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Trade-offs in habitat use and occupancy of bats across the gradient of urbanization and seasons

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Abstract

Urbanization that occurs 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 disturbances 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 the use of moderate and highly urbanized areas in the summer season where food and water resources were assumed to be greater compared with wildland areas. To evaluate these predictions, we used a stratified random sampling design to sample 50 sites with stationary acoustic bat monitors across the gradient of urbanization in the Phoenix metropolitan area, Arizona, USA during four seasons. We identified a total of 14 bat species during 1000 survey nights. Consistent with predictions, bat species exhibited different responses to urbanization, with most species exhibiting a negative relationship with urbanization, and some species exhibiting a quadratic or positive relationship with urbanization. Counter to predictions, most species did not appear to shift their response to urbanization across seasons. Consistent with predictions, plant productivity and water were important for some species in the summer season. Differences in the response of bat species to urbanization was likely related to species traits (e.g., wing morphology and echolocation call characteristics) and behavioral strategies that influence a species' sensitivity to anthropogenic disturbances and ability to access available resources in urbanized areas. Ultimately, to promote the management and conservation of bats, it is likely important to maintain resources in urbanized areas for bats that are more tolerant of urbanization and to conserve areas of undeveloped high-quality habitat with low anthropogenic disturbance in wildland areas for bats that are sensitive to urbanization.

KEYWORDS
acoustic monitoring, adapter, avoider, Chiroptera, exploiter, habitat use, population, urban ecology

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; Krausman, 1999; Mysterud & Ims, 1998). In addition, resources and costs can be dynamic. For example, although animals tend to select areas with food and water resources (Gedir et al., 2020; Hawkins et al., 2003; Marshal et al., 2006), these resources often vary seasonally, and wildlife populations can respond to resource fluctuations by spatially and temporally altering the use of areas (Rehnus et al., 2016; Wang et al., 2010; Zweifel-Schielly et al., 2009). It is unclear, however, 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 widespread and expanding driver of landscape change that can affect biodiversity, where some species benefit and others are negatively impacted (McDonald et al., 2008, 2013; Savard et al., 2000). Low to moderate levels of urbanization can provide increased food and water resources compared with wildland areas for some species (Falk, 1976; McKinney, 2002; Shochat et al., 2006). Areas with high levels of urbanization can also provide food and water resources, but these areas are typically characterized by greater amounts of impervious surfaces (e.g., houses, buildings, parking lots) and anthropogenic disturbances (e.g., human activity, sound and light pollution), and may lack resources for some species (McKinney, 2002, 2006; Shochat et al., 2006). Depending upon how wildlife responds to urbanization, species can be classified into four categories of urbanization: "Urbanization avoiders" reach their highest abundance in wildland areas, "urbanization adapters" peak in abundance at moderate levels of urbanization, "urbanization exploiters" reach their highest abundance in highly urbanized areas (Blair, 1996; McKinney, 2002), and "urbanization generalists" exhibit similar levels of abundance across the gradient of urbanization. However, species can exhibit additional trade-offs where 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 (de Ven et al., 2019; Gedir et al., 2020), where climate differs significantly among seasons and seasonal precipitation can create large fluctuations in food and water availability (de Ven et al., 2019; Gedir et al., 2020; Noy-Meir, 1973). 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 et al., 1997; Razgour et al., 2010; Shochat et al., 2006). Habitat use along the gradient of urbanization in arid regions, therefore, can involve seasonal trade-offs between obtaining available resources, such as food and water, and minimizing costs, such as anthropogenic disturbances (Acebes et al., 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.

In particular, 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 & Ancillotto, 2015). Yet, little research has focused on bat populations across seasons in urbanized environments. In addition to urbanization, habitat use of bat species is influenced by food and water availability (Korine & Pinshow, 2004; Shapiro et al., 2020; Threlfall et al., 2011) and other anthropogenic disturbances (Barré et al., 2021; Lehrer et al., 2021; Schoeman, 2016). 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; McCain, 2007; Mendes et al., 2017). Although each bat species exhibits varying patterns of use along the urbanization gradient (Jung & Kalko, 2011; Jung & Threlfall, 2018; Russo & Ancillotto, 2015), it is unclear whether the response of bats to urbanization will remain consistent across seasons or change seasonally relative to varying resource availability, especially in arid metropolitan areas.

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, Arizona, USA, which is one of the largest urbanized areas in the United States that continues to rapidly grow in population (Luck & Jianguo, 2002; Wu et al., 2011; U.S. Census Bureau, 2018), 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). Our first objective was to evaluate habitat use across a suite of bat species, where we predicted that bats could be classified into urbanization use categories (i.e., avoiders, adapters, exploiters, or generalists) based on their response to the gradient of urbanization within a season. Second, we evaluated whether the response of bats to urbanization changed seasonally, where we predicted that bats would increase their use of moderate and highly urbanized areas during the summer season when there may be greater food and water resources available in urbanized areas compared with wildland areas. And third, we evaluated whether bats exhibited stronger relationships with plant productivity and water in the summer season, when these resources were most likely limiting. We evaluated our objectives using acoustic monitoring and two types of models to examine the effect of urbanization, plant productivity, and water on bat habitat use and occupancy across seasons.

