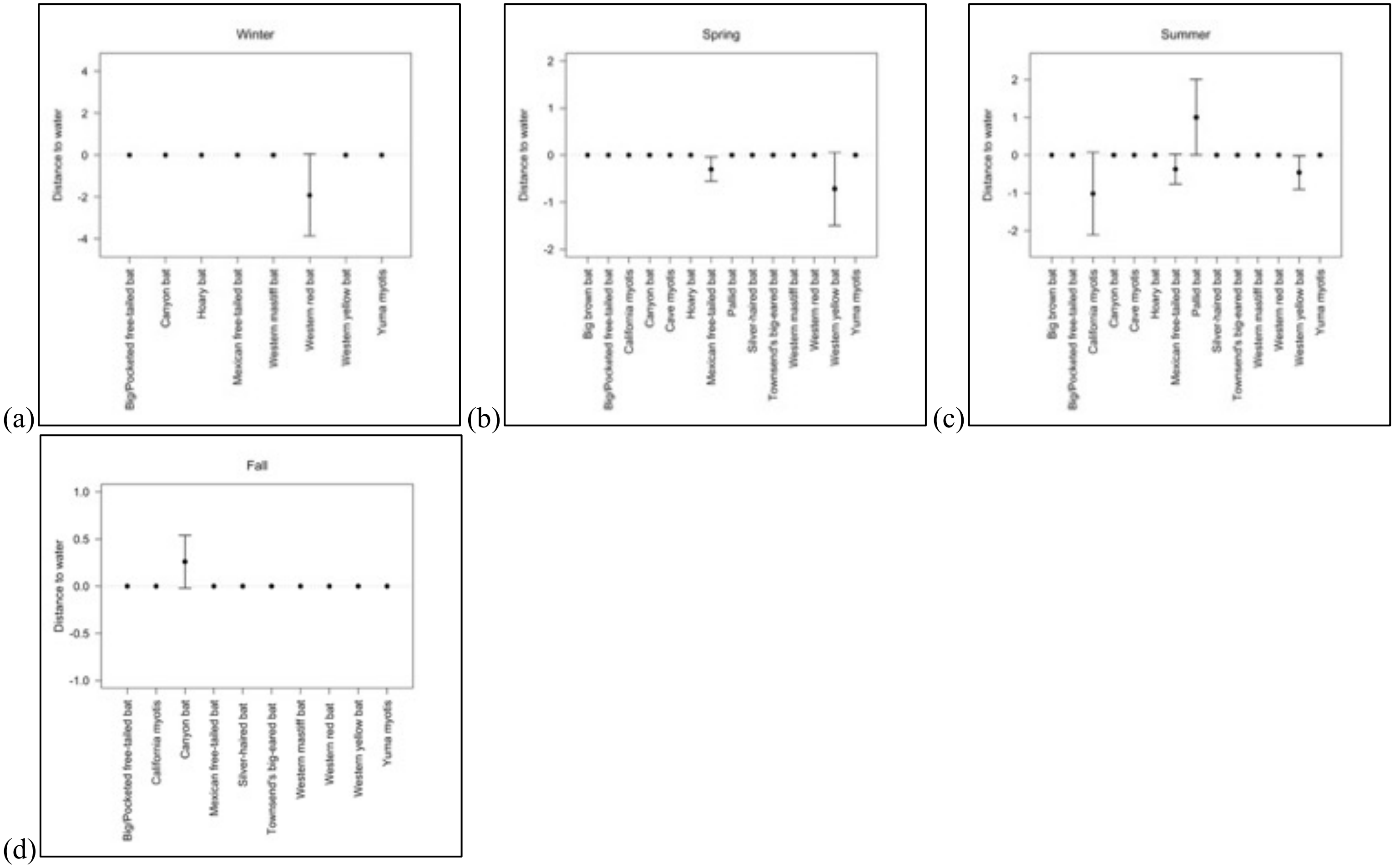


Figure E2: Bat species' relationships (based on RN models) with the variable "distance to water" in the (a) winter, (b) spring, (c) summer and (d) fall season.

APPENDIX F

SINGLE-SPECIES SINGLE-SEASON OCCUPANCY MODEL RESULTS

Appendix F: Occupancy model results for 14 bat species in the Phoenix metropolitan area, Arizona during four seasons in 2019. Species include the big brown bat (Table F1), the big/pocketed free-tailed bat (Table F2), the California myotis (Table F3), the canyon bat (Table F4), the hoary bat (Table F5), the Mexican free-tailed bat (Table F6), the pallid bat (Table F7), the silver-haired bat (Table F8), the Townsend's big-eared bat (Table F9), the western mastiff bat (Table F10), the western red bat (Table F11), the western yellow bat (Table F12), the Yuma myotis (Table F13) and the 40 kHz Myotis (Table F14). Parameters include detection probability (p) and occupancy probability (psi). Models include the intercept-only model (p(.) psi (.)) and the variables include detection probability variables minimum seasonal temperature (T) and average percent moon illumination (M), and occupancy variables urbanization (U), quadratic urbanization (UQ), plant productivity (P), the interaction between urbanization and plant productivity (UxP), and distance to water (W). The most supported spatial scale (i.e., 125- 2000 m radius buffers) of urbanization and plant productivity follows the associated variable in the model description. Result tables include the number of terms in the model (K), AICc value, delta AICc (ΔAICc), model weight (wt), and beta estimates for each variable, followed by the associated standard error (se).

Table F1: Occupancy model results for the big brown bat in spring and summer season.

						p		psi							
						M		U		UQ		P		W	
Season	Model	K	AICc	ΔAICc	wt	β	se	β	se	β	se	β	se	β	se
Spring	p(M) psi(U.125 + UQ.125)	5	94.71	0.00	0.38	-0.66	0.39	2.56	1.68	-1.44	1.07				
	p(M) psi(U.125 + UQ.125 + P.125)	6	96.24	1.53	0.17	-0.67	0.40	2.67	1.49	-1.44	0.98	0.62	0.66		
	p(M) psi(U.125 + UQ.125 + W)	6	96.80	2.09	0.13	-0.72	0.40	2.79	1.86	-1.44	1.10			0.49	0.82
	p(M) psi(.)	3	97.13	2.43	0.11	-0.86	0.37								
	p(M) psi(U.125 + UQ.125 + P.125 + W)	7	98.08	3.38	0.07	-0.73	0.40	3.00	1.79	-1.44	1.05	0.77	0.72	0.66	0.87
	p(M) psi(P.125)	4	98.54	3.83	0.06	-0.88	0.37					0.62	0.69		
	p(M) psi(W)	4	99.20	4.50	0.04	-0.83	0.38							-0.32	0.59
	p(.) psi(.)	2	100.34	5.63	0.02										
	p(M) psi(P.125 + W)	5	100.80	6.10	0.02	-0.85	0.37					0.59	0.70	-0.27	0.60
Summer	p(.) psi(P.125)	3	105.83	0.00	0.34							0.97	0.47		
	p(.) psi(U.125 + P.125)	4	105.86	0.02	0.34			0.61	0.40			1.16	0.56		
	p(.) psi(P.125 + W)	4	107.90	2.06	0.12							0.89	0.47	-0.30	0.58
	p(.) psi(U.125 + P.125 + W)	5	108.33	2.49	0.10			0.63	0.44			1.18	0.63	0.05	0.60
	p(.) psi(.)	2	110.23	4.39	0.04										
	p(.) psi(W)	3	110.74	4.91	0.03									-0.71	0.64
	p(.) psi(U.125)	3	111.63	5.79	0.02			0.32	0.34						
	p(.) psi(U.125 + W)	4	112.80	6.97	0.01			0.20	0.36					-0.61	0.65

Table F2: Occupancy model results for the big/pocketed free-tailed bat in the winter, spring, summer and fall season.

						p				psi							
						T		M		U		P		UxP		W	
Season	Model	K	AICc	ΔAICc	wt	β	se	β	se	β	se	β	se	β	se	β	se
Winter	p(M) psi(U.2000 + W)	5	125.26	0.00	0.81			0.20	0.29	-1.73	1.08					1.02	1.27
	p(M) psi(W)	4	128.19	2.93	0.19			0.26	0.29							2.50	1.13
	p(M) psi(.)	3	139.73	14.48	0.00			0.54	0.33								
	p(.) psi(.)	2	140.19	14.94	0.00												
Spring	p(T) psi(W)	4	130.36	0.00	0.44	-0.92	0.32									2.90	1.07
	p(T) psi(U.2000 + W)	5	132.13	1.77	0.18	-0.86	0.33			-0.70	0.75					2.10	1.17
	p(T) psi(P.1000 + W)	5	132.52	2.17	0.15	-0.89	0.32					0.28	0.49			2.89	1.06
	p(T) psi(U.2000)	4	133.43	3.08	0.09	-0.72	0.36			-1.54	0.60						
	p(T) psi(U.2000 + P.1000 + W)	6	134.69	4.33	0.05	-0.86	0.33			-0.62	0.89	0.10	0.55			2.20	1.30
	p(T) psi(U.2000 + P.1000)	5	135.46	5.10	0.03	-0.76	0.35			-1.73	0.69	-0.32	0.48				
	p(T) psi(U.2000 + P.1000 + UxP + W)	7	135.91	5.55	0.03	-0.90	0.32			-0.49	0.97	-0.20	0.68	-0.86	0.65	2.49	1.47
	p(T) psi(U.2000 + P.1000 + UxP)	6	136.21	5.85	0.02	-0.76	0.36			-1.82	0.70	-0.54	0.62	-0.72	0.70		
	p(T) psi(.)	3	140.97	10.61	0.00	-0.74	0.38										
	p(.) psi(.)	2	142.10	11.74	0.00												
	p(T) psi(P.1000)	4	142.85	12.49	0.00	-0.68	0.40					0.26	0.37				
Summer	p(T) psi(.)	3	86.97	0.00	0.60	2.21	0.98										
	p(T) psi(P.2000)	4	87.96	1.00	0.37	2.51	0.98					-0.69	0.65				
	p(.) psi(.)	2	92.99	6.02	0.03												
Fall	p(.) psi(W)	3	115.60	0.00	0.51											2.05	0.74
	p(.) psi(P.1000 + W)	4	115.68	0.09	0.49							0.75	0.53			2.59	1.08
	p(.) psi(.)	2	126.02	10.42	0.00												
	p(.) psi(P.1000)	3	127.60	12.01	0.00							0.30	0.36				

Table F3: Occupancy model results for the California myotis in the spring and summer season.

