Urban Ecosyst (2009) 12:197–214
DOI 10.1007/s11252-008-0075-6

Relationship between urbanization and bat community structure in national parks of the southeastern U.S.

Susan C. Loeb · Christopher J. Post · Steven T. Hall

Published online: 4 October 2008

Abstract Urbanization and development are predicted to increase considerably in the United States over the next several decades, and this is expected to result in large-scale habitat loss, fragmentation and loss of wildlife species. Thus, natural parks and preserves are becomingly increasingly important in the conservation of regional biodiversity. We used mist-nets and AnabatII acoustic detectors to survey bats in 10 national parks in the southeastern U.S. and examined the relationship between bat community structure and development in the surrounding 5 km. We predicted that species richness would increase with park size and that species richness and evenness would decrease with development. Species richness was not related to development or any other landscape characteristics including park size. In contrast, species evenness declined with increasing development. Percent Developed land in the surrounding 5 km area was the only variable that entered into the stepwise regression model. The decrease in species evenness in the urban parks was due to the dominance of big brown bats (*Eptesicus fuscus*) in these parks. The percentage of big brown bats in our captures was positively related to percent Developed land in the surrounding area. Our data suggest that urban parks may be important for conserving regional bat biodiversity. However, the low species evenness in these parks suggests that some bat species may be susceptible to the effects of urbanization and may be extirpated over time. Thus, management of urban as well as rural parks should strive to conserve as much bat roosting and foraging habitat as possible.

Keywords Bats · Chiroptera · Conservation · Urban development · Species richness · Species diversity

S. C. Loeb (✉)
USDA Forest Service, Southern Research Station, Department of Forestry & Natural Resources, Clemson University, Clemson, SC 29634, USA
e-mail: sloeb@fs.fed.us

C. J. Post · S. T. Hall
Department of Forestry & Natural Resources, Clemson University, Clemson, SC 29634, USA

Introduction

Urbanization and development are expected to increase substantially in the southeastern U.S. in the next few decades (Wear and Greis 2002; Alig et al. 2004). Due to urban sprawl, loss of land to development is predicted to be disproportional to population growth. For example, from 1994 to 2030 the population in the Charleston, South Carolina area is predicted to increase by 49% while the urban area is predicted to increase by 247% (Allen and Lu 2003). Consequently, loss and fragmentation of wildlife habitat will be considerable (Alig et al. 2003). Habitat loss and fragmentation are the major causes of species decline and extinction (Wilcove et al. 1998), and urbanization is the major factor contributing to this loss and fragmentation (Czech et al. 2000). Thus, continuing urbanization and development will likely have a significant impact on wildlife populations.

Approximately 24% of the world's bat species are threatened with extinction (Mickleburgh et al. 2002) and even common species may be declining (e.g., Whitaker et al. 2002). Although factors such as roost site disturbance and pesticides are important threats to bats, loss and degradation of important habitats such as forests and wetlands are the major threats to their populations (Mickleburgh et al. 2002; Racey and Entwistle 2003). Thus, urbanization and development have the potential to greatly impact bat populations. In addition to the loss of forests and wetlands, several other factors related to urbanization may impact bats. Natural roost sites, particularly snags and trees with hollows, are significantly reduced in urban areas (van der Ree and McCarthy 2005). Food availability may also be affected by urbanization. For example, insect abundance can be negatively affected by urbanization (McIntyre 2000; Kalcounis-Rueppell et al. 2007). Factors affecting arthropods in urban environments include habitat loss and alteration, loss of resources such as food plants, and pollution. Higher levels of traffic may also negatively impact bats in urban areas (Lodé 2000). However, several features of urban environments may be beneficial to some bats. For example, species such as the big brown bat (*Eptesicus fuscus*) and the Brazilian free-tailed bat (*Tadarida brasiliensis*) readily roost in buildings and bridges found in urban areas (Wilkins 1989; Duchamp et al. 2004; Neubaum et al. 2007) and some species commonly forage at street lights that attract insects (e.g., Hickey et al. 1996; Reddy and Fenton 2003).

Several studies have examined the use of urban areas by bats and have found that bats prefer wooded or riparian areas within cities and avoid high density residential and commercial–industrial areas (Gaisler et al. 1998; Gehrt and Chelsvig 2003; Duchamp et al. 2004; Sparks et al. 2005; Hourigan et al. 2006; Walters et al. 2007). However, only a few studies have examined the effects of urbanization on bat populations or community composition. These studies have found that bat communities in urban areas have lower species richness than surrounding rural areas (Avila-Flores and Fenton 2005) or are dominated by a few common species that have adapted well to urban environments (Kurta and Teramino 1992; Sparks et al. 1998; Ulrey et al. 2005). Results of these studies suggest that some species are more vulnerable to the effects of urbanization than others. However, few data are available to determine which species are the most vulnerable, or how bat communities will respond to increasing urbanization.

As the amount of privately owned land in forest and wetlands declines due to development, parks and other protected areas are becoming increasingly important for the conservation of biological diversity (Ferguson et al. 2001). Large natural parks and preserves are assumed to provide the greatest value for conservation due to species–area relationships, and are particularly important for large terrestrial species with large home ranges (Noss and Cooperrider 1994). However, even though large parks usually harbor more species, small parks often contain a greater proportion of unique species (Falkner and Stohlgren 1997). Small parks may also contribute to conservation of regional biodiversity by serving as refuges for endemic species with low mobility and as rest stops for species migrating among larger parks. Further, many small parks are in developed areas and therefore serve as local refugia.

Although there has been increased research on bats in urban environments in recent years, the importance of urban parks in the conservation of regional bat diversity has received little study. The objectives of our study were to examine the structure and composition of bat communities in 10 national parks in the southeastern U.S. and to relate measures of community composition and structure to park characteristics and the level of urbanization surrounding the parks. We predicted that: (1) bat species richness, evenness, and diversity would decrease as development increased, and (2) species richness would increase with park size.

Methods

Study areas

The study was conducted in 10 national park units, including one national park (NP), three national monuments (NM), two national historic sites (NHS), one national recreation area (NRA), one national battlefield (NB) and two national military parks (NMP) located in North Carolina, South Carolina, and Georgia (Fig. 1). Fort Sumter NM and Fort Pulaski NM are located in the Lower Coastal Plain Physiographic Region; Congaree NP and Ocmulgee NM are located in the Upper Coastal Plain Physiographic Region; Chattahoochee River NRA, Ninety Six NHS, Cowpens NB, Kings Mountain NMP, and Guilford Courthouse NMP are in the Piedmont Physiographic Region; and Carl Sandburg Home NHS is in the Mountains Physiographic Region. Most parks are contiguous units although Chattahoochee NRA consists of 14 individual land units extending along a 48-mi stretch of the Chattahoochee River and Fort Sumter NM consists of three administrative units (Fort Sumter, Fort Moultrie, and Charles Pinckney Home). Park size varies from approximately 42 ha to almost 9,000 ha (Table 1). Habitats in the parks include coastal hammock (Fort Pulaski NM), old-growth bottomland hardwood forest (Congaree NP), and mature pine, pine-hardwood and hardwood forests (Chattahoochee NRA, Cowpens NB, Guilford Courthouse NMP, Kings Mountain NMP, Ninety Six NHS, Ocmulgee NM and Carl Sandburg Home NHS). Many parks also have forested and herbaceous wetlands (e.g., Congaree NP, Fort Pulaski NM, Ocmulgee NM and Ninety Six NHS), extensive riparian areas (Chattahoochee NRA), and special habitats such as granitic domes (Carl Sandburg Home NHS). Four parks are found in large cities: Chattahoochee NRA is in Atlanta, GA; Fort Sumter NM is in Charleston, SC; Guilford Courthouse NMP is in Greensboro NC; and Ocmulgee NM is in Macon, GA. The other parks are in suburban or rural settings. Although most of the parks in the study were established to protect important cultural and historic resources, natural resource management is a priority in all the parks surveyed. Active management is practiced in some parks and consists primarily of prescribed burning and invasive species control.

