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Need for multiscale planning for conservation of urban bats

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Abstract: *For over a century there have been continual efforts to incorporate nature into urban planning. These efforts (i.e., urban reconciliation) aim to manage and create habitats that support biodiversity within cities. Given that species select habitat at different spatial scales, understanding the scale at which urban species respond to their environment is critical to the success of urban reconciliation efforts. We assessed species–habitat relationships for common bat species at 50-m, 500-m, and 1 km spatial scales in the Chicago (U.S.A.) metropolitan area and predicted bat activity across the greater Chicago region. Habitat characteristics across all measured scales were important predictors of silver-haired bat (*Lasionycteris noctivagans*) and eastern red bat (*Lasiurus borealis*) activity, and big brown bat (*Eptesicus fuscus*) activity was significantly lower at urban sites relative to rural sites. Open vegetation had a negative effect on silver-haired bat activity at the 50-m scale but a positive effect at the 500-m scale, indicating potential shifts in the relative importance of some habitat characteristics at different scales. These results demonstrate that localized effects may be constrained by broader spatial patterns. Our findings highlight the importance of considering scale in urban reconciliation efforts and our landscape predictions provide information that can help prioritize urban conservation work.*

Keywords: acoustic monitoring, Bayesian variable selection, Chiroptera, occupancy model

Necesidad de Planeación Multiescala para la Conservación de Murciélagos Urbanos

Resumen: *Durante más de un siglo ha habido esfuerzos continuos para incorporar a la naturaleza dentro de la planeación urbana. Estos esfuerzos (es decir, la reconciliación urbana) buscan administrar y crear hábitats que mantengan a la biodiversidad dentro de las ciudades. Ya que las especies seleccionan el hábitat a diferentes escalas espaciales, entender la escala a la que las especies urbanas responden a su ambiente es crítico para el éxito de los esfuerzos de reconciliación urbana. Evaluamos las relaciones especie-hábitat para especies comunes de murciélagos a escalas espaciales de 50 m, 500 m y 1 km en el área metropolitana de Chicago (E.U.A.) y pronosticamos la actividad de murciélagos en la región metropolitana de Chicago. Las características de hábitat en todas las escalas medidas fueron pronosticadores importantes de la actividad del murciélago plateado (*Lasionycteris noctivagans*) y del murciélago rojo occidental (*Lasiurus borealis*), y la actividad del gran murciélago marrón (*Eptesicus fuscus*) fue significativamente menor en los sitios urbanos que en los rurales. La vegetación abierta tuvo un efecto negativo sobre la actividad del murciélago plateado a escala de 50 m pero tuvo un efecto positivo a escala de 500 m, lo que indica cambios potenciales en la importancia relativa de algunas características de hábitat a diferentes escalas. Estos resultados demuestran que los efectos localizados pueden ser inhibidos por patrones espaciales más generales. Nuestros resultados resaltan la importancia de considerar la escala en los esfuerzos de reconciliación urbana y nuestros pronósticos de paisaje proporcionan información que puede ayudar a priorizar el trabajo de conservación urbana.*

Palabras Clave: Chiroptera, conservación urbana, ecología de reconciliación, escala, fauna urbana, modelo de ocupación, monitoreo acústico, selección de variable bayesiana

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Introduction

The effects of urbanization on biodiversity (e.g., habitat fragmentation, habitat loss, and altering of ecological processes) are well documented (Russo & Ancillotto 2015). Although cities are typically characterized by lower biodiversity (Aronson et al. 2014; Krauel & LeBuhn 2016), they can contain important habitat for wildlife (e.g., Fidino et al. 2016; Ives et al. 2016; Magle et al. 2016). Efforts to incorporate nature into urban planning could increase the quantity and quality of wildlife habitats within cities (Moskovits et al. 2004; Beatley 2011). These conservation efforts—known as urban reconciliation—aim to manage and create habitats that support wildlife populations, allow populations to remain resilient, and reduce biodiversity loss in cities (Rosenzweig 2003; Francis & Lorimer 2011). The long-term success of such efforts depends on a proper understanding of species–habitat relationships within cities. Yet, species perceive and respond to habitats at different scales (Levin 1992), and ecological studies in urban environments are often conducted at a single spatial scale (Pickett et al. 2016). Conservation actions may be ill-informed and miss their mark if they do not account for species-specific scale dependencies (e.g., Graf et al. 2005; Avelino et al. 2016). Therefore, understanding the scale at which urban wildlife responds to the environment is critical for urban reconciliation.