METHODS

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). The region is one of the most developed areas in the United States, which continues to rapidly

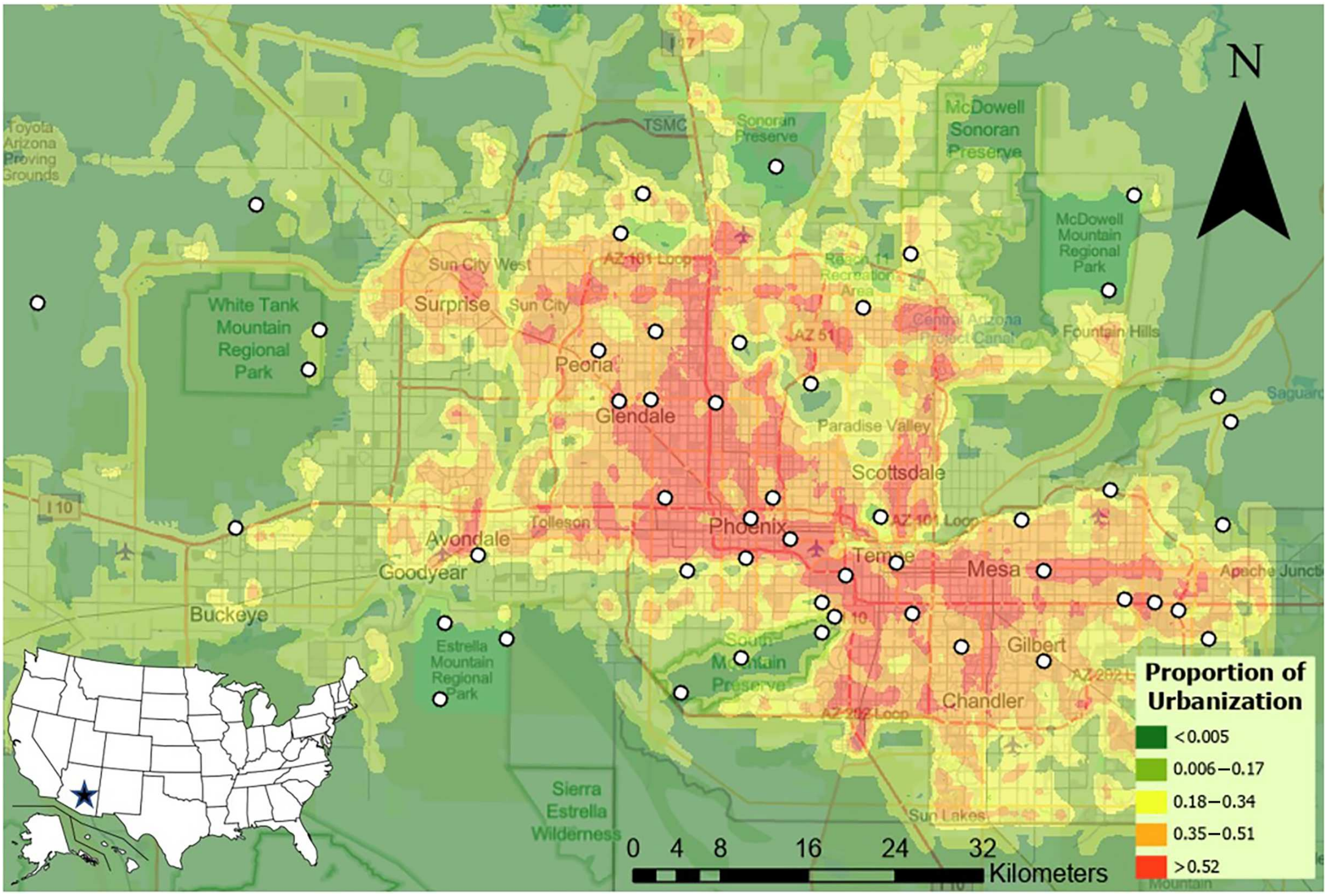

FIGURE 1 Fifty sampling locations (white circles) along the gradient of urbanization from wildland areas (dark green) to highly urbanized areas (red), in the Phoenix metropolitan area, Arizona.

urbanize (Luck & Jianguo, 2002; Wu et al., 2011; U.S. Census Bureau, 2018). 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 et al., 2010; Wu et al., 2011). Common vegetation includes the saguaro cactus (*Carnegiea gigantea*), paloverde (*Parkinsonia* spp.), creosote (*Larrea tridentata*), Fremont cottonwood (*Populus fremontii*), and Arizona willow (*Salix arizonica*) (Buyantuyev et al., 2010; Grimm & 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).

Sampling design

We used 2010 National Agriculture Imagery Program (NAIP) imagery with 1 × 1 m resolution (Li, 2015) to create an urbanization layer, which was calculated as the proportion of urbanization (impervious surfaces) within a 1000-m-radius buffer around each sampling location. To initially stratify the study area from low to high levels of urbanization, we used a 1000-m-radius buffer, which characterized broad levels of urbanization (Fidino et al., 2021; Magle et al., 2021). Across the gradient of urbanization, we used a stratified random sampling design to select 10 sites in each of five strata of urbanization ranging from undeveloped to highly developed (urbanization ranges for the categories included 0–0.005, 0.006–0.17, 0.18–0.34, 0.35–0.51, and 0.52–0.68). Although the proportion of urbanization ranged from 0.00 to 0.95 in the Phoenix metropolitan area, urbanized areas >0.68 were very rare because areas not classified as impervious surface (e.g., parks, vegetation, drainage ditches) were commonly intermixed within areas of development. We sampled sites below an elevation of 550 m to control for changes in temperature, topography, and vegetation, and we avoided sampling areas associated with agriculture. Sites were >2 km apart from each other, except for one site that was >1.5 km apart from nearby sites.