Bat survey methods

We surveyed each park with mist-nets and acoustic detectors. Surveys were conducted primarily from late May through mid-August 2004–2006 although brief spring (late

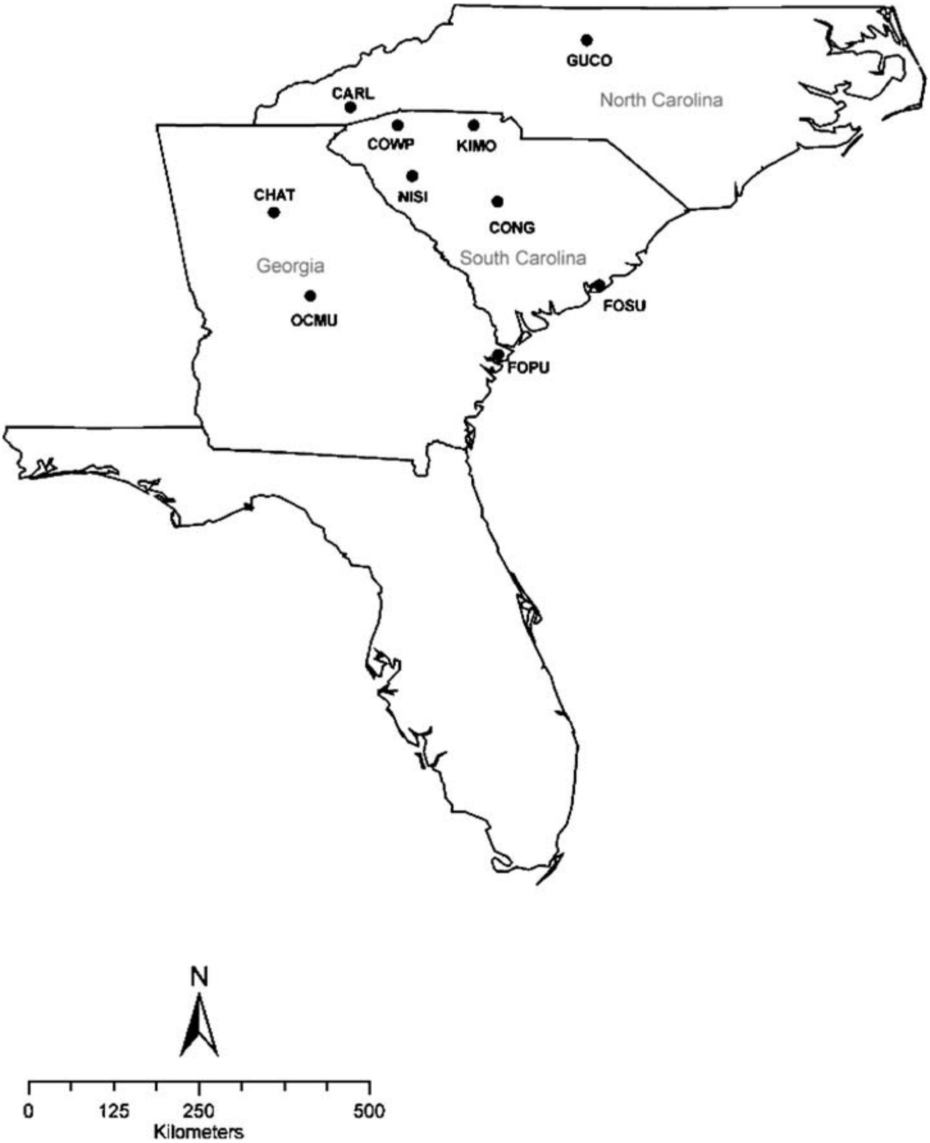


Fig. 1 Location of southeastern national parks surveyed for bats spring and summer 2004–2007. *CARL* Carl Sandburg National Historic Site, *CHAT* Chattahoochee National Recreation Area, *CONG* Congaree National Park, *COWP* Cowpens National Battlefield, *FOPU* Fort Pulaski National Monument, *FOSU* Fort Sumter National Monument, *GUCO* Guilford Courthouse National Military Park, *KIMO* Kings Mountain National Military Park, *NISI* Ninety Six National Historic Site, *OCMU* Ocmulgee National Monument

March–April) mist-net and acoustic sampling sessions were conducted at Fort Pulaski NM, Ninety Six NHS, and Ocmulgee NM in 2005–2007. No winter migrants were detected during the spring surveys. Capture and acoustic sampling efforts varied with park size and opportunities for mist-netting (Table 2). Netting was conducted in as many habitats as possible within each park and mist-nets were set across fly-ways such as streams, roads, and trails with over-hanging and side vegetation (Kunz and Kurta 1988). Mist nets were

Table 1 Characteristics of 10 southeastern U.S. national parks surveyed for bats during spring and summer 2004–2007

Park	Size (ha)	Region	Within park				5 km surrounding park						
			Canopy cover (%)	Forest (%)	Wetland (%)	Open (%)	Pop. density (people/km^2)	Canopy cover (%)	Devel. open (%)	Devel. (%)	Forest (%)	Wetland (%)	Agricul. (%)
CARL	107	Mtn	56.3	79.8	0.0	16.4	292.0	74.3	29.7	8.8	44.8	0.2	14.0
CHAT	4,047	Pied	48.0	56.6	5.3	12.6	993.3	58.0	26.5	34.6	28.5	0.9	3.5
CONG	8,988	UCP	62.2	4.6	91.4	0.9	17.5	63.8	3.5	0.7	37.1	31.7	10.8
COWP	341	Pied	45.8	73.8	1.7	22.0	72.8	65.7	9.1	3.3	36.8	1.3	40.9
FOPU	2,275	LCP	47.0	2.0	65.8	4.9	340.3	58.5	3.9	4.3	5.4	44.5	0.4
FOSU	42[a]	LCP	45.3	15.9	9.7	58.6	1,142.5	51.1	10.9	17.2	11.5	22.8	3.8
GUCO	89	Pied	54.3	76.0	0.0	0.9	739.6	53.8	35.8	30.1	21.5	1.0	4.9
KIMO	1,597	Pied	61.2	99.1	0.0	0.9	73.1	68.1	5.0	2.4	68.0	0.2	19.8
NISI	400	Pied	49.1	66.9	11.3	18.6	84.4	68.4	6.9	1.0	59.3	3.3	19.0
OCMU	284	UPC	49.8	40.8	36.2	15.9	930.3	62.5	15.7	23.5	30.8	17.2	2.7

CARL Carl Sandburg National Historic Site, *CHAT* Chattahoochee National Recreation Area, *CONG* Congaree National Park, *COWP* Cowpens National Battlefield, *FOPU* Fort Pulaski National Monument, *FOSU* Fort Sumter National Monument, *GUCO* Guilford Courthouse National Military Park, *KIMO* Kings Mountain National Military Park, *NISI* Ninety Six National Historic Site, *OCMU* Ocmulgee National Monument. *LCP* Lower Coastal Plain, *UCP* Upper Coastal Plain, *Pied* Piedmont, *Mtn* Mountains