						p		psi							
						M		U		UQ		P		W	
Season	Model	K	AICc	ΔAICc	wt	β	se	β	se	β	se	β	se	β	se
Spring	p(.) psi(U.2000 + UQ.2000)	4	85.76	0.00	0.54			-0.84	1.11	-3.13	1.36				
	p(.) psi(U.2000 + UQ.2000 + W)	5	87.98	2.22	0.18			-1.08	1.19	-2.85	1.45			-0.61	1.32
	p(.) psi(U.2000 + UQ.2000 + P.125)	5	88.17	2.42	0.16			-0.80	1.10	-3.11	1.35	-0.11	0.46		
	p(.) psi(U.2000 + UQ.2000 + P.125 + W)	6	90.44	4.68	0.05			-1.06	1.17	-2.76	1.46	-0.17	0.48	-0.74	1.42
	p(.) psi(W)	3	92.04	6.29	0.02									-1.12	0.95
	p(.) psi(.)	2	92.25	6.49	0.02										
	p(.) psi(P.125 + W)	4	94.02	8.26	0.01							-0.26	0.43	-1.22	1.00
	p(.) psi(P.125)	3	94.37	8.61	0.01							-0.17	0.45		
Summer	p(M) psi(P.1000 + W)	5	181.63	0.00	0.53	-0.34	0.49					1.27	0.68	-1.27	0.71
	p(M) psi(P.1000)	4	184.34	2.71	0.14	-0.60	0.50					1.18	0.52		
	p(M) psi(U.250 + UQ.250 + P.1000 + W)	7	184.59	2.96	0.12	-0.45	0.48	-0.15	0.88	-0.55	0.75	1.25	0.90	-1.52	1.10
	p(M) psi(U.250 + UQ.250 + P.1000)	6	185.46	3.83	0.08	-0.48	0.49	0.87	0.61	-1.17	0.68	1.13	0.57		
	p(M) psi(U.250 + UQ.250 + W)	6	186.17	4.53	0.06	-0.74	0.49	-0.39	0.83	-0.58	0.69			-1.71	1.00
	p(M) psi(W)	4	186.52	4.89	0.05	-0.48	0.52							-1.41	0.70
	p(M) psi(U.250 + UQ.250)	5	188.88	7.25	0.01	-0.86	0.52	0.62	0.63	-1.30	0.67				
	p(M) psi(.)	3	190.64	9.01	0.01	-0.90	0.46								
	p(.) psi(.)	2	191.01	9.38	0.00										

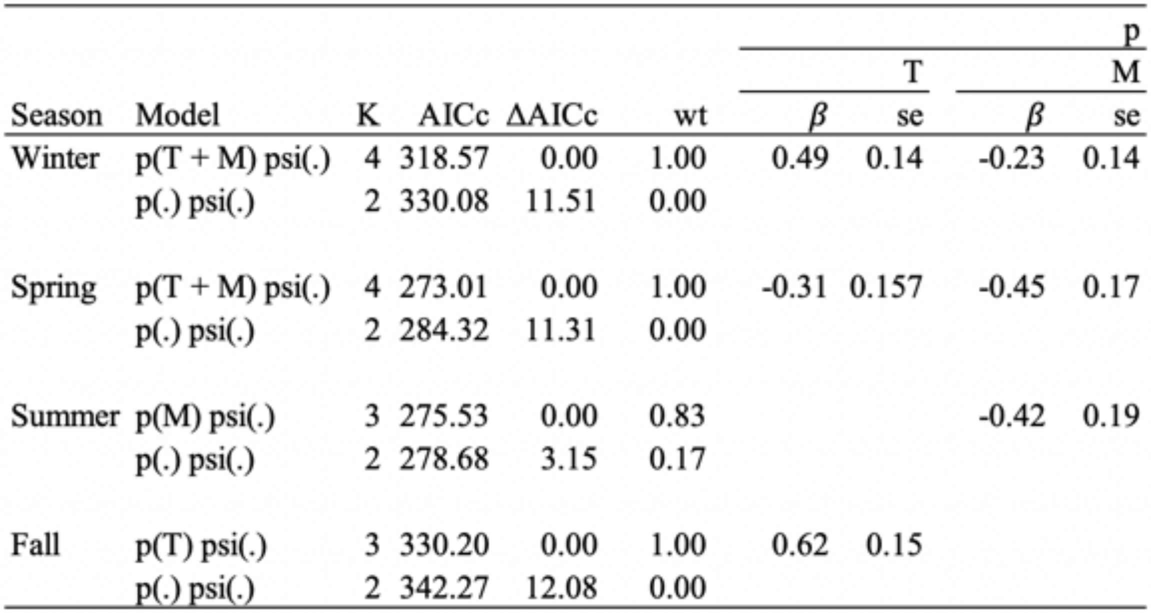
Table F4: Occupancy model results for the canyon bat in the winter, spring, summer and fall season. Note that there were no model results for landscape variables of the canyon bat in the summer season because the species occurred across most sites (psi = 0.98), and therefore variables could not inform occupancy probability.

						p				psi									
						T		M		U		UQ		P		UxP		W	
Season	Model	K	AICc	ΔAICc	wt	β	se	β	se	β	se	β	se	β	se	β	se	β	se
Winter	p(T) psi(U.1000)	4	179.44	0.00	0.30	0.68	0.26			-0.66	0.37								
	p(T) psi(P.125)	4	180.33	0.89	0.19	0.67	0.26							0.54	0.34				
	p(T) psi(.)	3	180.72	1.29	0.16	0.64	0.25												
	p(T) psi(W)	4	180.88	1.44	0.14	0.73	0.27											0.55	0.46
	p(T) psi(U.1000 + W)	5	181.61	2.17	0.10	0.71	0.26			-0.54	0.42							0.23	0.45
	p(T) psi(P.125 + W)	5	181.76	2.32	0.09	0.73	0.26							0.45	0.37			0.40	0.44
	p(.) psi(.)	2	185.07	5.64	0.02														
Spring	p(T + M) psi(U.1000)	5	238.99	0.00	0.52	0.54	0.21	0.40	0.22	-1.19	0.38								
	p(T + M) psi(U.1000 + P.1000)	6	240.83	1.84	0.21	0.53	0.21	0.39	0.22	-1.31	0.41			-0.33	0.38				
	p(T + M) psi(U.1000 + W)	6	241.54	2.55	0.14	0.53	0.21	0.40	0.22	-1.14	0.45							0.10	0.48
	p(T + M) psi(U.1000 + P.1000 + W)	7	243.54	4.55	0.05	0.53	0.21	0.39	0.22	-1.33	0.50			-0.33	0.40			-0.02	0.48
	p(T + M) psi(U.1000 + P.1000 + UxP)	7	243.54	4.55	0.05	0.53	0.21	0.39	0.22	-1.31	0.42			-0.33	0.38	0.00	0.36		
	p(T + M) psi(U.1000 + P.1000 + UxP + W)	8	246.38	7.39	0.01	0.53	0.21	0.39	0.22	-1.33	0.53			-0.33	0.40	-0.01	0.38	-0.02	0.50
	p(T + M) psi(W)	5	247.33	8.33	0.01	0.51	0.21	0.41	0.22									0.79	0.46
	p(T + M) psi(.)	4	249.17	10.18	0.00	0.51	0.22	0.43	0.23										
	p(T + M) psi(P.1000 + W)	6	249.47	10.48	0.00	0.51	0.21	0.42	0.23					0.21	0.32			0.81	0.47
	p(T + M) psi(P.1000)	5	251.24	12.24	0.00	0.51	0.22	0.44	0.24					0.20	0.32				
	p(.) psi(.)	2	262.29	23.29	0.00														
Summer	p(T + M) psi(.)	4	264.27	0.00	1.00	-0.56	0.20	0.53	0.16										
	p(.) psi(.)	2	281.75	17.49	0.00														
Fall	p(.) psi(U.125 + UQ.125)	4	247.73	0.00	0.41					-2.25	0.73	1.23	0.50						
	p(.) psi(U.125 + UQ.125 + P.1000)	5	248.58	0.85	0.27					-2.39	0.75	1.25	0.50	-0.44	0.35				
	p(.) psi(U.125 + UQ.125 + W)	5	249.31	1.58	0.19					-1.96	0.77	1.11	0.51					0.40	0.46
	p(.) psi(U.125 + UQ.125 + P.1000 + W)	6	250.76	3.03	0.09					-2.17	0.81	1.16	0.52	-0.38	0.36			0.28	0.45
	p(.) psi(W)	3	253.68	5.95	0.02													0.88	0.46
	p(.) psi(P.1000 + W)	4	255.80	8.07	0.01									-0.16	0.32			0.85	0.46
	p(.) psi(.)	2	256.88	9.15	0.00														
	p(.) psi(P.1000)	3	258.46	10.73	0.00									-0.25	0.30				

Table F5: Occupancy model results for the hoary bat in the spring season.

						p		psi							
						T		U		P		UxP		W	
Season	Model	K	AICc	ΔAICc	wt	β	se	β	se	β	se	β	se	β	se
Spring	p(T) psi(U.125)	4	100.13	0.00	0.20	-1.82	0.57	-1.68	1.05						
	p(T) psi(P.125 + W)	5	100.17	0.03	0.20	-1.79	0.54			0.86	0.53			1.86	1.23
	p(T) psi(W)	4	101.16	1.02	0.12	-1.83	0.54							1.47	1.05
	p(T) psi(U.125 + P.125)	5	101.55	1.42	0.10	-1.77	0.57	-1.43	1.06	0.53	0.56				
	p(T) psi(U.125 + W)	5	101.68	1.54	0.09	-1.84	0.55	-1.20	1.03					0.90	1.07
	p(T) psi(P.125)	4	101.76	1.62	0.09	-1.72	0.56			0.77	0.57				
	p(T) psi(.)	3	102.02	1.89	0.08	-1.77	0.56								
	p(T) psi(U.125 + P.125 + W)	6	102.33	2.20	0.07	-1.78	0.54	-0.64	1.05	0.72	0.56			1.44	1.32
	p(T) psi(U.125 + P.125 + UxP)	6	104.11	3.98	0.03	-1.77	0.57	-1.49	1.10	0.46	0.69	-0.25	1.39		
	p(T) psi(U.125 + P.125 + UxP + W)	7	105.04	4.91	0.02	-1.79	0.54	-0.60	1.18	0.75	0.72	0.08	1.32	1.46	1.34
	p(.) psi(.)	2	112.78	12.64	0.00										

Table F6: Occupancy model results for the Mexican free-tailed bat in the winter, spring, summer and fall season. Note that there were no model results for landscape variables of the Mexican free-tailed bat across seasons because the species occurred across most sites (psi ranging from 0.96 to 1.00), and therefore variables could not inform occupancy probability.



						p			
						T		M	
Season	Model	K	AICc	ΔAICc	wt	β	se	β	se
Winter	p(T + M) psi(.)	4	318.57	0.00	1.00	0.49	0.14	-0.23	0.14
	p(.) psi(.)	2	330.08	11.51	0.00				
Spring	p(T + M) psi(.)	4	273.01	0.00	1.00	-0.31	0.157	-0.45	0.17
	p(.) psi(.)	2	284.32	11.31	0.00				
Summer	p(M) psi(.)	3	275.53	0.00	0.83			-0.42	0.19
	p(.) psi(.)	2	278.68	3.15	0.17				
Fall	p(T) psi(.)	3	330.20	0.00	1.00	0.62	0.15		
	p(.) psi(.)	2	342.27	12.08	0.00				

Table F7: Occupancy model results for the pallid bat in the spring and summer season. Note that there were no model results for environmental or landscape variables of the pallid bat across seasons because there were too few detections to reliably evaluate relationships.