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 et al., 2013). All sites were surveyed during each of the four seasons in 2019: winter (January 7–March 1), spring (April 8–May 31), summer (July 8–August 30), and fall (October 7–November 29). 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 at a site 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 3–5 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 et al., 2013; Weller & 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 et al., 2013). Monitor settings were configured to maximize the likelihood of capturing calls from bats in the Phoenix region, with call frequencies ranging from 8 to 60 kHz, and to filter out ambient noise as much as possible (Reichert et al., 2018).

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, with a quality threshold of 0.80, 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 et al., 2013; Reichert et al., 2018). A species was 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 the western mastiff bat [*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 selected for each monitoring night a species was detected and used in analyses.

The expected regional pool of bat species for our study area was determined by the geographic and elevation range of Arizona bat species during each season. Of the 28 bat species that have been 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 S1). It can be difficult to confidently and 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, M. ciliolabrum, M. occultus, M. velifer*, and *M. volans*) were classified as "40 kHz *Myotis*" due to high overlap in call characteristics (Corcoran & Conner, 2012; Reichert et al., 2018). However, calls classified as 40 kHz *Myotis* species were most likely *M. velifer*, as the other species were either more likely to occur outside of the study area or at higher elevations (Appendix S1).

Landscape and environmental variables

We evaluated three landscape variables that we expected would influence bat habitat use and occupancy probability: urbanization, plant productivity, and distance to water. Because it was unknown at which spatial scale for a landscape variable that bats would most strongly respond to, and each species would likely respond to a different scale, we tested multiple spatial scales for a variable where possible (Grand & Cushman, 2003; Lewis et al., 2011; McGarigal et al., 2016) and selected the best scale based on model selection approaches (Burnham & Anderson, 2002). 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 (Li, 2015). To evaluate nonlinear 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; Landsat 8 Collection 1 Tier 1 8-Day NDVI Composite courtesy of the U.S. Geological Survey) associated with a site, averaged across multiple 8-day periods during each season at a resolution of 30 m, 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 & Billie Turner, 2020), we identified perennial water sources that were >7 m in length or width, including swimming pools (Hall et al., 2016; Nystrom & Bennett, 2019; Razgour et al., 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 & Whitford, 1989; Siemann, 1998) and water (Straka et al., 2020), which are important resources for insectivorous bats.

We evaluated two environmental variables that we expected to influence the detection of species: 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 h (UTC-7) across the five occasions within a season (Allen et al., 2009; NASA, 2019; Scanlon & 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 & West, 2002; Saldaña-Vázquez & Munguía-Rosas, 2013; Scanlon & Petit, 2008).

Statistical analysis

For our analysis, we used detection/nondetection data, where a species was either detected (1) or not detected (0) during an occasion (i.e., survey night). There were five occasions 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 & Nichols, 2003). We used program R (R Development Core Team, 2020) and the RMark package (Laake & Rexstad, 2008) to evaluate models in Program MARK (White & Burnham, 1999). First, we used Royle–Nichols (RN) models to evaluate heterogeneity in abundance (λ) across sites considering heterogeneity in detection probability (Royle & Nichols, 2003). Because we did not measure actual abundance in this study, 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 & 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 species-specific, where detection probability (r) is the probability of detecting a particular species during a survey if the species is present at that site (Donovan, 2007; Royle & Nichols, 2003).

Second, we used single-species single-season occupancy models to estimate (1) occupancy probability (ψ; the probability that a site was occupied or used by the species), and (2) 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.

For the occupancy 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 corrected Akaike information criterion (AIC_c) (Anderson & Burnham, 2004), then the detection variable(s) was included in all subsequent models evaluating occupancy probability.

For both the RN and occupancy 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 AIC_c for small sample size. To evaluate whether there was evidence of a nonlinear relationship with urbanization, we compared model support for the linear and quadratic relationships for urbanization using AIC_c. 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) (Arnold, 2010; White & Burnham, 1999). We further identified a variable as an "uninformative parameter" if it did not sufficiently improve the log-likelihood of models (Arnold, 2010; Leroux, 2019). Lastly, for a variable, we differentiated whether the 85% CIs (moderate support) or 95% CIs (high support) did not overlap 0 (Abrha et al., 2023; Arnold, 2010; Lewis et al., 2021). To aid in model convergence, all continuous variables were standardized by subtracting the sample mean and dividing by the SD (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.

Using results from the RN and single-season single-species occupancy modeling, we classified bat species into "urbanization avoider," "urbanization adapter," "urbanization exploiter" (Blair, 1996), and "urbanization generalist" categories based on where the species reached its highest relative habitat use or occupancy (or collectively referred to as "use") across the gradient of urbanization during each of the four seasons. A species was classified as an urbanization avoider if the species reached its highest use in wildland and low urbanization areas and exhibited a negative relationship with urbanization during that season (Blair, 1996; Callaghan et al., 2020). In contrast, a species was classified as an urbanization exploiter if the species reached its highest use in areas of high urbanization and exhibited a positive relationship with urbanization during that season (Blair, 1996; Callaghan et al., 2020). A species was classified as an urbanization adapter if the species exhibited their highest use in areas of intermediate urbanization and exhibited a unimodal, or quadratic, relationship with urbanization during that season (Blair, 1996). Lastly, a species was classified as an urbanization generalist if the species exhibited similar use across the gradient or urbanization and did not exhibit a strong relationship with urbanization during that season. If a species 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.