[a] Does not include approximately 48 ha of open water in Charleston Harbor

Table 2 Number of each species of bat captured in mist-nets in national parks during spring and summer 2004–2007

Park	Capture effort	CORA	EPFU	LABO	LAIN	LASE	MYAU	MYLE	MYLU	MYSE	NYHU	PESU	Total
CARL	7/21		4					1	6	17	1		29
CHAT	13/39		55	4					1			2	62
CONG	10/32	3	1	4			21				1	2	32
COWP	8/17												0
FOPU	5/14		1	4	1	11					1		18
FOSU	3/10					1							1
GUCO	6/16		39	4							2	2	47
KIMO	6/14		4	3								1	8
NISI	7/18		7	4		1					7		19
OCMU	7/16	2	9	1		2					1		15

Capture effort is the number of netting nights and the total number of net-nights (total number of nets set over all netting nights)

CARL Carl Sandburg National Historic Site, *CHAT* Chattahoochee National Recreation Area, *CONG* Congaree National Park, *COWP* Cowpens National Battlefield, *FOPU* Fort Pulaski National Monument, *FOSU* Fort Sumter National Monument, *GUCO* Guilford Courthouse National Military Park, *KIMO* Kings Mountain National Military Park, *NISI* Ninety Six National Historic Site, *OCMU* Ocmulgee National Monument. *LCP* Lower Coastal Plain, *UCP* Upper Coastal Plain, *Pied* Piedmont, *Mtn* Mountains; *CORA Corynorhinus rafinesquii*, *EPFU Eptesicus fuscus*, *LABO Lasiurus borealis*, *LAIN L. intermedius*, *LASE L. seminolus*, *MYAU Myotis austroriparius*, *MYLE M. leibii*, *MYLU M. lucifugus*, *MYSE M. septentrionalis*, *NYHU Nycticeius humeralis*, *PESU Perimyotis subflavus*

either 2.6 or 5.2 m high and 2.5, 6, 9 or 12 m wide depending on net sites. One to four mist-nets were set at each netting location. Nets were opened for 4–5 h depending on bat activity and weather, and were checked every 15 min. Bats were removed from the net, identified to species, and weighed. Sex, age (adult or juvenile), reproductive condition, and other pertinent information (e.g., parasites, injuries) were also recorded. A uniquely numbered aluminum-lipped band was placed on the forearm of each bat before it was released. Digital photographs were taken of each species encountered at each park for verification.

Acoustic sampling was conducted with AnabatII bat detectors (see Brigham et al. 2004). Detectors were connected either to laptop computers or programmable interface and recording modules with compact flash cards (CF-ZCAIMS). Detectors with CF-ZCAIMS were placed in waterproof containers with a 45° angled tube and attached to tripods set at approximately 1.3 m and oriented in the direction with the least vegetation or other obstructions (Weller and Zabel 2002). Detectors were set at mist-net sites to record species not captured in our nets as well as at sites that could not be mist-netted. In five of the parks (Carl Sandburg Home NHS, Cowpens NB, Guilford Courthouse NMP, Kings Mountain NMP, and Ninety Six NHS) 15–20 sampling points had been established by the Park Service in the dominant community types as well as in special habitats (Nichols et al. 2000). We sampled as many of these points with detectors as possible. In the other parks we sampled as many habitats types as possible with detectors including ponds, open fields, streams and a cross-section of forest types. Detectors were set for 1–3 nights per sampling session; some points were sampled during two or more sampling sessions.

We used Analook (Version 4.9j, 2004) to analyze bat calls. Two filters were applied to the files to delete noise and poor quality bat calls. The first filter removed insect and other extraneous noise. This filter selected passes that had ≥1 bat calls and allowed lower quality calls to pass the filter. The files that passed this filter provided an index of general bat activity in the area. These calls were subjected to a more stringent filter that selected primarily search phase calls with ≥5 pulses (Britzke and Murray 2000). Each of these files was examined visually to ensure that it contained search phase calls. A discriminant function model based on a call library of >23,000 calls was used to identify the remaining calls and passes to species (Britzke 2003). Because not all potential species were included in the model (e.g., Brazilian free-tailed bats), each pass was also examined qualitatively (O'Farrell et al. 1999) to confirm or correct the quantitative identification. We could not discriminate between the calls of red bats (*Lasiurus borealis*) and Seminole bats (*L. seminolus*). Therefore, we grouped these calls in parks where both species occurred or could potentially occur.

Landscape analysis

We used the 2000 population density by block for the conterminous United States dataset, obtained from the United States Geological Survey (http://water.usgs.gov/lookup/getspatial?uspopd00x10g) and the National Land Cover Dataset (NLCD) to determine human population density and land cover characteristics within 5 km of each park boundary. This area was based on the average foraging range for most bats in the eastern U.S. (Menzel et al. 2001; Duchamp et al. 2004; Elmore et al., 2005; Broders et al. 2006; Walters et al. 2007). Population density was estimated at 100 m grid cell resolution. Canopy cover and land cover data sets had a 30 m grid cell resolution and were obtained from the Multi-Resolution Land Characteristics consortium (http://www.mrlc.gov). Canopy cover and land cover datasets were derived primarily from high resolution Landsat 7 satellite imagery taken around 2001, with ancillary data such as digital elevation models and other existing spatial data layers used in the classification process (Homer et al. 2004). Canopy cover was based on empirical relationships developed between the satellite imagery and tree canopy density (Huang et al. 2001). Percent canopy cover and percent area in each land cover class were also calculated for the landscapes within each park. Summary statistics were calculated for each park and all corresponding percentages were calculated within ARCMAP 9.1 (ESRI, Redlands, California).

We classified the area surrounding the parks into seven land cover classes, some of which represent combinations of NLCD classes: (1) Developed/Open Space—<20% impervious surfaces; areas that are mostly vegetation but with some constructed material such as large-lot single-family homes, parks, and golf courses, (2) Developed—20–100% impervious surface, (3) Forest-areas dominated by trees >5 m in height and making up >20% of total vegetation; includes deciduous, evergreen, and mixed forests, (4) Woody Wetland—>20% of the area is forest or shrubland and the soil or substrate is periodically saturated or covered with water, (5) Herbaceous Wetland—>80% of the vegetation is perennial herbaceous and the soil or substrate is periodically saturated with water, (6) Total Wetland—Woody and Herbaceous Wetland, and (7) Agriculture—>20% of vegetation is pasture hay or cultivated crops. Many of the land classes in the area surrounding the parks did not exist within the parks or were present in small amounts. Thus, only three land classes were used for the area within parks: (1) Forest—defined above, (2) Total Wetland—defined above, and (3) Open—includes areas classified as shrub/scrub, grassland/herbaceous, pasture/hay, and developed/open space (primarily open space).

Statistical analysis

We calculated three measures of bat community structure for each park: species richness, the Shannon diversity index and the Shannon evenness index. Species richness was simply the total number of species documented at each park over the entire sampling period based on capture and acoustic data. The Shannon diversity and evenness indices incorporate the number of species captured as well as the number of individuals of each species (Magurran 2004). Although acoustic data can be used to estimate bat presence, relative activity and habitat use, it cannot be used to estimate bat abundance (Hayes 2000; Miller et al. 2003). Therefore, Shannon's diversity and evenness indices were based on capture data only.

