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COMMUNITY ECOLOGY OF BATS IN SOUTHERN LOWER MICHIGAN, WITH EMPHASIS ON ROOST SELECTION BY *MYOTIS*

By

Lisa Winhold

Thesis

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APPROVAL

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DEDICATION

This thesis is dedicated to my parents, who not only provided ample moral and financial support, but also took the time to introduce me to the outdoors through numerous camping, caving, kayaking, and hiking trips, which allowed me to develop an interest in ecology. This is also dedicated to D. Roberts and K. Roberts, who introduced me to caving, sparking my interest in bats and cave ecology.

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ABSTRACT

I studied the roosting niche of three sympatric species of *Myotis* (little brown bat, *M. lucifugus*; northern bat, *M. septentrionalis*; and Indiana bat, *M. sodalis*) and examined changes in composition of the entire bat community in southern Lower Michigan over long periods. Little brown bats roosted in buildings, whereas northern and Indiana bats used trees. Northern and Indiana bats differed primarily in species of tree used, whether the tree was living or dead, and use of cavities or loose bark. There were no differences among species in composition of landscapes surrounding roosts. I also netted bats during 2004–2006 and compared my captures to previous surveys. Over 26 years, composition of the entire community has changed with the addition of two new species, evening bats (*Nycticeius humeralis*) and eastern pipistrelles (*Pipistrellus subflavus*), and a drastic decline in relative abundance of red bats (*Lasiurus borealis*).

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CHAPTER 1

ROOSTING NICHE OF THREE SPECIES OF *MYOTIS* IN SOUTHERN LOWER MICHIGAN

INTRODUCTION

Effective management of a population requires knowledge of its ecological requirements. Quality habitats often are species specific in composition, size, and type, and knowledge of shelter and foraging requirements, spatial relationships, and connectivity of a population can help conservation efforts (Racey and Entwistle, 2003). However, obtaining such information requires a broad-scale approach.

A landscape is a mosaic of habitats in which each type is suitable for some species while potentially inhospitable to others (Krohne, 1998). Each patch of habitat varies in composition and area, and size of a patch contributes to the stability of a population and coexistence of multiple populations (Sanderson and Harris, 2000). Consequently, habitat fragmentation frequently leads to changes in natural processes and a loss in biodiversity. In addition, adjacent and nearby habitats can affect natural processes within a habitat of interest and, therefore, can affect the suitability of that patch for a particular species (Harris and Sanderson, 2000). With continuing agricultural development and urban sprawl, suitable habitats often are lost either through direct loss of land or disturbance by nearby anthropogenic activities, and, consequently, habitat loss or degradation is the most common cause of extinction of species (Krohne, 1998).

Bat roosts.—Approximately 1,100 species of bats exist worldwide, making bats the second most speciose group of mammals (Simmons, 2005). Despite this diversity, ca. 25% of bat species are either endangered or threatened (Hutson et al., 2001; Racey and Entwistle, 2003). In the United States and Canada, almost half of the 45 species are considered endangered or threatened at the national or local level, and destruction of habitat (roosting sites and foraging areas) is often believed to be the cause (Ellison et al., 2003; Racey and Entwistle, 2003).

Bats have numerous types of roosts that vary with the specific requirements of each species and availability of suitable structures in the immediate landscape (Kunz and Lumsden, 2003). These roosts provide protection from severe weather and predators, as well as a place to raise young, interact with other bats, and conserve energy while resting. Tree-dwelling bats often select roosts in dead trees, either under exfoliating bark or inside cavities, which provide protection from the environment and a desired microclimate. Furthermore, in temperate areas, roost trees often have low canopy cover, allowing exposure to sunlight for warmth (Barclay and Kurta, in press; Kunz and Lumsden, 2003). Dead trees, however, make unpredictable roosts, because they may fall, lose bark, or have fluctuating microclimates, and, consequently, members of a bat colony generally disperse among several trees in a stand and switch trees every few days (Kurta et al., 1996; Menzel et al., 2002).

Myotis *in Michigan*.—About 10% of bat species belong to the genus *Myotis* in the family Vespertilionidae, which are the largest genus and family of bats, respectively (Simmons, 2005). Fifteen species of *Myotis* are found in the United States, and three species have geographic ranges that include Michigan: the little brown bat (*M. lucifugus*), northern bat (*M. septentrionalis*), and Indiana bat (*M. sodalis*), which is on the federal list of endangered species. The Michigan myotines are similar in size (total body length of 73–100 mm) and mass (6–12 g) and superficially have similar foraging and roosting habits, suggesting potentially large niche overlap (Kurta, 1995; Foster and Kurta, 1998).

All three species of *Myotis* are uncommon in southern Lower Michigan during summer, and the low density of their populations is probably due to the distance to suitable underground hibernacula (mines and caves) and not to any particular effect of climate or general habitat (Kurta, 1982, 1995). All three species become more abundant as one moves south of Michigan into the farmlands of northern Ohio and Indiana (Mumford and Whitaker, 1982), and northern bats and little brown bats also become more abundant in summer as one heads north, into the forested areas of the northern Lower Peninsula (Kurta et al., 1987). All three species roost in trees and utilize buildings to varying degrees; the little brown bat commonly roosts in buildings in the East; the northern bat, occasionally; and the Indiana bat, rarely (Barbour and Davis, 1969; Fitch and Shump, 1979; Butchkoski and Hassinger, 2002). There is no reason to expect that suitable roosts are more available for any of these species either to the north or to the south. Consequently, roost selection by these bats in southern Lower Michigan is more likely to reflect true preferences of each species, rather than a compromise resulting from competition with related species.

Although roosting habits of the three *Myotis* seem similar, roost selection by all three species has never been examined across a broad geographic region. Radiotracking has been used extensively to study roosting habits of the Indiana bat (Kurta and Kennedy, 2002); however, published studies on northern bats and little brown bats are rare (Barclay and Kurta, in press), and most have been conducted in regions such as South Dakota (Cryan et al., 2001) or northern Alberta (Crampton and Barclay, 1998), which differ greatly in climate and in composition of the forest from southern Michigan. Moreover, these studies typically observe bats in extensive, intact forests, which contrast with the highly fragmented, agricultural landscape of southern Lower Michigan.

For all tree-dwelling bats, biologists seldom have examined roosting habits at the landscape level (e.g., Carter et al., 2002); instead, researchers typically focused on the roost tree itself and the habitat within a short distance of the roost tree (i.e., the roost plot). Although documenting habitat variables within 10–20 m of a roost is necessary for wildlife managers, such small-scale studies ignore the fact that bats are highly mobile animals, capable of traveling tens of kilometers in a single night (Murray and Kurta, 2004; Pierson, 1998). Because of the large home range of these animals, studies at the landscape level are required to develop effective management plans (Krusac and Mighton, 2002; Kurta et al., 2002; Racey and Entwistle, 2003).

My study determines how the myotines partition the roosting niche in the fragmented landscape of southern Lower Michigan. Specifically, I document aspects of the roosting niche of little brown, northern, and Indiana bats in southern Lower Michigan, concentrating on the roost tree, the roost plot, and the forest stand in which they are found (i.e., the roost stand). In addition, I provide the first study of roosting habitat of all three species at the landscape-level.

METHODS

Capturing and radio-tracking bats.—I studied habitat selection by mist-netting bats (Kunz and Kurta, 1988) and radiotracking them to their roosting sites. Mist-netting occurred at 83 locations in southern Lower Michigan, primarily in the four most southern rows of counties (Chapter 2). Field work occurred during 2004–2006, between 15 May and 15 August of each year, when captured bats were likely to be local residents and not migrants. I generally followed the netting protocol recommended by the United States Fish and Wildlife Service (1999) for Indiana bats, i.e., two large netting systems, ca. 100 m apart, on 2 nights, for 5 h each night, weather permitting.

After capture, I identified each bat to species, determined sex, and assigned an age, either adult or juvenile, based on extent of epiphyseal ossification of the wing phalanges (Anthony, 1988). I recorded reproductive status of adult females as pregnant, lactating, postlactating, or nonreproductive, based on palpation of the abdomen, condition of the nipples, and my ability to express milk from them (Racey, 1988). Bats were banded (Lambournes, Ltd., Leominster, Middlesex, United Kingdom) or punch-marked (Bonaccorso and Smythe, 1972) for future recognition.

Most *Myotis* that were mist-netted were radiotracked. I attached lightweight (<0.7-g) radio-transmitters (Holohil Systems, Ltd., Carp, Ontario, Canada) to the interscapular region with surgical glue, after trimming some dorsal hairs. Bats were tracked with a receiver (Wildlife Instruments, Carbondale, Illinois) and 3- and 5-element yagi antennas for 3–7 days after the transmitter was attached.

Characteristics of roost trees and buildings.—Once roost trees were located, I recorded characteristics of the roosts and of the surrounding habitat. Species of each tree was determined, although for statistical analysis trees were generally lumped into generic categories of elm (*Ulmus*), maple (*Acer*), ash (*Fraxinus*), and “other.” Diameter of the tree at breast height was measured with a tape, and height of the tree was determined with a clinometer. Location of the roost exit (entrance) was established by observing bats as they left to forage, between sunset and 50 min after sunset (Viele et al., 2002).

Solar radiation impinging on a roost helps bats maintain their body temperature while minimizing expenditure of endogenous energy (Kunz and Lumsden, 2003). Therefore, the number of hours that the roosting site was exposed to sunlight was estimated, and the roost was assigned a number from one to three, indicating low (≤5 h), medium (>5 but ≤10 h), or high (>10 h) solar exposure, respectively. Large trees retain more thermal energy than small trees, and, similarly, tree cavities retain more heat than roosts under loose bark (Kunz and Lumsden, 2003); consequently, in addition to measuring diameter and height of the tree, I recorded the type of roosting site on the tree (bark, cavity, or crevice).

Many roost trees were dead, so I also assigned each tree to a decay class, numbered from one to seven (Table 1.1—Bernardos et al., 2004). As a measure of potential roosting opportunities for bats, some investigators determine the total amount (percentage) of bark covering the trunk of a tree, whereas others assess only the amount of loose bark that remains (Kurta, 2005). I estimated both parameters in my study. Obstacles, such as foliage and twigs, may affect flight patterns, echolocation, and the ability of a bat to access a roost. Consequently, the amount of foliage and twigs (clutter) near the roost exit was categorized as low, medium, or high and assigned a corresponding number from one to three. Trees near the roost would contribute to the amount of clutter near the exit; therefore, I also measured the distance from the roost to the nearest tree taller and shorter than the roost tree.

For buildings, I recorded the type of structure and primary use (e.g., storage, livestock, and human activities) as an index of the amount of disturbance that occurred to the colony. In addition to estimating solar exposure and clutter around roosts, I also recorded the type (e.g., wood, shingles, or tin) and orientation of the roof, because those factors would also affect the amount of solar energy absorbed to warm the roost. Like the roost trees, I recorded height of the structure and maximum height of the exit. Location of exits was determined by monitoring the roost for 50 min starting at sunset.

Characteristics of the roost plot and the surrounding stand.—I assessed characteristics of the habitat within a circular plot (the roost plot) with a radius of 17.8 m (0.1 ha) around each roost tree. Within the roost plot, I determined the amount of canopy cover with a concave densiometer by calculating the mean of eight measurements—one at the base of the tree and one ca. 2 m away in each of the four cardinal directions. All woody stems with diameter ≥10 cm were counted and identified to species, and a decay class was assigned to each. I also measured diameter of each tree and used it to calculate total basal area of the plot (Brower and Zar, 1984).

To examine selectivity by the bats, I compared characteristics of each roost tree to a randomly chosen, potential roost tree within the roost plot. I identified potential roost trees based on published descriptions for each species (Foster and Kurta, 1999; Kurta, 2005) and my own observations. Potential roost trees were those with loose bark, crevices, or obvious cavities that were in dead trees for Indiana bats and live or dead trees for northern bats. All trees within the plot that had characteristics of a potential roost were numbered, and I selected one for comparison to the roost tree, using a table of random numbers (Zar, 1999). Data collected on this randomly chosen tree included species, diameter, height, canopy cover, decay status, solar exposure, percent bark remaining on the trunk, percent loose bark that covered the trunk, and distances to the nearest trees that were taller and shorter than the randomly selected potential roost. Because potential roosts did not have a specific exit point, I determined a category for clutter at a location halfway up the tree.

In addition to plot-level traits, I examined characteristics of the surrounding forest stand. To do so, I first randomly selected a tree within the same stand as the roost tree, by using a table of random numbers to choose a compass direction and a distance from the roost tree. Randomly chosen trees were located a minimum of 36 m from the roost tree (i.e., twice the diameter of a roost plot) and within an arbitrary maximum distance of 200 m. Once the distance and direction were selected, I chose the closest potential roost to that point based on the criteria used for random trees within roost plots. For each randomly selected tree in the same stand, I recorded species, decay status, height, diameter, canopy cover, amount of clutter halfway up the tree, solar exposure, percent bark remaining, percent loose bark, and distances to the nearest trees that were taller and shorter than the randomly selected potential roost. After delineating a 0.1-ha plot around the randomly chosen tree, I recorded the species, decay status, and diameter of all woody stems (≥10 cm) within this stand plot.

If the roost was a building, then the plot consisted of a buffer strip, 17.8-m wide, surrounding the building. The same measurements were recorded for trees within the buffer strip as those within tree roost plots. No random buildings were selected for comparison because the nearest comparable structure was often 1 km or farther away.

Characteristics of the surrounding landscape.—The location (North American Datum, 1983) of each roost was recorded using a global positioning system (Garmin GPS II Plus, Olathe, Kansas), and data were later downloaded into ArcGIS 9.1 (ESRI, Redlands, California). These points were overlain onto digital orthophoto quadrangles taken in 1998 and digital raster graphs, and using the North American Datum, 1983, Michigan Georeference projection, I created digital maps of roost locations. For landscape analyses, the roost tree arbitrarily was assumed to be at the center of the animal's home range, and landcover was analyzed within a 5-km radius surrounding each roost. I selected this radius based on the potential home range of *Myotis sodalis* (Kurta et al., 2002). If multiple roosting structures (trees or buildings) were discovered for a colony, only a central point that was equidistant from all roosts was used as the center of landcover analysis to preserve independence.

In addition to analyzing landcover within 5 km of the roost, I determined the type of landcover at which a roost was found, although the maximum resolution that I could attain was an area of 0.9 ha surrounding the roost (the size of a single pixel). For colonies with multiple roosts, I determined landcover within 0.9 ha of only the primary roost (i.e., the roost that had either the most bats at emergence or that was visited on the most nights) to preserve independence.

The National Oceanic and Atmospheric Agency created a digital landcover file based on data obtained in 2000, which divided the state of Michigan into 18 landcover categories, 15 of which were found in southern Lower Michigan—bare land, cultivated land, deciduous forest, evergreen forest, grassland, high-intensity developed, low-intensity developed, mixed forest, palustrine aquatic bed, palustrine emergent wetland, palustrine forested wetland, palustrine shrub/scrub wetland, scrub/shrub, unconsolidated shore, and water (Figure 1.1—NOAA, 2000). I condensed these 15 categories into developed (bare land, high-intensity developed, and low-intensity developed), open (cultivated land and grassland), upland deciduous forest (deciduous forest, mixed forest, and scrub/shrub), lowland deciduous forest (palustrine forested wetland), coniferous forest (evergreen forest), non-forested wetlands (palustrin aquatic bed, palustrine emergent wetland, palustrine shrub/scrub wetland, and unconsolidated shore), and open water (water).