Bats currently face a multitude of anthropogenic threats, including energy development (Kunz et al. 2007), roads (Fensome & Mathews 2016), and pesticide exposure (Bayat et al. 2014) and play numerous beneficial roles in natural and human-dominated ecosystems through pest control, crop pollination, and forest regeneration (Kunz et al. 2011). Many bat species can live in urban spaces (Kurta & Teramino 1992; Gehrt & Chelsvig 2003; Krauel & LeBuhn 2016) and directly or indirectly provide ecosystem services to such environments (Kunz et al. 2011); thus, creating, managing, and monitoring bat habitat in urban environments should be a conservation priority.

The Chicago, Illinois, region (Fig. 1) in the United States is highly urbanized but contains a significant portion of protected lands (Moskovits et al. 2004). Following the Great Chicago Fire in 1871, city planners created an array of protected natural areas in and around the city (Moskovits et al. 2004). Tallgrass prairies, oak woodlands, oak savannas, sedge meadows, and prairie wetlands make up the ecosystems still intact within the Chicago region (Wang & Moskovits 2001). These protected areas, along with cemeteries, right-of-ways, and golf courses, act as habitat patches for urban wildlife (Magle et al. 2016). Regional conservation organizations are engaged in coordinated efforts to restore, connect, and manage these urban habitats in the greater Chicago area (Moskovits et al. 2004)—making Chicago an ideal place to study species–habitat relationships that can be implemented into science-based urban conservation plans.

We assessed species–habitat relationships for common bat species at varying spatial scales in the Chicago metropolitan area. We hypothesized that bat activity is best predicted by habitat characteristics (i.e., proportion of tree cover, open vegetation, and impervious surface) at multiple scales. Furthermore, the influence of habitat characteristics may vary in magnitude and direction depending on species' life-history strategies (e.g., foraging and roosting habitat preferences). We sought to recognize scale-dependent species-habitat relationships that can better inform future bat-conservation efforts in urban areas such as Chicago.

Methods

Study Area and Data Collection

To estimate bat activity, we deployed passive acoustic bat detectors throughout Cook, Lake, and Kane Counties, Illinois, from 2013 to 2015 (Fig. 1). Cook County is the second most populous county in the United States and includes the city of Chicago, the third most populous city (approximately 2.7 million residents; average population density of 7355 people/km^2; U.S. Census Bureau 2015). Lake County is directly north of Cook County, has an average population density of 612 people/km^2 (U.S. Census Bureau 2015), and is predominately suburban. Kane County is directly west of Cook County, has an average population density of 383 people/km^2 (U.S. Census Bureau 2015), is the most rural of the three counties, and consists predominantly of low-density development and small towns.

In the summer of 2013 we randomly selected 11 sites in the urban core of Chicago or suburban areas of Cook and Lake counties (hereafter urban sites) and 9 sites in exurban or rural locations in eastern Kane County (hereafter rural sites; Fig. 1). Rural sites were >50 km from the Chicago city center. In 2015, we added 2 additional urban sites for a total of 13 urban sites and 9 rural sites ($n = 22$). Sites were randomly selected from a comprehensive list of urban green spaces in the Chicago metropolitan area. Selected sites included remnant natural areas, city parks, and golf courses that encompassed a variation of land cover and tree cover within their vicinity. At each site, we deployed one SM2BAT+ stationary acoustic detector equipped with one SMX-US omnidirectional microphone (Wildlife Acoustics, Maynard, MA). Within each randomly selected site, detector location was chosen based on accessibility and suitability for acoustic sampling. Each detector and microphone was attached to a tree with little overhead canopy. Microphones were affixed to poles and extended roughly 3 m aboveground.