We tested each variable for normality using the Shapiro–Wilk Test (SAS 2002; PROC UNIVARIATE). When a variable did not approximate a normal distribution, we applied a $\log_{10}$ and square-root transformation and used the transformed variable that resulted in the best approximation of a normal variate. However, even after transformation, the diversity index was not normally distributed. Therefore, we only used species richness and evenness in our statistical analyses. We used correlation analysis (PROC CORR; α=0.05) to test whether species richness and evenness were related to sampling effort and we used stepwise regression (PROC REG; α=0.05) to examine the relationships between species richness and evenness and park and landscape characteristics. Although there are some problems with the use of stepwise regression as a model building procedure, it is a good tool for exploratory data analysis (Thayer 2002). Before conducting the stepwise regression analyses we eliminated variables that were highly correlated (r>0.70). Remaining variables were park size, percent Forest within the park, percent Open area within the park, percent Developed land in the area surrounding the park, percent Forest in the area surrounding the park, percent Total Wetland in the area surrounding the park, and percent Agriculture in the area surrounding the park.

Results

Landscape and population characteristics

Although canopy cover inside the parks did not vary greatly, there was considerable variation in the amount of forest and wetland within park boundaries (Table 1). Because Congaree NP contains primarily floodplain forest, most of the area was classified as Total Wetland (primarily Woody Wetland) and only 4.6% was classified as Forest. Population density in the 5 km area surrounding the parks ranged from 17.5 people/km^2 to 1,142 people/km^2 (Table 1). Percent Developed land in the area surrounding the parks ranged from 1% to 35% (Table 1). Based on population density and percent Developed land, we considered Chattahoochee NRA, Fort Sumter NM, Guilford Courthouse NMP, and Ocmulgee NM as urban (739.6–1,142 people/km^2 and 17.2–34.6% Developed land), Congaree NP, Cowpens NB, Kings Mountain NMP, and Ninety Six NHS as rural (17.5–84.4 people/km^2 and 3.5–9.1% Developed land), and Carl Sandburg Home NHS and Fort Pulaski NM as intermediate or suburban (292.0–340.3 people/km^2 and 4.3–8.8% Developed land).

Bat species richness and evenness

The number of netting nights (number nights×number of locations) per park ranged from three to 13 and the number of net-nights (total number of nets set over all netting nights) ranged from 10 to 39 (Table 2). Although the number of individual bats captured at each park was positively correlated with the number of net-nights (r=0.75, P=0.011), the number of species captured was not (r=0.41, P=0.242). We recorded 17,940 bat passes and were able to identify 4,790 (26.7%) of these passes to species. The number of acoustic sampling nights (total number of acoustic detectors set over all nights) per park ranged from 13 to 61 (Table 3) but the number of species recorded was not related to the number of sampling nights (r=0.316, P=0.374). Therefore, although sampling effort varied among the parks, it did not affect our measures of species richness or evenness.

We captured a total of 231 bats of 11 species in the 10 parks during 72 nights of netting (Table 2). No bats were captured in Cowpens NB despite considerable effort, and only one bat was captured in Fort Sumter NM. However, appropriate capture sites were very limited in Fort Sumter NM. The big brown bat, red bat, evening bat (*Nycticeius humeralis*) and eastern pipistrelle (*Perimyotis subflavus*) were the most common species and were captured in eight, seven, five, and five parks, respectively. Four species of special concern were captured: Rafinesque's big-eared bat (*Corynorhinus rafinesquii*) in Congaree NP and Ocmulgee NM, the southeastern myotis (*Myotis austroriparius*) in Congaree NP, the small-footed bat (*M. leibii*) in Carl Sandburg Home NHS, and the northern yellow bat (*L. intermedius*) in Fort Pulaski NM. Pregnant, lactating, or post-lactating bats were captured in every park in which we had captures except Fort Sumter NM (Appendix). However, the one bat captured in Fort Sumter NM was a juvenile. We were not able to compare the proportion of animals in reproductive condition among the various parks because the captures occurred over a large range of dates. Bats were recorded acoustically in every park and the number of species recorded ranged from three to seven (Table 3). Big brown bats and eastern pipistrelles were detected in every park as were red bats or red bats/ Seminole bats.

Species richness based on capture and acoustic records ranged from three in Cowpens NB and Kings Mountain NMP to eight in Carl Sandburg House NHS (Table 4). Species richness was not significantly related to any of the variables entered in the linear regression model. Species diversity ranged from 0.46 to 1.22 and species evenness ranged from 0.33 to 0.88 (Table 4). Percent Developed land in the surrounding 5 km was the only variable that was included in the model for species evenness (P=0.019, R^2=0.63). Species evenness was negatively related to the amount of development in the area (Fig. 2a). Chattahoochee NRA and Guilford Courthouse NMP, both urban parks, had the lowest species diversity and evenness, while Ocmulgee NM and Ninety Six NHS, an urban and a rural park, had the highest species diversity, and Ninety Six NHS and Kings Mountain NMP, both rural parks, had the highest species evenness (Table 4).

Bat community structure

Big brown bats dominated the bat communities of Chattahoochee NRA and Guilford Courthouse NMP (88.7% and 83.0% of captures, respectively) and accounted for a large percentage of the captures in Ocmulgee NM (60%), another urban park (Table 2). In contrast, big brown bats comprised <50% of the captures in other parks. The percentage of big brown bats in our captures was positively related to percent Developed land in the surrounding area (Fig. 2B; P=0.008, R^2=0.72). No other variables were included in the model. Captures of the second most common group (red bats and/or Seminole bats) were not related to any of the variables in the regression model, including percent Developed land (Fig. 2c). Northern long-eared bats (*M. septentrionalis*) were the dominant species in Carl Sandburg Home NHS, and southeastern bats dominated the bat community in Congaree NP.

Table 3 Bats recorded with AnabatII bat detectors at each of the national parks during spring and summer 2004–2007

Park	No. sampling nights	No. species	EPFU	LABO	LABO[a]/ LASE	LANO	MYLE	MYLU	MYSE	NYHU	PESU	TABR
CARL	61	7	+	+		+	+	+	+		+	
CHAT	34	4	+	+						+	+	
CONG	25	4	+		+					+	+	
COWP	48	3	+	+							+	
FOPU	13	5	+		+					+	+	+
FOSU	21	5	+		+					+	+	+
GUCO	34	5	+	+		+				+	+	
KIMO	32	3	+	+							+	
NISI	34	4	+		+					+	+	
OCMU	18	5	+		+					+	+	+

CARL Carl Sandburg National Historic Site, *CHAT* Chattahoochee National Recreation Area, *CONG* Congaree National Park, *COWP* Cowpens National Battlefield, *FOPU* Fort Pulaski National Monument, *FOSU* Fort Sumter National Monument, *GUCO* Guilford Courthouse National Military Park, *KIMO* Kings Mountain National Military Park, *NISI* Ninety Six National Historic Site, *OCMU* Ocmulgee National Monument. *LCP* Lower Coastal Plain, *UCP* Upper Coastal Plain, *Pied* Piedmont, *Mtn* Mountains; *EPFU Eptesicus fuscus*, *LABO Lasiurus borealis*, *LASE L. seminolus*, *LANO Lasionycteris noctivagans*, *MYLE M. leibii*, *MYLU M. lucifugus*, *MYSE M. septentrionalis*, *NYHU Nycticeius humeralis*, *PESU Perimyotis subflavus*, *TABR Tadarida brasiliensis*

[a] It is not possible to distinguish between LABO and LASE calls. Thus, in areas where they both occur calls were assigned to LABO/LASE

Discussion

Because the parks included in this study were located in three physiographic regions, the bat communities were drawn from somewhat different species pools. For example, species associated with more northern latitudes (e.g., little brown bat) were captured at Carl Sandburg NHS and Chattahoochee NRA while species associated with coastal pine and hardwood forests (Seminole bat, northern yellow bat, southeastern bat) were captured at Congaree NP, Fort Pulaski NM, and Fort Sumter NM. However, the parks with the highest species richness were in the mountains and Coastal Plains (Carl Sandburg NHS, Ocmulgee NM, and Fort Pulaski NM) while the two parks with the lowest species richness (Kings Mountain NMP and Cowpens NB) were in the Piedmont region. The Piedmont regions of South Carolina and Georgia have a lower number of summer resident bat species than either the Coastal Plains or Mountains (Menzel et al. 2000, 2003), and therefore, the potential number of species in these parks was lower. Because our urban or intermediate parks were found in all three physiographic regions, the effect of physiographic region should have had little effect on our results.