Distance from each roost (or central point) to permanent water sources, treelines or forest edges, roads, buildings, and towns was measured through ArcGIS. Because some roosts were within forests whereas others were in the open, I indicated distance from the open to the nearest treeline or forest patch as a positive number and those from within the forest to the edge as negative numbers. For every roost (or central point), I selected a location between 10 and 20 km from the roost, using a table of random numbers, and determined the same landscape-level variables (i.e., distances and landcover types) that I used for roosts. I was not always able to locate the roost of a bat that was fitted with a radio-transmitter, and if this occurred, I used the capture location of the bat as the central point around which landscape variables were measured. To increase my sample size, I also analyzed the landscape surrounding capture locations from previous surveys, including the Three Rivers State Game Area, St. Joseph Co.; Shiawasee State Game Area, Livingston Co.; and Ives Road Fen, Lenawee Co. (A. Kurta, in litt.).

Statistics.—To analyze differences among most continuous variables, I used multivariate analysis of variance (MANOVA). MANOVA, however, may not perform well if dependent variables are highly correlated or if there are a large number of variables (Zar, 1999). Consequently, before conducting the MANOVA, I calculated parametric correlations between my variables (Appendix A), and if variables were highly correlated, I eliminated one from the MANOVA. I considered variables highly correlated if the absolute value of r was greater than 0.5, an arbitrary value I selected. I usually decided which variable to drop based on which was measured with the least accuracy. For example, if height and diameter of trees were highly correlated, I eliminated height, because the ground-based measurement of diameter with a tape was probably more accurate than height measured with the clinometer. For landcover analyses, most landcover types were highly correlated with each other, often with $|r| > 0.8$, so I performed one-way analyses of variance (ANOVA) for each variable rather than a MANOVA on the set of variables.

Furthermore, I checked for equality of variances with Levene’s test prior to any MANOVA or ANOVA. If variances were heterogeneous for a particular variable, I replaced it with a rank transformation (Conover and Iman, 1981), which usually solved the problem. However, on two occasions with landcover data, transformations did not result in equal variances; consequently, I examined them for significance using t-tests for unequal variances rather than ANOVA. If the MANOVA or ANOVA indicated a significant difference among three groups (i.e., the three species of *Myotis*), I then performed multiple comparisons using Fisher’s protected least-significant difference test (Carmer and Swanson, 1973).

For categorical variables (e.g., species of tree) or ordinal variables with only three levels (e.g., solar exposure or clutter near the exit), I used Fisher's exact test because most expected values were less than five, making chi-squared tests inappropriate (Zar, 1999). All percentages were arcsine transformed before any analysis. Most calculations were performed using Excel (Microsoft, Redmond, Washington) or the Statistical Package for the Social Sciences (SPSS, Inc., Chicago, Illinois). VassarStats (Lowry, 2006) was used to calculate Fisher's exact tests. Alpha was set at 0.05 for all statistical tests. Means are presented with the associated standard error.

RESULTS

Radio-tracking.—On 155 nights during summers 2004–2006, I netted 1,025 bats at 83 sites throughout southern Lower Michigan, including some sites that were netted intentionally because of past captures of *Myotis* (Appendix C; Chapter 2). Seventy-nine captured bats (7.7%) were of the genus *Myotis*—48 little brown bats, 24 Indiana bats, and 7 northern bats (Appendix D). *Myotis* of any kind was found at 18 sites (21.7%), whereas individual species were caught at only 8.4–13.3% of the sites.

Multiple individuals of the same species often were caught at the same site, but not all could be radiotracked because of limited personnel and equipment. In addition, *Myotis* from the same species that were captured at a particular site likely were from the same colony, and I was attempting to locate as many colonies as possible. I was able to radio-track 10 little brown bats to seven roosts, six northern bats to 10 roosts, and 15 Indiana bats to 14 roosts (Table 1.2). In addition, Kurta (1980) reported a roost of little brown bats near Dowagiac, Cass County, in 1978. I visited that site in 2005, verified that the colony still existed, and included it in my study as an eighth roost for little brown bats.

Characteristics of roosts.—All roosts of little brown bats were in buildings, usually barns or sheds, and all appeared to be more than 100 years old (Appendix B). Most buildings were used for storage, although livestock had access to portions of three buildings, and one structure was used exclusively for human social events. Roofs were made of metal (62.5%) or shingles (37.5%), and oriented north-south (37.5%) east-west (37.5%), or in both directions (25.0%). Mean height of the building and exit were 10.3 ± 1.1 m and 9.3 ± 0.9 m, respectively (Table 1.3). As one might expect, buildings typically had low canopy cover (12.1 ± 7.8%), low clutter around the exits (1.0 ± 0.0 or 0–33%), and high amounts of solar exposure (2.75 ± 0.1 or >10 h).

All northern bats roosted in trees. Although the roosting site of one northern bat could not be determined, the other nine bats roosted in either crevices (44%) or under loose bark (56%), either on the main trunk (78%) or a major lateral branch (22%—Appendix B). Northern bats roosted in trees of varying species, size, and decay class (Table 1.3). Although most (60%) trees were living, decay stage was highly variable, ranging from 1 to 6.5. Trees typically had moderate canopy cover (59.4 ± 7.7%), solar exposure (1.8 ± 0.3), and clutter around the exit (1.6 ± 0.3). Trees used as roosts by northern bats were not significantly different from randomly selected trees in the roost or stand for any of the measured variables (Table 1.4). Most (70%) roosts were maples (Table 1.5), but composition did not differ between randomly selected trees in the roost (P = 1.00) or stand (P = 0.36) plots.

All Indiana bats roosted in trees, usually on the trunk (72%) but occasionally on a lateral branch (28%—Appendix B). All Indiana bats roosted under the loose bark of dead trees, with a mean decay class of 5.4 ± 0.8 (range: 4.5–7; Table 1.3). Trees typically had moderate canopy cover (58.2 ± 9.1%), solar exposure (2.1 ± 0.2), and clutter around the exit (1.1 ± 0.1). Roost trees of the Indiana bat did not differ from random trees in the same stand in any of the variables, but roost trees were significantly larger in diameter than random trees in the roost plot (Table 1.4). Most (93%) roosts were elms (Table 1.5), but species composition of roost trees did not differ from randomly selected potential roosts in the roost plot (P = 0.33) or stand plot (P = 0.16).

Characteristics of the roost plot and surrounding stand.—Roosts of the little brown bat were located on farms where basal area of trees (13.1 ± 8.0 m^2/ha) was low and half the roosts had no trees within 17.8 m of the building. In addition, many trees were planted so that plots around roosts of the little brown bat were high in coniferous (31%) and non-native trees (22%), such as Colorado blue spruce (*Picea pungens*) and Douglas fir (*Pseudotsuga menziesii*).

Plots around roosts of the northern bat contained 41.6 ± 8.0 trees and had a basal area of 25.6 ± 4.6 m^2/ha, which were similar to random plots in the same stand (Tables 1.6 and 1.7). Trees were comprised primarily of elms (*Ulmus*, 20%), maples (*Acer*, 43%), and ashes (*Fraxinus*, 14%; Table 1.8); proportion of elms and maples was higher in roost plots than trees around random plots within the same stand ($P = 0.01$). In addition, trees in roost plots of the northern bat had a higher mean decay class than trees in stand plots (Tables 1.6 and 1.7). There was no statistical difference in distance between the roost tree or randomly selected tree in the stand to the nearest taller or shorter tree (Tables 1.6 and 1.7)

Roost plots of the Indiana bat contained 40.8 ± 5.2 trees and had a mean basal area of 22.1 ± 4.6 m^2/ha, which was similar to random plots in the same stand (Table 1.6). Overall species composition of trees in roost plots of the Indiana bat also differed significantly ($P < 0.001$) from that of stand plots, with elms (26%), maples (34%), and ashes (18%) dominating in the roost plot. There was no statistical difference in distance between the roost tree or randomly selected tree in the stand to the nearest taller or shorter tree (Tables 1.6 and 1.7).

Characteristics of the surrounding landscape.—Little brown bats were located in agricultural areas dominated by open cropland and grassland (73 ± 5%) and upland deciduous forests (12 ± 3%; Table 1.9). Total area of each landcover type did not differ between roost and random landscapes (Tables 1.9 and 1.10). Their roosts were closer to roads than random points and typically located in open areas, as indicated by the positive distance to wooded edges or treelines (Tables 1.11 and 1.12).

In terms of landcover, five colonies of the little brown bat were in open land, and one roost was in lowland deciduous forest. Seven random locations in the surrounding landscape also were in open land, and five other random sites were in other types of landcover. A 2-by-4 Fisher's exact test (analyzing colony versus random and the categories of upland deciduous forest, lowland deciduous forest, nonforested wetland, and other landcover) indicated no significant difference ($P = 0.99$) and that colonies and random locations were equally likely to be in open land.

Landscapes surrounding roosts of northern bats were dominated by open areas (55 ± 10%) and upland deciduous forests (19 ± 4%), but total area of each landcover type did not differ between roost and random landscapes (Tables 1.9 and 1.10). Roost trees were found within forests (79.7 ± 34.4 m from the forest edge) and located in secluded (185.8 ± 35.9 m from roads) rural areas (3.9 ± 0.6 km from towns). However, roosts of the northern bat did not differ in landscape variables or landcover from random points in the landscape (Tables 1.10 and 1.12).

Six colonies of northern bats were located in lowland deciduous forest (3 colonies) and nonforested wetlands (3). For randomly selected points in the surrounding landscape, only one site was in lowland deciduous forest, one was in nonforested wetland, and ten were in other landcover types (six open land and four upland deciduous forest). A 2-by-3 Fisher's exact test (analyzing colony versus random and the categories of lowland deciduous forest, nonforested wetland, and other landcover) indicated a significant difference (*P* = 0.002) and that colonies of northern bats were found more often in wetlands (lowland deciduous forest and nonforested wetlands) than randomly chosen points.

Indiana bats roosted in landscapes dominated by open areas (64 ± 4%) and upland deciduous forests (17 ± 2%), but total area of each landcover type did not differ between roost and random landscapes (Tables 1.9 and 1.10). As with northern bats, roost trees of Indiana bats were found within forests (8.7 ± 17.4 m from the forest edge) and located in secluded (311.6 ± 50.2 m from roads) rural areas (4.3 ± 0.5 km from towns). Unlike northern bats, however, roosts of the Indiana bat were significantly farther from towns and closer to water than were random points in the landscape (Tables 1.11 and 1.12).

Actual colony sites of Indiana bats were located in lowland deciduous forest (5 colonies) and nonforested wetlands (2). For randomly selected points, however, only one site was in lowland deciduous forest, one was in nonforested wetland, and 12 were in other landcover types (11 open and 1 upland deciduous forest). A 2-by-3 Fisher's exact test (analyzing colony versus random and the categories of lowland deciduous forest, nonforested wetland, and other landcover) indicated a significant difference (*P* = 0.0004) and that colonies of Indiana bats were found more often in wetlands (lowland deciduous forest and nonforested wetlands) than randomly chosen points.

Interspecific comparisons.—Overall, species composition of all trees that were found in roost plots of northern bats did not differ from trees in roost plots of the Indiana bat (*P* = 0.42; Table 1.8), although species composition of actual roost trees was significantly different. Ninety-three percent of roost trees of Indiana bats were elms, whereas 70% of roost trees of northern bats were maples. A 2-by-3 Fisher's exact test analyzing species of bat and the categories of elm, maple, and other species was significantly different (*P* = 0.0001). In addition, roost trees of northern bats were more often living (*P* = 0.002) than were those of Indiana bats. Although a significantly greater proportion of northern bats than Indiana bats roosted in crevices (*P* = 0.01), both species typically were found on the trunk, as opposed to major lateral branches (*P* = 0.55 — Appendix B).

There were a few other differences in roost-tree parameters between northern and Indiana bats. A MANOVA indicated that rank-transformed decay class was significantly different between Indiana and northern bats (Table 1.4), with roosts of northern bats typically less advanced in decay. The original data, before transformation, also showed a significant difference in the variance in decay class between species ($F_{1,20} = 14.87$; $P < 0.01$); roosts of northern bats were more variable in stage of decay (coefficient of variation = 64%) than were those of Indiana bats (14%). Furthermore, trees used by northern bats had significantly less loose bark (13.6 ± 4.1 %) as did roost trees of Indiana bats (31.1 ± 5.1 %; Tables 1.3 and 1.4), which reflects the difference in decay stage.

Use of MANOVA indicated statistical differences in only two landscape (distance) variables (Tables 1.11 and 1.12) among the species, and multiple-comparison tests showed that the only significant differences were between little brown bats and the northern bats and Indiana bats. Average distance to treelines or forest edges was positive for little brown bats and negative for northern and Indiana bats, indicating that little brown bats typically roosted in open areas compared with northern bats and Indiana bats that usually roosted within forested patches or along edges.

Amount of land in different landcover types within 5 km of the roost also did not vary among the three species (Tables 1.9 and 1.10). However, 83% of colonies of little brown bats were in open land, but all colonies of both northern bats and Indiana bats were located in lowland deciduous forest and nonforested wetlands.

DISCUSSION

Myotis are rare in southern Lower Michigan, with each species being caught at less than 22% of the 83 netting sites, whereas other species, such as big brown bats, are captured at 90% of these sites. This lack of *Myotis* presumably is caused by the great distance (>200 km) to suitable hibernacula, which are located primarily in the karst areas of southern Indiana and Kentucky (e.g., Winhold and Kurta, 2006), as well as the inherent danger and high energetic cost associated with migration (Fleming and Eby, 2003). Consequently, this low density of *Myotis* should reduce or eliminate the potential for interspecific competition, allowing the bats to select roosting habitat that most fits their needs.

Roosts of little brown bats.—In the West, little brown bats usually roost in trees, whereas in the East, these bats typically roost in buildings (Barbour and Davis, 1969; Fenton and Barclay, 1980; Williams and Brittingham, 1997). Although Kurta (2000) demonstrated through radiotracking that some female little brown bats alternated between buildings and trees in northern Lower Michigan, I found no evidence for use of trees by little brown bats in southern Michigan. Kurta (2000), however, worked in the Manistee National Forest, in an area with a lower human population than in southern Lower Michigan. It could be that little brown bats are more likely to use trees in areas where people and buildings are uncommon but trees are abundant (the West and northern Michigan), whereas suitable buildings are used where available (most of the East).

The frequent adoption of building roosts by these bats suggests that buildings are in some way superior to natural roosts in trees. In buildings, little brown bats often roost in spaces where the daytime air temperature frequently exceeds 30°C, and the thermal inertia of such a large structure provides a warm roosting environment even at night (Anthony et al., 1981; Kunz, 1980). It is doubtful whether trees can consistently achieve such warmth, and perhaps the preference for buildings is associated with selection of warm roost sites. The fact that building roosts in my study had few adjacent trees that might shade the building and decrease solar insolation is consistent with the bats' choice of warm roosting sites. In any event, data suggest that there is no overlap in the roosting niche of little brown bats with either northern bats or Indiana bats in southern Lower Michigan, in terms of the type of structure that is used (building or tree).