Season	Model	K	AICc	ΔAICc	wt
Spring	p(.) psi(.)	2	34.12	0.00	1.00
Summer	p(.) psi(.)	2	58.28	0.00	1.00

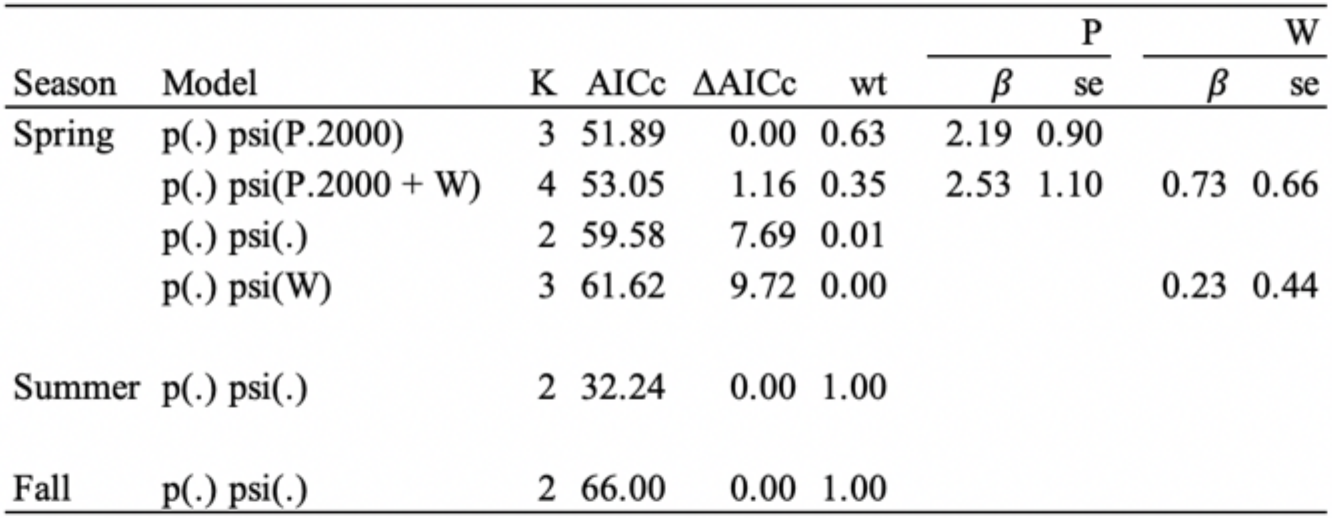
Table F8: Occupancy model results for the silver-haired bat in the summer and fall season. Note that there were no model results for environmental or landscape variables of the silver-haired bat across seasons because there were too few detections to reliably evaluate relationships.

Season	Model	K	AICc	ΔAICc	wt
Summer	p(.) psi(.)	2	32.24	0.00	1.00
Fall	p(.) psi(.)	2	74.56	0.00	1.00

Table F9: Occupancy model results for Townsend’s big-eared bat in the summer season. Note that there were no model results for environmental or landscape variables of the Townsend’s big-eared bat in the summer season because there were too few detections to reliably evaluate relationships.

Season	Model	K	AICc	ΔAICc	wt
Summer	p(.) psi(.)	2	32.24	0.00	1.00

Table F10: Occupancy model results for the western mastiff bat in the spring, summer, and fall season. Note that there were no model results for environmental or landscape variables of the western mastiff bat in the summer and fall season because there were too few detections to reliably evaluate relationships.



						P		W	
Season	Model	K	AICc	ΔAICc	wt	β	se	β	se
Spring	p(.) psi(P.2000)	3	51.89	0.00	0.63	2.19	0.90		
	p(.) psi(P.2000 + W)	4	53.05	1.16	0.35	2.53	1.10	0.73	0.66
	p(.) psi(.)	2	59.58	7.69	0.01				
	p(.) psi(W)	3	61.62	9.72	0.00			0.23	0.44
Summer	p(.) psi(.)	2	32.24	0.00	1.00				
Fall	p(.) psi(.)	2	66.00	0.00	1.00				

Table F11: Occupancy model results for the western red bat in the winter, spring, and fall season.

						p		psi							
						M		U		UQ		P		W	
Season	Model	K	AICc	ΔAICc	wt	β	se	β	se	β	se	β	se	β	se
Winter	p(M) psi(.)	3	91.16	0.00	0.73	0.77	0.39								
	p(.) psi(.)	2	93.15	1.99	0.27										
Spring	p(M) psi(.)	3	56.70	0.00	0.39	1.00	0.49								
	p(M) psi(P.250)	4	57.36	0.66	0.28	1.03	0.50					0.60	0.44		
	p(M) psi(W)	4	58.86	2.16	0.13	1.01	0.50							-0.27	0.66
	p(.) psi(.)	2	59.19	2.49	0.11										
	p(M) psi(P.250 + W)	5	59.79	3.09	0.08	1.03	0.50					0.57	0.45	-0.13	0.64
Fall	p(.) psi(P.125)	3	96.42	0.00	0.33							1.02	0.51		
	p(.) psi(P.125 + W)	4	98.66	2.24	0.11							0.98	0.53	-0.19	0.56
	p(.) psi(U.500 + UQ.500)	4	99.67	3.25	0.07			-0.47	0.76	-1.89	1.27				
	p(.) psi(.)	2	100.34	3.92	0.05										
	p(.) psi(U.500 + UQ.500 + W)	5	101.06	4.64	0.03			-0.96	0.89	-1.23	1.32			-0.80	0.90
	p(.) psi(W)	3	101.57	5.15	0.03									-0.53	0.58

Table F12: Occupancy model results for the western yellow bat in the winter, spring, summer and fall season.

						p				psi									
						T		M		U		UQ		P		UxP		W	
Season	Model	K	AICc	ΔAICc	wt	β	se	β	se	β	se	β	se	β	se	β	se	β	se
Winter	p(T) psi(.)	3	107.59	0.00	0.61	1.67	0.55												
	p(T) psi(P.125)	4	108.48	0.90	0.39	1.72	0.55							-0.93	0.90				
	p(.) psi(.)	2	120.29	12.70	0.00														
Spring	p(T + M) psi(P.125 + W)	6	197.03	0.00	0.42	0.71	0.30	-0.29	0.22					1.87	1.05			-0.74	0.50
	p(T + M) psi(P.125)	5	197.05	0.01	0.42	0.74	0.30	-0.33	0.22					1.80	0.94				
	p(T + M) psi(U.1000 + UQ.1000 + P.125)	7	199.91	2.88	0.10	0.71	0.29	-0.29	0.22	0.54	0.49	-0.86	0.64	1.91	0.97				
	p(T + M) psi(U.1000 + UQ.1000 + P.125 + W)	8	201.95	4.92	0.04	0.72	0.30	-0.29	0.22	0.09	0.72	-0.50	0.76	1.89	1.05			-0.59	0.71
	p(T + M) psi(W)	5	204.66	7.63	0.01	0.66	0.28	-0.33	0.21									-0.84	0.48
	p(T + M) psi(.)	4	206.44	9.41	0.00	0.68	0.29	-0.37	0.22										
	p(T + M) psi(U.1000 + UQ.1000)	6	207.73	10.70	0.00	0.69	0.28	-0.32	0.22	0.50	0.40	-0.89	0.53						
	p(.) psi(.)	2	208.31	11.28	0.00														
	p(T + M) psi(U.1000 + UQ.1000 + W)	7	208.91	11.88	0.00	0.69	0.28	-0.32	0.22	-0.02	0.59	-0.45	0.64					-0.74	0.68
Summer	p(.) psi(W)	3	280.39	1.14	0.62													-1.00	0.45
	p(.) psi(N.2000 + W)	4	282.28	3.03	0.24									0.30	0.44			-0.98	0.45
	p(.) psi(.)	2	284.06	4.80	0.10														
	p(.) psi(N.2000)	3	285.56	6.31	0.05									0.36	0.41				
Fall	p(T) psi(U.2000)	4	147.75	0.00	0.41	0.99	0.35			1.96	1.10								
	p(T) psi(U.2000 + P.125)	5	150.22	2.47	0.12	0.99	0.35			1.90	1.28			0.05	0.62				
	p(T) psi(U.2000 + P.125 + UxP)	6	151.19	3.43	0.07	0.91	0.36			2.15	1.33			-0.20	0.59	1.89	1.70		
	p(T) psi(W)	4	151.31	3.56	0.07	1.00	0.36											-1.03	0.66
	p(T) psi(.)	3	152.18	4.42	0.04	1.07	0.38												
	p(T) psi(P.125 + W)	5	153.13	5.38	0.03	0.98	0.36							0.39	0.51			-0.90	0.64
	p(T) psi(P.125)	4	153.17	5.42	0.03	1.02	0.38							0.52	0.48				
	p(.) psi(.)	2	159.07	11.32	0.00														

Table F13: Occupancy model results for the Yuma myotis in the winter, spring, summer and fall season. Note that there were no model results for environmental or landscape variables of the Yuma myotis in the winter season because there were too few detections to reliably evaluate relationships.

						p				psi									
						T		M		U		UQ		P		UxP		W	
Season	Model	K	AICc	ΔAICc	wt	β	se	β	se	β	se	β	se	β	se	β	se	β	se
Winter	p(.) psi(.)	2	51.16	0.00	1.00														
Spring	p(T + M) psi(U.125)	5	161.86	0.00	0.44	-0.62	0.30	-0.82	0.26	-1.41	0.68								
	p(T + M) psi(U.125 + W)	6	163.28	1.41	0.22	-0.56	0.32	-0.77	0.27	-1.66	0.77							-0.68	0.60
	p(T + M) psi(U.125 + P.1000)	6	164.33	2.46	0.13	-0.60	0.31	-0.82	0.26	-1.37	0.69			0.14	0.40				
	p(T + M) psi(U.125 + P.1000 + W)	7	165.78	3.92	0.06	-0.52	0.33	-0.76	0.27	-1.61	0.77			0.19	0.41			-0.69	0.60
	p(T + M) psi(.)	4	166.26	4.39	0.05	-0.65	0.31	-0.74	0.28										
	p(T + M) psi(U.125 + P.1000 + UxP)	7	166.89	5.03	0.04	-0.60	0.31	-0.83	0.26	-1.38	0.68			0.08	0.44	-0.28	0.72		
	p(T + M) psi(P.1000)	5	168.05	6.18	0.02	-0.58	0.33	-0.73	0.28					0.31	0.37				
	p(T + M) psi(U.125 + P.1000 + UxP + W)	8	168.25	6.39	0.02	-0.51	0.33	-0.77	0.27	-1.66	0.78			0.09	0.45	-0.46	0.75	-0.77	0.63
	p(T + M) psi(W)	5	168.69	6.83	0.01	-0.64	0.32	-0.73	0.29									-0.12	0.56
	p(T + M) psi(P.1000 + W)	6	170.52	8.65	0.01	-0.56	0.34	-0.70	0.29					0.33	0.37			-0.19	0.53
	p(.) psi(.)	2	171.53	9.67	0.00														
Summer	p(.) psi(P.2000)	3	173.89	0.00	0.39									1.60	0.62				
	p(.) psi(P.2000 + W)	4	174.66	0.78	0.27									1.50	0.63			-0.58	0.51
	p(.) psi(U.2000 + UQ.2000 + P.2000)	5	175.01	1.13	0.22					-0.11	0.46	-1.21	0.71	1.64	0.90				
	p(.) psi(U.2000 + UQ.2000 + P.2000 + W)	6	176.83	2.95	0.09					-0.52	0.64	-0.80	0.78	1.39	0.75			-0.72	0.89
	p(.) psi(U.2000 + UQ.2000 + W)	5	180.92	7.03	0.01					-0.81	0.57	-0.83	0.64					-1.25	0.88
	p(.) psi(U.2000 + UQ.2000)	4	181.42	7.53	0.01					-0.17	0.42	-1.36	0.57						
	p(.) psi(W)	3	183.21	9.32	0.00													-0.86	0.52
	p(.) psi(.)	2	185.11	11.22	0.00														
Fall	p(.) psi(U.250 + P.2000)	4	140.99	0.00	0.29					-1.06	0.60			0.78	0.47				
	p(.) psi(U.250)	3	141.72	0.73	0.20					-1.18	0.63								
	p(.) psi(U.250 + P.2000 + W)	5	143.00	2.01	0.11					-1.27	0.71			0.74	0.48			-0.35	0.52
	p(.) psi(P.2000)	3	143.03	2.04	0.10									0.81	0.44				
	p(.) psi(U.250 + W)	4	143.17	2.18	0.10					-1.42	0.72							-0.50	0.51
	p(.) psi(U.250 + P.2000 + UxP)	5	143.42	2.43	0.09					-1.09	0.62			0.88	0.68	0.20	0.96		
	p(.) psi(.)	2	144.87	3.87	0.04														
	p(.) psi(P.2000 + W)	4	145.32	4.32	0.03									0.83	0.44			0.13	0.46
	p(.) psi(U.250 + P.2000 + UxP + W)	6	145.54	4.54	0.03					-1.29	0.73			0.85	0.71	0.22	1.01	-0.35	0.52
	p(.) psi(W)	3	147.13	6.14	0.01													-0.01	0.48

