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BAT SPECIES DIVERSITY AT AN

URBAN-RURAL INTERFACE: DOMINANCE BY ONE SPECIES IN AN URBAN AREA

A Thesis

Presented to

The College of Graduate and Professional Studies

Department of Biology

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In Partial Fulfillment

of the Requirements for the Degree

Jason Philip Damm

by

Jason Philip Damm

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COMMITTEE MEMBERS

Committee Chair: John O. Whitaker, Jr., Ph.D.

Professor, Department of Biology

Indiana State University

Committee Member: William A. Mitchell, Ph.D.

Associate Professor, Department of Biology

Indiana State University

Committee Member: Peter E. Scott, Ph.D.

Associate Professor, Department of Biology

Indiana State University

ABSTRACT

The growth of urban areas is known to affect different species of wildlife in varying ways. Many organisms have exhibited declines in abundance due to habitat loss, while overall species diversity decreases. Bats can serve as reliable indicators of habitat quality and level of anthropogenic disturbance. To investigate urbanization impacts on a Midwestern bat community, I analyzed nine years of mist-net captures from a study area on the edge of Indianapolis, Indiana, where the percentage of urbanized ground cover ranged from zero to 26%, within 1.3-km of a net site. I used Pearson correlation statistics to examine the effect of urban ground cover on each species' abundance, and the Shannon-Wiener Diversity Index was used to quantify species diversity at the study area. To test the effect of urbanization on diversity, linear mixed models were constructed using percentage of urban ground cover and year. A total of 10 species were captured over nine years, seven of them annually. The big brown bat (*Eptesicus fuscus*) was the dominant species at all urbanized sites and at five of six rural sites. Most species were more common at rural sites than at urbanized sites. Urbanization was significantly and negatively related to bat species diversity, although one species, the northern myotis (*Myotis septentrionalis*), showed a significant positive correlation with urban ground cover. Two bat species, the eastern pipistrelle (*Perimyotis subflavus*) and the little brown myotis (*Myotis lucifugus*) both displayed significant negative correlations with

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the percentage of urban ground cover. The Indiana myotis (*Myotis sodalis*) had a marginal negative correlation, but not significant.

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CHAPTER 1

BAT SPECIES DIVERSITY AT AN

URBAN-RURAL INTERFACE: DOMINANCE BY ONE SPECIES IN AN URBAN AREA

Introduction

Growth of urban areas (i.e. urban sprawl) is known to affect different species of wildlife in varying ways (McKinney 2002; Duchamp and Swihart 2008). Additionally, urbanization is a relatively long-term anthropogenic habitat alteration (McKinney 2002; McDonald et al. 2008). Many organisms have been shown to exhibit declines in abundance due to habitat loss, while overall species composition often trends toward homogeneity (Marchetti et al. 2006; McKinney 2006; Duchamp and Swihart 2008). Urban sprawl has been implicated as a likely variable in the decline of many species (Dickman 1987). Some organisms, however, have demonstrated varying abilities to adapt to urban habitat alterations (Gehrt and Chelsvig 2004; Ordenana et al. 2010).

Bats often serve as reliable indicators of habitat quality and level of disturbance (Medellin et al. 2000). While some species do well in an anthropogenically-disturbed environment (Gehrt and Chelsvig 2004; Oprea et al. 2009; Jung and Kalko 2010), other species are rarely found in association with humans. Many species of bats are found in greater numbers in areas with a greater abundance of natural features. In the east-central United States, most bat species are recognized as species of special concern or are federally listed as endangered, with many of these species showing a decrease in abundance. There is a paucity of research on the effects of urban development on bat species diversity, although studies by Kurta and Teramino (1992) and Gehrt and Chelsvig (2004) have shown that bat species diversity declines as a function of urban area.

The Indianapolis International Airport (IND), as part of a plan to mitigate the effects of airport expansion in 1991, began purchasing lands to the south of Interstate 70 (I-70) and funding annual studies in an attempt to assess the impact on a community of federally endangered Indiana myotis (*Myotis sodalis*). Additional construction began in 2001, and a Habitat Conservation Plan (American Consulting, Inc.) was designed and implemented shortly thereafter to help direct land managers and ensure conservation of the local bat population, particularly the Indiana bat (*Myotis sodalis*). Aside from the southern habitat mitigation lands, land was also purchased to provide a buffer for airport noise to the north of I-70. Due to the consistency of net site protocol since the HCP began, we have many data on the distribution, abundance, and richness of the bat species at this urban-rural study site (Whitaker et al. 2004; Ulrey et al. 2005; Damm et al. 2011; Whitaker et al. 2011). At the time of this study, White-Nose Syndrome (*Geomyces destructans*) had not been found in Indiana, although the fungus was later discovered in Endless Cave, Washington County, Indiana on 23 January, 2011 [\(http://www.fws.gov/WhiteNoseSyndrome/pdf/IndianaWNS.pdf\)](http://www.fws.gov/WhiteNoseSyndrome/pdf/IndianaWNS.pdf).