Roosts of the little brown bat were closer to roads than were the roosts of northern and Indiana bats. Although such selectivity may reflect a preference for more developed areas, roosts of little brown bats were not any closer to urban areas than were roosts of the tree-dwelling species (Table 1.11). Closeness to roads probably is related to their choice of buildings for roosts, because most old barns and houses were constructed near roads for ease of human access. Use of roosts in open areas by little brown bats, compared with northern or little brown bats, may be associated with greater solar exposure, as indicated earlier, or it too may be an artifact related to human behavior. Landowners typically remove most trees from around their barns and sheds and, of course, farms must contain open land for crops or pasture.

Although roosts of little brown bats were in open landscapes, these structures were only 59.8 m from treelines that connected the roosting area to forested patches and other habitats (Table 1.11). Little brown bats feed primarily on insects that have aquatic larval stages, such as many dipterans, trichopterans, and ephemeropterans, and are known to forage along forest edges (e.g., Patriquin and Barclay, 2003) and over ponds and slowmoving streams (e.g., Anthony and Kunz, 1977). However, roosts of the little brown bat were not closer to standing water than were randomly chosen points. This lack of a difference may simply reflect the ubiquity of standing water in southern Lower Michigan. Average distance from the roost to water was less than 300 m—a distance that a bat can travel in only a few minutes.

Roosts of northern bats.—Northern bats are believed to forage within intact woodlands (e.g., Patriquin and Barclay, 2003), and my study shows that they typically roosted within wooded areas, even in the fragmented habitat of southern Lower Michigan, as shown by the large proportion (70%) of roosts that were found in lowland deciduous woods and by their negative mean distance (-79.7 m) to wooded edges (Table 1.11). I found northern bats roosting in live or dead trees of varying decay classes, in crevices or under loose bark, and in a variety of tree species typical of lowland areas, primarily maples. Foster and Kurta (1999), who studied a single colony in Eaton Co., Michigan, detected similar patterns. They also found that northern bats roosted in living trees about half the time, chose crevices about half the time, and were found on major branches about half the time; roost trees were usually maples, and canopy cover was highly variable, reflecting use of both living and dead trees. Hence, my study extends their observations to a wide geographic area and suggests that these traits are typical of the species.

Other studies that were conducted in different types of habitats have found northern bats roosting in various other trees, such as elms, beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*—Menzel et al., 2002; Mumford and Cope, 1964; Sasse and Pekins, 1996). Owen et al. (2002) demonstrated that northern bats in an intensively managed forest in the Appalachian Mountains selected black locust (*Robinia pseudoacacia*) and black cherry (*Prunus serotina*) more often than would be expected based on their abundance. It seems that northern bats do prefer certain species of tree, but apparently a number of different species of tree are capable of providing suitable roosts for these bats. However, which species of tree actually used likely depends on the type of habitat where the bats live and the area of the continent where the study is conducted, similar to what has been suggested for Indiana bats (Kurta, 2005).

I found no significant differences among tree variables between identified roosts of northern bats and randomly selected potential roosts, suggesting that other trees within the same stand are available for roosting, which could be beneficial to these bats, given the ephemeral nature of tree roosts (Barclay and Kurta, in press). Foster and Kurta (1999) also noted that roost trees of northern bats differed little from potential roosts in surrounding roost plots. Although Owen et al. (2002) reported that northern bats in the Appalachians chose roosts that were smaller in diameter and lower in height than randomly selected potential roosts from the same stand, Sasse and Pekins (1996) detected the opposite trend for northern bats in the White Mountains of New Hampshire.

Roosts of Indiana bats.—All Indiana bats in my study roosted under loose bark of dead trees. This seems to be the preferred roosting site for Indiana bats. In an analysis of more than 600 roost trees used by Indiana bats, throughout their range, Kurta (2005; A. Kurta, pers. comm.) indicated that more than 95% of roosting sites were under bark.

Thirteen of my 14 roosts were American elms, and one was green ash. In the eastern United States, more than 40 species of trees have been used as roosts by Indiana bats, but more than 80% were some form of elm, maple, ash, hickory (*Carya*), or oak

(*Quercus*—Kurta, 2005). Although some species of seemingly common tree, such as box elder (*Acer negundo*), are rarely or never used, which one of the many acceptable species that is occupied apparently depends on local abundance (Kurta, 2005). In my study, roost and stand plots were comprised of 21–26% elms, and species composition of roost trees and randomly selected trees from the plots did not differ, suggesting that Indiana bats were roosting in elms because they were readily available, rather than selecting the species of tree for specific characteristics.

Although roost trees did not differ from randomly selected trees in most respects, I found diameter of the roost tree to be significantly larger than randomly selected potential roost trees in the same plot, similar to what was reported by Kurta et al. (1996, 2002). Occupancy of roost trees that are taller or wider than those that are available is a common behavior of many species of tree-roosting bat in North America (Barclay and Kurta, in press). Larger trees presumably create a more stable microclimate within the roost, thus reducing the amount of energy required for thermoregulation, and are perhaps easier to locate in extensive woodlands.

Previous studies of specific colonies in Michigan indicated that canopy cover around roost trees of Indiana bats was low, possibly increasing solar exposure for these southern bats on the northern edge of their range (Kurta et al., 1996, 2002). At 23 trees in Eaton Co., average canopy cover was less than 20%, and at 38 trees along the border between Washtenaw and Jackson counties, average canopy cover was only 31% (Kurta et al., 2002). These values are about one half to one third of the average (58%) in my study. Although this might reflect some variation among colonies, it also might be related to climatic differences. The multi-year study in Eaton Co. included data obtained in 1992, during the second coldest summer since 1870, following eruption of Mount Pinatubo in the Philipines (Deedler, 2005). Summer 2005, in contrast, was the second warmest summer on record in southern Michigan (NOAA, 2005), with temperatures frequently above 32°C. During late June 2005, I witnessed an entire colony of Indiana bats in the Crane Pond State Game Area, Cass County, move from a tree with moderate canopy cover (59%) and a southern exposure to a well-shaded tree (90%) during a heat wave. A colony of nearly 30 bats roosted in the tree with higher solar exposure (ca. 6–10 h) during the 1st 4 days of monitoring when daily maximum ambient temperature ranged from 22 to 31°C (72–88°F). Starting on the 5th day, the colony switched to the shaded tree, ca. 82 m from the original roost tree, and remained in this tree for at least 3 days while daily maximum ambient temperature ranged from 29 to 35°C (84–95°F).

Roost trees of Indiana bats were located closer to standing water but farther from developed areas than were randomly chosen points (Tables 1.11 and 1.12). Kurta et al. (2002) reported that roost trees of one colony of Indiana bats were closer to perennial streams than were random points, but there was no difference in distance to lakes or ponds. Although insects with aquatic larval stages comprise a large proportion of the diet of Indiana bats in Michigan, these bats also eat significant amounts of beetles and moths (Kurta and Whitaker, 1998; Murray and Kurta, 2002) and seem less reliant on aquatic-based prey than little brown bats. In addition, most foraging by Indiana bats seems to occur in wooded areas, especially wooded wetlands, rather than over open water (Gardner et al., 1991; Murray and Kurta, 2004; Sparks et al., 2005). Hence, it seems unlikely that Indiana bats are locating their roost trees close to water sources that might provide potential foraging grounds. Although I did not analyze distance to streams and lakes separately, perhaps the closeness to water that I detected is more reflective of these bats locating their roosts close to wooded streams that can act as travel corridors among various sites in their home range (Murray and Kurta, 2004; Sparks et al., 2005).

Roost trees of Indiana bats also were found farther from developed areas than were randomly chosen points (Tables 1.11 and 1.12). Indiana bats seem less able to adapt to using human-made structures for roosts than the other two species, which may suggest a greater sensitivity to disturbance. Nevertheless, colonies of Indiana bats have been discovered in disturbed sites, such as rapidly developing areas near the Indianapolis Airport (Sparks et al., 2005). Indiana bats are extremely loyal to their home range (Kurta and Murray, 2002), and continued presence of the colony near this busy airport likely represents an attempt by the colony to hold on as the habitat around them disappears, rather than a tolerance for disturbance.

In Michigan, 93% of previously discovered roosts of Indiana bats were elm, maple, or ash, reflecting the fact that most roost trees were located in forested wetlands (Kurta and Rice, 2002; Kurta et al., 2002). In my study, 93% of roost trees of Indiana bats also were in wetlands, either lowland deciduous forest or nonforested wetlands (Appendix B). Although Indiana bats do roost in upland habitats in other parts of their range, such as New England (Britzke et al., 2003) and Missouri (Callahan et al., 1997), this behavior is not common in Michigan. Murray and Kurta (2002) speculated that agricultural practices in glaciated areas of the central Great Lakes region resulted in removal of most forests except in areas that were too wet to be farmed, whereas rocky uplands were not farmed in other regions. However, in my analyses of landcover (Table 1.9), the amount of upland deciduous forest was generally twice that of lowland deciduous forest, both in landscapes surrounding roosts and around random points. Although there may be a greater area of upland woods available, it is possible that lowland woods are more difficult to log and, therefore, the trees may be older and larger than in most upland forests. Indiana bats apparently are more common in areas of large-sized trees (Miller et al., 2002) and perhaps northern bats are, too.

Summary and final comments.—Little brown bats roost in buildings, and their roosting niche in southern Lower Michigan does not overlap those of the northern bat or Indiana bat. Although species composition of trees in the roosting plots of northern and Indiana bats is similar, northern bats often roost in crevices of live trees and tend to select maples, whereas Indiana bats invariably roost under bark, primarily in dead elms. Thus, species of tree, decay stage, and roosting site (crevice or bark) appear to be the only avenues of partial resource partitioning between these two species of bat. Density of each species is low in the region, and competition between northern bats and Indiana bats is unlikely, despite the similarity of roosting niches.

Landcover within 5 km of a roost or capture site does not seem useful in predicting occurrence of any species of *Myotis* in southern Lower Michigan. In this region of very low density of populations of *Myotis*, each species has a home range of superficially similar composition, although further analysis might reveal fine-grained differences that I could not detect. For example, I compared only total area of each landcover type; however, average size of individual patches of woods, wetlands, or agricultural fields may be more important than the aggregate (Carter et al., 2002), and presence or absence of wooded connections (travel corridors) between these patches may determine whether they are even available to a species (Murray and Kurta, 2004;

Verboom and Huitema, 1997; Winhold et al. 2005). Another factor to consider in future studies is the age or size of trees in wooded areas (Miller et al., 2002) and not just the existence of the woods, because older forests may provide more large trees for roosting and a more open subcanopy that would provide easier access to roosts and perhaps more open space for foraging by woodland bats.

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Table 1.1. Decay classification of trees, modified from Vonhof and Barclay (1996) as cited in Bernardos et al. (2004).

Decay class	Description
1	Live and apparently healthy
2	Live, declining (dead top branches, dead side branches)
3	Dead with top and most of all limbs intact, tight bark, base solid
4	Dead with broken top and/or missing limbs, most bark tight, base solid
5	Dead with broken top, most of limbs missing, exfoliating bark, more than 50% bark remaining, some decay at base
6	Dead with broken top, most of limbs missing, few stubs present, exfoliating bark, less than 50% bark remaining, sapwood decay evident
7	Little or no bark remaining, advanced sapwood decay, few or no stubs present

Figure 1.1. Landcover of southern Lower Michigan as classified by the National Oceanic and Atmospheric Agency (NOAA, 2000).

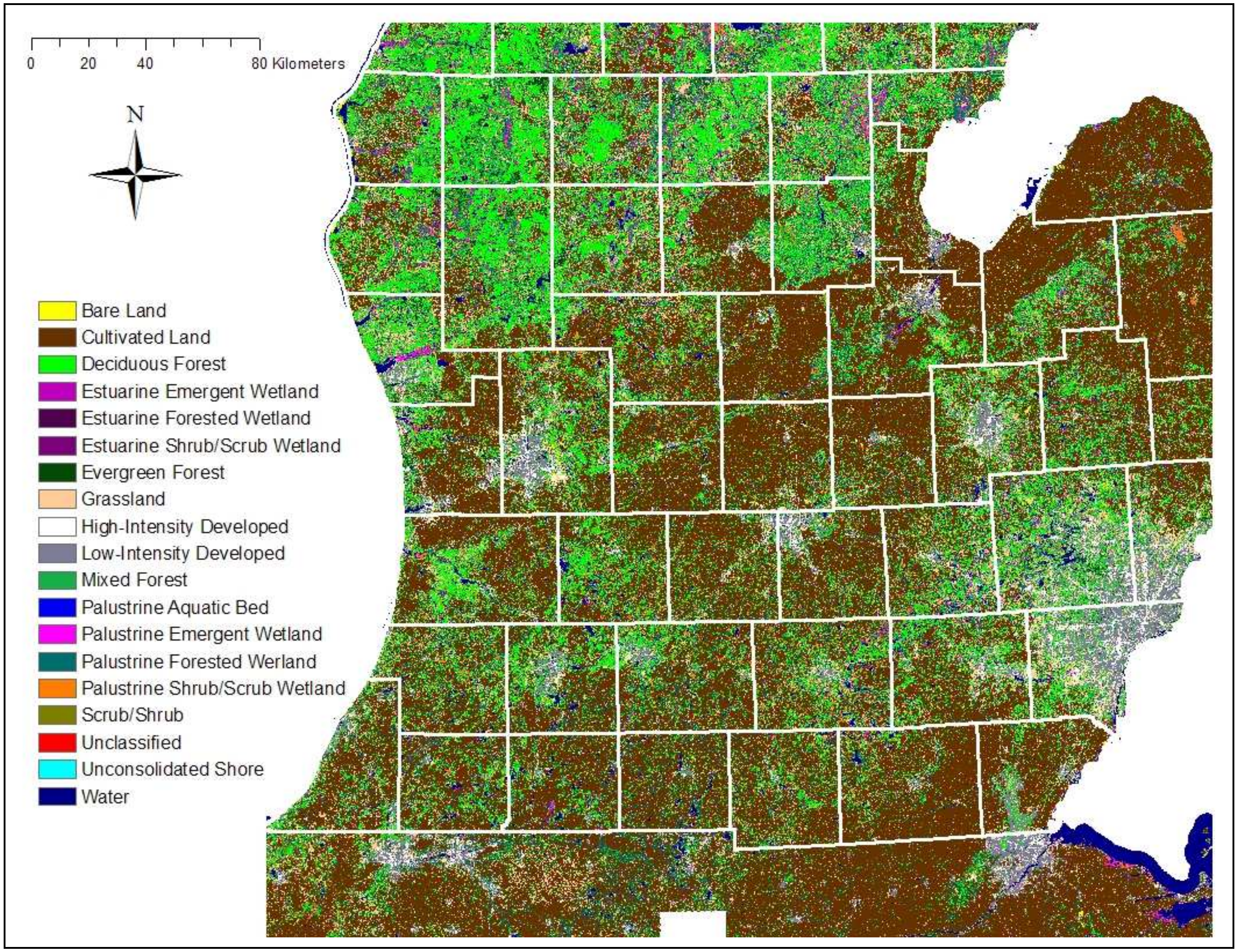

Table 1.2. Bats that were radio-tracked in 2004–2006. Potential reproductive statuses of adult females are not palpably pregnant (NPP), pregnant (P), lactating (L), postlactating (PL), or nonreproductive (NR).