Table F14: Occupancy model results for the 40 kHz Myotis spring and summer season.

						p		psi							
						M		U		P		UxP		W	
Season	Model	K	AICc	ΔAICc	wt	β	se	β	se	β	se	β	se	β	se
Spring	p(M) psi(P.2000)	4	92.11	0.00	0.35	1.28	0.46			1.73	0.74				
	p(M) psi(P.2000 + W)	5	93.53	1.42	0.17	1.33	0.46			1.78	0.78			-0.63	0.69
	p(M) psi(U.2000 + P.2000 + W)	6	93.56	1.45	0.17	1.29	0.45	-1.47	1.01	1.54	0.86			-1.83	1.32
	p(M) psi(U.2000 + P.2000)	5	94.41	2.30	0.11	1.26	0.47	-0.26	0.62	1.67	0.75				
	p(M) psi(U.2000 + P.2000 + UxP + W)	7	94.90	2.79	0.09	1.30	0.46	-1.90	1.23	1.25	0.94	-1.19	1.04	-2.18	1.41
	p(M) psi(U.2000 + W)	5	96.21	4.09	0.05	1.16	0.48	-1.92	0.90					-2.26	1.27
	p(M) psi(U.2000 + P.2000 + UxP)	6	96.42	4.31	0.04	1.24	0.48	-0.34	0.62	1.51	0.74	-0.53	0.62		
	p(M) psi(.)	3	100.19	8.07	0.01	1.10	0.50								
	p(M) psi(U.2000)	4	100.64	8.53	0.00	1.00	0.52	-0.61	0.47						
	p(M) psi(W)	4	101.15	9.04	0.00	1.20	0.49							-0.58	0.56
	p(.) psi(.)	2	103.06	10.95	0.00										
Summer	p(.) psi(.)	2	139.80	0.00	0.18										

APPENDIX G

SUMMARY OF HOW DETECTION PROBABILITY AND OCCUPANCY VARIED IN RELATION TO ENVIRONMENTAL AND LANDSCAPE VARIABLES

Appendix G: Summary of how detection probability and occupancy based on the top model for 12 bat species varied with average minimum temperature (T), average lunar illumination (M), urbanization (U), plant productivity (P), and distance to water (W) in the Phoenix metropolitan area, Arizona during four seasons in 2019. For each variable, we report the general relationship of the beta estimate (positive relationship = +; negative relationship = -; quadratic relationship = Q) and the most supported spatial scale (i.e., 125- 2000 m radius buffers).

		p		psi				
		T	M	U		P		W
Species	Season	Beta	Beta	Beta	Scale	Beta	Scale	Beta
Big brown bat	Spring		-	Q	125			
	Summer			+	125	+	125	
Big/pocketed free-tailed bat	Winter		+	-	2000			+
	Spring	-						+
	Summer	+						
	Fall							+
California myotis	Spring			Q	2000			
	Summer		-			+	1000	-
Canyon bat	Winter	+		-	1000	+	125	
	Spring	+	+	-	1000			
	Summer	-	+			+	2000	
	Fall			Q	125			
Hoary bat	Spring	-		-	125	+	125	+
Mexican free-tailed bat	Winter	+	-					
	Spring	-	-					
	Summer		-					
	Fall	+						
Pallid bat	Summer							
Silver-haired bat	Fall							
Western mastiff bat	Spring					+	2000	
	Fall							
Western red bat	Winter		+					
	Spring		+					
	Fall					+	125	
Western yellow bat	Winter	+						
	Spring	+	-			+	125	-
	Summer							-
	Fall	+		+	2000			
Yuma myotis	Spring	-	-	-	125			
	Summer					+	2000	
	Fall			-	250	+	2000	
40 kHz Myotis	Spring		+			+	2000	
	Summer							

APPENDIX H

PREDICTED OCCUPANCY ACROSS THE GRADIENT OF URBANIZATION

Appendix H: Predicted occupancy (with associated 95% confidence intervals) based on the top occupancy model across the gradient of urbanization for 7 bat species in the Phoenix metropolitan area, Arizona during four seasons in 2019. Species include the big brown bat (Figure H1), the big/pocketed free-tailed bat (Figure H2), the California myotis (Figure H3), the canyon bat (Figure H4), the hoary bat (Figure H5), western yellow bat (Figure H6), and the Yuma myotis (Figure H7). Note that the y-axes are on different scales.

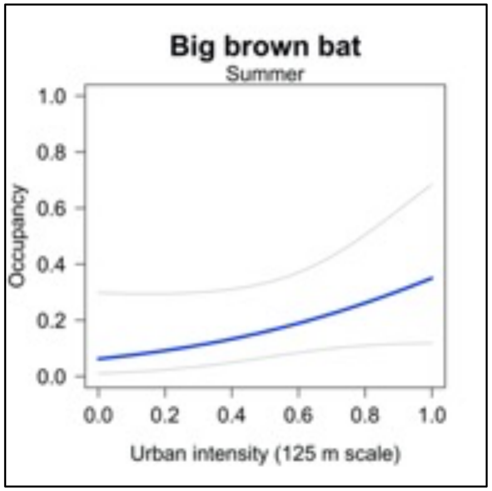


Figure H1: Predicted occupancy across the gradient of urbanization for the big brown bat (i.e., urbanization exploiter) in the summer season.

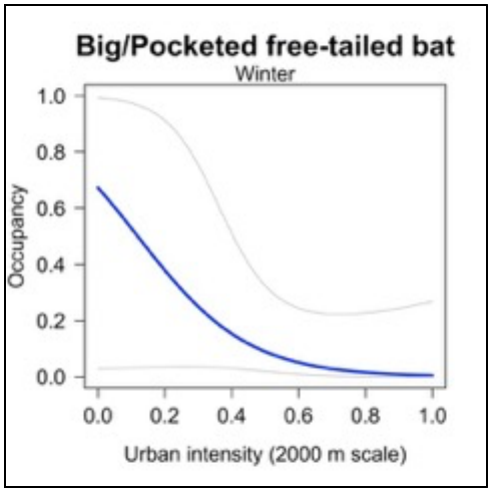
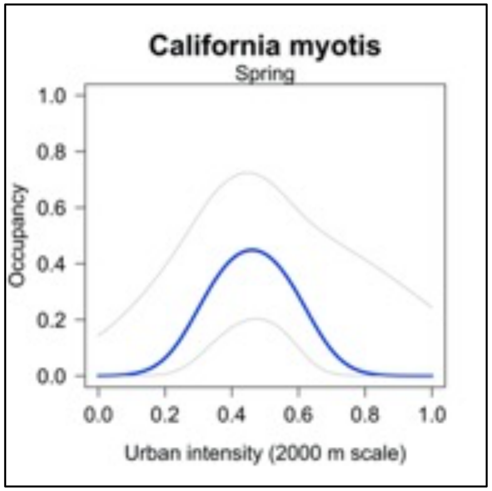


Figure H2: Predicted occupancy across the gradient of urbanization for the big/pocketed free-tailed bat (i.e., urbanization avoider) in the winter season.



(a)

Figure H3: Predicted occupancy across the gradient of urbanization for the California myotis (i.e., urbanization adapter) in the spring season.

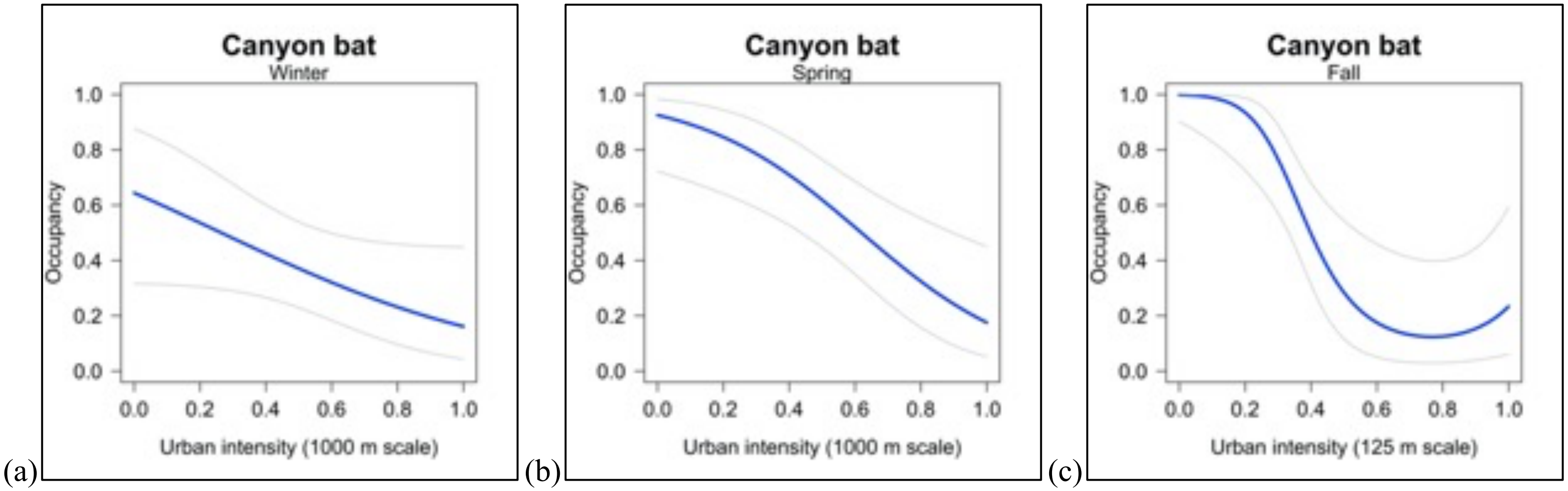


Figure H4: Predicted occupancy across the gradient of urbanization for the canyon bat (i.e., urbanization avoider) in the (a) winter, (b) spring, and (b) fall season.