Previous studies at IND have focused on bat foraging (Duchamp et al. 2004; Sparks et al. 2005a, b; Walters et al. 2007) and roosting habits (Ritzi et al. 2005; Whitaker et al. 2006). Herein I ask what differences, if any, occur in the northern, more urbanized, portions of the project area north of I-70 versus the more rural area to the south. Both of these areas were purchased by the airport to mitigate for habitat loss. The urban impact is much greater at the northern sites, with development increasing annually. Besides comparing the two areas, I look at the amount of urbanization present in the areas surrounding net sites to examine for an effect of urban landscape. I use long-term netting data (2002 through 2010) to quantify possible differences in bat community diversity.

Methods

Study Area

The Indianapolis International Airport (IND; 39°42'57", 86°16'07") is situated on the southwestern edge of Indianapolis, a major US metropolis. The study area is located to the southwest of IND on lands purchased by the Indianapolis Airport Authority and is bordered by US Highway 40 and Indiana Highway 67 to the north and south, respectively (Fig. 1). Indiana Highway 267 borders the study site to the west. Interstate Highway 70 (I-70) bisects the study site into a northern and southern section, with the area north of I-70 being more developed due to an increasing warehouse district. The southern half of the area is a matrix of agricultural and residential parcels with many small, scattered woodlots ranging approximately 30 – 40 ha in area. All 10 of the net sites used in this study are located along the East Fork of White Lick Creek (WLC), a medium-sized perennial stream which runs north to south through the study

area. This stream bisects the study area from the east side of Mooresville in the south to the west side of Indianapolis to the north. The banks of WLC are mostly wooded, with the dominant species being box elder (*Acer negundo*), eastern cottonwood (*Populus deltoides*), hackberry (*Celtis occidentalis*), sycamore (*Platanus occidentalis*), green ash (*Fraxinus pennsylvanicus*), and black walnut (*Juglans nigra*). Most open areas are either cultivated or developed. The woodlots that are not adjacent to the WLC are dominated by black walnut (*Juglans nigra*), bitternut hickory (*Carya cordiformis*), shagbark hickory (*Carya ovata*), shellbark hickory (*Carya laciniosa*), red oak (*Quercus rubra*), white oak (*Quercus alba*), sugar maple (*Acer saccharum*), honey locust (*Gleditsia triacanthos*), and American elm (*Ulmus americana*). As part of the airport's mitigation procedures, properties are being purchased and small woodlots are being planted along the WLC.

Mist-netting

The bat community was sampled annually from 15 May – 15 August of 2002 - 2010. Mist-netting was conducted for two primary reasons: 1) to monitor and annually assess the overall bat community at the airport, and 2) to radio-tag Indiana myotis for roosting and foraging data. Standardized data taken from every bat included species and sex, reproductive status, length of right forearm, and body mass in grams. Each individual also received an individually numbered aluminum wing band (Porzana Ltd., United Kingdom) placed on the right or left forearm for male and female, respectively.

Netting sessions were conducted at 10 semi-permanent sites along White Lick Creek, four to the north and six to the south of I-70, and at other supplementary sites within the study

area. One creek site to the north of I-70 was lost after the 2002 season and has been removed from analyses. Only creek site data from the 10 sites along White Lick Creek were used in analyses because all non-creek sites are south of I-70 and any additional creek netting was irregular and inconsistent. On each net night, two mist nets were placed in such a way as to seal the flyway along the creek. All nets were set in place by dusk (approximately 2100 hrs) and consisted of two and/or three tier 9 m x 2 m mist nets. A bat detector (Anabat II, Titley Electronics, Australia) was used during each night to audibly assess bat activity. Nets remained in place until at least 0115, unless adverse weather required them to be taken down earlier. On occasion, nets were left in place later than 0115 when bat activity warranted such action. Much netting was done in the study area from 1991 – 1999 (Whitaker et al. 2004), using different netting protocols. All analyses herein use data from 2002-2010.