Species	Sex	Age	Reproductive status	County	Date captured
Little brown bat	Male	Juvenile		Lenawee	29 July 2004
	Female	Adult	PL	Lenawee	2 August 2004
	Male	Adult		Lenawee	6 August 2004
	Male	Adult		St. Joseph	22 July 2005
	Male	Adult		St. Joseph	22 July 2005
	Male	Adult		Eaton	2 August 2005
	Female	Adult	PL/NR	Eaton	2 August 2005
	Female	Adult	PL/NR	Eaton	2 August 2005
	Male	Adult		Washtenaw	8 August 2005
	Female	Adult	L	Clinton	22 July 2006
Northern bat	Female	Adult	NPP	Washtenaw	24 May 2004
	Female	Adult	P	Livingston	7 June 2004
	Male	Adult		Washtenaw	2 July 2004
	Male	Juvenile		Lenawee	29 July 2004
	Male	Juvenile		Calhoun	14 July 2005
	Female	Adult	PL	Eaton	2 August 2005
Indiana bat	Female	Adult	NPP	Jackson	27 May 2004
	Female	Adult	PL	Lenawee	29 July 2004
	Male	Juvenile		Lenawee	5 August 2004
	Female	Adult	P	Cass	18 June 2005
	Female	Adult	L	Cass	19 June 2005
	Female	Adult	P	Cass	25 June 2005
	Female	Adult	L	Cass	25 June 2005
	Female	Adult	L	Calhoun	14 July 2005
	Female	Adult	PL	Jackson	22 July 2005
	Male	Juvenile		St. Joseph	22 July 2005
	Female	Juvenile		St. Joseph	22 July 2005
	Male	Juvenile		Van Buren	4 August 2005
	Female	Adult	PL	Van Buren	4 August 2005
	Female	Juvenile		Washtenaw	8 August 2005
	Male	Adult		Barry	7 June 2006

Table 1.3. Mean ± SE followed by n for characteristics of roost trees and randomly selected trees from roost plots and roost stands of northern bats and Indiana bats and characteristics of the roost for little brown bats.

Variable	Little brown bat	Northern bat			Indiana bat		
	Roost	Roost tree	Plot tree	Stand tree	Roost tree	Plot tree	Stand tree
Diameter (cm)		47.9 ± 9.5, 10	43.6 ± 5.9, 9	37.3 ± 4.3, 10	34.4 ± 3.7, 14	20.6 ± 2.2, 13	27.3 ± 4.2, 14
Tree height (m)	10.3 ± 1.1, 8	19.9 ± 2.5, 10	17.9 ± 2.3, 10	18.7 ± 1.8, 10	20.5 ± 2.6, 13	12.0 ± 1.6, 13	16.1 ± 1.6, 14
Exit height (m)	9.3 ± 0.9, 5	9.2 ± 1.2, 9			10.4 ± 1.6, 14		
Decay class (1–7)		3.0 ± 0.6, 10	3.6 ± 0.6, 10	4.0 ± 0.7, 10	5.4 ± 0.2, 14	5.3 ± 0.2	4.7 ± 0.2, 14
Canopy cover (%)	12.1 ± 7.8, 8	59.4 ± 7.7, 10	64.6 ± 8.7, 10	70.2 ± 6.7, 10	58.2 ± 9.1, 14	61.4 ± 9.2, 13	64.5 ± 14.0, 14
Total bark (%)		70.5 ± 9.6, 10	68.2 ± 10.6, 10	74.0 ± 9.0, 10	49.5 ± 7.8, 14	73.7 ± 5.0, 13	67.4 ± 6.4, 14
Loose bark (%)		13.6 ± 4.2, 10	14.8 ± 5.6, 10	14.8 ± 6.0, 10	31.1 ± 5.1, 14	46.9 ± 8.4, 13	33.0 ± 5.1, 14
Solar class (1–3)	2.8 ± 0.2, 8	1.8 ± 0.3, 10	2.0 ± 0.3, 9	1.6 ± 0.3, 10	2.1 ± 0.2, 14	1.7 ± 0.3, 12	1.7 ± 0.3, 12
Clutter class (1–3)	1.0 ± 0.0, 7	1.6 ± 0.3, 10	1.5 ± 0.1, 10	1.9 ± 0.1, 10	1.14 ± 0.1, 14	1.5 ± 0.2, 13	1.64 ± 0.2, 14

Table 1.4. Results of MANOVAs performed on roost and random tree variables for northern and Indiana bats. Blank cells occur because variables were dropped from the analysis due to high correlation with other variables (Appendix A).

Variable	Roost of northern bat compared with randomly selected tree in the roost plot			Roost of northern bat compared with randomly selected tree in the stand			Roost of Indiana bat compared with randomly selected tree in the roost plot			Roost of Indiana bat compared with randomly selected tree in the stand			Roost of northern bat compared with roost of Indiana bat		
	F	*P*	*d.f.*	*F*	*P*	*d.f.*	*F*	*P*	*d.f.*	*F*	*P*	*d.f.*	*F*	*P*	*d.f.*
Diameter	0.17	0.69	1, 17	1.09	0.31	1, 18	8.15	0.01	1, 25	1.58	0.22	1, 26	0.84	0.37	1, 20
Exit height													0.32	0.58	1, 20
Decay class							0.15	0.70	1, 25	4.17	0.051	1, 26	8.09	0.01	1, 20
Canopy cover	0.18	0.68	1, 17	1.15	0.30	1, 18	0.09	0.76	1, 25	0.36	0.55	1, 26	0.41	0.53	1, 20
Total bark				0.43	0.84	1, 18									
Loose bark	0.08	0.78	1, 17	0.04	0.84	1, 18	3.05	0.09	1, 25	0.06	0.81	1, 26	4.66	0.04	1, 20

Table 1.5. Genera of roost trees and randomly selected trees from roost plots and roost stands of northern bats and Indiana bats.

Genera	Northern bat			Indiana bat		
	Roost tree	Plot tree	Stand tree	Roost tree	Plot tree	Stand tree
Elm	2 (20%)	3 (30%)	2 (20%)	13 (93%)	10 (77%)	9 (64%)
Maple	7 (70%)	6 (60%)	4 (40%)	0	0	1 (7%)
Other	1 (10%)	1 (10%)	4 (40%)	1 (7%)	3 (23%)	4 (29%)
Total	10	10	10	14	13	14

Table 1.6. Mean ± SE followed by n for characteristics of 0.1-ha roost plots and randomly selected plots within roost stands for northern bats and Indiana bats and characteristics of the roost plot for little brown bats. Plots surrounding building roosts of little brown bats were variable in area, but always larger than those of northern and Indiana bats.

	Little brown bat	Northern bat		Indiana bat	
Variable	Roost plot	Roost plot	Stand plot	Roost plot	Stand plot
Basal area (m^2/ha)	13.1 ± 8.0, 8	25.6 ± 4.6, 10	23.9 ± 3.6, 10	22.1 ± 4.6, 13	23.3 ± 2.7, 14
Number of stems	8.4 ± 3.5, 8	41.6 ± 8.0, 10	44.3 ± 5.8, 10	40.8 ± 5.2, 13	46.0 ± 3.7, 14
Mean decay class (1–7)	1.1 ± 0.1, 4	1.9 ± 0.2, 10	1.3 ± 0.1, 10	2.6 ± 0.5, 13	1.9 ± 0.2, 14
Distance to taller tree (m)	4.4 ± 2.5, 4	6.8 ± 0.8, 9	5.4 ± 0.8, 9	6.0 ± 1.1, 14	3.5 ± 0.7, 14
Distance to shorter tree (m)	2.9 ± 1.2, 3	3.5 ± 0.8, 10	4.0 ± 0.6, 9	3.1 ± 0.7, 14	3.0 ± 0.7, 14

Table 1.7. Results of MANOVAs performed on roost and random plot variables for northern and Indiana bats. Blank cells occur because variables were dropped from the analysis due to high correlation with other variables (Appendix A).

Variable	Roost plot of northern bat compared with randomly selected plot in the same stand			Roost plot of Indiana bat compared with randomly selected plot in the same stand			Roost plot of northern bat compared with roost plot of Indiana bat		
	F	*P*	*d.f.*	*F*	*P*	*d.f.*	*F*	*P*	*d.f.*
Basal area	0.19	0.67	1, 16	0.05	0.83	1, 25	0.92	0.35	1, 20
Mean decay class	5.97	0.03	1, 16				0.07	0.80	1, 20
Distance to taller tree	1.78	0.20	1, 16	0.06	0.81	1, 25	0.24	0.63	1, 20
Distance to shorter tree	1.63	0.22	1, 16	2.31	0.14	1, 25			

Table 1.8. Mean ± SE followed by n of trees of different genera that were found within roost plots of little brown, northern, and Indiana bats and randomly selected plots within roost stands.

Genera	Little brown bat	Northern bat		Indiana bat	
	Roost plot	Roost plot	Stand plot	Roost plot	Stand plot
Elm	2.0 ± 1.4, 4	8.3 ± 3.5, 10	3.4 ± 1.3, 10	10.8 ± 2.9, 13	9.4 ± 2.4, 14
Maple	3.5 ± 0, 4	18.0 ± 7.1, 10	14.9 ± 4.3, 10	13.9 ± 3.4, 13	14.9 ± 3.9, 14
Other	11.3 ± 1.4, 4	15.3 ± 3.6, 10	26.0 ± 5.6, 10	16.1 ± 4.5, 13	21.7 ± 4.0, 14
Total	16.8 ± 3.0, 4	41.6 ± 8.0, 10	44.3 ± 5.8, 10	40.8 ± 5.2, 13	46.0 ± 3.7, 14

Table 1.9. Mean ± SE followed by n for area (ha) of different types of landcover within a 5-km radius of randomly selected points and roosts of little brown, northern, and Indiana bats.

Landcover	Little brown bat		Northern bat		Indiana bat	
	Roost tree	Random point	Roost tree	Random point	Roost tree	Random point
Developed land	196 ± 42, 6	400 ± 85, 12	326 ± 126, 6	274 ± 60, 12	220 ± 28, 12	407 ± 116, 24
Open land	5,708 ± 370, 6	5,852 ± 288, 12	4,322 ± 795, 6	5,254 ± 351, 12	4,983 ± 321, 12	5,256 ± 286, 24
Upland deciduous forest	949 ± 206, 6	772 ± 127, 12	1,521 ± 337, 6	1,170 ± 172, 12	1,326 ± 180, 12	1,054 ± 118, 24
Lowland deciduous forest	556 ± 91, 6	408 ± 56, 12	693 ± 151, 6	599 ± 67, 12	674 ± 73, 12	541 ± 53, 24
Coniferous forest	58 ± 27, 6	43 ± 9, 12	115 ± 42, 6	56 ± 17, 12	96 ± 25, 12	72 ± 20, 24
Non-forested wetland	309 ± 75.4, 6	235 ± 59.8, 12	709 ± 229, 6	397 ± 76, 12	433 ± 65, 12	344 ± 45, 24
Open water	79 ± 24, 6	142 ± 62, 12	168 ± 84, 6	104 ± 46, 12	122 ± 18, 12	180 ± 47, 24

Table 1.10. One-way ANOVA results of comparisons of landcover within 5 km radius of roost and random points of little brown, northern, and Indiana bats.

Landcover	Roost of little brown bat compared to random point			Roost of northern bat compared to random point			Roost of Indiana bat compared to random point			Comparison among roosts of all three species		
	F	*P*	*d.f.*	*F*	*P*	*d.f.*	*F*	*P*	*d.f.*	*F*	*P*	*d.f.*
Developed land	2.80	0.11	1, 16	0.18	0.68	1, 16	1.27	0.27	1, 34	1.00	0.38	2, 21
Open land	0.09	0.77	1, 16	1.57	0.23	1, 16	0.34	0.56	1, 34	1.40	0.27	2, 21
Upland deciduous forest	0.59	0.46	1, 16	1.08	0.32	1, 16	1.69	0.20	1, 34	1.21	0.32	2, 21
Lowland deciduous forest	2.13	0.16	1, 16	0.57[a]	0.59	16	2.15	0.15	1, 34	0.46	0.64	2, 21
Coniferous Forest	0.40	0.54	1, 16	2.44	0.14	1, 16	0.50	0.49	1, 34	0.69	0.52	2, 21
Non-forested wetland	0.54	0.47	1, 16	0.48	0.50	1, 16	1.30	0.26	1, 34	1.12	0.35	2, 21
Open water	0.51	0.49	1, 16	0.54	0.47	1, 16	-1.13[a]	0.27	34	0.73	0.50	2, 21

[a] Comparison resulted in unequal variances and so a *t*-test was used rather than an ANOVA.

Table 1.11. Mean ± SE followed by n for distances between landscape features randomly selected points and roosts of little brown, northern, and Indiana bats. Distances from open areas to treelines or forests were recorded as positive numbers and distances from within forests to the edge were recorded as negative numbers. Distances are in meters, except distance to town, which is in kilometers.

Feature	Little brown bat		Northern bat		Indiana bat	
	Roost	Random point	Roost	Random point	Roost	Random point
Water	298.3 ± 90.6, 8	218.4 ± 54.7, 12	276.4 ± 96.9, 10	277.4 ± 61.7, 12	167.7 ± 60.6, 19	470.2 ± 115.7, 24
Treeline/edge	59.8 ± 34.0, 8	167.1 ± 59.1, 12	-79.7 ± 34.4, 10	4.4 ± 29.1, 12	-81.7 ± 17.4, 19	46.3 ± 18.9, 24
Road	57.4 ± 12.8, 8	123.7 ± 22.2, 12	185.8 ± 35.9, 10	261.1 ± 49.7, 12	311.6 ± 50.2, 19	270.6 ± 73.7, 24
Building	17.5 ± 5.1, 8	106.8, 22.5, 12	348.0 ± 56.0, 10	263.4 ± 33.2, 12	321.4 ± 39.6, 19	272.0 ± 80.2, 23
Town	3.2 ± 0.6, 8	2.2 ± 0.3, 12	3.9 ± 0.6, 10	2.8 ± 0.5, 12	4.3 ± 0.5, 19	2.6 ± 0.4, 24

Table 1.12. Results of MANOVAs performed on distances to landscape features from roost and randomly selected points for little brown, northern, and Indiana bats. Blank cells occur because variables were dropped from the analysis due to high correlation with other variables (Appendix A).

	Roosts of little brown bats compared with randomly selected points in the landscape			Roosts of northern bats compared with randomly selected points in the landscape			Roosts of Indiana bats compared with randomly selected points in the landscape			Comparison among roosts of all three species		
	F	*P*	*d.f.*	*F*	*P*	*d.f.*	*F*	*P*	*d.f.*	*F*	*P*	*d.f.*
Water	0.64	0.43	1, 18	< 0.001	0.99	1, 20	5.62	0.02	1, 41	0.88	0.43	2, 34
Treeline/edge	0.47	0.50	1, 18	3.54	0.08	1, 20	23.69	0.001	1, 41	7.70	0.002	2, 34
Road	5.12	0.04	1, 18	0.98	0.34	1, 20	0.19	0.67	1, 41	13.00	< 0.001	2, 34
Building				1.83	0.19	1, 20						
Town	1.01	0.33	1, 18	2.10	0.16	1, 20	6.30	0.02	1, 41	0.74	0.48	2, 34

Chapter 2.