RESULTS

Across our 50 sites during four seasons, we identified a total of 14 bat species during 1000 nightly occasions (Table 1). For most species, the greatest number of occasions (i.e., survey nights) that a species was detected occurred in the spring or summer season (Table 1). We obtained sufficient data to evaluate habitat use and occupancy of 14 species for at least one season, 12 of which were detected across multiple seasons, and 10 of which allowed for comparing variables across multiple seasons (Table 1; Appendix S2). Three species (i.e., pallid bat [*Antrozous pallidus*], Townsend's big-eared bat [*Corynorhinus townsendii*], and western mastiff bat [in the spring and summer season]) had too few detections to evaluate their response to urbanization using RN and occupancy modeling, but were only detected in wildland areas, and therefore were considered a potential urbanization avoider.

Relative habitat use modeling

Response to urbanization

Relative habitat use estimated from RN models supported our prediction that some bat species would be more sensitive to urbanization than others (Figure 2; Appendices S2–S4). Some species (i.e., big/pocketed

TABLE 1 Total number of nightly occasions and total number of sites where 14 bat species were detected across 50 sites in the Phoenix metropolitan area, Arizona, during four seasons in 2019.

	Winter		Spring		Summer		Fall	
Bat species	**Occasions**	**Sites**	**Occasions**	**Sites**	**Occasions**	**Sites**	**Occasions**	**Sites**
Big brown bat	0	0	**13**	**9**	**18**	**9**	0	0
Big/pocketed free-tailed bat	**22**	**13**	**23**	**13**	**12**	**8**	**21**	**11**
California myotis	0	0	**16**	**7**	**40**	**18**	6	6
Canyon bat	**43**	**17**	**92**	**29**	**184**	**48**	**77**	**27**
Hoary bat	7	7	**16**	**10**	6	6	0	0
Mexican free-tailed bat	**157**	**48**	**188**	**50**	**160**	**42**	**120**	**44**
Pallid bat	0	0	**4**	**2**	**8**	**4**	0	0
Silver-haired bat	0	0	2	2	**3**	**2**	**8**	**7**
Townsend's big-eared bat	0	0	1	1	**3**	**2**	1	1
Western mastiff bat	6	6	**10**	**4**	**3**	**2**	**8**	**5**
Western red bat	**11**	**9**	**9**	**4**	3	3	**13**	**9**
Western yellow bat	**16**	**12**	**41**	**21**	**63**	**35**	**25**	**16**
Yuma myotis	**5**	**4**	**32**	**16**	**44**	**17**	**21**	**15**
40 kHz *Myotis*	0	0	**14**	**9**	**26**	**12**	0	0

Note: There were 5 nightly occasions at each of the 50 sites per season, for a total of 250 nightly occasions each season. Values in boldface 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.

free-tailed bat, canyon bat [*Parastrellus hesperus*], hoary bat [*Lasiurus cinereus*], western mastiff bat, western red bat [*Lasiurus blossevillii*], Yuma myotis [*Myotis yumanensis*], and 40 kHz *Myotis*) exhibited a negative relationship with urbanization in one or more seasons (Table 2; Appendix S2). In contrast, other species (i.e., Mexican free-tailed bat [*Tadarida brasiliensis*]) exhibited a positive relationship with urbanization in one or more seasons (Table 2; Appendix S2). Other bats (i.e., big brown bat [*Eptesicus fuscus*], California myotis [*Myotis californicus*], western yellow bat [*Lasiurus xanthinus*], and Yuma myotis) exhibited their highest use of areas of intermediate urbanization (i.e., quadratic relationship) in one or more seasons (Table 2; Appendix S2). Lastly, one species (i.e., big brown bat) exhibited similar relative habitat use across the gradient of urbanization (Appendices S2 and S4). Based on results in one or more seasons, species were classified into the categories of urbanization avoider (i.e., big/pocketed free-tailed bat, canyon bat, hoary bat, western mastiff bat, western red bat, Yuma myotis, and 40 kHz *Myotis*), urbanization exploiter (i.e., Mexican free-tailed bat), urbanization adapter (i.e., big brown bat [spring season], California myotis, western yellow bat, and Yuma myotis), and urbanization generalist (i.e., big brown bat [summer season]) (Table 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 yellow bat) did not appear to shift their response to urbanization across seasons, such as during the summer (Table 2; Figure 2; Appendices S2–S4). However, some bat species did vary their response to urbanization across seasons (Table 2; Appendices S2–S4). For example, the Yuma myotis exhibited a quadratic relationship with urbanization in the summer season (i.e., urbanization adapter) and a negative relationship with urbanization during the fall season (i.e., urbanization avoider) (Tables 2 and 4; Appendix S2). In addition, the big brown bat exhibited an urbanization adapter pattern in the spring and an urbanization generalist pattern in the summer season (Tables 2 and 3; Appendices S2 and S4).