Habitat Analysis

I overlaid buffers ranging in size from 200-m to 2-km diameter around each net site using MapWindow v.4.8.4. Open Source software. Using habitat class maps (updated from those used in Duchamp et al. 2004, Sparks et al. 2005, and Walters et al. 2007), the areas within each buffer were grouped as either wooded or open/agricultural habitat, water, and urban developed. Urban land cover consisted of commercial, industrial, and high-density residential zones, as well as major transportation routes (i.e. I-70). The relative proportions of each of these habitat-classes were then derived for these groups. Wooded and open habitat that was not classed as urban was considered rural, and water was omitted from any analyses because bodies of water often overlapped into different buffers. Due to buffer overlap, three sites were

used for the north and three for the south in analyses. Three of the southern sites and one northern site was omitted to keep independence of the buffers. Buffers measuring 1.3-km diameter were used because they were the largest possible without sacrificing independence. These buffers were selected based on the distance apart to get the largest buffers possible. Sites A, B, and C were all within 1-km from one another, so site B was selected. Sites D and F were far enough from one another; however site E was removed due to overlap with D and F. In the north, site J was the only one that needed to be omitted. The proportion of urban ground cover was used as a fixed independent factor in analyses.

Data analysis

The Shannon-Wiener Diversity Index (Zar 1999) was used to quantify diversity by net site and by region (north and south of I-70). Relative evenness (J') was derived by dividing H' by the natural log of the maximum number of species present (H_{max}) to acquire a percentage. Shannon diversity values and relative evenness were calculated using Microsoft Excel 2007.

I used Pearson's correlation statistic (Pearson's *r*) to test the hypothesis that abundance of each bat species was dependent on the proportion of urban ground cover within 1.3-km diameter buffers centered on each net site. Student's *t*-tests were used to test the significance of correlations with urban ground cover. Pearson correlations were run in R v.2.13.1 (R Development Core Team). Each of the retained net sites (*n* = 6) was at least 1.3-km from one another.

Differences in Shannon diversity values were tested using linear mixed models constructed in the program R v.2.13.1 using the package lme4 (Bates et al. 2008) with full

maximum likelihood. Year and percentage of urban ground cover were used as independent variables. Year was set as a random factor, and urban ground cover was a fixed factor. Shannon values were the dependent variable. Two models were constructed and compared, one including the proportion of urban ground cover and year and another examining the effect of year with the intercept. The best fit model was chosen using AIC.

Results

One species, the big brown bat (*Eptesicus fuscus*), dominated the bat community in the urbanized northern regions surrounding White Lick Creek, accounting for 65-82% of all captures. *Eptesicus fuscus* was the most abundant (*n* = 956, 54.6%) species at the Indianapolis International Airport conservation properties (Table 1, 2). It was the most common species netted each year (Table 1). The big brown bat was also dominant at each net site except for net site A, which was dominated by *Myotis* species, namely *M. sodalis* (Table 2). The eastern pipistrelle (*Perimyotis subflavus*; *n* = 179), eastern red bat (*Lasiurus borealis*; *n* = 173), Indiana myotis (*M. sodalis*; *n* = 163), and little brown myotis (*M. lucifugus*; *n* = 115) comprised 36.0% of captures (10.2, 9.9, 9.3, and 6.6%, respectively). Other bats captured annually were the evening bat (*Nycticeius humeralis*, *n* = 71, 4.1%) and the northern myotis (*M. septentrionalis*, *n* = 83, 4.7%). The evening bat, Indiana myotis, and the northern myotis all showed high variability in abundance among sites. The evening bat occurred very seldom, if at all, at most sites; however, the species occurred in relatively large numbers at one site, Site E (Fig. 1). The silver-haired bat (*Lasionycteris noctivagans*; *n* = 6), hoary bat (*Lasiurus cinereus*; *n* = 4), and the gray myotis (*M. grisescens*; *n* = 1) together comprised 0.6% of the captures.

The urbanized northern region had a much lower species diversity value (H') than did the southern region (Table 3). There was a similar number of *E. fuscus* in both the northern and southern regions in all years (*n* = 457 and *n* = 499, respectively), but a much higher percentage (75.8%) of *E. fuscus* occurred in the north compared to the south (43.9%). The correlation between this dominant species and urban ground cover was positive, but not significant (*p* = 0.2665; Fig. 2a).