Long-term Changes in the Bat Community of Southern Lower Michigan

INTRODUCTION

Approximately 1,100 species of bats exist worldwide, making bats the second most speciose group of mammals (Simmons, 2005). Despite this diversity, ca. 25% of bat species are either threatened or endangered around the world (Hutson et al., 2001; Racey and Entwistle, 2003). In the United States and Canada alone, almost half of the 45 species are considered endangered or threatened at the national or local level (Ellison et al., 2003). Of the nine species that live in Michigan, one species is considered endangered in the United States, one has been proposed for threatened status in the state, and a third is listed as a species of special concern by the Michigan Department of Natural Resources.

No single reason for the decline in populations of bats is known, but habitat loss often is proposed as a direct cause (Racey and Entwistle, 2003), although indirect effects are also possible. Temperate bats, for example, rely on the availability of appropriate roosts and insects for survival, and the relative abundance of each species of bat in a region potentially affects the intensity of inter- and intraspecific competition (Findley, 1993). In any given landscape, the intensity of competition is minimized by partitioning available resources among local bats, but changing the composition of the bat community could alter in unknown ways the availability of food and roosts for other species.

Whether the threats are direct or indirect, effective management of communities, species, and populations of bats requires some information concerning the number of animals involved or, at the least, knowledge of whether numbers are increasing or decreasing (O'Shea and Bogan, 2003). Unfortunately, small size, nocturnal behavior, and cryptic roost sites make it impossible to obtain total estimates of population size or even regional approximations for most species (Kunz, 2003), except a few highly colonial species, such as the Indiana bat, *Myotis sodalis* (Clawson, 2002). Nevertheless, it is possible to obtain information on long-term changes in relative abundance of species and to infer whether a population is increasing or decreasing by replicating community surveys in different years (e.g., Whitaker et al., 2002). It is essential, though, that such studies have comparable methodology for meaningful analyses (Baker and Lacki, 2004).

This report summarizes a 3-year (2004–2006) study of the bat community in southern Lower Michigan. The purpose of my investigation was three-fold. First, I wanted to perform a comprehensive, mist-netting survey of bats in southern Lower Michigan to provide the Michigan Department of Natural Resources with baseline information that would be pertinent to the management of this important group of mammals. Second, I examined the efficacy of specific aspects of recommended survey protocols (U.S. Fish and Wildlife Service, 1999), such as length of a netting session, 1 versus 2 nights of netting at a site, and influence of habitat on netting success. Finally, I investigated whether long-term changes in composition of the bat community had occurred in Michigan. I did so by comparing data obtained in my netting survey with those reported in a similar regionwide survey that was performed 26 years earlier (Kurta, 1980a), as well as by evaluating other paired sets of unpublished data that allowed comparisons over spans of 12 or more years.

METHODS

Netting Survey during 2004–2006

Study area.—I predominantly netted bats at rural sites that were located in the southern three rows of counties in Michigan and occasionally farther north. Southern Lower Michigan is characterized by low relief and a maximum elevation of ca. 250 m. The region is composed of lake plains and moraine ecosystems that are fine-to-coarse textured, with primarily deciduous forests scattered throughout (Albert et al., 1986). Dominant types of forest are beech-sugar maple and oak-hickory; hardwood swamps are interspersed throughout the region, and a few oak savannas and grasslands occur, especially in the southwestern part of the state (Barnes and Wagner, 2004). Forests are highly fragmented, and agriculture is the dominant land use, although significant urban sprawl is occurring in some areas (Levy, 2001). Small streams, lakes, and ponds are common.

Netting and handling techniques.—Netting occurred from sunset to ca. 5 hours after sunset, between 15 May and 15 August, as suggested by the U.S. Fish and Wildlife Service (1999) for studies involved with Indiana bats (Chapter 1). Most nets were made from 50-denier, braided nylon. A typical netting system was 9-m high and either 9- or 13-m wide, although 4.3-m-high nets occasionally were used at sites with low canopy. Most sites were netted for 2 nights, usually consecutively, with netting systems that were stretched across potential foraging/commuting corridors, such as county roads, primitive roads (two-tracks), trails through the woods, pipeline corridors, and streams; two netting systems were used at most sites, but occasionally one or three nets were used. Nets were placed a minimum of 100 m apart. Each net typically was checked at a maximum of 15-min intervals.

Captured bats were identified to species, sexed, and aged as either adult or juvenile, based on extent of epiphyseal ossification of the wing phalanges (Anthony, 1988). I recorded reproductive status of adult females as pregnant, lactating, post-lactating, or nonreproductive, based on palpation of the abdomen, condition of the nipples, and my ability to express milk from them (Racey, 1988). Bats were either punch-marked (Bonaccorso and Smythe, 1972) or banded (Lambournes, Ltd., Leominster, Middlesex, United Kingdom) for future identification. Marked bats occasionally were recaptured later in the same evening (6.3%) and even more rarely on the 2nd night (1.3%), but to preserve independence, these repeat captures were not used in any analysis. As part of a companion study, I also placed a radio-transmitter (Holohil Systems, Ltd., Carp, Ontario, Canada) on most bats belonging to the genus *Myotis* (Chapter 1).

Surveys at caves.—Caves are extremely rare in Michigan (Davies, 1955), but in addition to mist-netting in summer, I surveyed swarming and hibernating bats at Bear Cave. Bear Cave is located on the west bank of the St. Joseph River, 5.5 km N of Buchanan, Berrien Co (Figure 2.1). The cave formed within tufa, a carbonate rock that precipitated from surface water on top of unconsolidated sand and gravel after the glaciers retreated (Davies, 1955; Winkler and Van Besien, 1963). The present-day cave is only ca. 60-m long, but despite its small size, the cave became commercialized between 1936 and 1940. Humans enter through a door inside a gift shop built on top of the cave, whereas bats enter through a small opening through the tufa in the northeastern part of the cave. This latter opening is 0.2-m wide and 0.6-m tall; it is located ca. 2.5 m above the ground, in the side of a 6-m-high bluff, next to a pond. The cave is found in an end- and ground-moraine ecosystem dominated by beech-sugar maple forests (Albert et al., 1986).

On 30 August 2005, I searched for bats in Bear Cave during the day, and I then set three mist nets and two harp traps (Kunz and Kurta, 1988) near the bat's entrance and caught bats from sunset to sunrise. Captured individuals were banded or punch-marked before release. I made additional daytime visits to the cave on 10 and 25 September 2005, during the swarming season, and on 20 December 2005, during hibernation.

Silas Doty Cave is an even smaller cave that only recently has come to the attention of scientists in Michigan. Although there is no published literature on this cave, it also appears to be made from tufa that was deposited on top of a sandy substrate. Silas Doty Cave contains ca. 10–15 m of passage, but the cave has multiple entrances, and no underground point is more than 5.5 m from an entrance. The cave is located on the side of a wooded stream valley, in the Lost Nation State Game Area, southwest of Pittsford, Hillsdale Co (Figure 2.1).

On 2 September 2004, I erected two mist nets near the entrances to Silas Doty Cave and monitored them from sunset until 5 h after sunset in an attempt to capture swarming bats. I also placed a broadband ultrasonic detector (Titley Electronics, Ballina, Australia) near the entrances to detect any passing bats that were not caught by the nets. In addition to this visit, the cave was searched during the day on 26 March 2006, when any resident bats should have been hibernating.

Netting Survey during 1978–1979

Netting.—I compared my data with those of Kurta (1980a), who netted bats at 31 rural sites, primarily over stream corridors, throughout the southern three tiers of counties in Lower Michigan and occasionally farther north (Figure 2.1). Original data sheets indicate that netting occurred intensively through 18 August and continued sporadically from 24 August into September (A. Kurta, in litt.). Consequently, I restricted comparison to sites that he netted before 18 August to make the data comparable to mine. As in my study, Kurta (1980a) used mist nets that were made from 50-denier, braided nylon. Most of his netting systems were 9–13 m in length and 4.3–9 m in height, although smaller nets often were used in 1978. Multiple, small nets occasionally were placed in 1978, whereas in 1979, one large netting system typically was employed. Each site was netted from sunset until ca. 4 h after sunset. Type of data recorded and handling techniques were identical to those used in my study, except that no bats were banded or radiotracked in the earlier survey.

Bear Cave.—Kurta (1980b) also visited Bear Cave on multiple occasions. He made daytime visits to search for bats in the cave on 6 June, 12 July, and 7 September 1978 and on 5 September 1979. In addition, he performed all-night surveys of swarming bats using mist nets on 2 nights during September 1978 and mist nets and a bat trap on 5 nights during September 1979.

Other Paired Surveys

Netting surveys along the Thornapple River.—The Thornapple River in west-central Eaton Co. (Figure 2.1) runs through a medium-textured ground-moraine ecosystem, with surrounding land use dominated by agriculture. Beech-sugar maple forests occur in regions that are moderately or well drained, while hardwood swamps are found along the poorly drained floodplain (Albert et al., 1986). This area supports a high diversity of bats and is one of the few sites in southern Lower Michigan where all three species of *Myotis* that live in the state coexist (Kurta, 1980a).

During summer 1978 and 1979, Kurta (1980a) netted bats along a 5-km section of the Thornapple River, south and east of Vermontville, and much of that netting was done in conjunction with a study of spatial use by foraging big brown bats (*Eptesicus fuscus*) and little brown bats (*Myotis lucifugus*—Kurta, 1982a). He used single netting systems that were 9-m high and 13-m wide, just spanning the river, and nets that were made from 50-denier, braided threads. Netting lasted for ca. 4 h after sunset. As with the regional comparison, I used only data from Kurta (1980a) that were obtained before 18 August.

During summer 1993 and 1994, Foster and Kurta (1999; Foster, 1997; A. Kurta, in litt.) netted bats near Vermontville, while studying roosting behavior of the northern bat (*Myotis septentrionalis*) and Indiana bat (*Myotis sodalis*). They used systems similar in size to those of Kurta (1980a), although nets in the later studies were made from 30-denier braided threads or monofilament nylon. I examined the unpublished netting data from 1993–1994 and extracted nights for which netting occurred over the Thornapple River for ca. 4-h. Basic handling techniques and type of data recorded were identical in the two studies, except that many northern bats and Indiana bats were banded and/or received radio-transmitters in the later study (Foster and Kurta, 1999; Kurta et al., 1996).

Netting surveys at the Fort Custer Training Center.—The Fort Custer Training Center is a 3,066-ha facility of the Michigan National Guard that is located in Kalamazoo and Calhoun Counties, on the western edge of the city of Battle Creek (Figure 2.1). It was founded in 1917 and expanded in 1940. Much of the land comprising the fort was originally farmland; consequently, landcover currently varies from "sparsely stocked old farm fields, which have not naturally reforested, to well-stocked sawtimber stands on areas which were never cleared for farming" (Forest and Land Managers, Inc., 1990:4). The general area is an outwash and ground-moraine ecosystem dominated by various types of oak-hickory forest (Albert et al., 1986; Forest and Land Managers, Inc., 1990). Lakes, ponds, and other wetlands are common. However, the most significant stream on the property is only ca. 2–3 m in width, and it flows slowly for only a few kilometers, mostly through open wetlands. Buildings are found only in the cantonment in the northeastern part of the installation, and outside the cantonment, there are few roads; these roads are primarily surfaced with gravel and are not open to the public.

Bats at Fort Custer were surveyed from 15 July to 3 August 1993 (Kurta, 1993) and again from 5 to 19 July 2005 (Kurta and Foster, 2005). In 1993, nets were placed across forested roads at 19 sites and over the single small stream at one site. Most netting systems were 9-m high and 9- or 13-m wide. A single net was placed at each site and monitored from sunset to 5 h after sunset. Nineteen of the 20 sites were netted for 2 nights. Netting sites were generally 0.1–1 km apart.

In 2005, 10 sites were netted for 2 nights each, using two mist nets that were monitored from sunset until 5 h after sunset, following the protocol for Indiana bats (U.S. Fish and Wildlife Service, 1999). Like the earlier survey (Kurta, 1993), most nets were 9-m high and 9- or 13-m wide. All nets were over forested roads in 2005. Nets at individual sites usually were 0.1–0.3 km apart, and this was the only difference in protocol between years. Both studies primarily used nets made from monofilament or

30-denier braided nylon. Type of data recorded and handling techniques were identical in both studies at Fort Custer and were the same as in the regional surveys.

Bats submitted for rabies testing—In addition to mist-netting, bats that are submitted by citizens to public health departments for rabies testing provide a statewide sample that can be analyzed for changes in relative abundance (e.g., Whitaker et al., 2002). In Michigan, all bats that are to be tested for rabies are sent to the Michigan Department of Community Health in Lansing, except those from certain communities around Detroit. I reviewed published data covering bats that were submitted and identified in 1968–1978 (Kurta, 1979) and 1993 (Feller et al., 1997), and I obtained unpublished data for 1979–1982 (A. Kurta, in litt.) and 1997–2005 (P. Clark, in litt.). Identifications of bats between 1965 and 1982 were made by mammalogists at the Michigan State University Museum, whereas identifications after 1982 were made by personnel of the Michigan Department of Community Health.

Statistics

To determine whether long-term changes have taken place in the structure of bat communities in Michigan, I looked primarily at potential differences in relative abundance of species. I used a chi-squared test to examine differences in relative abundance between subsets of my data and to make comparisons between studies. However, because of the extremely small number of captures for hoary bats (*Lasiurus cinereus*), silver-haired bats (*Lasionycteris noctivagans*), and evening bats (*Nycticeius humeralis*), I eliminated these species from all analyses of relative abundance. In addition, I combined the three species of *Myotis* (little brown bats, northern bats, and Indiana bats) into one category, for all analyses of relative abundance, to avoid small expected values. Hence, tests of relative abundance generally used a 3-by-2 contingency table, with big brown bat, red bat (*Lasiurus borealis*), and *Myotis* as the three "species" categories. If the null hypothesis of no change in relative abundance was rejected, I used the sum of the partial chi-squared value for each species as an indication of which species was most responsible for the overall change (Steele and Torrie, 1960).

I also characterized each bat community by calculating a value for species diversity and evenness. As a measure of species diversity, I used Simpson's Index, which is equal to: $1 - 1 / \sum p_i^2$, where p_i is the proportion of each species in the total catch (Brower and Zar, 1984). I compared values of species diversity between studies using a *t*-test with infinite degrees of freedom (Brower and Zar, 1984). Evenness was calculated by taking the ratio of observed diversity and maximum possible diversity for a community with a given number of individuals and species (Brower and Zar, 1984). Maximum diversity was calculated as: $[(S - 1) / S] * [N / (N - 1)]$, where N represents the number of individuals in the community, and S equals the number of species. Unlike my procedure with the chi-squared tests, each species was included in calculations of species diversity and evenness.

Calculations were performed using Excel (Microsoft, Redmond, Washington). Alpha was set at 0.05 for all statistical tests. Means are presented with the associated standard error.