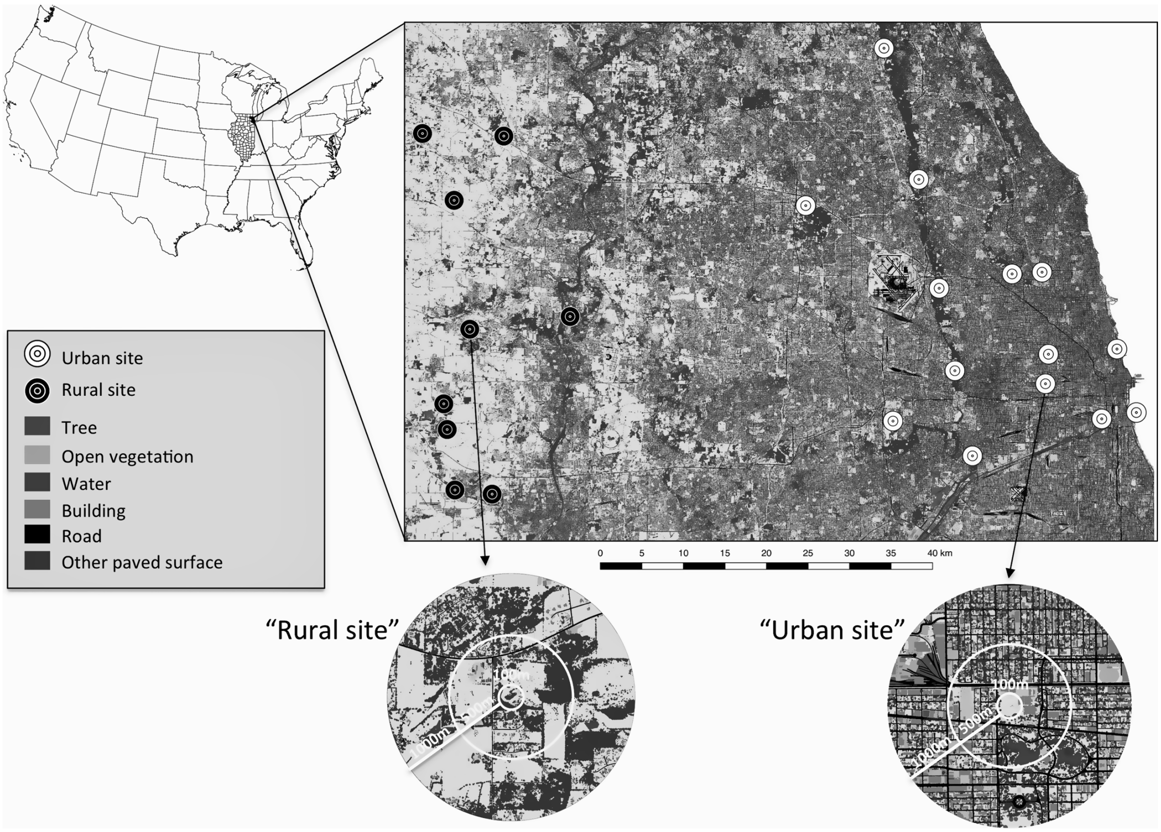

Figure 1. The distribution and an example of land cover of urban and rural study sites where bats were sampled in the Chicago metropolitan area (U.S.A.).

Each year sampling was concentrated in 3, 1-week recording sessions that took place throughout May, July, and September. The exception was 2013, when sampling was conducted only in July and September. In each month, a minimum of 3 urban and 3 rural sites were sampled simultaneously per week, and detectors were rotated to the next group of sites after a minimum of 6 nights. Detectors were set to record ultrasonic calls in full spectrum format, beginning at sunset and recording for 6 hours. Due to logistical constraints, the mean number of recording nights per session per site was 4.14. Recordings were scrubbed using SonoBat Batch Scrubber Utility version 5.5 (Sonobat, Arcata, CA). Bat calls were identified to species with SonoBat version 3.2.1, with the exception of *Myotis* spp., which are difficult to distinguish acoustically and were combined as *Myotis*. See Supporting Information for acoustic-detector settings and SonoBat specifications.

Predictor Variables

To assess species–habitat relationships for bat species at different scales, we created spatial fixed-radius buffers of 100 m (local), 500 m (medium), and 1 km (broad) around each sampling site with QGIS (QGIS Development Team 2009). We chose 100 m as our local scale because it was the smallest scale we could analyze with sufficient variation in land-cover data. We chose 1 km as our broad scale because it encompasses the general foraging range of the bat species identified to have sufficient numbers of detections for analysis (Kunz 1982; Shump & Shump 1982; Kurta & Baker 1990). The medium scale was chosen to be partway between the other scales.

We extracted the proportions of tree cover, open vegetation, and impervious cover within each buffer (Table 1) from the 2010 High-resolution (1-m) Land Cover Data Set for northeastern Illinois and northwestern Indiana (hereafter HRLC data set) (Chicago Metropolitain Agency for Planning 2016) with the raster package in R version 3.3.2 (R Core Team 2016). We chose these habitat characteristics because they are categorically broad, can be generalizable across urban areas, and tree cover and areas of open vegetation represent a majority of roosting and foraging habitats for bats, whereas impervious cover describes the relative lack of natural habitat in urban environments (Gehrt & Chelsvig 2003; Russo & Ancillotto 2015; Krauel & LeBuhn 2016). We considered impervious cover to be the combination of building, road, and other paved surface categories in the HRLC data set (Fig. 1). We included a regional-level predictor by denoting sites in Cook and Lake Counties as urban sites and sites in Kane County as rural sites (Fig. 1). Open water may be

Table 1. Predictor variables used to assess the influence of habitat characteristics at varying scales on bat activity in Chicago, Illinois (U.S.A.).