The northern myotis abundance was significantly and positively correlated with urban ground cover (*p* = 0.01532; Fig. 2b). Red bat (*L. borealis*) relative abundance was approximately the same between the two regions ($n = 64$ and $n = 109$ in the north and south, respectively) representing 9.6% of all bats in the north and 10.6% in the south (*p* =0.7049; Fig. 2c).

The Indiana myotis (*n* = 9, 154), *M. sodalis*, showed a marginal negative correlation with urban ground cover (*p* = 0.06993; Fig. 2d). The eastern pipistrelle, *P. subflavus*, (*n* = 18, 161) and the little brown myotis, *M. lucifugus* (*n* = 8, 107) both showed a significant decrease as urban ground cover increased ($p = 0.002541$ and $p = 0.0358$, respectively; Fig. 2e, f). In contrast, captures of northern myotis increased significantly as urban ground cover increased. The evening bat, *N. humeralis*, (*n* = 5, 66) showed no change between north and south (*t* = - 0.0452; *d.f.* = 4; *p* = 0.9661; *r* =-0.02259). This species was captured in relatively high numbers at one net site (net site E; Fig.1), which followed a corridor from a known roost for this species. There were additionally *L. cinereus* (*n* = 1, 3) and *L. noctivagans* (*n* = 1, 5). The one *M. grisescens* was captured in the north. The proportion of species in the north and south are summarized in Tables 1 and 2.

The southern section of the project site consistently displayed greater diversity than the north (Fig. 3; Table 3). The Shannon diversity value for the south was higher in all years (Range $= 1.434 - 1.763$), whereas the northern sites had lower H'-values (0.589 – 1.073). Overall diversity for all years studied was also greater in the south than the north (H'_s = 1.641; H'_n = 0.898). Relative evenness (J') for the region south of I-70 ranged from 0.737 – 0.906, while the northern region ranged from 0.302 – 0.551 (Fig. 3). Mean evenness for years combined in the south and north was 0.843 and 0.462, respectively.

Urban ground cover percentages were greater in the north (Table 4) than in the south. Percentages of urban ground cover became greater as the buffer sizes grew, up to 1.3-km, at all but one site. As buffer size went from 1.3-km to 2.0-km, urban percentage declined for some sites and increased for others. At 1.3 km diameter, the buffer zones to the south contained 0.0 – 5.6% urban land, while the more urban north contained 18.1 – 26.4% urban ground cover.

The model that explained the most variance in Shannon diversity values was that which included the percent of urban ground cover and year as opposed to the model including year alone with the intercept (Table 5). This model had an AIC value of 51.56 and a relative weight of 99.78% (0.9978). The model with urban ground cover removed had an AIC weight of 0.22% (0.00219), and a ΔAIC equal to 12.24. A comparison of the two models using a Chi-Square test showed that the model with urban ground cover was significantly better at explaining the data (*p* = 0.000161; *d.f .*= 1).

Discussion

Previous studies of the effects of urbanization have shown that some species thrive in an increasingly urban setting (Marchetti et al. 2006; Ordenana et al. 2010). Marchetti et al. (2006) found that urbanization causes declines in many native fishes in California, while also facilitating the spread of non-native fishes. Ordenana et al. (2010) showed that as proximity to urban areas increased, many species of carnivores declined. This study coincides with previous reports on the effects that urban landscapes impose on wildlife (Marchetti et al. 2006; McKinney 2006; Duchamp and Swihart 2008; Ordenana et al. 2010; Fitzsimmons et al. 2011). My results show that urbanization likely contributes to the decline of overall diversity, while benefiting a minority of species.

The big brown bat was expected to be abundant relative to other species, as this species is often captured and is believed to be the most common bat in Indiana (Whitaker and Mumford 2009). The relative abundance of the red bat remained similar in the two areas. Gehrt and Chelsvig (2004) found the red bat to have a positive response to nearby industrial and commercial areas. The primary use of foliage by the red bat could be a reason for no change in abundance between northern and southern regions in my study area. Red bats rarely use man-made structures as roosts; however, they are known to forage near street lamps (Geggie and Fenton 1985; Hickey et al. 1996; Duchamp et al. 2004). Interestingly, the northern myotis showed a strong positive correlation with urban ground cover. The total captures for this species were approximately the same in the north and south, however the relative abundance was almost double in the north. This result could possibly be due to roosting requirements, as many northern myotis have been radio-tracked to woodlots in the northern

region of this study area in the past (unpublished data) and are primarily a forest-dwelling species.