RESULTS

Netting in 2004–2006

Overall captures.—Over 3 years, netting occurred on 155 nights at 83 sites (Figure 2.2, Appendix C). On some dates, cold temperatures (<10°C) or prolonged rain dramatically shortened the duration of netting, and these data were eliminated from further analysis. Furthermore, another goal of my netting was to capture and radiotrack individuals in the genus *Myotis* (Chapter 1), so some sites that I netted were chosen specifically because *Myotis* had been captured there in earlier studies. Given the strong philopatry shown by many bats (e.g., Kurta and Murray, 2002; Winhold et al., 2005), I felt that these sites biased my estimates of regional relative abundance, so they too were excluded from further analysis. Therefore, my final data set reflected netting that occurred on 135 nights, for 266 net-nights, at 75 sites.

I captured 948 bats at these 75 sites, including eight of the nine species known to live in Michigan (Table 2.1). The big brown bat was the most commonly captured species and represented 81% of the catch. The red bat was second most abundant at 12%. All other species were uncommon and contributed <4% each to the total. Species diversity was 0.33, and evenness was 0.37. The big brown bat also was the most ubiquitous of the species, being captured at 93% of the 75 sites (Table 2.1). Red bats also were widespread and found at 64% of sites. All other species were encountered at <10% of the sites.

Netting over land versus over water.—Does habitat make a difference in capture success or relative proportion of species captured? Two major types of habitat were sampled in this study. These were comprised of netting sites that were on land (e.g., roads, trails, forest edges) and sites that were over or adjacent to water (e.g., streams, pond edges, riparian forest).

Occasionally during my study, the specific net in which a bat was captured accidentally was not recorded. This generally did not interfere with later determining the habitat in which the bat was caught; however, at a few sites, one of the nets may have been placed in upland woods, while the other may have been set near a pond or river. Consequently, I eliminated from analysis 35 bats that were taken at these dual-habitat sites and for which the net was not specified. This left 913 big brown bats, red bats, and *Myotis* from 72 sites (Table 2.3). Of the 253 net-nights in this modified data set, 131 were over water, and 122 were over land.

Number of bats captured per night over water (3.9 ± 0.4 bats) was slightly but not significantly ($t_{251} = 1.06$; $P = 0.15$) greater than number of captures over land (3.3 ± 0.4 bats). There was, however, a significant difference ($X^2_2 = 27.78$; $P < 0.001$) in relative abundance of species between habitats (Table 2.2). Although big brown bats contributed ca. 80% to total captures in either habitat, *Myotis* was encountered more frequently over water, whereas red bats were slightly more common over land, as indicated by the magnitude of the individual contributions to overall X^2 (Table 2.3). Species diversity over land (0.30) was significantly lower ($t_\infty = 2.43$; $P < 0.01$) than water (0.35), and evenness was 10% lower over land (0.36) than water (0.40).

Netting in the 5th h versus the 1st 4 h after sunset.—Many investigators net for 4 h or less after sunset, yet the protocol recommended by the U.S. Fish and Wildlife Service (1999) calls for netting for 5 h after sunset. What proportion of captures actually occurs in the 5th h, and are some species more likely to be caught than others during this period?

In other words, does species composition or relative abundance in the 5th h differ from the first 4 h?

Occasionally, the time at which a bat was captured was not recorded, so I eliminated 42 bats from this analysis, which left 906 big brown bats, red bats, and *Myotis* from 75 sites (Table 2.3). If captures were equally distributed over the night, 20% of captures should occur in the 5th h after sunset. However, only 11% of captures during my study occurred during the 5th h (Table 2.2). This is significantly less than expected ($X^2_1 = 50.08$; $P < 0.0001$), indicating that netting is less productive during this period than earlier in the night.

A significant difference ($X^2_2 = 9.82$; $P < 0.001$) in relative abundance of species that were captured also was detected (Table 2.3). This difference is mostly attributable to a doubling of the proportion of *Myotis* that were netted in the last hour. In addition, red bats increased their contribution from 12% of the catch in the 1st 4 h to 18% in the 5th hour. As one might surmise from these changes in relative abundance, species diversity was significantly higher ($t_\infty = 5.18$; $P < 0.001$) in the 5th h (0.48) compared with the 1st 4 h (0.29) after sunset. Evenness was almost twice as great in the 5th h (0.57) than earlier in the evening (0.33).

Netting on the 1st night versus the 2nd night at a site.—Netting for 2 nights at a site obviously entails a considerable expense in time and money for field biologists. What proportion of the total catch occurs on the 2nd night? Are some species more likely to be captured on the 1st or 2nd nights?

To answer these questions, I examined data that I obtained, after excluding 15 sites at which netting only occurred on 1 night. At the remaining 60 sites, 542 bats were captured on the 1st night and 325 bats on the 2nd night, indicating a 40% decline in number of bats caught (Table 2.2). An average of 9.0 ± 1.1 bats was netted on the 1st night, but only 5.4 ± 0.7 bats were caught during the 2nd night (paired $t_{59} = 4.50$; $P < 0.0001$). Although number of captures was different between nights, relative abundance did not differ ($X^2_2 = 0.18$; $P > 0.75$; Table 2.3). Similarly, species diversity during the 1st night (0.31) was indistinguishable ($t_\infty = 1.71$; $P > 0.05$) from that on the 2nd night (0.34), and evenness was virtually identical on both nights (0.37–0.39).

Nevertheless, netting for a 2nd night did lead to increased species richness at some sites. Big brown bats, for example, were caught at a total of 58 sites, and at six (10%) of these sites, they were encountered only on the 2nd night. Similarly, the number of sites that yielded red bats only on the 2nd night was seven (17%); hoary bats, four (57%); silver-haired bats, one (100%); northern bats, one (17%); and evening bats, one (100%). Although the protocol established for Indiana bats (USFWS, 1999) requires 2 nights of netting to establish presence/absence of the species, all sites that yielded Indiana bats in my study did so on the 1st night.

Caves.—Examination of Bear Cave during the day on 30 August 2005 yielded four northern bats and four eastern pipistrelles (*Pipistrellus subflavus*), and captures during all-night swarming yielded 91 northern bats, 51 little brown bats, and 9 eastern pipistrelles. Species diversity during that single night of swarming was 0.52, and evenness was 0.78. I also visited the cave during the day on 10 September 2005 and found 63 bats roosting in the cave. Sixty of these were *Myotis*, but I did not attempt to identify each to species because most were tucked into inaccessible crevices within the rock. The other three bats were eastern pipistrelles, one of which had been banded on 30

August. During the day on 25 September, I observed 87 *Myotis* and 5 unbanded eastern pipistrelles in the cave. On 20 December 2005, after the bats had entered hibernation, I saw only 52 bats, but 32 were eastern pipistrelles, including nine that had been previously banded. The remainder consisted of 19 *Myotis* and one big brown bat. Air temperatures in the cave were 9–10°C in December.

No bats were captured and no bats were heard with an ultrasonic detector at Silas Doty Cave on 2 September 2004. In addition, no bats were present in the cave on 26 March 2006. Air temperature within the cave was 3.9–5.0°C on the latter date, which was similar to the external temperature of 4.4°C. The site was highly disturbed. A trail had been blazed through the woods directly to the cave, and an abandoned bonfire in front of the cave was still smoldering at 1600 h. Trash and old blankets that had not been there in 2004 were present inside the cave in 2006, and it was not likely that bats used such a disturbed site.

Comparisons over Long Periods

Regionwide netting in 1978–1979 versus 2004–2006.—In his netting survey of bats in southern Lower Michigan, Kurta (1980a) captured 139 bats on or before 18 August 1978 and 1979 (Table 2.4). Before comparing my data with those of Kurta (1980a), I first deleted all my captures from the 5th h after sunset, because Kurta (1980a) only netted for 4 h and my analysis demonstrated that relative abundance differed in the 5th h compared with earlier in the evening. Similarly, I deleted data from all my land sites because Kurta (1980a) netted primarily over water, and my data indicated a difference in relative abundance between land and water sites. Although I showed earlier that number of bats captured was significantly reduced on a 2nd night of netting at the same site, I included both nights in this comparison, because relative abundance of species did not change from the 1st night to the 2nd night. Modifying the data set in these ways resulted in 430 captures for comparison with Kurta (Table 2.4).

Both studies had similar results in that the big brown bat and red bat were the two most abundant species, and various species of *Myotis* were present, albeit uncommonly. Hoary, silver-haired, and evening bats were rare or undetected in both surveys (Table 2.4). Despite similarity in the overall pattern, relative abundance differed between periods ($X^2_2 = 7.17$; $P < 0.05$), with red bats decreasing and big brown bats increasing in relative abundance between 1978–1979 and 2004–2006. The partial X^2 for red bats, however, is the largest contributor (65%) to overall X^2 (Table 2.5), which suggests that the decline of red bats is driving the overall difference. Species diversity declined ($t_\infty = 4.00$; $P < 0.001$) from 0.44 in 1978–1979 to only 0.31 during the 1st 4 h in 2004–2006. Evenness also was very different, with a value of 0.55 in 1978–1979 and 0.36 in 2004–2006.

Netting over the Thornapple River in 1978–1979 versus 1993–1994.—In addition to his regional survey (Table 2.4), Kurta (1980a) performed a separate, concentrated study of bats along the Thornapple River, where he captured 223 bats on 23 nights (Table 2.4). The most common species was the big brown bat (56%), followed by the little brown bat (25%) and red bat (9%). Along the same stretch of river, R. Foster and A. Kurta (in litt.) captured 217 bats on 21 nights, between 11 May and 18 August 1993 and 1994, and like the earlier survey on the Thornapple River, most captures were big brown bats (66%) and little brown bats (21%), although Indiana bats were the third most abundant (6%).

There was a significant change in relative abundance between surveys (X^2_2 = 15.02; $P < 0.001$). The partial X^2 for red bats represented 90% of total X^2, indicating that most observed change is due to a decrease in red bats (Table 2.5). Use of identical protocols allowed me to make comparisons of nightly rates of capture. Number of red bats captured per night significantly declined (unequal variances, $t_{29} = 3.62$; $P = 0.001$) from 0.91 ± 0.2 bats/night in 1978–1979 to only 0.14 ± 0.08 bats/night in 1993–1994. Number of captures of big brown bats, however, did not differ ($t_{42} = 1.03$; $P = 0.31$), with 6.9 ± 1.1 captures/night in 1978–1979 and 5.4 ± 0.9 bats/night in 1993–1994. Species diversity declined significantly ($t_\infty = 2.89$; $P < 0.01$), with values of 0.62 in the earlier study and 0.51 in the later one. Evenness declined by 12% from 0.72 in 1978–1979 to 0.61 in 1993–1994.

Netting at Fort Custer in 1993 versus 2005.—Kurta (1993) captured 208 bats in 39 net-nights at Fort Custer in 1993, most of which were either big brown bats (54%) or red bats (45%; Table 2.4). Twelve years later in 2005, Kurta and Foster (2005) captured 118 bats in 40 net-nights, all of which were big brown bats (78%) or red bats (22%).

Statistical comparison of relative abundance between studies was performed on only two categories—big brown bats and red bats—because of low expected values for the other groups. Proportions of species captured in the two surveys were statistically different (X^2_1= 17.52; $P < 0.001$), suggesting a decline of red bats relative to big brown bats; the partial X^2 for red bats accounted for 63% of total X^2 (Table 2.5). Number of big brown bats captured per net-night did not differ (unequal variances, $t_{56} = 0.74$; $P = 0.56$) between 1993 (2.9 ± 0.4 bats/night) and 2005 (2.3 ± 1.1 bats/night). Red bats, in contrast, showed a significant decline, from 2.3 ± 0.7 bats/net-night in 1993 to only 0.7 ±

0.4 bats/net-night in 2005 (unequal variances, $t_{51} = 3.46$; $P = 0.001$). Species diversity declined ($t_{\infty} = 3.95$; $P < 0.001$) over the 12 years from 0.51 in 1993 to 0.33, while evenness decreased slightly from 0.68 to 0.66.

Rabies submissions.—Data on bats submitted for rabies testing (Table 2.6) existed for four periods: 1965–1978 (Kurta, 1979), 1979–1982 (A. Kurta, in litt.), 1993 (Feller et al., 1999), and 1997–2005 (P. Clark, in litt.; Table 2.6). As in netting, several species, such as hoary bats or evening bats, were extremely uncommon in the samples. Furthermore, technicians at the Michigan Department of Community Health, who made identifications in 1993 and 1999–2005, had difficulty distinguishing *Myotis* from big brown bats (A. Kurta, pers. comm.). Consequently, I restricted the analysis of relative abundance to a simple comparison of easily identified red bats to all other species.

Only a small number of red bats are turned in each year in Michigan because tree-roosting red bats are less apt to come into contact with humans than building-dwelling species, such as the big brown bat, and because the red bat is migratory and not a resident for much of the year. The low number of red bats that typically were submitted forced me to pool the two older sets of data and the two newer sets to avoid expected values less than five. The proportion of red bats from 1965–1982 was 1.9%, whereas the proportion from 1993–2005 was 0.2%. These proportions were significantly different ($X^2_1 = 67.45$; $P < 0.0001$), indicating a decrease in relative abundance of red bats over this 38-year span (Table 2.5).

Bear Cave.—Kurta (1980b) conducted all-night swarming surveys of Bear Cave on 7 nights in September 1978 and 1979, when he captured 356 bats. Most were little brown bats (75%) and northern bats (24%), although two red bats (1%) also were netted.

In 2005, I captured 155 bats, including little brown bats (36%), northern bats (59%), and eastern pipistrelles (6%). I excluded red bats from the comparative analysis because of the small sample, and because red bats typically do not enter caves or participate in autumn swarming (Barbour and Davis, 1969).

Relative abundance differed significantly between the two surveys ($X^2_2 = 83.65$; $P < 0.001$), with northern bats and eastern pipistrelles more abundant and little brown bats less abundant in the current study compared with 1978–1979. Species diversity was greater ($t_\infty = 3.48$; $P < 0.001$) in 2005 (0.52) than in 1978–1979 (0.38). The catch in 2005 was less dominated by little brown bats than in 1978–1979, which led to a large increase in evenness from 0.57 in the first study to 0.78 in the second. Nevertheless, these statistical results should be interpreted with caution, because only 1 night of netting occurred during my study.

Discussion

Netting Protocols

My data indicate that different results can be obtained depending on the timing of netting and location of nets. For example, species diversity and relative abundance of bats caught during the 5th h after sunset are significantly different from results obtained during the 1st 4 h. Consequently, studies that are designed to obtain data from a broad sample of the local community, as opposed to a single target species, should net for longer periods each night. A smaller number of bats, however, was captured in the 5th h, so investigators must weigh the desirability of the increased diversity of the catch against the value of a smaller return in number of bats captured.

The intra-night differences that I observed are most likely due to different species-specific patterns of nocturnal behavior, with some bats concentrating their foraging closer to sunset and others later in the evening (Kunz, 1973). Although such temporal patterns may be genetically determined, they also may reflect differences in preferred prey. Flies (Diptera), for example, typically are most active close to sunset, whereas moths (Lepidoptera) peak in activity later in the night (Jones and Rydell, 1994); hence, the timing of a bat's activity may be controlled by activity of its prey.