Species richness was not related to percent Developed land, the measure of urbanization included in the regression analysis. Species richness in urban parks ranged from five to seven whereas species richness in rural parks ranged from three to six. While some studies have found a reduction in bat species richness in urban areas compared to surrounding rural areas (Avila-Flores and Fenton 2005), others have found that bat species richness is not affected by urbanization (Kurta and Teramino 1992; Sparks et al. 1998; Ulrey et al. 2005). However, within cities, bat species richness often declines with the amount of urbanization (Gaisler et al. 1998; Hourigan et al. 2006). Thus, parks within urban areas may serve as important refuges for bats and may explain why species richness was preserved in the urban parks we studied.

Table 4 Species richness, Shannon's diversity index, and Shannon's evenness index of bats in 10 national parks in the southeastern U.S.

Park	Potential species richness[b]	Species richness	Species diversity	Species evenness
CARL[a]	9	8	1.14	0.71
CHAT	7	5	0.46	0.33
CONG	8	6	1.15	0.64
COWP[a]	6	3		
FOPU	9	7	1.12	0.69
FOSU[a]	9	5		
GUCO	6	5	0.63	0.46
KIMO	6	3	0.97	0.89
NISI	6	5	1.22	0.88
OCMU	8	7	1.20	0.75

Species richness was based on capture and acoustic surveys whereas diversity and evenness indices were based on capture data only

CARL Carl Sandburg National Historic Site, *CHAT* Chattahoochee National Recreation Area, *CONG* Congaree National Park, *COWP* Cowpens National Battlefield, *FOPU* Fort Pulaski National Monument, *FOSU* Fort Sumter National Monument, *GUCO* Guilford Courthouse National Military Park, *KIMO* Kings Mountain National Military Park, *NISI* Ninety Six National Historic Site, *OCMU* Ocmulgee National Monument. *LCP* Lower Coastal Plain, *UCP* Upper Coastal Plain, *Pied* Piedmont, *Mtn* Mountains

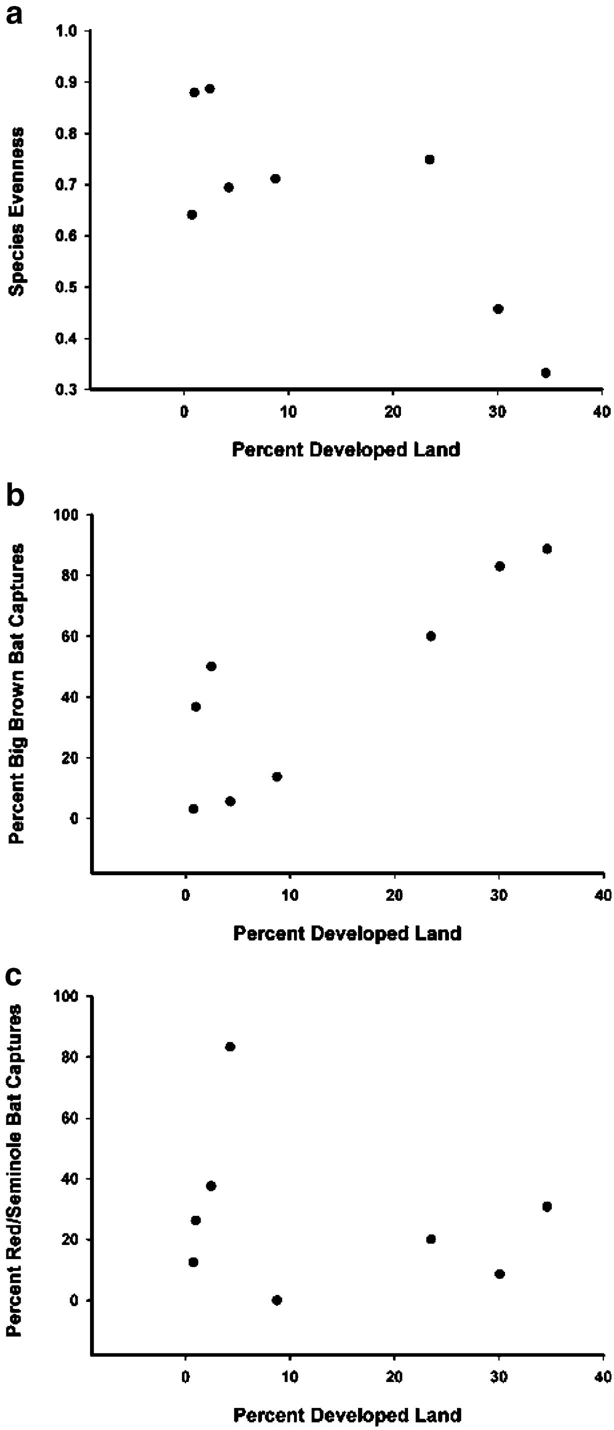
[a] No or only one bat were captured in these parks

[b] Potential species richness is the number of species that could be in a park based on range maps

The two intermediate parks (Carl Sandburg Home NHS and Fort Pulaski NM) had the highest species richness (7 and 8). Species richness is higher in suburban areas in a number of taxa (McKinney 2002) and this is often explained by the intermediate disturbance hypothesis (e.g., Marzluff 2005; McKinney 2008). Although our sample size was small, the higher bat species richness in parks that were surrounded by a moderate degree of development and urbanization suggests that the balance of local extinction and invasion in suburban areas may result in higher species richness in suburban bat communities, as in other taxa. However, further work will be needed to test this hypothesis more fully.

Contrary to our prediction, species richness was not related to park size. In contrast, herpetofaunal species richness in 16 national parks in the southeastern U.S., including some of the parks surveyed in this study, had a strong positive relationship with park size (Tuberville et al. 2005). There have been few studies of species–area relationships in bats, particularly in temperate regions. Although bat species richness increases with island area in Scandinavia and the Lesser Antilles (e.g., Ahlén 1983; Ricklefs and Lovette 1999; Pedersen et al. 2003), the effect of forest patch size (i.e., forest islands) on bat species is equivocal. Lesiński et al. (2007) found that bat species richness increased with forest patch size but that significant increases in species richness did not occur in patches >100 ha. Montiel et al. (2006) also found that forest fragment area had a positive effect on species richness in northwest Yucatan, but Estrada et al. (1993) found that fragment size was not an important factor explaining species richness in forest patches in the same area. However, like Lesiński et al. (2007), Estrada et al. (1993) found that the number of species appeared to increase as patch size increased up to about 100 ha. Most of the parks in our study were >100 ha in size and therefore, may have been larger than the maximum size at which area would be an important factor. Further, the effective size of some parks may have been larger than the actual size of those parks depending on the amount of suitable habitat in the surrounding area.