The Indiana myotis, little brown myotis, and eastern pipistrelles all showed either a significant or a marginally significant decline in abundance relative to urban ground cover (Figs. 2d, e, f). They did not disappear from the urbanized areas, but declined in relative abundance, compared to rural areas along the same creek. The evening bat had one site at which they were regularly captured, along a corridor to a known roosting area, so it is likely that the greater southern abundance of this species is not related to urbanization, but to proximity to roost.

My results show that some bat species seem to be more able to cope with a heavily modified anthropogenic landscape and occur in a greater abundance in these sites, while other species show declines in numbers relative to urbanization. The more urbanized northern region was consistently dominated by the big brown bat in all years examined. Jung and Kalko (2010) found that species of bats in Panama also showed species-specific land use with respect to urban-forest interface. They found that many (18 out of 25) bats in their study used street lamps to varying degrees for foraging. Duchamp et al. (2004) examined foraging areas used by the big brown bat and the evening bat at this site in Indianapolis. They found that the evening bat showed more fidelity to a foraging patch than the big brown bat. Perhaps of greater importance to this study was their finding that the big brown bat used some low-density residential areas for foraging. Additionally, Duchamp and Swihart (2008) found greater bat diversity as urban area decreased and the total forested area grew in north-central Indiana

along the Upper Wabash River Basin (approximately 100 km to the north). Although my study did not examine the effects of forested area, urban ground cover did have an effect on several species examined.

Although my results suggest that urbanization plays a role in bat species diversity and abundance at this study site, urban ground cover alone is probably not the only factor involved. Much of the difference in bat species richness may likely be attributed to specific roosting and foraging requirements. Many of the bat species in this study roost in natural situations (i.e. trees); however, *E. fuscus* is well known and documented to use anthropogenic roosts such as warehouses and residential buildings (Whitaker and Gummer 1992; Williams and Brittingham 1997; Duchamp et al. 2004; Whitaker et al. 2006; Neubaum et al. 2007) and are best described as urban exploiters. Ordenana et al. (2010) found similar trends in carnivore species richness using areas described as urban-edge in southern California. They found that certain species (i.e. raccoon, coyote) were more likely to occur as the percentage of urban cover increased, with more sensitive species such as the striped skunk and gray fox decreasing with urbanization.

Another possible factor involved in the lack of wildlife diversity in urban areas is the relatively heavy use of roads. Oprea et al. (2009) found urban parks, fragments of habitat within an urban matrix, to have much greater bat diversity than wooded and non-wooded streets in Brazil. This result implies that, even with tree cover, many species are absent or rare in urban and suburban areas. Zurcher et al. (2010) found bats at the IND study area to be significantly averse to road traffic, and this behavior could likely help explain avoidance of urban areas by some species of bats. An examination of individual recaptures between the

north and south regions could give more insight into the effects of roadways, especially major high-traffic ones such as I-70.

Three bat species were captured occasionally: the silver-haired bat (*Lasionycteris noctivagans*), hoary bat (*Lasiurus cinereus*), and gray bat (*Myotis grisescens*). Due to the rarity of these three species (see Methods), they were removed from the analyses. The silver-haired bat is a spring and fall migrant through the area (Whitaker and Mumford 2009), and as such, is not captured often enough at this site to be considered for analyses. Additionally, during the studied years, this species was only captured in mid-late May until early June. The hoary bat was only captured five times at this study site from 2002 – 2010, with three of these captures occurring in 2003. This species is likely underrepresented as it often flies high above the canopy and mist-netting alone is a relatively non-efficient method for capture. The single capture of a gray bat occurred in the northern region in 2005. The individual was thought to be vagrant to the site (Tuttle et al. 2005), possibly due to approaching stormy weather (J. Helms, pers. comm.), although the species has a colony of about six thousand bats at Sellersburg, Indiana (Brack et al. 1984), and isolated captures have been netted mostly along the Ohio River in eastern parts of the state (Whitaker and Gummer 2001; Whitaker et al. 2001).

Although these data coincide with other research on the effects of urbanization on species diversity (Kurta and Teramino 1992; Gehrt and Chelsvig 2004; Marchetti et al. 2006; Ordenana et al. 2010), much more research is warranted in this field. The lands that have been studied at this urban-rural interface were purchased to mitigate for habitat loss due to airport expansion, as well as to provide a noise buffer for airport traffic, and my results demonstrate

the positive effect of these southern mitigation efforts on bat species diversity. Given the relatively large home range of many bats, this work should be easily applied to other species of vertebrates. In particular, studies focusing on how urbanization affects individuals at the species level, both positively and negatively, would provide beneficial knowledge into the adaptive thresholds of species.