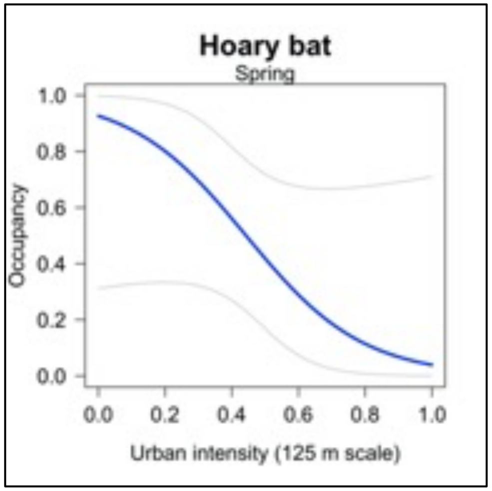


Figure H5: Predicted occupancy across the gradient of urbanization for the hoary bat (i.e., urbanization avoider) in the spring season.

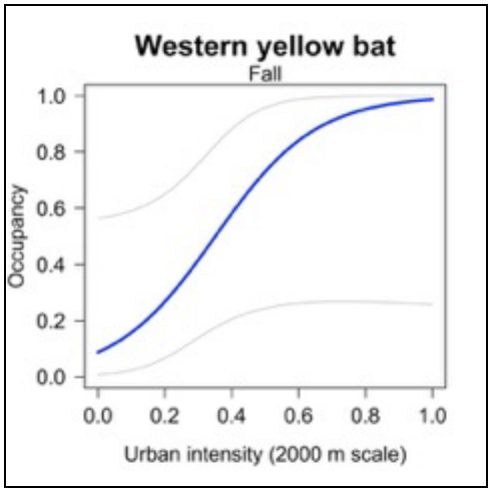
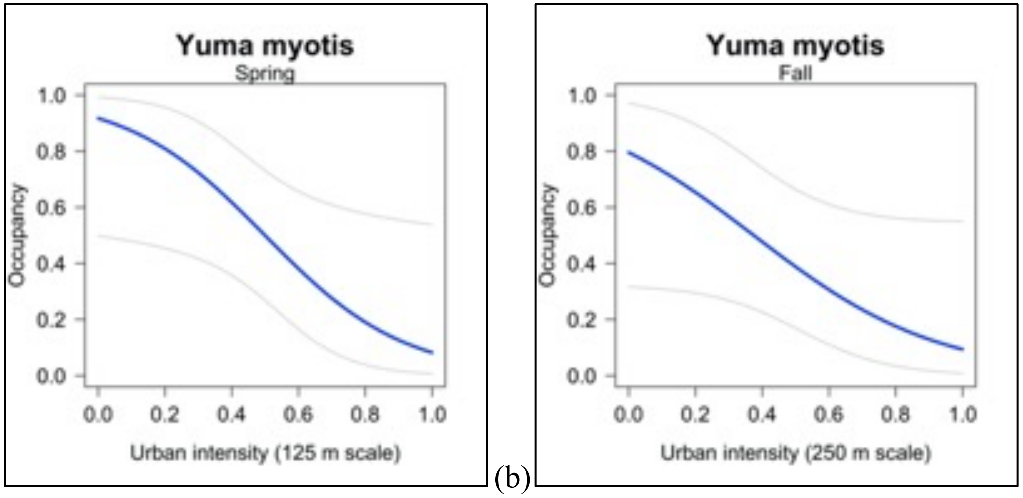


Figure H6: Predicted occupancy across the gradient of urbanization for the western yellow bat (i.e., urbanization exploiter) in the fall season.



(a) (b)

Figure H7: Predicted occupancy across the gradient of urbanization for the Yuma myotis (i.e., urbanization avoider) in the (a) spring and (b) fall season.

APPENDIX I

OCCUPANCY PROBABILITY ACROSS URBAN INTENSITY CATEGORIES

Appendix I: Estimates of occupancy probability across three categories of urban intensity at a 1000 m scale (low (0-0.01), moderate (0.02-0.30), and high urban intensity (0.31-0.61)) for 12 bat species in the Phoenix metropolitan area, Arizona during four seasons in 2019. Species include the big brown bat (Figure I1), the big/pocketed free-tailed bat (Figure I2), the California myotis (Figure I3), the canyon bat (Figure I4), the hoary bat (Figure I5), the pallid bat (Figure I6), the Townsend's big-eared bat (Figure I7), the western mastiff bat (Figure I8), the western red bat (Figure I9), the western yellow bat (Figure I10), the Yuma myotis (Figure I11) and the 40 kHz Myotis (Figure I12). The error bars represent 95% confidence intervals. Note that the y-axes are on different scales.

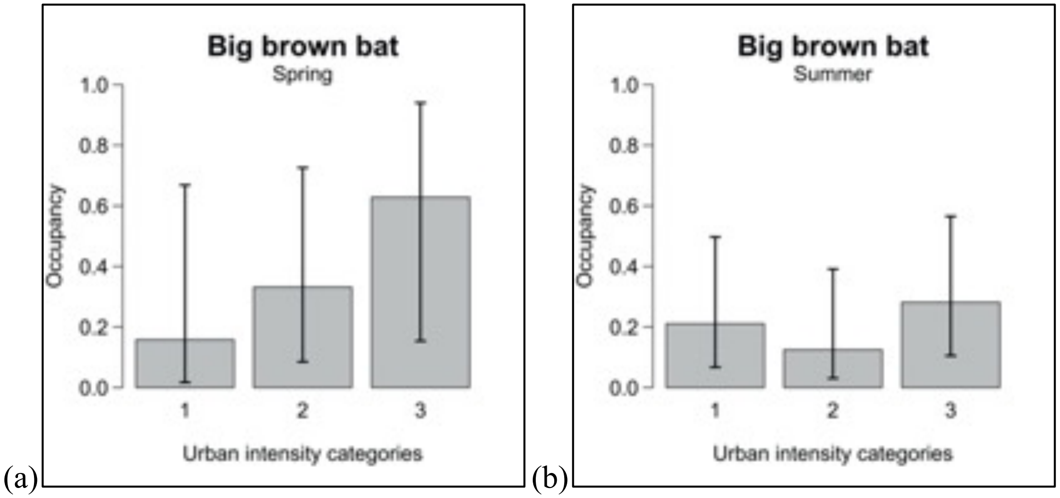


Figure I1: Occupancy across urban intensity categories for the big brown bat in the (a) spring and (b) summer season.

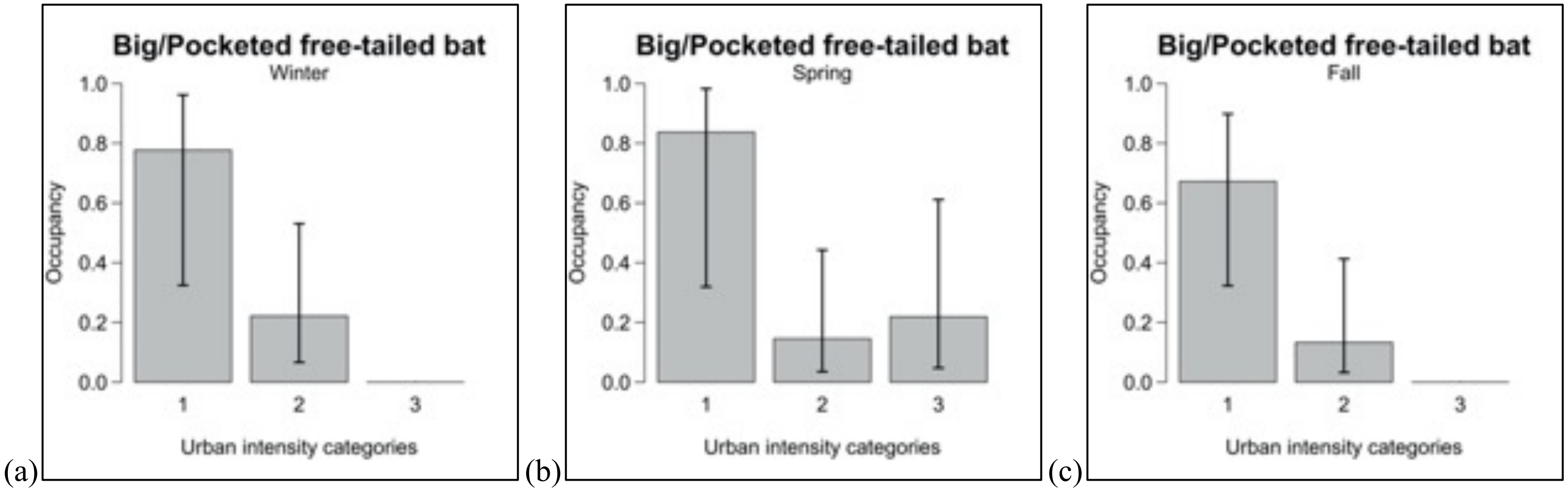


Figure I2: Occupancy across urban intensity categories for the big/pocketed free-tailed bat in the (a) winter, (b) spring, and (b) fall season.

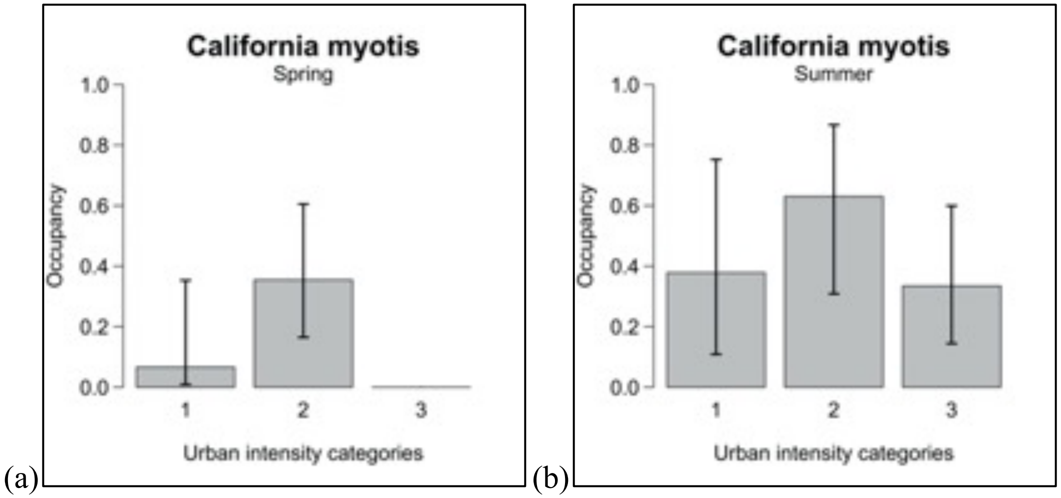


Figure I3: Occupancy across urban intensity categories for the California myotis in the (a) spring and (b) summer season.