Although netting for an additional hour improves diversity of the catch, netting for a 2nd consecutive 5-h night had little impact. Both species diversity and relative abundance did not change on the 2nd night compared with the 1st night, although occasionally species that were not captured on the 1st night were netted on the 2nd night. Total number of bats caught declined by 40%, from 9.0 bats/night to 5.4 bats/night (Table 2.4). The large decrease in number of bats captured on the 2nd night suggests that bats either learn the position of a net on the 1st night and avoid it on the 2nd evening, or that disturbance involved with netting causes the bats to change the location of their activity for the 2nd night (Kunz and Brock, 1975). In any event, studies that need to capture a large number of bats would have greater success by establishing a new site rather than spending a 2nd night at a single site.

Netting over land yielded the same number of bats captured per night as did netting over water, but differences in relative abundance existed between the habitats. Although big brown bats were ubiquitous, red bats were more common over land, and *Myotis* were more common over water. My results are consistent with those of Furlonger et al. (1987), who relied on acoustic detection of flying bats rather than netting captures to establish differences in activity among habitats.

Differences in use of habitat likely reflect, at least partly, dietary differences and the location of suitable prey. Little brown bats, for example, feed primarily on insects with aquatic larval stages, such as caddisflies (Trichoptera), mayflies (Ephemeroptera), and many true flies (Anthony and Kunz, 1977), and Indiana bats in Michigan also prey heavily on aquatic-based dipterans and trichopterans (Kurta and Whitaker, 1998; Murray and Kurta, 2002). The red bat, on the other hand, includes few of these small insects in its diet, concentrating instead on moths and bugs (Homoptera—Mumford and Whitaker, 1982). Obviously, studies that target red bats or *Myotis* should preferentially sample terrestrial or aquatic habitats, respectively.

Changes in Species Richness

Only seven species of bat were thought to be residents of southern Lower Michigan before my study (Kurta, 1982a; 1995). Nevertheless, I was able to document the presence of nine species of bat in this region during my surveys in 2004–2006. Of particular interest were my captures of an evening bat (*Nycticeius humeralis*), near Palmyra, ca. 10 km N of the border with Ohio, in Lenawee Co. (Appendix D), in July 2004, and the presence of eastern pipistrelles at Bear Cave in August and September 2005.

Evening bat.—There are no records of the evening bat from northern Indiana or northern Ohio (Gottschang, 1981; Whitaker and Gummer, 2003), and prior to 2004, only three records of the species existed in Michigan, with single specimens taken in 1938, 1956, and 1969 (Burt, 1939; Kurta 1982b). Consequently, the evening bat captured in Lenawee Co., a lactating female, is the first individual of this species found in Michigan in 37 years.

Previous evening bats caught in Michigan were believed to be vagrants or lost migrants (Kurta, 1982b). However, the individual from 2004 was radio-tracked after capture to a roost tree, and netting near the tree resulted in the capture of another 10 evening bats, including one lactating female and nine volant juveniles, thus documenting presence of a maternity colony (Kurta et al., 2005). Subsequent counts during evening emergence at this and two other trees indicated the presence of at least 68 evening bats, including juveniles. This was the first colony of evening bats reported in Michigan and the northernmost ever discovered in North America (Kurta et al., 2005).

The range of many species of bats is changing due to global warming (LaVal, 2004; Scheel et al., 1996), and it is possible that the evening bats at Palmyra are recent arrivals, with this southern species expanding its maternity range northward as average temperatures increase. Kurta (1980a) found no evening bats during his study, which suggests that their presence at Palmyra may be new, although Kurta (1980a) did not net near Palmyra and he may have missed this apparently isolated colony. Regardless, over 40 adults are in the colony as of 2006 (O. Munzer, pers. comm.), and movement of such a large group of tree-roosting bats, from one site to another over long distances, has never been documented (Barclay and Kurta, in press). Thus, it seems likely that the colony of evening bats near Palmyra has been in Michigan for a number of years, although the exact length of time is unknown.

Eastern pipistrelle.—Like the evening bat, the eastern pipistrelle was not thought to be a resident of southern Lower Michigan (Unger and Kurta, 1998). Unger and Kurta (1998) described a single male pipistrelle captured near Stevensville, Berrien Co., in November 1966, and the only other report of this species from the region was that of an unsexed animal that unsuccessfully attempted to hibernate in a garage, near Grand Haven, Ottawa Co., in December 1999 (Martinus and Kurta, 2001). As with the evening bat, there were no records from northern Indiana or northern Ohio prior to 2004 (Brack and Mumford, 1984; Kurta, 1995; J. O. Whitaker, Jr., pers. comm.), suggesting that the eastern pipistrelles from Grand Haven and Stevensville were wandering or lost individuals.

Despite this lack of records, I obtained 44 eastern pipistrelles at Bear Cave during swarming and hibernation in 2005. Kurta (1980b) did not find any pipistrelles in 1978–1979, even after four daytime visits to the cave and 7 nights of netting during swarming. In addition to my bats at Bear Cave, two lactating eastern pipistrelles were netted in Porter Co., Indiana, ca. 64 km southwest of Bear Cave, in July 2005, thus providing the first records of this species in northern Indiana (Kurta et al., in press). Although I encountered eastern pipistrelles only during swarming and hibernation, these bats do not migrate far (<140 km) from their hibernaculum to their summer range (Griffin, 1940), and it seems likely that some individuals summer in southwestern Michigan.

The lack of eastern pipistrelles in 1978–1979 and their abundance in 2005 suggest that the species arrived at Bear Cave in the intervening 26 years. The appearance of this species is not related to global warming, because eastern pipistrelles are found much farther north in Quebec and Minnesota (Barbour and Davis, 1969). Instead, Kurta et al. (in press) speculate that modifications of Bear Cave in 1936–1940, which coincided with commercialization of the cave, increased the volume of the cave, and changed the microclimate to an environment suitable for hibernation by eastern pipistrelles. The pipistrelles at Bear Cave presumably originated from hibernating colonies found in other human-made hibernacula (mines) that are found in central Indiana or northern Illinois, and over the last century, pipistrelles expanded their range northward, from karst areas of the Ohio River Valley, as these mines became available (Kurta et al., in press).

Comparisons over Long Periods

Using my data from 2004–2006 and a variety of unpublished data sets with comparable methods, I made quantitative comparisons of relative abundance and species diversity of bat communities in Michigan spanning periods of 12 (Fort Custer) to 38 years (rabies submissions). These comparative data sets also were valuable because they were obtained at different geographic scales. For example, bats submitted for rabies testing came from all over the state, whereas broad regional surveys involving mist-netting were performed in southern Lower Michigan. In addition, localized areas of southern Lower Michigan were intensively sampled at Fort Custer and along the Thornapple River.

Earlier netting studies of bats in southern Lower Michigan demonstrated that the bat community typically was dominated by big brown bats, with red bats usually second in abundance (Table 2.4). Although that general pattern remains true today, paired data from Fort Custer, the Thornapple River, and regional surveys of southern Lower Michigan indicate that a change in the bat community has occurred over the past few decades. Specifically, the proportion of red bats has decreased compared with the proportion of big brown bats and *Myotis* in each study (Table 2.4). Red bats yielded the highest individual chi-squared values in each analysis, suggesting that the overall change in abundance is primarily due to a decrease in red bats and not necessarily an increase in other species. In addition, a comparison of netting success at Fort Custer and along the Thornapple River, the two studies with the most comparable sampling methods, indicates no significant change in number of big brown bats/net-night but a 52–85% decrease in number of red bats/net-night. A decrease in proportion of red bats and increase in proportion of big brown bats also is reflected in the decreased species diversity and lower species evenness that was detected in all recent surveys.

Furthermore, red bats have decreased in abundance among bats turned in for rabies testing in Michigan (Table 2.6), and a similar trend also has been documented in more southern states, where this migratory species can be found during some or all of the year. In Indiana, Whitaker et al. (2002) analyzed data on rabies submissions that were collected over 4 decades, from 1966 to 2000. These authors showed that red bats decreased significantly from 23% of the total submitted in the 1960s to 19% in the 1990s.

In Arkansas, Carter et al. (2003) reported that the absolute number of red bats submitted each year declined from ca. 65 animals/year in the early 1980s to only 25–30 bats/year in the late 1990s, despite an increased awareness of bats and rabies and an increased human population, two factors that should have led to increased submissions. The decline in Arkansas was statistically significant for both male and female red bats, as well as the total population.

Thus, a decrease in number of red bats appears to be occurring throughout the East, from Arkansas to Michigan, and it may have been going on for a long time. A number of older reports claim that red bats were commonly seen migrating during daylight (Allen, 1939; Howell, 1908). Similarly, Mearns (1898:344) describes seeing (and shooting at) "great flocks" of red bats migrating through New York "during the whole of the day." Nevertheless, there have been no observations of flocks or diurnal migration that were published in the last 50 years or more (Carter et al., 2003).

There are several possible causes for decreasing populations of red bats, including reduction and/or fragmentation of forested habitat (Dickmann and Leefers, 2003; Levy, 2001), increased use of pesticides and production of environmental pollutants (Clark, 1981; Clark and Shore, 2001), and collisions with tall buildings (Terres, 1956; Timm, 1989), airplanes (Martin et al., 2005), wind turbines (Johnson, 2005; Johnson et al., 2004), and even automobiles (Farmer, 1999). In addition, recent literature describes red bats hibernating in leaf litter in the South—a strategy that makes them vulnerable to the controlled burns that foresters have used with increasing frequency in winter (Moorman et al., 1999). Which of these issues is contributing to the decline of red bats is unknown, and the observed decrease actually may be the cumulative result of all these human-related factors. In any event, further study of the ecology, behavior, and physiology of red bats is warranted to prevent its population from declining to the point that this seemingly common bat must be placed on a national list of endangered species.

Management implications.—Estimates of population size are not available for most species of bat (O'Shea and Bogan, 2003), but simple knowledge of whether a population is decreasing or increasing can be valuable to a wildlife manager. Identifying trends can be accomplished through studies of relative abundance, such as the present report, but meaningful comparison of relative abundance over time or between sites requires the use of similar protocols (Baker and Lacki, 2004; this study). I was fortunate in having access to data and unpublished notes that were produced by field biologists with similar training, thus insuring similar techniques. Although estimates of relative abundance exist for other communities of bats at other locations and times, based on mist-netting (e.g., Kunz, 1973; Lacki and Bookhout, 1983) and rabies submissions (e.g., Biggler et al., 1975), such studies typically have not been replicated. I recommend that biologists attempt to duplicate these studies so that any changes over time can be documented and potential problems identified as early as possible, before a population or an entire species suffers irreparable harm.

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Figure 2.1. Counties surveyed in 1978–1979 (shaded), as well as locations of the Thornapple River, Fort Custer, Bear Cave, and Silas Doty Cave.

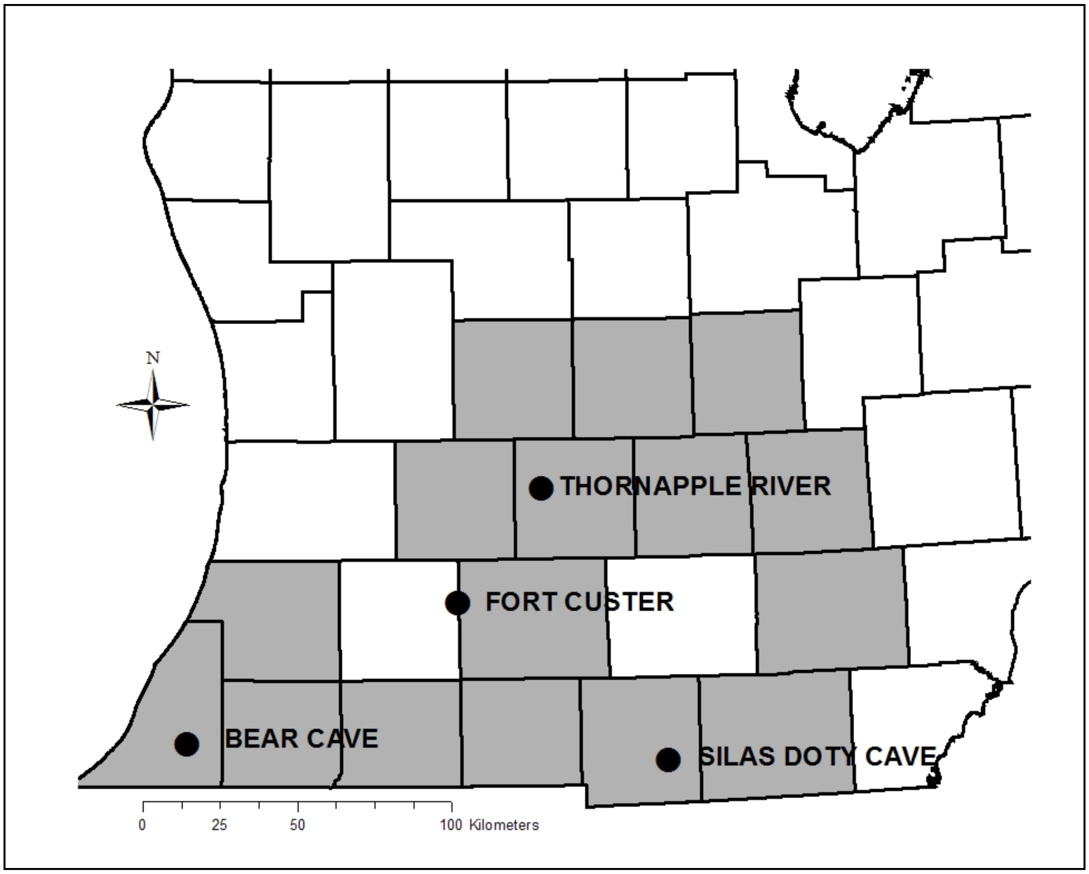

Figure 2.2. Location of 83 sites that were netted in 2004–2006.