Fig. 2 Relationship between **a** species evenness of bat communities in 10 national parks in the southeastern U.S. and percent developed land in the surrounding 5 km, **b** the percent of big brown bats in mist net captures and percent developed land in the surrounding 5 km, and **c** the percent of red bats and/or Seminole bats in mist net captures and percent developed land in the surrounding 5 km



In addition to maintaining species richness, urban and intermediate parks may serve as refuges for species of concern. Rafinesque's big-eared bats are species of high conservation concern (Global Status G3G4, NatureServe 2007). Two Rafinesque's big-eared bats were captured in Ocmulgee NM, a highly urbanized park. We radio-tracked one adult female and confirmed that the bats were roosting in the park (Loeb, unpublished data). Small-footed bats are also a species of conservation concern (Global Status G3, NatureServe 2007) and were captured in Carl Sandburg Home NHS, a park that is surrounded by an intermediate amount of urbanization. Northern yellow bats are not considered to be vulnerable to extinction, but because little is known about their distribution and status in the U.S., many states list them as species of special concern. This species was captured in Fort Pulaski NM, a park on the outskirts of Savannah, Georgia. Thus, urban and intermediate parks may be important refuges for rare and declining bat species if they provide the habitat required by these species.

In contrast to species richness, species evenness was not maintained in urban parks. Species evenness declined as percent Developed land in the 5 km surrounding the parks increased. Similarly, Kurta and Teramino (1992) found lower species diversity and evenness in urban parks than in rural areas in the Detroit area, despite similarities in species richness.

The decline of species evenness with increasing urbanization was due to the dominance of big brown bats in urban park communities. Big brown bats made up the majority of captures in the three urban parks in which we were able to mist-net throughout the parks (i.e., Chattahoochee NRA, Guilford Courthouse NMP, and Ocmulgee NM) but made up <50% of the captures in the intermediate and rural parks. In the mid-Atlantic region of the U.S., big brown bat activity is greatest in urban forest parks and lowest in fragmented rural parks (Johnson et al. 2008) and big brown bats dominate all of the North American urban bat communities that have been studied to date (Kurta and Teramino 1992; Sparks et al. 1998; Everette et al. 2001; Ulrey et al. 2005; Kalcounis-Rueppell et al. 2007). Big brown bats commonly roost in buildings in urban areas (Everette et al. 2001; Duchamp et al. 2004; Neubaum et al. 2007) and forage in urban habitats, although they prefer to forage in rural habitats (Geggie and Fenton 1985; Duchamp et al. 2004). Within urban habitats, foraging activity is greatest in parkland and residential areas and lowest in commercial areas (Geggie and Fenton 1985). Thus, the urban parks in our study may have provided important foraging habitat for big brown bats that were roosting in buildings on or in the vicinity of the parks.

While other bat species are found in urban areas, they do not appear to be as adapted to urban environments as big brown bats. For example, big brown bats near Indianapolis use low density developed and urban areas more than evening bats which prefer agricultural and wooded habitats (Duchamp et al. 2004). Evening bats also direct their foraging activity away from residential areas whereas big brown bats do not. Red bats and Indiana bats (*M. sodalis*) near Indianapolis also avoid developed areas including transportation corridors, extraction sites, and commercial areas (Sparks et al. 2005; Walters et al. 2007). Big brown bats are one of the largest species of bats in North America, and are able to fly long distances from their roost sites to foraging areas (Everette et al. 2001). In contrast, red bats in urban areas appear to restrict their foraging to areas close to the roost (Mager and Nelson 2001; Walters et al. 2007). Because flight efficiency increases with body size (Speakman and Thomas 2003), the energetic costs of flying farther to suitable foraging is greater for smaller species. Thus, in the eastern U.S., smaller species such as pipistrelles, evening bats, and red bats may be more heavily impacted by the effects of urbanization than big brown bats which can better afford to fly to distant foraging sites if necessary.

We could not compare the reproductive status of bats in urban parks with that of bats in rural parks because the capture season was relatively long and sample sizes were small in some parks. However, our data suggest that urban parks do not serve as sinks for non-reproductive individuals. We captured pregnant and lactating females or young of the year in all the parks in which we captured bats. However, even though Kurta and Teramino (1992) captured many pregnant, lactating, or post-lactating big brown bats in urban parks in Detroit, the proportion of reproductive females in urban areas was significantly lower than in rural areas. Further, little is known about bat survival and the factors that affect it. If predation or other mortality factors are higher in urban parks than in rural parks, these parks may in fact act as sinks. Thus, future studies of bats in urban parks should address demographic characteristics as well community composition and structure.

Urbanization and development may occur gradually, particularly around rural parks and other natural areas. Thus, managers need early warning signs to mitigate potential impacts of development on bats and other wildlife. For bats in the eastern U.S., increasing proportions of big brown bats in mist-net captures may be a good indicator of encroaching urbanization. Thus, mist-net surveys conducted on an annual or bi-annual basis may be a good way to monitor urbanization and its effects on bat communities in parks and preserves in the eastern U.S.

Our data suggest that urban parks may play an important role in the conservation of regional biodiversity. High bat species richness and the presence of sensitive bat species in urban parks suggest that these parks may serve as refuges for bats. However, to fully test the importance of urban parks to bats, future studies should compare the bat community structure and composition in the parks to those in the surrounding urban matrix. Further, although species richness is maintained in urban parks, the low species evenness and the dominance of big brown bats in these parks suggest that some species may be more susceptible than others to the effects of urbanization and may be extirpated from the urban environment over time. Management of parks and green spaces within urban environments to provide foraging and roosting habitats for bats may slow or reverse this trend.

Acknowledgements Funding for this project was provided by the National Park Service, Southeast Coast Inventory and Monitoring Network and the Cumberland Piedmont Inventory and Monitoring Network. We thank C. A. Dachelet, S. Buranek, J. Fernandez, L. Staples, T. Torongeau, and K. Wolcott for assistance in the field and personnel at all of the parks for logistical support. We thank P. G. R. Jodice, J. M. O'Keefe, D. W. Sparks, S. J. Zarnoch and two anonymous reviewers for helpful comments on previous drafts of the manuscript.

Appendix

Table 5 Number of juvenile, adult male and adult female bats of each species captured at each of 10 national parks in the southeastern U.S. and the number of adult females that were pregnant, lactating or post-lactating

Park	Species	Juvenile	Adult male	Adult female	Pregnant	Lactating	Post lactating
CARL	EPFU	0	2	2	0	2	0
	MYLE	0	0	1	0	1	0
	MYLU	0	0	6	0	6	0
	MYSE	0	2	15	1	7	0
	NYHU	0	1	0	–	–	–
CHAT	EPFU	6	10	39	0	14	1
	LABO	1	4	0	–	–	–
	MYLU	0	1	0	–	–	–
	PESU	0	0	2	0	1	0

Table 5 (continued)

Park	Species	Juvenile	Adult male	Adult female	Pregnant	Lactating	Post lactating
CONG	CORA	2	1	0	–	–	–
	EPFU	0	1	0	–	–	–
	LABO	1	0	3	1	2	0
	MYAU	1	4	16	11	0	1
	NYHU	1	0	0	–	–	–
	PESU	2	0	0	–	–	–
FOPU	EPFU	0	0	1	0	0	0
	LABO	1	0	3	0	3	0
	LAIN	0	1	0	–	–	–
	LASE	5	1	5	0	0	1
	NYHU	1	0	0	–	–	–
FOSU	LASE	1	0	0	–	–	–
GUCO	EPFU	22	16	1	0	1	0
	LABO	2	1	1	0	1	0
	NYHU	1	1	0	–	–	–
	PESU	1	0	1	0	1	0
KIMO	EPFU	0	4	0	–	–	–
	LABO	1	1	1	0	1	0
	PESU	0	1	0	–	–	–
NISI	EPFU[a]	0	3	3	0	3	0
	LABO	0	1	3	3	0	0
	LASE	0	1	0	–	–	–
	NYHU	0	1	6	4	1	0
OCMU	CORA	0	0	2	0	0	0
	EPFU	0	8	2	0	1	0
	LABO	0	1	0	–	–	–
	LASE	1	1	0	–	–	–
	NYHU	0	1	0	–	–	–