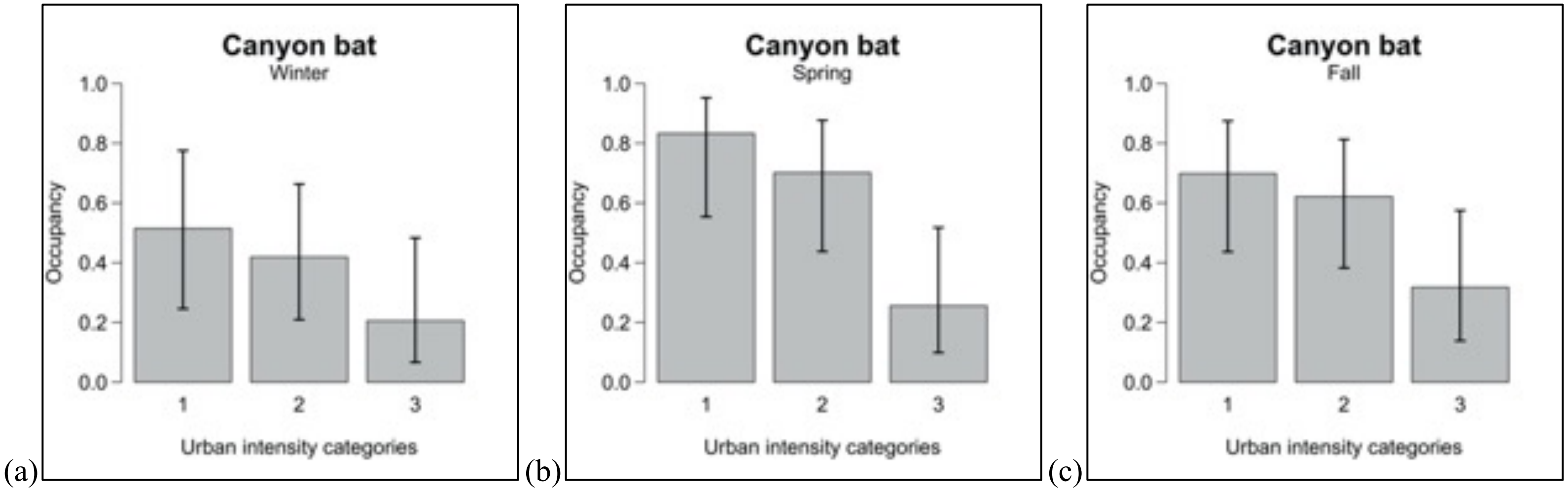


Figure I4: Occupancy across urban intensity categories the canyon bat in the (a) winter, (b) spring, and (b) fall season.

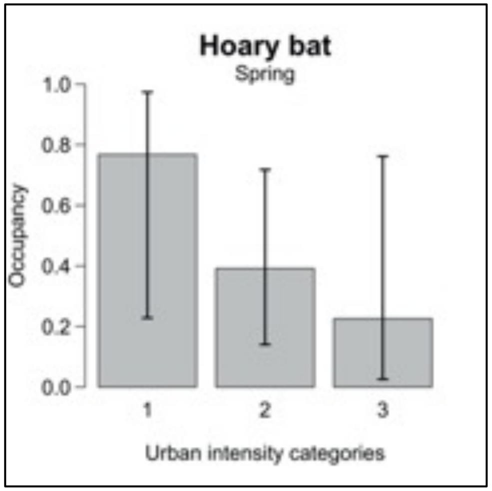


Figure I5: Occupancy across urban intensity categories for the hoary bat in the spring season.

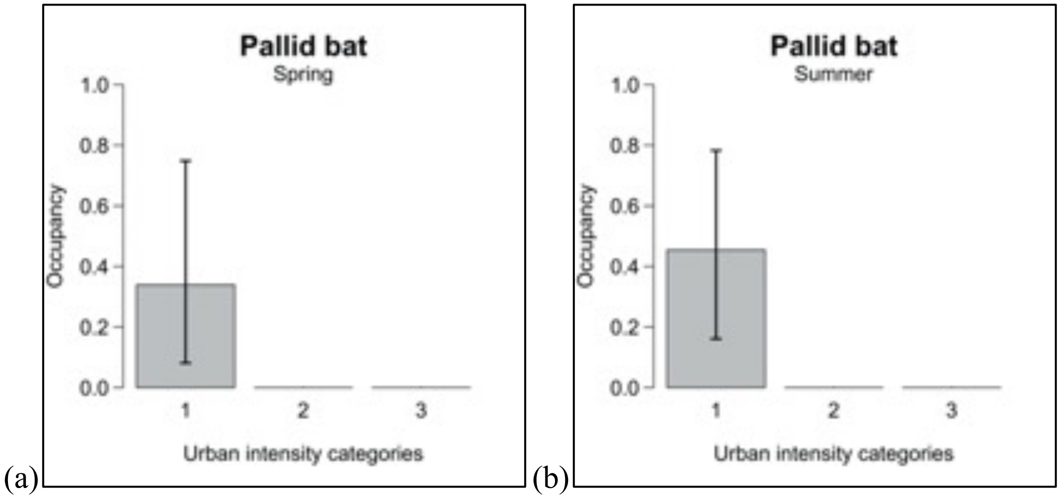


Figure I6: Occupancy across urban intensity categories for the pallid bat in the (a) spring and (b) summer season.

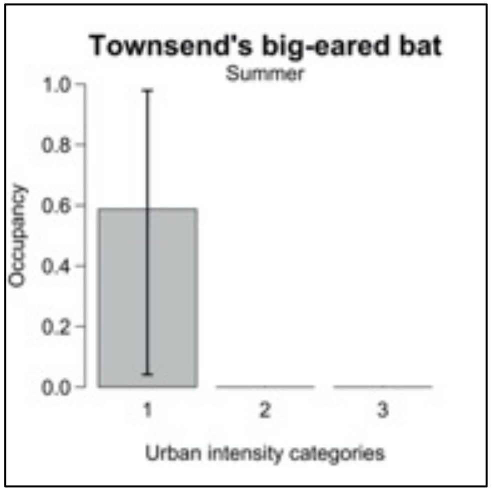


Figure I7: Occupancy across urban intensity categories for the Townsend's big-eared bat in the summer season.

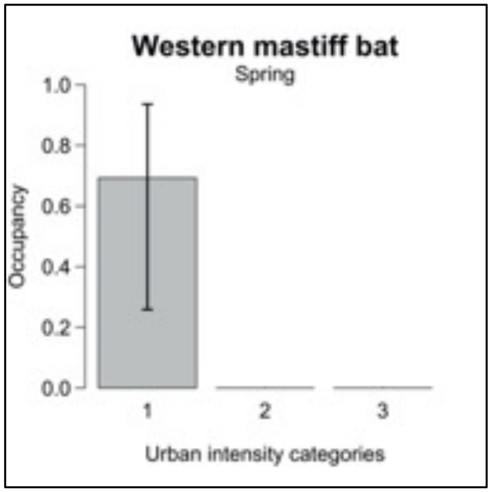
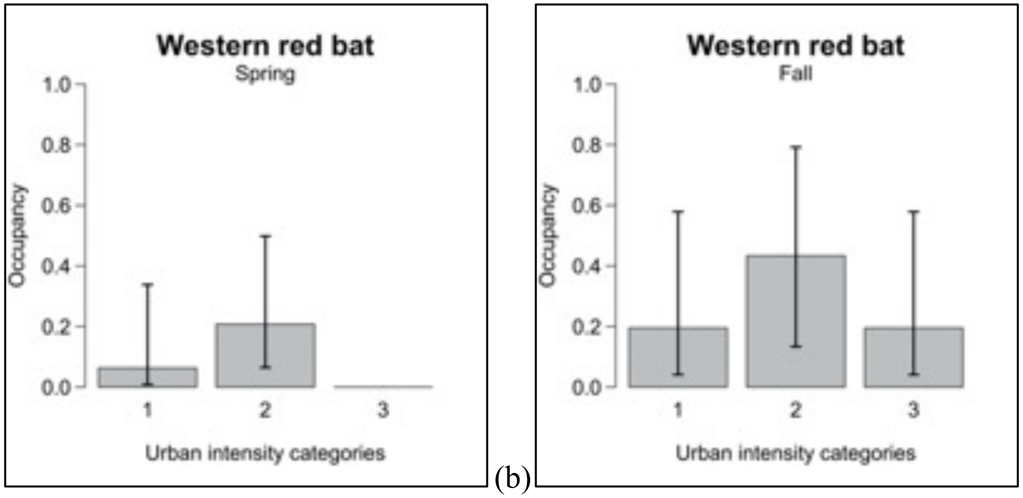


Figure I8: Occupancy across urban intensity categories for the western mastiff bat in the spring season.



(a) (b)

Figure I9: Occupancy across urban intensity categories for the western red bat in the (a) spring and (b) fall season.

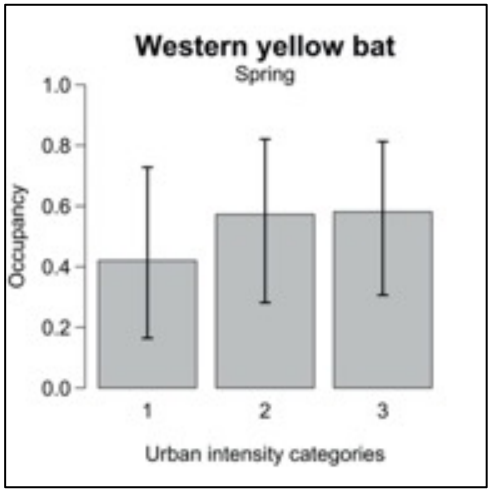
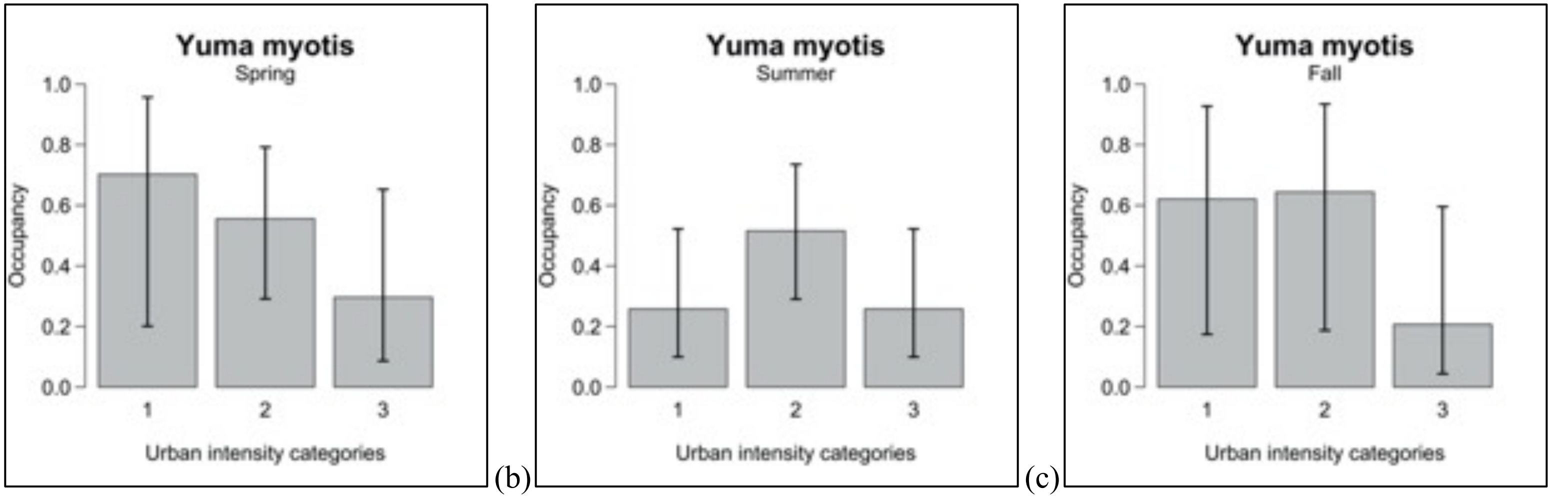


Figure I10: Occupancy across urban intensity categories for the western yellow bat in the spring season.