Variable	*Description*
TREE100	proportion of tree cover within 100 m of a site
TREE500	proportion of tree cover within 500 m of a site
TREE1000	proportion of tree cover within 1 km of a site
OPENVEG100	proportion of shrub and grass cover within 100 m of a site
OPENVEG500	proportion of shrub and grass within 500 m of a site
OPENVEG1000	proportion of shrub and grass within 1 km of a site
IMP100	proportion of impervious cover within 100 m of a site
IMP500	proportion of impervious cover within 500 m of a site
IMP1000	proportion of impervious cover within 1 km of a site
REGIONAL	a binary indication whether a site was urban (1) or rural (0)

an important predictor variable for bat activity (Gehrt & Chelsvig 2003; Straka et al. 2016). However, we were unable to analyze this metric because the presence of open water was often absent at the local and medium-sized scales around our sites (Fig. 1). Thus, there was little variation in open-water availability across our study region (Supporting Information).

Predictor variables were scaled to have a mean of 0 and SD 1. All predictor variables were tested for correlation ($|r|$) among both variables and scales ($|r| \geq 0.70$; correlation results in Supporting Information). We found moderate correlation between open vegetation at 100 m and tree cover at 100 m ($|r| = 0.82$) and moderate correlation between impervious cover at 100 and 500 m (($|r| = 0.84$). Correlation between some scales for specific land-cover characteristics was high, but correlation between the different land-cover characteristics within the same scale were not high. Correlation between tree cover at 500 and 1000 m was 0.94, correlation between open vegetation at 500 and 1000 m was 0.93, and correlation between impervious cover at 500 and 1000 m was 0.94. Although correlation among predictor variables can result in high variability in regression coefficients, our implementation of lasso regression—described below—is a well-established method to reduce this variability when multicollinearity exists (Oyeyemi et al. 2015).

Data Analyses

Occupancy Models

Most bats were detected at a majority of sites resulting in high estimates of occupancy throughout the study area. Bat foraging calls, specifically, can be difficult to record in urban areas due to high rates of attenuation (Parkins & Clark 2015). Therefore, high occupancy rates based on bat calls alone offer little information about habitat selection at a site. Repeated activity at a location may provide a useful metric to determine where bats occur most frequently (Manly et al. 1993). In the occupancy-modeling framework, the detection probability of a species is a function of a species' presence and activity at a site and can be modeled using habitat covariates to estimate the relative activity (habitat use) of a species (Royle & Nichols 2003; Lewis et al. 2015). This approach offers a useful metric of habitat use for species, such as bats, that exhibit high occupancy rates across a landscape. Using a Bayesian hierarchical occupancy model (MacKenzie et al. 2006; Royle & Dorazio 2008), we assessed site-level bat activity by examining the relationship between predictor variables and detection probability (Lewis et al. 2015). For each species, we included only the intercept on the occupancy parameter (Ψ) and modeled the detection probability (p) as a function of our predictor variables. To account for pseudoreplication (here repeated samples across years) and control for variability in bat activity across seasons and years, we used a nested random effects design in which sampling season was nested within year for the intercept values of Ψ and p (model-formulation details in Supporting Information).

Variable Selection

For each species, we fitted a single model including all predictor variables and used Bayesian lasso regression and variable selection to determine the most parsimonious model and relative variable importance (Lykou & Ntzoufras 2013). We followed Lykou and Ntzoufras (2013) and specified the priors for each model coefficient to be a mixture of Laplace (0, λ) and Bernoulli (Ω) distributions (Supporting Information). The Laplace distribution shrinks values for variables that have low explanatory value toward 0 based on the tuning parameter λ and reduces the variability of estimates when multicollinearity exists (Oyeyemi et al. 2015). At each step in the Markov chain Monte Carlo (MCMC) if a given Bernoulli trial for a variable had a value of 1, we sampled from its respective Laplace distribution. If the Bernoulli trial took a value of 0, the parameter was not included in the model at that sample step. Thus, the probability that a variable would be included in the model (variable inclusion probability [vip]) was the proportion of times a model coefficient's Bernoulli trial took a value of 1 across all MCMC samples. For each model, we assessed the relative importance of each variable by comparing the vip of each variable with the mean inclusion probability of the full variable set. Variables with a vip lower than the mean inclusion probability were removed from the final model structure of each species. We retained all other variables because collectively they provide the best information as to what habitat characteristics explain variability in bat activity. We considered a variable to have evidence of an effect on bat activity if the 95% Bayesian credible intervals (BCI) did not overlap 0. We also considered moderate trends in our data if 90% BCIs do not overlap 0.

Model Implementation and Predictive Check

Posterior distributions of model parameters were estimated using an MCMC algorithm implemented in JAGS version 4.2.0 (Plummer 2003) with the runjags package (Denwood 2016) in R. Seven parallel chains were run from random starting values for 20,000 iterations after discarding 20,000 burn-in samples. Model convergence was assessed by checking that the Gelman-Rubin diagnostic statistic for each parameter was <1.1 (Gelman & Rubin 1992) and by visually inspecting the trace plots of MCMC samples.