Table 1: Numbers of bat species captured in the study area between 2002 and 2010 at ten net sites along the East Fork of White Lick Creek, Hendricks County, Indiana, USA. Percentages are given (in parentheses) for each species in each year, and for all species in the total column.

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Table 2: Total number of each bat species captured in all years (2002 – 2010), listed by net site. Percentages are given for the dominant species, *Eptesicus fuscus*. Net sites A – F are located to the rural south of Interstate 70, and sites H – K are located to the north (urbanized area). All net sites are located along the East Fork of White Lick Creek in Hendricks County, Indiana, USA.

Table 2 (con't): Total number of each bat species captured in all years (2002 – 2010), listed by net site. Percentages are given for the dominant species, *Eptesicus fuscus*. Net sites A – F are located to the rural south of Interstate 70, and sites H – K are located to the north (urbanized area). All net sites are located along the East Fork of White Lick Creek in Hendricks County, Indiana, USA.

Table 3: Yearly number of captures and Shannon-Wiener Diversity Index values (H') for bat netting to the south and north of Interstate 70 at the Indianapolis International Airport. Relative evenness (J') is the value of H' divided by the maximum attainable diversity (H_{max}), measured as the natural log of the species richness (S). Bats Netted is the total number of bats captured per year. Seven species were captured annually. The three species that were rarely captured (*Lasionycteris noctivagans, Lasiurus cinereus,* and *Myotis grisescens*) were omitted from analyses.

Table 4: The percentage of urban ground cover contained within different buffer sizes. Buffer diameters are in meters. Net sites A – F are located to the south of I-70, and H – K are north. Urban ground cover consisted of industrial, commercial, and high-density residential zones, as well as heavy transportation (i.e. airport, I-70). The 1300-m diameter buffers from sites B, D, F, H, I, and K were used for analyses.

Table 5: Models used to explain the species diversity relative to year and percentage of urban ground cover from the nine years studied, 2002 through 2010. Urban ground cover was derived from 1.3 km buffers around three net sites in each region, north and south of I-70. Urban ground cover is a fixed factor and year was a random factor in analysis. The first model contained both percentage urban ground cover within 1.3-km buffers and the year. The second model was testing the effect of year alone.

Figure 1: Location of the study area within the state of Indiana (top left) and greater Indianapolis Metroplex (top right). Bottom shows an overview of the study area, with major roads and the East Fork of White Lick Creek. Net sites are labeled and denoted by black triangles. Thatched area represents the Indianapolis International Airport (IND). The net sites are labeled. Net sites A – F are located to the south of Interstate 70, and net sites H – K are to the north.

Figure 2: The abundance (total captures per site) of the bat species captured at the Indianapolis International Airport relative to the proportion of urban ground cover. Species shown are the a) big brown bat (*Eptesicus fuscus*), b) red bat (*Lasiurus borealis*), c) little brown myotis (*Myotis lucifugus*), d) northern myotis (*M. septentrionalis*), e) Indiana myotis (*M. sodalis*), and eastern pipistrelles (*Perimyotis subflavus*). The black dots represent the six net site buffers that were used in analyses. The crosses are the net sites that were omitted from analyses because of overlap. Statistics test the null hypothesis that the two variables are not correlated.

Figure 2 (con't): The abundance (total captures per site) of the bat species captured at the Indianapolis International Airport relative to the proportion of urban ground cover. Species shown are the a) big brown bat (*Eptesicus fuscus*), b) red bat (*Lasiurus borealis*), c) little brown myotis (*Myotis lucifugus*), d) northern myotis (*M. septentrionalis*), e) Indiana myotis (*M. sodalis*), and eastern pipistrelles (*Perimyotis subflavus*). The black dots represent the six net site buffers that were used in analyses. The crosses are the net sites that were omitted from analyses because of overlap. Statistics test the null hypothesis that the two variables are not correlated.

Figure 3: The top figure shows the Shannon-Wiener diversity values (H') by year for the northern urbanized (squares) and southern rural (diamonds) regions of the Indianapolis International Airport conservation properties, Hendricks County, Indiana, USA. The maximum attainable diversity (H_{max} = 1.946) is represented by triangles. The bottom figure represents the relative evenness (J') for the northern (squares) and southern (diamonds) regions.

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