(a) (b) (c)

Figure I11: Occupancy across urban intensity categories for the Yuma myotis in the (a) spring, (b) summer, and (b) fall season.

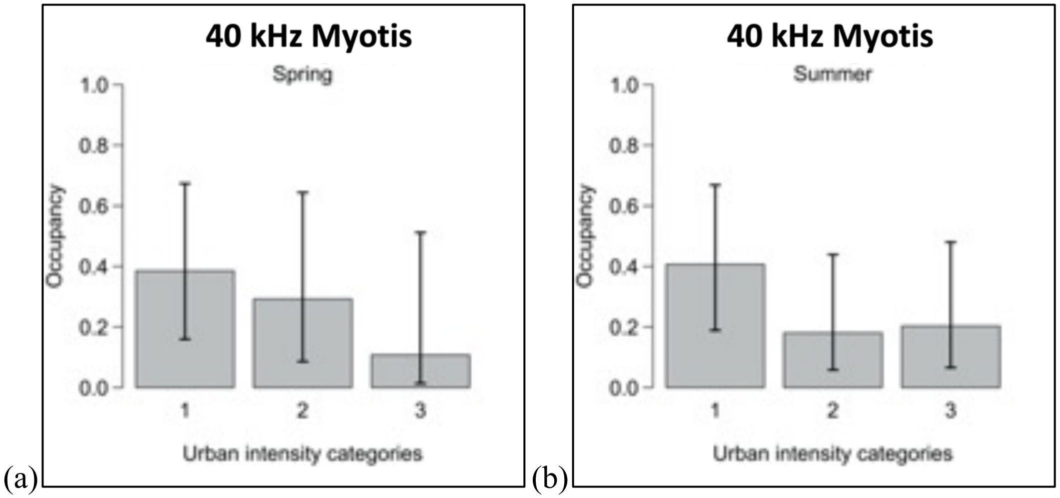


Figure I12: Occupancy across urban intensity categories for the 40 kHz Myotis in the (a) spring and (b) summer season.

APPENDIX J

SPECIES RELATIONSHIPS WITH ENVIRONMENTAL AND LANDSCAPE VARIABLES ACROSS SEASONS BASED ON OCCUPANCY MODELS

Appendix J: Summary of how detection probability and occupancy (based on the top occupancy models) varied in relation to the variables average minimum temperature (Figure J1), average lunar illumination (Figure J2), plant productivity (Figure J3), and distance to water (Figure J4) among 14 species and four seasons in the Phoenix metropolitan area, Arizona in 2019. The error bars represent 95% confidence intervals. Note that the y-axes are on different scales.

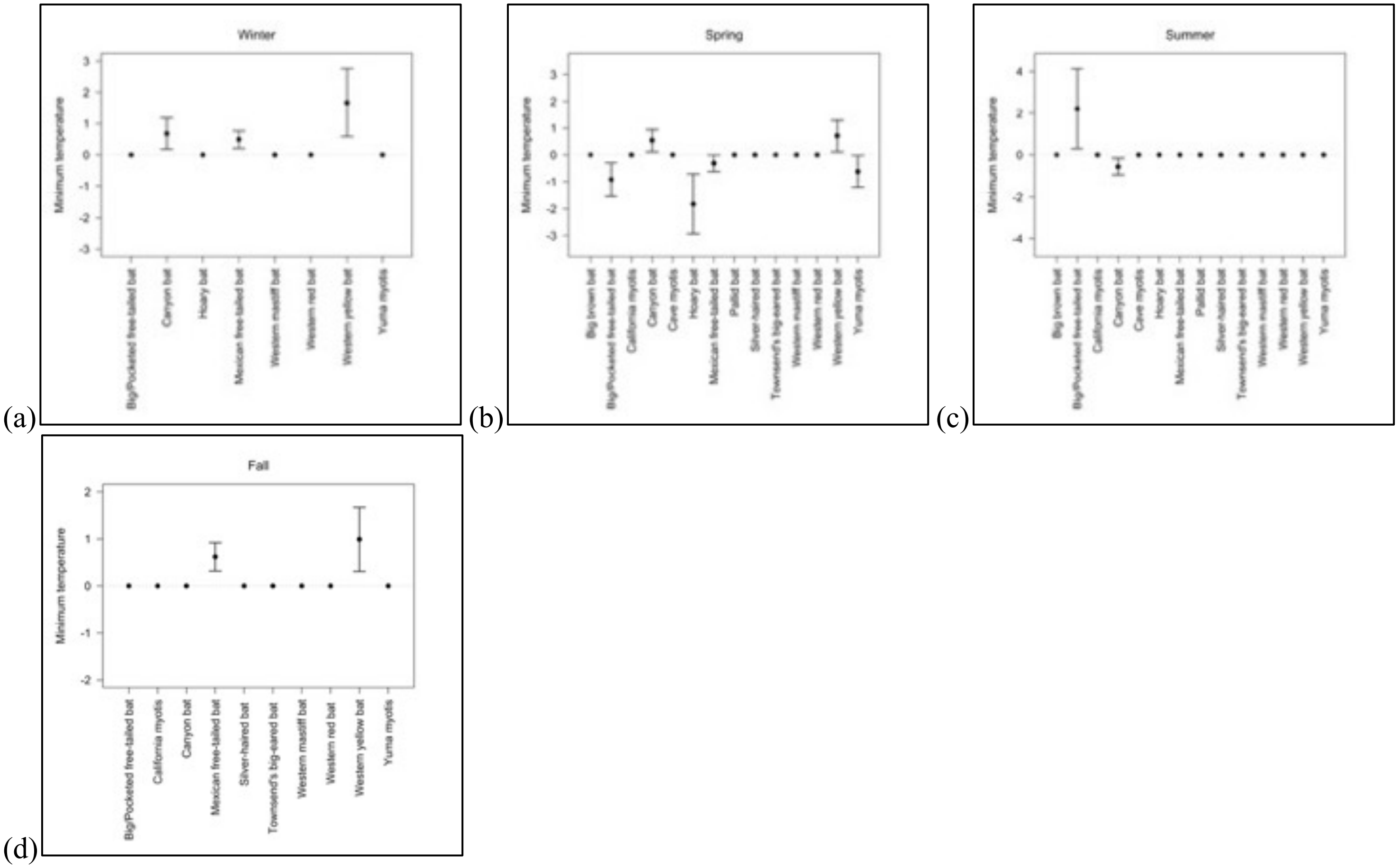


Figure J1: Bat species' relationships with the detection probability variable "minimum temperature" in the (a) winter, (b) spring, (c) summer and (d) fall season.

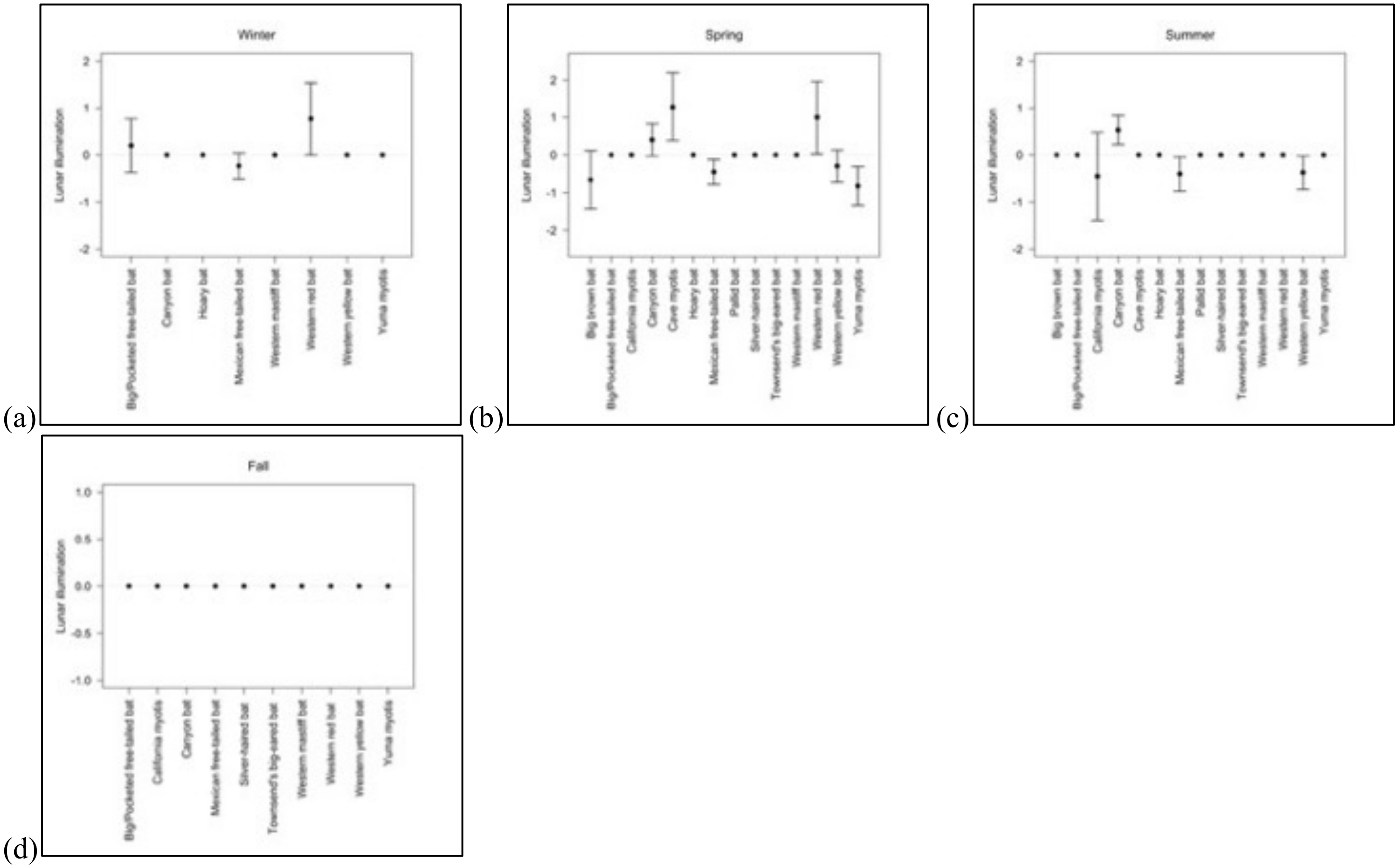


Figure J2: Bat species' relationships with the detection probability variable "lunar illumination" in the (a) winter, (b) spring, (c) summer and (d) fall season.