Response to plant productivity and distance to water

In addition to urbanization, habitat use of bats varied in relation to plant productivity and water (Table 2; Appendices S2 and S5). Although variable across species and seasons, 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 during one or more seasons; however, some species (i.e., canyon bat, Mexican free-tailed bat,

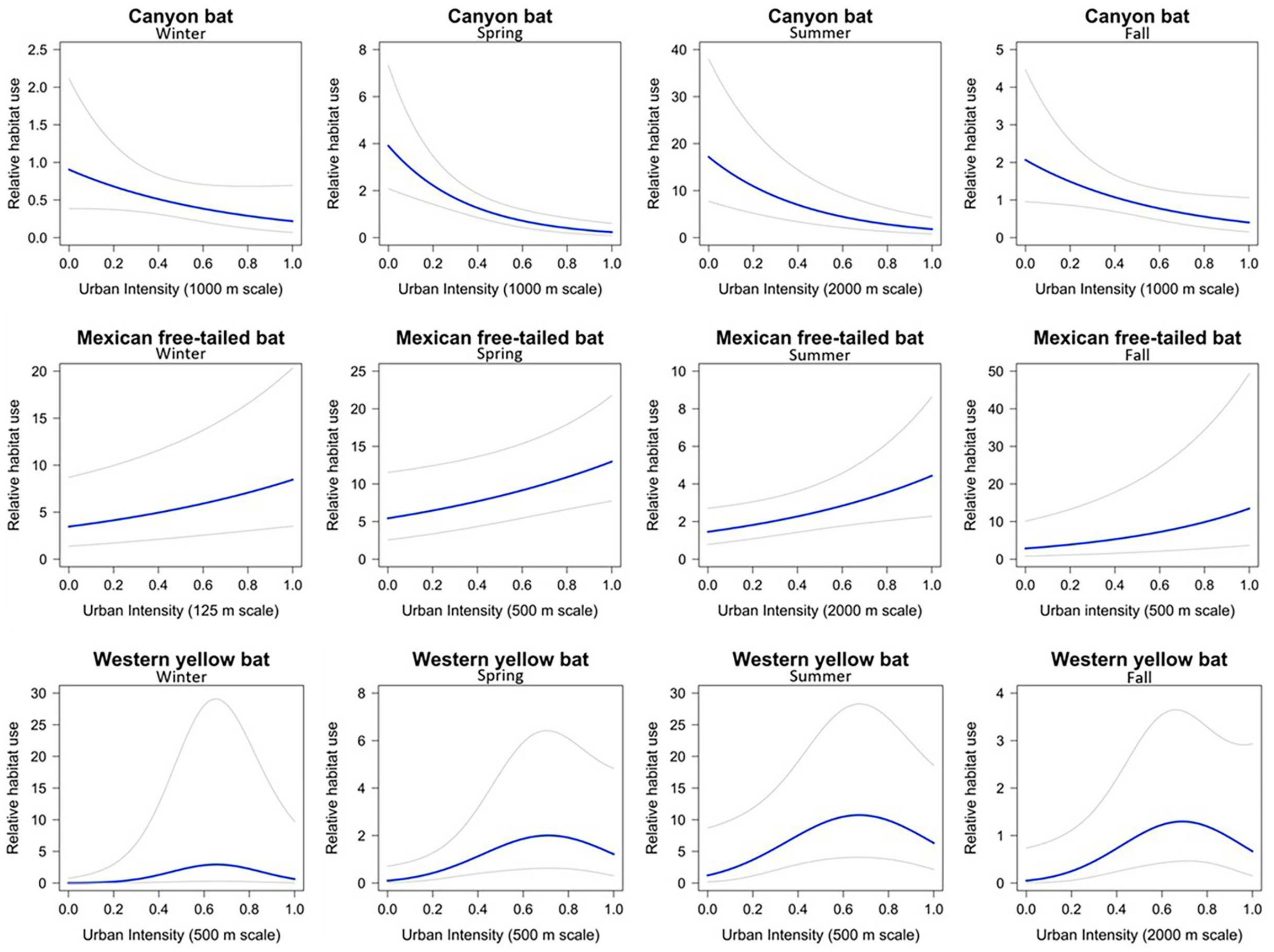

FIGURE 2 Several bat species exhibited consistent relationships with urbanization across seasons. Predicted relative habitat use (with associated 95% CIs) based on Royle–Nichols (RN) models across the gradient of urbanization (from low to high urbanization) for the canyon bat (i.e., urbanization avoider), the Mexican free-tailed bat (i.e., urbanization exploiter), and the western yellow bat (i.e., urbanization adapter). Note the different *y*-axis scales.

and silver-haired bat [*Lasionycteris noctivagans*]) exhibited a negative relationship with plant productivity in winter, spring, or fall (Table 2; Appendices S2 and S5). In addition, there was variation in how bats responded to distance to water. For some species and seasons, bats (i.e., California myotis, Mexican free-tailed bat, western red bat, and western yellow bat) exhibited a negative relationship with distance to water, indicating that habitat use decreased as distance to water increased (Table 2; Appendix S5). In contrast, other bats (i.e., canyon bat and pallid bat) exhibited a positive relationship with distance to water (Table 2; Appendix S5). Consistent with predictions, plant productivity was a particularly important variable for some species (i.e., big brown bat, California myotis, pallid bat, Yuma myotis) in the summer season compared with other seasons (Appendices S2 and S5). In addition, water appeared to be a more important variable for some species (i.e., California myotis, Mexican free-tailed bat, western yellow bat) in the summer season, when it occurred in top models, compared with other seasons, when it did not occur in top models (Appendices S2 and S5).

Occupancy modeling

Occupancy

Naïve occupancy of bats ranged from 0.02 to 1.00 (Table 1) and occupancy of bats ranged from 0.05 to 1.00 (Table 4). The results of occupancy models were often similar to the results of habitat use from RN models for several bat species. As observed with the RN models, bat species tended to follow three general patterns with occupancy

TABLE 2 Habitat use for 13 bat species in relation to urbanization, plant productivity, and distance to water in the Phoenix metropolitan area, Arizona, during four seasons in 2019.