To assess model fit and predictive performance, we used a leave-one-out approach (Hooten & Hobbs 2015) to predict the likelihood that the final model for each species could provide a prediction of an out of sample data points. Using these likelihoods, we calculated a Macfadden's pseudo-R^2 ($1 - \Sigma L/\Sigma L_0$; Domencich & McFadden 1975), where L is the log likelihood of each removed data point in our final model and L_0 is the log likelihood of each data point in a null model. This approach estimates the power of the model to predict an out-of-sample data point relative to a null model. Macfadden's pseudo-R^2 values from 0.2 to 0.4 indicate a model has strong fit to the data (Domencich & McFadden 1975; Louviere et al. 2000).

Landscape Predictions

Using the final model for each species, we extrapolated bat activity probabilities across our study region. To predict bat activity across the greater Chicago metropolitan area, we created a grid of points (n = 507,792) spaced 100 m apart over the region of interest with QGIS. The same predictor variables were extracted at each grid point and at each scale following the methods described above. Large, developed cities expand slowly and in relatively concentric rings (Seto et al. 2010), and this pattern of growth is evident in the Chicago metropolitan area (Fig. 1). Taking this pattern into consideration and staying consistent with the original study design, we classified points within a 50-km fixed-radius area around the city center as urban and points outside of this radius as rural. For each species, we used the final model structure and calculated the probability of bat activity at each grid point. These values were then converted to a spatial raster with the raster package in R.

Results

From 726 sampling nights (mean [SD] = 33 [12.17] nights/site) resulting in 26,903 identifiable calls, we detected 7 bat species across our study area: big brown bat (*Eptesicus fuscus*), eastern red bat (*Lasiurus borealis*), evening bat (*Nycticeius humeralis*), hoary bat (*Lasiurus cinereus*), silver-haired bat (*Lasionycteris noctivagans*), tricolored bat (*Perimyotis subflavus*), and *Myotis*. All species were detected at both urban and rural study sites. The most frequently detected species at urban (204 days) and rural sites (234 days) was the big brown bat. The *Myotis* species were detected least frequently at urban sites (combined 18 days), and tricolored bat was detected least frequently at rural sites (42 days). The three most common bat species detected were the big brown bat, eastern red bat, and silver-haired bat. These species were detected at all sites, and we were able to appropriately fit our occupancy model to these three species and assess their site-level activity.

Top Predictor Variables

Mean vip for the big brown bat model was 0.39. Final predictor variables selected and retained for this model were the regional-level indicator (i.e., urban or rural sites; vip = 0.86), TREE100 (0.68), and OPENVEG100 (0.41) (Fig. 2). The regional indicator was the only predictor variable that had a significant effect (95% BCI did not bound 0) on big brown bat activity ($\beta = -0.70$; 95% BCI, -1.32 to -0.13), indicating these bats were more active at rural sites (Fig. 2).

The final model for silver-haired bat contained TREE100 (vip = 0.54), TREE500 (0.52), TREE1000 (0.50), OPENVEG100 (0.72), OPENVEG500 (0.66), and IMP100 (0.64). Mean vip was 0.47. Relationships between the retained predictor variables and silver-haired bat activity were all nonsignificant (all 95% BCI overlap 0). However, OPENVEG100 ($\beta = -0.70$; 90% BCI, -1.03 to -0.07) and IMP100 ($\beta = -0.54$; 90% BCI, -1.04 to -0.05) both showed a moderate negative trend and OPENVEG500 ($\beta = 0.45$; 90% BCI, 0.01 to 1.04) showed a moderate positive trend with silver-haired bat activity (Fig. 2).

Eastern red bat had a final model that included TREE1000 (vip = 0.95), OPENVEG100 (0.77), OPENVEG500 (0.79), and IMP100 (0.99). Mean vip for this bat model was 0.56. All retained predictor variables had a significant positive effect on eastern red bat activity (Fig. 2).

Landscape Predictions

McFadden's pseudo-R^2 values were 0.20, 0.09, and 0.15 for big brown bat, silver-haired bat, and eastern red bat models, respectively. These results indicate strong fit for