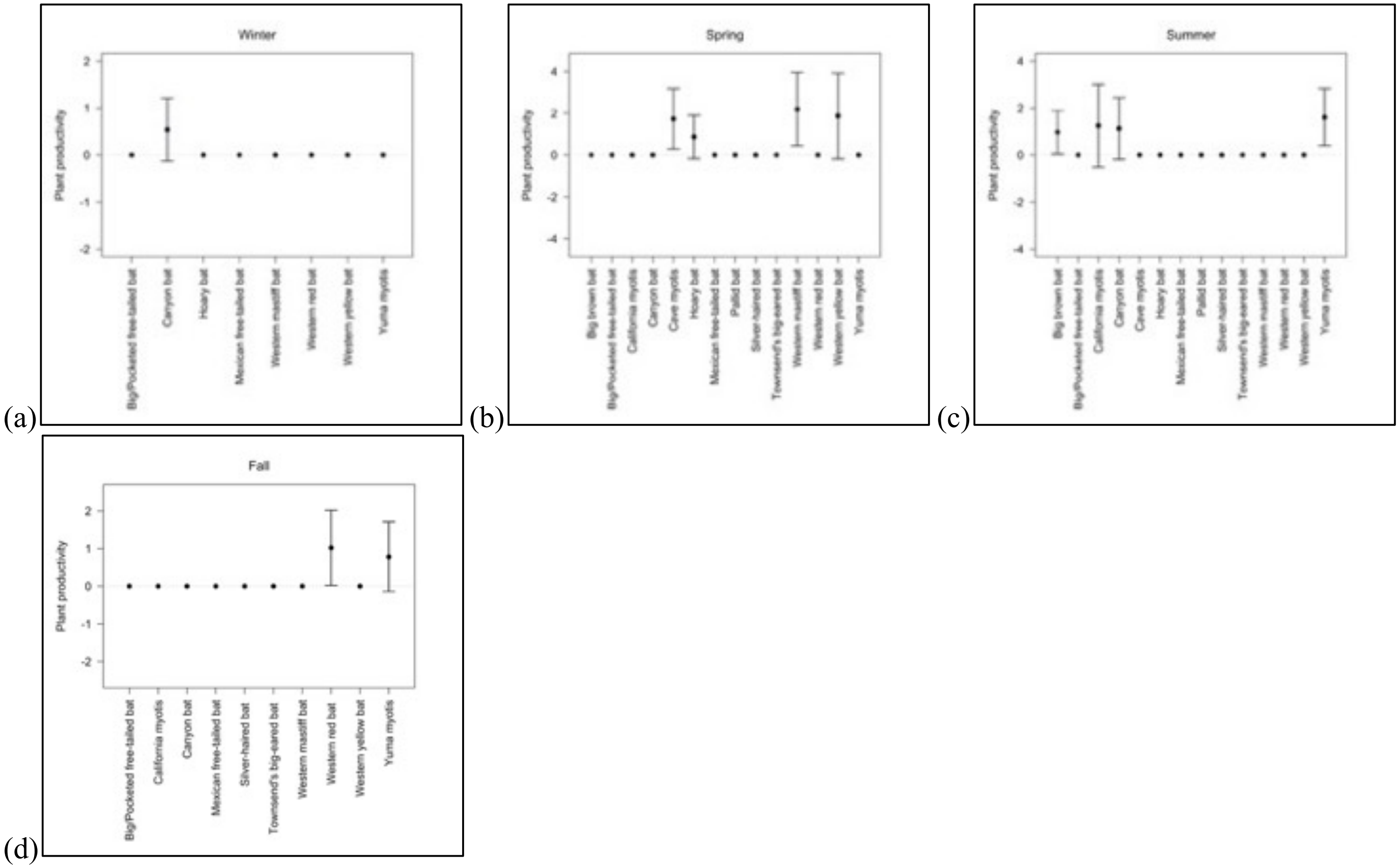


Figure J3: Bat species' relationships with the occupancy probability variable "plant productivity" in the (a) winter, (b) spring, (c) summer and (d) fall season.

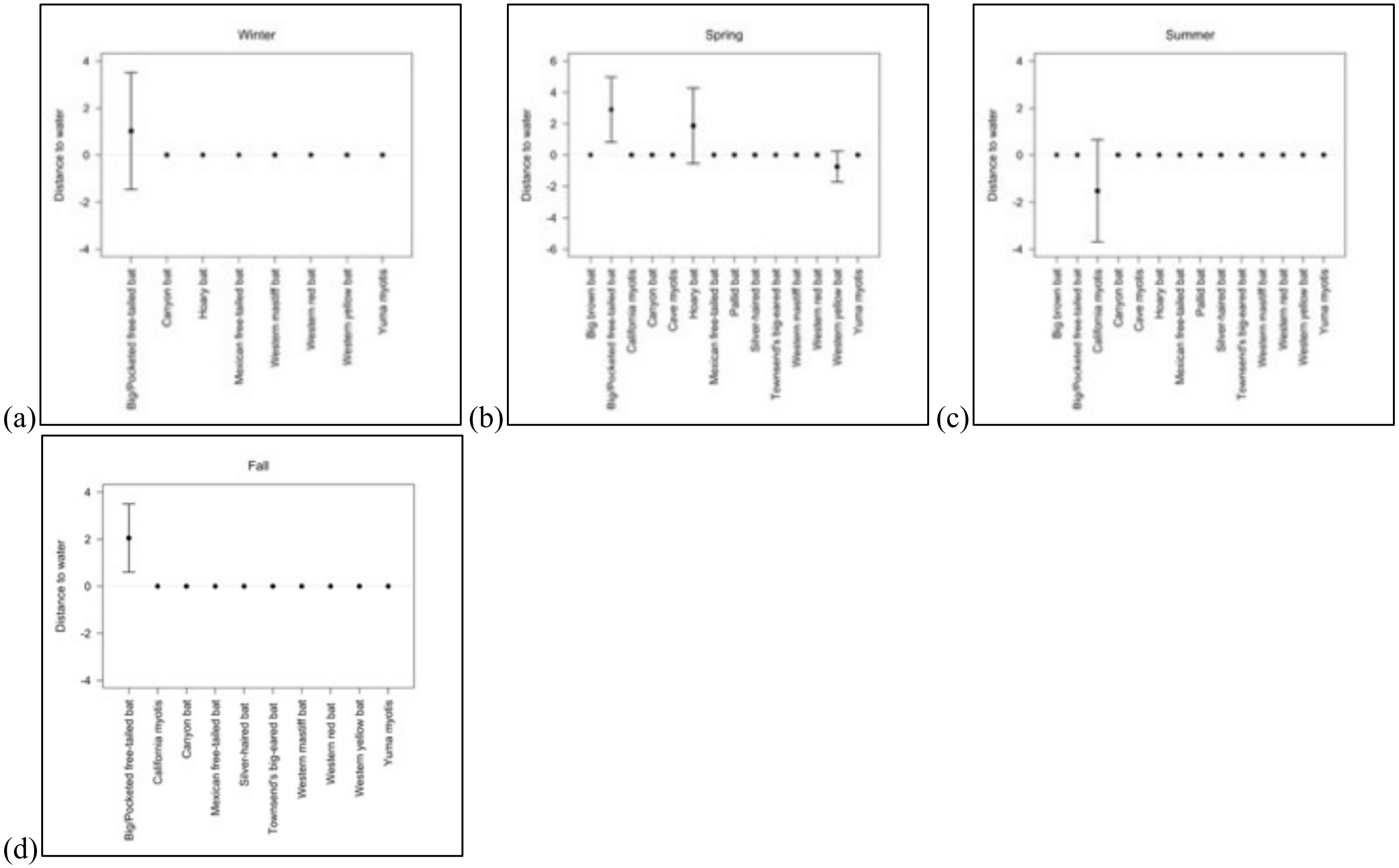


Figure J4: Bat species' relationships with the occupancy probability variable "distance to water" in the (a) winter, (b) spring, (c) summer and (d) fall season.

APPENDIX K

DORAZIO-ROYLE COMMUNITY MODEL RESULTS

Appendix K: Results from the top Dorazio-Royle (DR) model (p(T + M) psi(U.1000 +W)) for the bat community in the Phoenix metropolitan area, Arizona in the summer of 2019. Parameters include community-average beta estimates of detection probability variables average minimum temperature (mu.T) and average lunar illumination (mu.M), and community-average beta estimates of occupancy variables urbanization (mu.U) and distance to water (mu.W), total metacommunity size (Ntotal), species richness at each site (Nsite).

parameter	estimate	se	parameter	estimate	se
mu.T	0.16	0.22	Nsite[24]	5.77	1.17
mu.M	-0.19	0.23	Nsite[25]	6.15	1.01
mu.U	-1.35	0.65	Nsite[26]	7.47	1.00
mu.W	-0.90	0.36	Nsite[27]	4.92	1.19
Ntotal	16.40	1.29	Nsite[28]	6.53	1.03
Nsite[1]	9.63	0.98	Nsite[29]	4.45	1.04
Nsite[2]	4.55	1.23	Nsite[30]	7.08	0.88
Nsite[3]	3.50	1.17	Nsite[31]	5.45	0.65
Nsite[4]	5.47	1.49	Nsite[32]	4.12	0.91
Nsite[5]	8.13	1.12	Nsite[33]	5.61	0.73
Nsite[6]	6.25	1.49	Nsite[34]	3.96	0.91
Nsite[7]	7.80	1.24	Nsite[35]	5.58	0.72
Nsite[8]	6.09	1.20	Nsite[36]	4.72	0.81
Nsite[9]	6.71	1.41	Nsite[37]	4.71	0.77
Nsite[10]	3.70	1.34	Nsite[38]	4.80	0.80
Nsite[11]	5.80	0.87	Nsite[39]	7.01	0.82
Nsite[12]	7.91	1.27	Nsite[40]	5.06	0.89
Nsite[13]	4.95	1.29	Nsite[41]	5.54	0.71
Nsite[14]	6.46	1.26	Nsite[42]	6.43	0.63
Nsite[15]	9.97	0.98	Nsite[43]	4.27	0.72
Nsite[16]	6.25	1.21	Nsite[44]	4.73	0.82
Nsite[17]	4.63	1.40	Nsite[45]	4.44	0.76
Nsite[18]	13.10	0.61	Nsite[46]	3.63	0.76
Nsite[19]	5.41	1.32	Nsite[47]	3.68	0.78
Nsite[20]	5.72	1.09	Nsite[48]	4.64	0.77
Nsite[21]	8.61	1.11	Nsite[49]	3.67	0.78
Nsite[22]	3.60	0.90	Nsite[50]	3.39	0.62
Nsite[23]	8.79	0.82			