		Urbanization		Plant productivity		Water
Species	**Season**	**Beta**	**Scale**	**Beta**	**Scale**	**Beta**
Big brown bat	Spring	Q	250			
	Summer			+	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			*–	2000	
Western mastiff bat	Spring			+	1000	
	Fall	*–	1000	+	2000	
Western red bat	Winter	–	250			*–
	Fall			+	500	
Western yellow bat	Winter	Q	500			
	Spring			+	125	*–
	Summer	Q	500			–
	Fall	Q	2000			
Yuma myotis	Spring	Q	500	+	2000	
	Summer			+	2000	
	Fall	*–	250	*+	2000	
40 kHz *Myotis*	Spring			+	2000	
	Summer	–	2000	*+	2000	

Note: Results based on top Royle–Nichols (RN) model results. Urbanization and plant productivity were correlated in the winter season, so if both variables are included in the winter season, then the top two models were used. For each variable, we report the general relationship (+, positive; –, negative; or Q, quadratic) of the beta estimate and the most supported spatial scale (i.e., 125–2000 m radius buffers). Lastly, we also differentiated whether the 85% CIs (asterisk) or 95% CIs (no asterisk) did not overlap 0.

where bats exhibited a negative, positive, or quadratic relationship across the gradient of urbanization and consistent patterns across seasons (Appendices S6–S9). However, there were some differences between RN and occupancy models. 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 (Appendices S2 and S6). Relative habitat use and predicted occupancy across the gradient of urbanization indicated that the Yuma myotis was present in low and intermediate levels of urbanization and exhibited the lowest relative abundance and occupancy at

TABLE 3 Urbanization categories[a] 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 or occupancy across the gradient of urbanization.

Bat species	Winter	Spring	Summer	Fall
Big brown bat		Adapter	Generalist	
Big/pocketed free-tailed bat	Avoider	Avoider	Avoider	Avoider
California myotis		Adapter	NA	
Canyon bat	Avoider	Avoider	Avoider	Avoider
Hoary bat		Avoider		
Mexican free-tailed bat	Exploiter	Exploiter	Exploiter	Exploiter
Pallid bat		*Avoider	*Avoider	
Silver-haired bat			NA	NA
Townsend's big-eared bat			*Avoider	
Western mastiff bat		*Avoider	*Avoider	Avoider
Western red bat	Avoider	NA		NA
Western yellow bat	Adapter	NA	Adapter	Adapter
Yuma myotis	NA	Adapter	NA	Avoider
40 kHz *Myotis*		NA	Avoider	

Note: Habitat use is based on the top model for Royle–Nichols (RN) model analyses and occupancy is based on single-species single-season occupancy model results.

[a] A bat was classified as an (1) "urbanization avoider" if the species reached its highest relative habitat use or occupancy in wildland areas and exhibited a negative relationship with urbanization, (2) "urbanization exploiter" if the species reached its highest relative habitat use or occupancy in highly urbanized areas and exhibited a positive relationship with urbanization, (3) "urbanization adapter" if the species reached its highest relative habitat use or occupancy in moderately urbanized areas and exhibited a quadratic relationship with urbanization, and (4) "urbanization generalist" if the species reaches similar levels of relative habitat use or occupancy across the urbanization gradient and did not exhibit a strong 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 species that did not have sufficient data to evaluate their response to urbanization was noted as "NA" and any species that was not detected during the season was left blank.

sites with high levels of urbanization (Appendices S4 and S8). Thus, due to the high relative abundance in intermediate levels of urbanization, Yuma myotis appeared most consistent with an urbanization adapter in the spring season. 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 (Appendices S2 and S6). Relative habitat use and occupancy across the gradient of urbanization indicated that the western yellow bat was present at sites with intermediate and high levels of urbanization. Therefore, the western yellow bat appeared most consistent as an urbanization adapter in the fall season (Figure 2; Appendices S4 and S8). In addition to urbanization, occupancy of bats varied in relation to plant productivity and water (Appendices S6, S7, and S10). Consistent with predictions, plant productivity was an important variable for some species (i.e., big brown bat, California myotis, Yuma myotis) in the summer season compared with other seasons (Appendices S6 and S10). In addition, water was a particularly important variable for some species (i.e., California myotis, western yellow bat) in the summer season compared with other seasons (Appendices S6 and S10).

Detection probability

Detection probability in occupancy models of bat species ranged from 0.07 to 0.77 (Table 4) and was influenced by average minimum temperature and average lunar illumination for some species (Appendices S6, S7, and S10). Although variable, detection probability for several 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 one or more 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 (Appendices S7 and S10). Furthermore, consistent with predictions, the 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 with lunar illumination across all seasons the species was detected (Appendices S7 and S10).

TABLE 4 Estimates (the real estimates) and SEs of occupancy probability (ψ) and detection probability (*p*) from the intercept-only 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	0.28	0.11	0.19	0.08
	Summer	0.20	0.06	0.36	0.08
Big/pocketed free-tailed bat	Winter	0.33	0.09	0.27	0.07
	Spring	0.32	0.08	0.29	0.07
	Summer	0.23	0.10	0.20	0.08
	Fall	0.26	0.08	0.30	0.07
California myotis	Spring	0.15	0.05	0.43	0.09
	Summer	0.39	0.07	0.41	0.06
Canyon bat	Winter	0.35	0.07	0.49	0.06
	Spring	0.58	0.07	0.63	0.04
	Summer	0.96	0.03	0.77	0.03
	Fall	0.55	0.07	0.56	0.04
Hoary bat	Spring	0.27	0.09	0.24	0.08
Mexican free-tailed bat	Winter	0.97	0.03	0.65	0.03
	Spring	1.00	0.00	0.75	0.03
	Summer	0.84	0.05	0.76	0.03
	Fall	0.90	0.05	0.53	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	0.08	0.04	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	0.44	0.26	0.10	0.06
	Spring	0.09	0.04	0.42	0.12
	Fall	0.28	0.11	0.19	0.08
Western yellow bat	Winter	0.44	0.18	0.14	0.06
	Spring	0.48	0.08	0.34	0.05
	Summer	0.84	0.09	0.30	0.04
	Fall	0.44	0.11	0.23	0.06
Yuma myotis	Winter	0.18	0.15	0.11	0.10
	Spring	0.36	0.08	0.36	0.06
	Summer	0.35	0.07	0.50	0.06
	Fall	0.50	0.16	0.17	0.06
40 kHz *Myotis*	Spring	0.25	0.09	0.22	0.08
	Summer	0.26	0.07	0.40	0.07