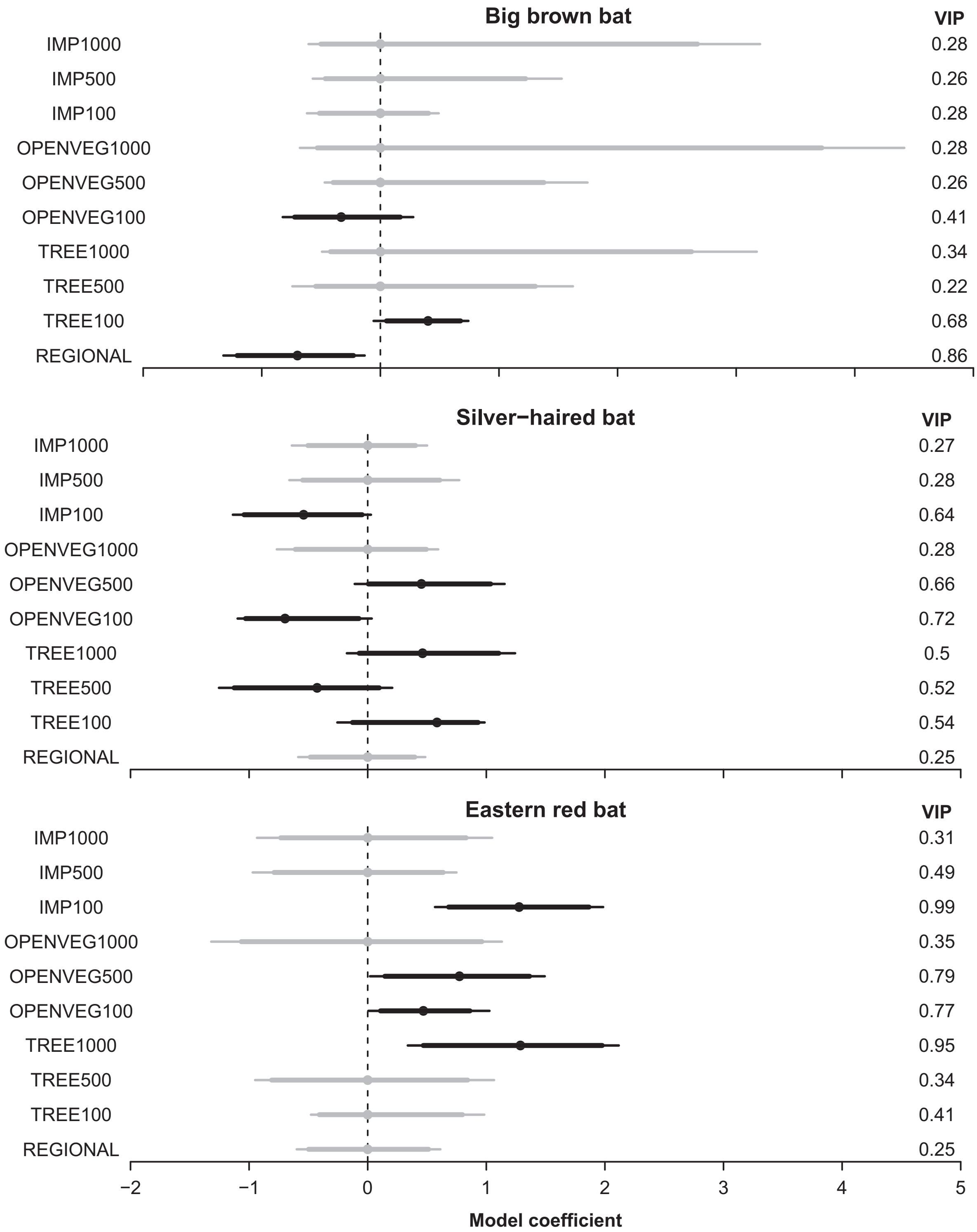

Figure 2. Median posterior distribution values (points), 95% Bayesian credible intervals (BCI) (thin lines), 90% BCI (thick lines), and variable inclusion probability (vip) for 3 bat species in all habitats and scales (see Table 1). Variables with a vip lower than the mean overall inclusion probability were set to 0 (grey points and lines).

big brown bat, adequate to poor fit for silver-haired bat, and good fit for eastern red bat. Due to poor model fit, we excluded silver-haired bat from our landscape-prediction analysis. The mean predicted activity probability for big brown bats across our study region was 0.45. We predicted high activity ($p > 0.70$) in 6% of our study area and low activity ($p < 0.30$) in 5% of our study area. Big brown bat was the most common species detected