CARL Carl Sandburg National Historic Site, *CHAT* Chattahoochee National Recreation Area, *CONG* Congaree National Park, *COWP* Cowpens National Battlefield, *FOPU* Fort Pulaski National Monument, *FOSU* Fort Sumter National Monument, *GUCO* Guilford Courthouse National Military Park, *KIMO* Kings Mountain National Military Park, *NISI* Ninety Six National Historic Site, *OCMU* Ocmulgee National Monument. *LCP* Lower Coastal Plain, *UCP* Upper Coastal Plain, *Pied* Piedmont, *Mtn* Mountains; *CORA Corynorhinus rafinesquii*, *EPFU Eptesicus fuscus*, *LABO Lasiurus borealis*, *LAIN L. intermedius*, *LASE L. seminolus*, *MYAU Myotis austroriparius*, *MYLE M. leibii*, *MYLU M. lucifugus*, *MYSE M. septentrionalis*, *NYHU Nycticeius humeralis*, *PESU Perimyotis subflavus*

[a] One bat escaped before age, sex and reproductive condition were determined

References

Ahlén I (1983) The bat fauna of some isolated islands in Scandinavia. Oikos 41:352–358. doi:10.2307/3544093

Alig RJ, Platinga AJ, Ahn S, Kline JD (2003) Land use changes involving forestry in the United States: 1952 to 1997, with projections to 2050. Gen. Tech. Report-587, Pacific Northwest Research Station, USDA Forest Service, Portland, OR

Alig RJ, Kline JD, Lichtenstein M (2004) Urbanization on the US landscape: looking ahead in the 21st century. Landsc Urban Plan 69:219–234. doi:10.1016/j.landurbplan.2003.07.004

Allen J, Lu K (2003) Modeling and prediction of future urban growth in the Charleston region of South Carolina: a GIS-based integrated approach. Conserv Ecol 8:2 Available online at http://www.consecol.org/vol8/iss2/art2

Avila-Flores R, Fenton MB (2005) Use of spatial features by foraging insectivorous bats in a large urban landscape. J Mammal 86:1193–1204. doi:10.1644/04-MAMM-A-085R1.1
Brigham RM, Kalko EK, Jones G, Parson S, Limpens HJGA (2004) Bat echolocation research: tools, techniques and analysis. Bat Conservation International, Austin
Britzke ER (2003) Use of ultrasonic detectors for acoustic identification and study of bat ecology in the eastern United States. PhD Dissertation. Tennessee Technological University, Cookville, TN
Britzke ER, Murray KL (2000) A quantitative method for selection of identifiable search-phase calls using the Anabat system. Bat Res News 41:33–36
Broders HG, Forbes GJ, Woodley S, Thompson ID (2006) Range extent and stand selection for roosting and foraging in forest-dwelling northern long-eared bats and little brown bats in the Greater Fundy Ecosystem, New Brunswick. J Wildl Manage 70:1174–1184. doi:10.2193/0022-541X(2006)70[1174:REASSF]2.0.CO;2
Czech B, Krausman PR, Devers PK (2000) Economic associations among causes of species endangerment in the United States. Bioscience 50:593–601. doi:10.1641/0006-3568(2000)050[0593:EAACOS]2.0.CO;2
Duchamp JE, Sparks DW, Whitaker JO Jr (2004) Foraging-habitat selection by bats at an urban–rural interface: comparison between a successful and a less successful species. Can J Zool 82:1157–1164. doi:10.1139/z04-095
Elmore LW, Miller DA, Vilella FJ (2005) Foraging area size and habitat use by red bats (*Lasiurus borealis*) in an intensively managed pine landscape in Mississippi. Am Midl Nat 153:405–417. doi:10.1674/0003-0031(2005)153[0405:FASAHU]2.0.CO;2
Estrada A, Coates-Estrada R, Meritt D Jr (1993) Bat species richness and abundance in tropical rain forest fragments and in agricultural habitats at Los Tuxtlas, Mexico. Ecography 16:309–318. doi:10.1111/j.1600-0587.1993.tb00220.x
Everette AL, O'Shea TJ, Ellison LE, Stone LA, McCance JL (2001) Bat use of a high-plains urban wildlife refuge. Wildl Soc Bull 29:967–973
Falkner MB, Stohlgren TJ (1997) Evaluating the contribution of small National Park areas to regional biodiversity. Nat Areas J 17:324–330
Ferguson HL, Robinette K, Stenberg K (2001) Wildlife of urban habitats. In: Johnson DH, O'Neil TA (eds) Wildlife–habitat relationships in Oregon and Washington. Oregon State University Press, Corvallis, pp 317–341
Gaisler J, Zukal J, Rehak Z, Homolka M (1998) Habitat preference and flight activity of bats in a city. J Zool (Lond) 244:439–445. doi:10.1111/j.1469-7998.1998.tb00048.x
Geggie JF, Fenton MG (1985) A comparison of foraging by *Eptesicus fuscus* (Chiroptera: Vespertilionidae) in urban and rural environments. Can J Zool 63:263–267
Gehrt SD, Chelsvig JE (2003) Bat activity in an urban landscape: patterns at the landscape and microhabitat scale. Ecol Appl 13:939–950. doi:10.1890/02-5188
Hayes JP (2000) Assumptions and practical considerations in the design and interpretation of echolocation-monitoring studies. Acta Chiropt 2:225–236
Hickey MBC, Acharya L, Pennington S (1996) Resource partitioning by two species of vespertilionid bats (*Lasiurus cinereus* and *Lasiurus borealis*) feeding around street lights. J Mammal 77:325–334. doi:10.2307/1382804
Homer C, Huang C, Yang L, Wylie B, Coan M (2004) Development of a 2001 national land cover database for the United States. Photogramm Eng Remote Sensing 70:829–840
Hourigan CL, Johnson C, Robson SKA (2006) The structure of a micro-bat community in relation to gradients of environmental variation in a tropical urban area. Urban Ecosyst 9:67–82. doi:10.1007/s11252-006-7902-4
Huang C, Yang L, Wylie B, Homer C (2001) A strategy for estimating tree canopy density using Landsat 7 ETM+ and high resolution images over large areas. In: Third International Conference on Geospatial Information in Agriculture and Forestry; November 5–7, 2001; Denver, Colorado. CD-ROM, 1 disk
Johnson JB, Gates JE, Ford WM (2008) Distribution and activity of bats at local and landscape scales within a rural–urban gradient. Urban Ecosyst 11:227–242. doi:10.1007/s11252-008-0055-x
Kalcounis-Rueppell MC, Payne VH, Huff SR, Boyko AL (2007) Effects of wastewater treatment plant effluent on bat foraging ecology in an urban stream system. Biol Conserv 138:120–130. doi:10.1016/j.biocon.2007.04.009
Kunz TH, Kurta A (1988) Capture methods and holding devises. In: Kunz TH (ed) Ecological and behavioral methods for the study of bats. Smithsonian Institution Press, Washington, DC, pp 1–29
Kurta A, Teramino JA (1992) Bat community structure in an urban park. Ecography 15:257–261. doi:10.1111/j.1600-0587.1992.tb00032.x
Lesiński G, Kowalski M, Wojtowicz B, Gulatowska J, Lisowska A (2007) Bats on forest islands of different size in an agricultural landscape. Folia Zool (Brno) 56:153–161