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. For most bats, the costs of urbanization appeared to outweigh the benefits, where habitat use decreased with urbanization, and was greatest in wildland areas. In contrast, the benefits appeared to outweigh the costs for other species; although costs appeared to vary across the gradient of urbanization for different bat species. Counter to our predictions, species did not appear to switch their categories of urbanization to use resources in urbanized areas more during the hot and dry summer season, when resources were predicted to be most limiting in wildland areas. Thus, it appeared that costs outweighed the benefits across the gradient of urbanization during all seasons for nearly all bats in our study.

Although the classification of how bats responded to urbanization appeared to be similar for a given species across seasons, differences in how each bat species responded to urbanization were likely related to species traits and behavioral characteristics. First, one of the most important species traits for bats is wing morphology, or wing shape, which influences flight speed and strength, as well as maneuverability and mobility (Jung & Threlfall, 2018). The resources in highly urbanized areas can be spread across a broad landscape interspersed with buildings, roads, and artificial lights. Therefore, the ability of a bat to use areas of higher urbanization is likely influenced by its flight speed and strength. For example, bats with short and wide wings tend to be highly maneuverable, but relatively weak flyers with lower mobility. Thus, these species are less likely to use areas of urbanization (i.e., urbanization avoiders) (Avila-Flores & Brock Fenton, 2005; Jung & Kalko, 2011; Jung & Threlfall, 2018; Threlfall et al., 2011). In contrast, bats with long and narrow wings tend to be less maneuverable, but strong flyers with higher mobility, and more likely to use areas of urbanization (i.e., urbanization exploiters) (Avila-Flores & Brock Fenton, 2005; Jung & Kalko, 2011; Jung & Threlfall, 2018; Schoeman, 2016; Threlfall et al., 2011). Lastly, bats with intermediate wing morphology exhibit traits in-between the first two categories and might be the most likely to use areas of moderate urbanization (i.e., urbanization adapters) or may be habitat generalists (Adams, 2003; Avila-Flores & Brock Fenton, 2005; Gehrt & Chelsvig, 2004; Norberg & Rayner, 1987; Schimpp et al., 2018). For example, the big brown bat, classified as an urbanization generalist in the summer season, has intermediate wing morphology and occurs across a range of urbanization levels throughout its distribution (Agosta, 2002; Avila-Flores & Brock Fenton, 2005; Johnson et al., 2008). However, not all bats fit neatly into the above urbanization categories, indicating that there are other important considerations that can determine how bats respond to the gradient of urbanization.

Additional factors that can influence how bats respond to urbanization include roosting strategy, diet or foraging strategy, and overall sensitivity to anthropogenic disturbances. For example, bats may prefer to roost in natural areas that provide specific roosting requirements for a species. However, some bats may be able to use roosting sites in urbanized areas to take advantage of buildings, bridges, attics, or trees in people's yards (Avila-Flores & Brock Fenton, 2005). For example, although the big/pocketed free-tailed bat and western mastiff bat share many traits with urbanization exploiters, they tend to avoid urbanized areas, which is possibly due to the species' roosting requirements of high cliffs and complex rock features that are more widely available in wildland areas (Adams, 2003; Hinman & Snow, 2003; Remington, 2006). Roost availability is different for other species, such as the Mexican free-tailed bat that may use human structures (e.g., bridges) as roosts (Adams, 2003; Allen et al., 2009; Avila-Flores & Brock Fenton, 2005), and the western yellow bat, which may use trees in urbanized areas as roosts (Adams, 2003).

Diet and foraging strategy can also influence bat use across the gradient of urbanization (Avila-Flores & Brock Fenton, 2005; Russo & Ancillotto, 2015). Given the specific diet requirements of each species, bats are most likely to use areas where their preferred food resources are available; if their preferred food resources are unavailable in urbanized areas, then bats might avoid using these areas. The abundance of some food resources for bats can be negatively influenced by urbanization (Conrad et al., 2006; Dar & Jamal, 2021; Piano et al., 2020). However, abundance of some species of prey can increase in urbanized areas, such as beetles and moths in residential yards (Bang & Faeth, 2011; Bates et al., 2014) or mosquitos near standing water (Rochlin et al., 2016; Wilke et al., 2019). In addition, urbanization could potentially interfere with the foraging strategy and echolocation calls of bats (Barré et al., 2021; Bolliger, Hennet, Wermelinger, Bösch, et al., 2020). Lights and sounds associated with urbanization could potentially cause bats to be less efficient foragers, even if prey items are present in these areas. Bats with quiet echolocation calls might be especially challenged to successfully forage in areas with anthropogenic sounds (Reichert et al., 2018). Ultimately, due to the multiple considerations, bats might exhibit varying sensitivities to human disturbances, where some bats might avoid human disturbance and light pollution, while other bats might be more tolerant and able to exploit resources in proximity to human development (Mena et al., 2002; Russo & Ancillotto, 2015; Schoeman, 2016).