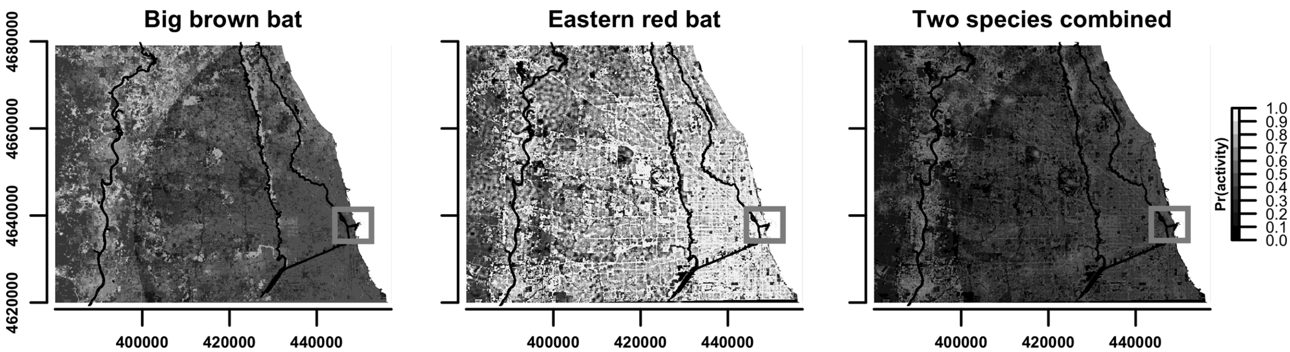

Figure 3. Predicted bat activity across the Chicago, Illinois (U.S.A.), region based on the final bat-activity model for each species (black lines, major waterways; grey boxes, downtown Chicago). The species-combined map is the probability of big brown bats and eastern red bats being active at the same location.

across the study area, yet higher activity was predicted in more rural areas (Fig. 3). Eastern red bat had a mean activity probability of 0.55 across the study region. We predicted high activity of eastern red bat in 42% of our study region, and most of the high activity was predicted in urban or suburban areas (Fig. 3). We predicted low activity for eastern red bat across 23% of the region. The mean probability that both species were active in the same location was 0.25 (Fig. 3).

Discussion

Habitat characteristics at multiple scales influenced the activity rates of all 3 bat species we examined. Local-, medium-, and broad-scale features were included in the silver-haired and eastern red bat models, and the largest and smallest scale features were included in the final model for big brown bat. These habitat characteristics, calculated at appropriate spatial scales, were used to predict bat activity across our entire study area (including unsampled locations), revealing potential hotspots for urban bat conservation. Our results reinforce the idea that scale is a critical concept in species–habitat relationships and that multiple scales should be considered when managing and creating urban bat habitat.

Tree cover and open vegetation were included in the final models of all species. These results are unsurprising because all three species depend, to some degree, on tree cover for roosting and open vegetation for foraging and travel corridors (Betts 1998; Agosta 2002; Limpert et al. 2007). The effects of open vegetation (Fig. 2) on silver-haired bats at the local (positive influence) and medium (negative influence) scales are more difficult to explain. At broad scales, patterns, and distributions of habitat characteristics may influence the importance of characteristics at finer scales (Turner & Gardner 2015). Urban bats may select forest edges for foraging (Krauel & LeBuhn 2016). Perhaps open vegetation at larger scales is indicative of increased forest edge and thus increased foraging habitat. The spatial arrangement and patterns of forest edge at a medium-sized scale may not be recognized by local-scale measurement. Assessing additional processes and patterns, such as edge effects, could further explain diverging effects of unique habitat characteristic at different scales. Similarly, this could explain why medium- and broad-scale tree cover had opposite, yet nonsignificant, effects on silver-haired bats. However, these two variables were highly correlated, and we urge caution when interpreting their effects. Although we used lasso regression to reduce variability between correlated variables, the weakness of their effects combined with their high degree of correlation may have generated the equivocal effects we observed.

Urbanization is generally considered to have a negative effect on bat species (Kurta & Teramino 1992; Duchamp et al. 2004). Our results showed no effect of urbanization on silver-haired bat and eastern red bat relative to rural sites (Fig. 2). Gehrt and Chelsvig (2004) also found that big brown bat, silver-haired bat, and eastern red bat were detected more frequently in urban areas of Chicago than in rural and agricultural lands surrounding the city. Although our results do not indicate bats had higher activity in urban areas, they confirm that urbanization in general does not have a negative effect on the occurrence of these species in the Chicago area. We found that big brown bats were less active in urban areas, contrary to Gehrt and Chelsvig (2004). However, big brown bat was the most common species detected across our study region. Thus, our results may not indicate a negative effect of urbanization per se, but merely that big brown bats were more active at rural sites. Our results are difficult to compare directly with previous research in the Chicago area (e.g., Gehrt & Chelsvig 2003, 2004) because we did not distinguish agriculture from the open-vegetation land cover. However, our findings further signify that urban areas may provide natural and artificial habitats that are otherwise limited in rural landscapes (Gehrt & Chelsvig 2004). Thus, managing and monitoring bat habitat in urban environments should be a conservation priority.

Our landscape predictions (Fig. 3) revealed hotspots that could be designated for creating or improving bat habitats in the Chicago region. Because our predictor variables were categorically broad and generalizable, this approach could also be used in other cities beyond Chicago. Predicting across broad but relevant land-cover categories may reveal other potential and important predictors of bat activity. For example, big brown bats had consistently higher rates of predicted activity along major waterways (Fig. 3). Riparian areas are important habitats for urban bats (Krauel & LeBuhn 2016; Salvarina 2016; Straka et al. 2016). Although we were unable to include open water as a variable, our landscape predictions illustrate that it is an important feature on the landscape for bats.