Lodé T (2000) Effect of a motorway on mortality and isolation of wildlife populations. Ambio 29:163–166. doi:10.1639/0044-7447(2000)029[0163:EOAMOM]2.0.CO;2

Mager KJ, Nelson TA (2001) Roost-site selection by eastern red bats (*Lasiurus borealis*). Am Midl Nat 145:120–126. doi:10.1674/0003-0031(2001)145[0120:RSSBER]2.0.CO;2

Magurran AE (2004) Measuring biological diversity. Blackwell, Oxford

Marzluff JM (2005) Island biogeography for an urbanizing world: how extinction and colonization may determine biological diversity in human-dominated landscapes. Urban Ecosyst 8:157–177. doi:10.1007/s11252-005-4378-6

McIntyre NE (2000) Ecology of urban arthropods: a review and a call to action. Ann Entomol Soc Am 93:825–835. doi:10.1603/0013-8746(2000)093[0825:EOUAAR]2.0.CO;2

McKinney ML (2002) Urbanization, biodiversity, and conservation. Bioscience 52:883–890. doi:10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2

McKinney ML (2008) Effects of urbanization on species richness: a review of plants and animals. Urban Ecosyst 11:161–176. doi:10.1007/s11252-007-0045-4

Menzel MA, Chapman BR, Ford WM, Menzel JM, Laerm J (2000) A review of the distribution and roosting ecology of bats in Georgia. Ga J Sci 58:143–178

Menzel MA, Menzel JM, Ford WM, Edwards JW, Carter TC, Churchill JB et al (2001) Home range and habitat use of male Rafinesque's big-eared bats (*Corynorhinus rafinesquii*). Am Midl Nat 145:402–408. doi:10.1674/0003-0031(2001)145[0402:HRAHUO]2.0.CO;2

Menzel JM, Menzel MA, Ford WM, Edwards JW, Sheffield SR, Kilgo JC et al (2003) The distribution of the bats of South Carolina. Southeast Nat 2:121–152. doi:10.1656/1528-7092(2003)002[0121:TDOTBO]2.0.CO;2

Mickleburgh SP, Hutson AM, Racey PA (2002) A review of the global conservation status of bats. Oryx 36:18–34

Miller DA, Arnett EB, Lacki MJ (2003) Habitat management for forest-roosting bats of North America: a critical review of habitat studies. Wildl Soc Bull 31:30–44

Montiel S, Estrada A, León P (2006) Bat assemblages in a naturally fragmented ecosystem in the Yucatan Peninsula, Mexico: species richness, diversity and spatio-temporal dynamics. J Trop Ecol 22:267–276. doi:10.1017/S026646740500307X

NatureServe (2007) NatureServe Explorer: An online encyclopedia of life [web application]. Version 6.2. NatureServe, Arlington, Virginia. Available at http://www.natureserve.org/explorer. Accessed: October 21, 2007

Neubaum DJ, Wilson KR, O'Shea TJ (2007) Urban maternity-roost selection by big brown bats in Colorado. J Wildl Manage 71:728–736. doi:10.2193/2005-684

Nichols B, Jenkins M, Rock J, Langdon K, Leibfreid T (2000) Study plan for vertebrate and vascular plant inventories in Cumberland Piedmont and Appalachian Highlands Networks. National Park Service

Noss RF, Cooperrider AY (1994) Saving nature's legacy: protecting and restoring biodiversity. Island, Washington DC

O'Farrell MJ, Miller BW, Gannon WL (1999) Qualitative identification of free-flying bats using the Anabat detector. J Mammal 80:11–23. doi:10.2307/1383203

Pedersen SC, Genoways HH, Morton MN, Johnson JW, Courts SE (2003) Bats of Nevis, northern Lesser Antilles. Acta Chiropt 5:251–267

Racey PA, Entwistle AC (2003) Conservation ecology of bats. In: Kunz TH, Fenton MB (eds) Bat ecology. University of Chicago Press, Chicago, pp 680–743

Reddy E, Fenton FB (2003) Exploiting vulnerable prey: moths and red bats (*Lasiurus borealis*; Vespertilionidae). Can J Zool 81:1553–1560. doi:10.1139/z03-146

Ricklefs RE, Lovette IJ (1999) The roles of island area *per se* and habitat diversity in the species–area relationships of four Lesser Antillean faunal groups. J Anim Ecol 68:1142–1160. doi:10.1046/j.1365-2656.1999.00358.x

SAS Institute (2002) SAS/STAT user's guide. Version 9. SAS Institute, Cary

Sparks DW, Laborda JA, Whitaker JO Jr (1998) Bats of the Indianapolis International Airport as compared to a more rural community of bats at Prairie Creek. Proc Indiana Acad Sci 107:171–179

Sparks DW, Ritzi CM, Duchamp JE, Whitaker JO Jr (2005) Foraging habitat of Indiana myotis (*Myotis sodalis*) at an urban/rural interface. J Mammal 86:713–718. doi:10.1644/1545-1542(2005)086[0713:FHOTIB]2.0.CO;2

Speakman JR, Thomas DW (2003) Physiological ecology and energetics of bats. In: Kunz TH, Fenton MB (eds) Bat ecology. University of Chicago Press, Chicago, pp 209–253

Thayer JD (2002) Stepwise regression as an exploratory data analysis procedure. Presented at the Annual Meeting of the American Educational Research Association, April 2, 2002, New Orleans, Louisiana. 11 pp

Tuberville TD, Willson JD, Dorcas ME, Gibbons JW (2005) Herpetofaunal species richness of southeastern national parks. Southeast Nat 4:537–569. doi:10.1656/1528-7092(2005)004[0537:HSROSN]2.0.CO;2
Ulrey WA, Sparks DW, Ritzi CM (2005) Bat communities in highly impacted areas: comparing Camp Atterbury to the Indianapolis Airport. Proc Indiana Acad Sci 114:73–76
van der Ree R, McCarthy MA (2005) Inferring persistence of indigenous mammals in response to urbanisation. Anim Conserv 8:308–319
Walters BL, Ritzi CM, Sparks DW, Whitaker JO Jr (2007) Foraging behavior of eastern red bats (*Lasiurus borealis*) at an urban–rural interface. Am Midl Nat 157:365–373. doi:10.1674/0003-0031(2007)157[365:FBOERB]2.0.CO;2
Wear DN, Greis JG (2002) Southern forest resource assessment. Gen Tech Report-53, USDA, Forest Service, Southern Research Station, Asheville, NC
Weller TJ, Zabel CJ (2002) Variation in bat detections due to detector orientation in a forest. Wildl Soc Bull 30:922–930
Whitaker JO Jr, Brack V Jr, Cope JB (2002) Are bats in Indiana declining. Proc Indiana Acad Sci 111: 95–106
Wilcove DS, Rothstein D, Dubow J, Phillips A, Losos E (1998) Quantifying threats to imperiled species in the United States. Bioscience 48:607–615. doi:10.2307/1313420
Wilkins KT (1989) *Tadarida brasiliensis*. Mamm Species 331:1–10. doi:10.2307/3504148