Due to dynamic resource availability across the gradient of urbanization, some species might shift their response (i.e., urbanization category) to urbanization across seasons. Counter to our predictions, however, most bat species in our study exhibited a consistent response to urbanization across seasons, even though some food and water resources were assumed to be greater in urbanized areas compared to wildland areas during the summer season (Buyantuyev & Jianguo, 2009, 2012). Thus, for bats that were sensitive to urbanization, the cost of accessing resources in urbanized environments appeared to outweigh the benefit of obtaining available resources during the summer season, which was likely related to constraints of species traits, roosting strategies, diet and foraging strategies, and sensitivity to human disturbances described above. However, consistent with predictions, one bat species (i.e., Yuma myotis) shifted their response to urbanization, increasing their use of moderate and highly urbanized areas in the summer season compared with other seasons. 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; Braun et al., 2015; Hinman & Snow, 2003).

In addition to urbanization, habitat use and occupancy of bats were 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 & Brock Fenton, 2005; Haddad et al., 2001; Lightfoot & Whitford, 1989; Siemann, 1998), and that those resources would be most abundant in urbanized areas during the hot and dry summer season, compared with wildland areas. Although some bat species exhibited high use of areas with higher plant productivity in the summer season (i.e., big brown bat, California myotis, Yuma myotis, 40 kHz *Myotis*), it appeared to be important to bats in other seasons as well (i.e., canyon bat, hoary bat, Mexican free-tailed bat, western mastiff bat, western red bat, western yellow bat, Yuma myotis, 40 kHz *Myotis*). In addition, some bats exhibited high use of areas closer to water during the summer season (i.e., California myotis, Mexican free-tailed bat, western yellow bat), though it also appeared to be important to bats during other seasons (i.e., Mexican free-tailed bat, western red bat, western yellow bat). We assumed that areas with increased plant productivity and water likely exhibited increased insect abundance, which was the main food resource for the insectivorous bats in this study (Avila-Flores & Brock Fenton, 2005; Haddad et al., 2001; Lightfoot & 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 et al., 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.

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 seasons (Bender & Hartman, 2015; Scanlon & 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. Desert-adapted bat species can be tolerant of high temperatures, even during the summer (Bondarenco et al., 2014, 2016). However, our study demonstrated variation among species, which is potentially related to variation in heat tolerance among species (Bondarenco et al., 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 & Munguía-Rosas, 2013). Lunar phobia (i.e., decreased activity during nights with increased moonlight) is potentially due to predation risk or prey availability, and is 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 & 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 moonlight (Appel et al., 2017, 2019; Vásquez et al., 2020). Although little research has documented increased bat activity during nights with increased lunar illumination, this behavior could potentially occur 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 to 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 some species, such as the pallid bat and Townsend's big-eared bat, and possibly contributed to not detecting the California leaf-nosed bat, which is reported to live in the study area (Adams, 2003; Hinman & Snow, 2003). Second, 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 limited levels of 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 with 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 & Chelsvig, 2004; Lintott et al., 2016; Neece et al., 2018; Patriquin et al., 2019; Rodríguez-Aguilar et al., 2017; Zuñiga-Palacios et al., 2021).

The trade-off between bats using resources within urbanized areas and avoiding anthropogenic disturbance 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 & Brock Fenton, 2005; Jung & Kalko, 2011; Jung & 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, such as strong flight and high mobility, that allow them to access resources in highly urbanized environments (Avila-Flores & Brock Fenton, 2005; Jung & Kalko, 2011; Jung & Threlfall, 2018; Schoeman, 2016). Further, bats that appeared to use habitat across the entire gradient of urbanization (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 & Brock Fenton, 2005; Gehrt & Chelsvig, 2004; Norberg & Rayner, 1987; Schimpp et al., 2018).

Results from this study have important management and conservation implications for bats across the gradient of urbanization. Bats can serve as indicator or umbrella species, which may effectively conserve other species with similar habitat requirements (Jones et al., 2009; Russo et al., 2021; Scanlon & Petit, 2015). Overall, many bat species appeared to fit within the broad categories of urbanization avoiders, adapters, and exploiters. The majority of bat species were classified as urbanization avoiders, indicating that urbanization can have negative effects on habitat use for many species. Further, bats were consistently classified as avoiders across seasons and did not appear to access resources in urbanized areas during the summer when some resources (e.g., water) might be most limited. For bats that tend to avoid urbanization and use wildland areas, it is likely important to maintain a large connected landscape of high-quality undeveloped habitat and with low anthropogenic disturbance in these areas (Ancillotto et al., 2019; Grindal et al., 1999; Korine et al., 2016). For other bat species that exploit moderate to high levels of urbanization, outdoor parks, green-spaces, trees, water, travel ways (such as along water canals), and other landscape features may provide important resources for bats that enable them to use these areas (Dalhoumi et al., 2018; de Araújo et al., 2016; Johnson et al., 2008; Russo & Ancillotto, 2015). Ultimately, each bat species exhibits species-specific habitat requirements across the gradient of urbanization that managers may consider when aiming to conserve bat populations across landscapes affected by human activities.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Lewis et al., 2024) are available from Dryad: https://doi.org/10.5061/dryad.w6m905qx2.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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