The landscape predictions further illustrate stark differences in the effect that broad-scale patterns of urbanization have on predicted bat activity for each species. Higher levels of activity in the Chicago urban core were predicted for eastern red bats, whereas lower activity was predicted for big brown bats (Fig. 3). These predictions offer baseline information that can help prioritize urban reconciliation efforts. Although our predictive models were constructed using general landscape variables, there are likely other factors related to urbanization that influence bat activity. Future research should assess region-specific landscape patterns (e.g., riparian zones, urban intensity, human densities, light pollution, anthropogenic noise) that may also influence urban bat activity.

Manley et al. (1993) recognized that habitat selection is determined by criteria at a hierarchy of scales (O'Neill 1986), starting from geographical characteristics and extending to local-scale conditions. Studies in more rural and remote locations demonstrate that bats select habitat at multiple scales (Limpert et al. 2007; Mendes et al. 2017). Our results indicate this is true for urban bats as well (Fig. 2). Both silver-haired and eastern red bats had multiple scales of the same habitat characteristic retained in their final models. These findings are generally inconsistent with previous work conducted in the Chicago area. Gehrt and Chelsvig (2003) found that microhabitats had a stronger effect on urban bat activity relative to landscape features. However, they did not evaluate tree cover beyond the microhabitat scale (Gehrt & Chelsvig 2003), and tree cover was the only broad-scale land-cover variable included in a final model for any species in our study (Fig. 2). These results highlight the importance of multiscale approaches to urban bat conservation because noticeable patterns at one scale may be driven by habitat selection at another scale (Limpert et al. 2007; Turner & Gardner 2015).

In light of limited funding for conservation (Primack 2014), decisions should be based on the most up-to-date scientific information. If conservation decisions are ill informed, efforts may be made at inappropriate scales and diverge from important species-habitat relationships. For example, if management decisions for the silver-haired bat were made from information obtained at our local scale (100 m), one might attempt to reduce vegetative open spaces and increase core areas of woodlands. Consequently, this would reduce forest patterns and configurations that have a positive effect on silver-haired bat activity at a broader scale (Fig. 2). Our study further reinforces Levin's (1992) claim that there is no single correct scale to view ecosystems. We recommend that practitioners take a multiscale hierarchy approach (O'Neill 1986) to understand the scales at which species–habitat relationships exist in urban environments.

An important limitation or constraint of our analysis was the number of parameters modeled. To be cautious of overparameterization, we limited our analysis to three important land-cover categories we hypothesized influenced bat activity. Although these land-cover categories can be generalizable to other cities, they will differ in their spatial extent and distribution. For example, we found no significant correlation between vegetation cover and impervious cover at our sampling sites, which may be unique to our study area or study design. City-specific variation should be considered when assessing species-habitat relationships across multiple cities. Further, patch-level characteristics such as urban complexity, forest complexity, or tree-cover configuration may also influence urban bats. For instance, site-specific forest composition was an important factor influencing silver-haired bat and eastern red bat activity in restored urban forests throughout Chicago (Smith & Gehrt 2009). Including field-collected attributes at the patch level will help further elucidate additional relationships between bat activity and landscape characteristics. As high-resolution land-cover data become more broadly available, more categories describing urban, suburban, and rural areas should be assessed. Finally, understanding the predictive power of models is important for policy and management decisions. Our model for silver-haired bats had poor model fit. Our results indicated that the final model for silver-haired bats offered more information than a null model, but it offered weak predictive power for extrapolating predictions across the landscape. Thus, long-term monitoring of urban bat activity should be prioritized to collect more data that will allow for stronger and more reliable predictions.

Our results demonstrated that urban bats select habitat at multiple scales. Silver-haired bat and eastern red bat activity were correlated with habitat characteristics at all three scales and big brown bat activity was correlated with habitat characteristics at local and broad scales. Our study also highlights important habitat characteristics that can predict activity of some bat species in urban environments. These findings have broad implications for urban wildlife conservation and urban habitat reconciliation. Although it is important to understand what habitat characteristics are most important for bat activity, it is just as important to understand at what scale bats are selecting these habitats. Working within the proper scale for target species will effectively connect urban restoration efforts with species-habitat relationships—resulting in more impactful urban reconciliation.

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Supporting Information

Acoustic detector settings and SonoBat specifications (Appendix S1), variation in the proportion of open-water data across (Appendix S2), correlation results between and among scales and land-cover categories (Appendix S3), detailed model formulation (Appendix S4), and R code for JAGS model used to select variables and estimate bat activity (Model S1) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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