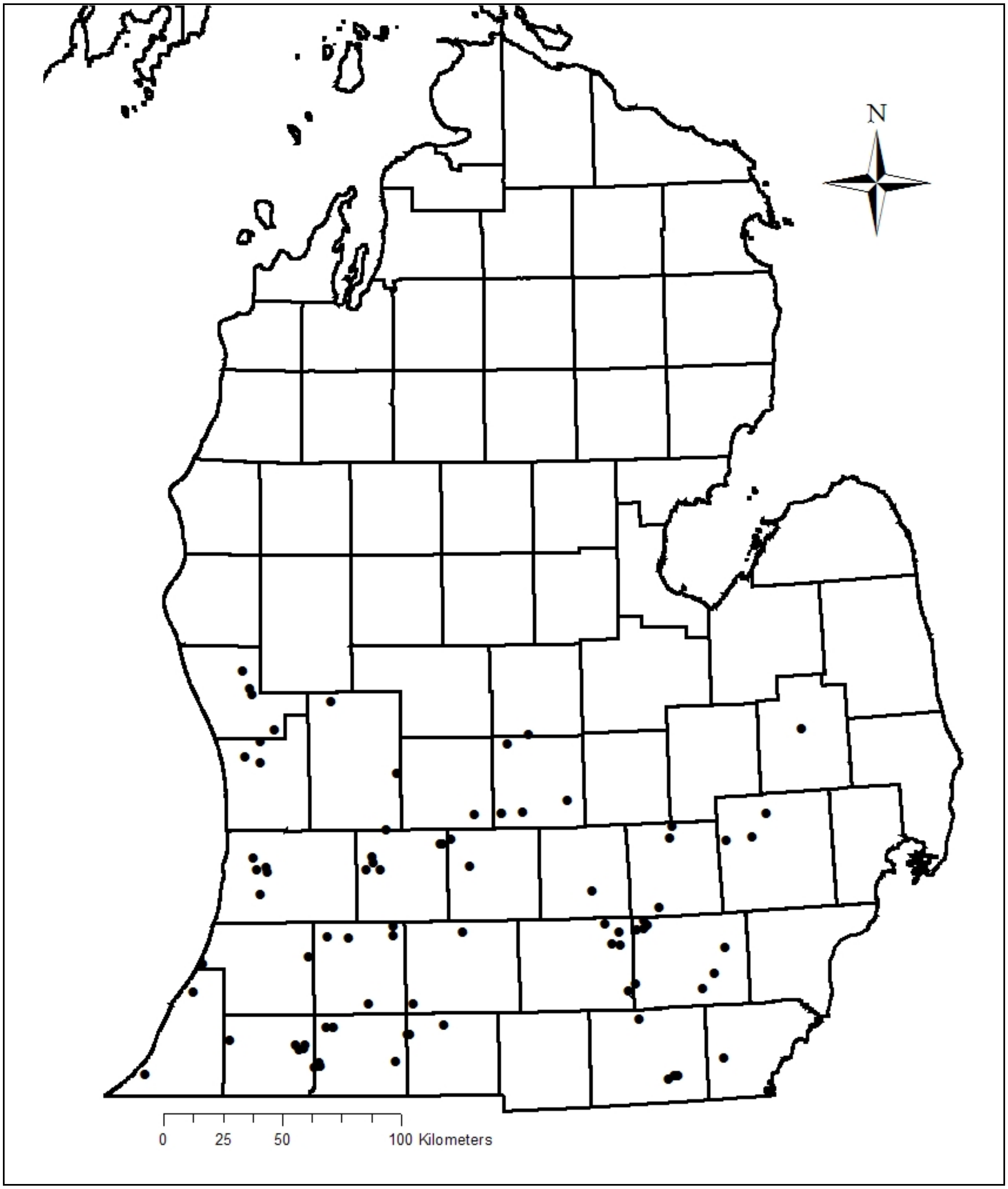

Table 2.1. Bats captured during 2004–2006 regional survey.

Species	Number of bats	Number of sites
Big brown bat	768 (81.0%)	70 (93.3%)
Red bat	116 (12.2%)	48 (64.0%)
Hoary bat	7 (0.7%)	7 (9.3%)
Silver-haired bat	1 (0.1%)	1 (1.3%)
Little brown bat	37 (3.9%)	5 (6.7%)
Northern bat	6 (0.6%)	6 (8.0%)
Indiana bat	12 (1.3%)	7 (9.3%)
Evening bat	1 (0.1%)	1 (1.3%)
Total	948	75
Species diversity	0.33	
Species evenness	0.37	

Table 2.2. Bats captured in various habitats, at different times of night, and on different days in 2004–2006.

Species	Habitat		Time of night		Repeat netting	
	Land	Water	1st 4 hours	5th hour	Night 1	Night 2
Big brown bat	332 (82.2%)	414 (79.9%)	680 (83.3%)	69 (69.7%)	447 (82.5%)	261 (80.3%)
Red bat	62 (15.3%)	50 (9.7%)	97 (11.9%)	18 (18.2%)	61 (11.3%)	38 (11.7%)
Hoary bat	2 (0.5%)	5 (1.0%)	4 (0.5%)	3 (3.0%)	3 (0.6%)	4 (1.2%)
Silver-haired bat	1 (0.2%)		1 (0.1%)			1 (0.3%)
Little brown bat		37 (7.1%)	22 (2.7%)	3 (3.0%)	18 (3.3%)	17 (5.2%)
Northern bat	3 (0.7%)	3 (0.6%)	3 (0.4%)	2 (2.0%)	5 (0.9%)	1 (0.3%)
Indiana bat	4 (1.0%)	8 (1.5%)	8 (1.0%)	4 (4.0%)	8 (1.5%)	2 (0.6%)
Evening bat		1 (0.2%)	1 (0.1%)			1 (0.3%)
Total	404	518	816	99	542	325
Species diversity	0.30	0.35	0.29	0.48	0.31	0.34
Species evenness	0.36	0.40	0.33	0.57	0.37	0.39

Table 2.3. Chi-squared comparison of various netting procedures based on bats captured during 2004–2005.

Species	Habitat			Time of night			Repeat netting		
	Land	Water	X^2	1st 4 hours	5th hour	X^2	Night 1	Night 2	X^2
Big brown bat	332	414	0.10	680	69	1.51	447	261	0.03
Red bat	62	50	5.95	97	18	3.10	61	38	0.06
Myotis	7	48	21.73	33	9	5.20	31	20	0.09
Total	401	512	27.78	810	96	9.82	539	319	0.18

Table 2.4. Number and percentage of bats captured during each of the three pairs of surveys.

Species	Regional		Thornapple River		Fort Custer	
	1978–1979	2004–2005	1978–1979	1993–1994	1993	2005
Big brown bat	100 (71.9%)	354 (82.3%)	124 (55.6%)	144 (66.4%)	112 (53.8%)	92(78.0%)
Red bat	26 (18.7%)	45 (10.5%)	21 (9.4%)	3 (1.4%)	93 (44.7%)	26 (22.0%)
Hoary bat	4 (2.9%)	3 (0.7%)	4 (1.8%)	2 (0.9%)	2 (1.0%)	
Silver-haired bat			4 (1.8%)			
Little brown bat	6 (4.3%)	22 (5.1%)	56 (25.1%)	45 (20.7%)	1 (0.5%)	
Northern bat		1 (0.2%)	4 (1.8%)	10 (4.6%)		
Indiana bat	3 (2.2%)	4 (0.9%)	10 (4.5%)	13 (6.0%)		
Evening bat		1 (0.2%)				
Total	139	430	223	217	208	118
Species diversity	0.44	0.31	0.62	0.51	0.51	0.33
Species evenness	0.55	0.36	0.72	0.61	0.68	0.66

Table 2.5. Chi-squared comparison of each pair of surveys. The category of big brown bat for bats submitted for rabies testing includes all species except red bats.

Species	Regional			Thornapple River			Fort Custer			Rabies testing		
	1978–1979	2004–2005	X^2	1978–1979	1993–1994	X^2	1993	2005	X^2	1965–1982	1993–2005	X^2
Big brown bat	100	354	1.03	124	96	1.49	112	92	6.46	1,379	7,119	0.34
Red bat	26	45	6.13	21	2	13.50	93	26	11.07	27	16	67.11
Myotis	9	27	0.02	70	60	0.03						
Total	135	426	7.17	215	158	15.02	205	118	17.52	1,406	7,135	67.45

Table 2.6. Bats submitted for rabies testing.

Species	1965–1978	1979–1982	1993	1997–2005
Red bat	16 (2.1%)	11 (1.7%)	1 (0.4%)	15 (0.2%)
Other	744 (97.9%)	635 (98.3%)	245 (99.6%)	6,874 (99.8%)
Total	760	646	246	6,889

APPENDICES

Appendix A. Tables containing results of Pearson's, 2-tailed, correlation analyses for various groups of variables. Percentages were arc-sine transformed before determining the correlation coefficient (*r*). If |*r*| > 0.5 for any pair of variables, then one of these variables, indicated by an asterisk, was not used in subsequent MANOVAs.

Table A1. Correlation coefficient (*r*) followed by probability (*P*) for characteristics of roost trees of northern bats and randomly selected trees within the roost plot. Unless indicated, sample size is 20.

Variable	Diameter	Tree height*	Decay class*	Canopy cover	Total bark*	Loose bark
Diameter						
Tree height*	0.26, 0.28[a]					
Decay class*	-0.24, 0.33[a]	-0.50, 0.02				
Canopy cover	0.06, 0.80[a]	-0.75, < 0.001	-0.56, 0.01			
Total bark*	-0.01, 0.97[a]	0.37, 0.11	-0.86, < 0.001	0.48, 0.03		
Loose bark	0.06, 0.81[a]	-0.47, 0.04	0.63, 0.003	-0.50, 0.02	-0.54, 0.01	

[a] Sample size is 19.

Table A2. Correlation coefficient (*r*) followed by probability (*P*) for characteristics of roost trees of northern bats and randomly selected trees within the roost stand. For all comparisons, sample size is 20.

Variable	Diameter	Tree height*	Decay class*	Canopy cover	Total bark	Loose bark
Diameter						
Tree height*	0.16, 0.49					
Decay class*	-0.05, 0.82	-0.35, 0.13				
Canopy cover	-0.04, 0.88	0.66, 0.002	-0.14, 0.56			
Total bark	-0.06, 0.81	0.36, 0.12	-0.71, < 0.001	0.41, 0.07		
Loose bark	0.24, 0.32	-0.22, 0.35	0.60, 0.01	-0.10, 0.68	-0.48, 0.03	

Table A3. Correlation coefficient (*r*) followed by probability (*P*) for characteristics of roost trees of Indiana bats and randomly selected trees within the roost plot. For all comparisons, sample size is 27.

Variable	Diameter	Tree height*	Decay class	Canopy cover	Total bark*	Loose bark
Diameter						
Tree height*	0.75, < 0.001					
Decay class	-0.29, 0.14	-0.42, 0.03				
Canopy cover	0.28, 0.16	0.39, 0.04	-0.15, 0.46			
Total bark*	-0.21, 0.30	-0.09, 0.66	-0.63, < 0.001	0.20, 0.32		
Loose bark	-0.33, 0.09	-0.10, 0.61	-0.25, 0.21	-0.08, 0.71	0.53, 0.005	

Table A4. Correlation coefficient (*r*) followed by probability (*P*) for characteristics of roost trees of Indiana bats and randomly selected trees within the roost stand. For all comparisons, sample size is 28.

Variable	Diameter	Tree height*	Decay class	Canopy cover	Total bark*	Loose bark
Diameter						
Tree height*	0.66, < 0.001					
Decay class	-0.33, 0.09	-0.33, 0.09				
Canopy cover	0.09, 0.63	0.36, 0.06	-0.35, 0.07			
Total bark*	0.15, 0.45	-0.02, 0.94	-0.61, 0.001	0.31, 0.10		
Loose bark	-0.10, 0.60	0.30, 0.12	-0.11, 0.58	0.22, 0.27	0.28, 0.15	

Table A5. Correlation coefficient (*r*) followed by probability (*P*) for characteristics of roost trees of northern bats and Indiana bats. Unless indicated, sample size is 24.

Variable	Diameter	Tree height*	Exit height	Decay class	Canopy cover	Total bark*	Loose bark
Diameter							
Tree height*	0.28, 0.18						
Exit height	0.24, 0.28[a]	0.89, < 0.001[a]					
Decay class	-0.31, 0.14	-0.30, 0.16	-0.14, 0.54[a]				
Canopy cover	0.07, 0.74	0.60, 0.002	0.48, 0.02[a]	-0.21, 0.33			
Total bark*	0.01, 0.97	0.18, 0.40	0.10, 0.67[a]	-0.74, < 0.001	0.34, 0.10		
Loose bark	0.10, 0.64	0.19, 0.38	0.24, 0.29[a]	0.35, 0.09	0.21, 0.33	-0.02, 0.92	

[a] Sample size is 22.

Table A6. Correlation coefficient (*r*) followed by probability (*P*) for characteristics of roost plots of northern bats and randomly selected plots within the roost stand. Unless indicated, sample size is 20.

Variable	Basal area	Number of stems*	Mean decay class	Distance to taller tree	Distance to shorter tree
Basal area					
Number of stems*	0.62, 0.003				
Mean decay class	-0.06, 0.81	-0.31, 0.18			
Distance to taller tree	-0.16, 0.53[a]	0.12, 0.63[a]	0.12, 0.65[a]		
Distance to shorter tree	-0.37, 0.12[b]	-0.68, 0.001[b]	0.46, 0.05[b]	-0.42, 0.08[a]	

[a] Sample size is 18.

[b] Sample size is 19.

Table A7. Correlation coefficient (*r*) followed by probability (*P*) for characteristics of roost plots of Indiana bats and randomly selected plots within the roost stand. Unless indicated, sample size is 27.

Variable	Basal area	Number of stems*	Mean decay class*	Distance to taller tree	Distance to shorter tree
Basal area					
Number of stems*	0.56, 0.002				
Mean decay class*	-0.53, 0.005	-0.58, 0.002			
Distance to taller tree	-0.31, 0.12	-0.49, 0.01	0.44, 0.02		
Distance to shorter tree	-0.30, 0.13	-0.34, 0.08	0.41, 0.03	0.34, 0.07[a]	

[a] Sample size is 28.

Table A8. Correlation coefficient (*r*) followed by probability (*P*) for characteristics of roost plots of northern bats and Indiana bats. Unless indicated, sample size is 23.

Variable	Basal area	Number of stems*	Mean decay class	Distance to taller tree	Distance to shorter tree*
Basal area					
Number of stems*	0.63, 0.001				
Mean decay class	-0.46, 0.03	-0.51, 0.01			
Distance to taller tree	-0.25, 0.26[a]	-0.33, 0.13[a]	0.26, 0.25[a]		
Distance to shorter tree*	-0.51, 0.01	-0.65, 0.001	0.59, 0.003	0.34, 0.11	

[a] Sample size is 22.

Table A9. Correlation coefficient (*r*) followed by probability (*P*) for types of landcover around roosts of little brown bats and randomly selected points. For all comparisons, sample size is 18.

Variable	Developed land	Open land	Upland deciduous forest	Lowland deciduous forest	Coniferous forest	Nonforested wetland	Open water
Developed land							
Open land	-0.28, 0.27						
Upland deciduous forest	-0.10, 0.69	-0.86, < 0.001					
Lowland deciduous forest	-0.09, 0.73	-0.66, 0.003	0.51, 0.03				
Coniferous forest	-0.03, 0.92	-0.78, < 0.001	0.79, < 0.001	0.55, 0.02			
Nonforested wetland	0.09, 0.72	-0.88, < 0.001	0.76, < 0.001	0.58, 0.01	0.70, 0.001		
Open water	0.26, 0.30	-0.74, < 0.001	0.52, 0.03	0.34, 0.17	0.48, 0.05	0.64, 0.004	

Table A10. Correlation coefficient (*r*) followed by probability (*P*) for types of landcover around roosts of northern bats and randomly selected points. For all comparisons, sample size is 18.

Variable	Developed land	Open land	Upland deciduous forest	Lowland deciduous forest	Coniferous forest	Nonforested wetland	Open water
Developed land							
Open land	-0.37, 0.13						
Upland deciduous forest	0.39, 0.11	-0.94, < 0.001					
Lowland deciduous forest	-0.01, 0.98	-0.85, < 0.001	0.69, 0.002				
Coniferous forest	0.45, 0.06	-0.86, < 0.001	0.85, < 0.001	0.61, 0.01			
Nonforested wetland	-0.02, 0.94	-0.85, < 0.001	0.67, 0.002	0.88, < 0.001	0.66, 0.003		
Open water	0.19, 0.46	-0.82, < 0.001	0.67, 0.002	0.78, < 0.001	0.62, 0.01	0.77, < 0.001	

Table A11. Correlation coefficient (*r*) followed by probability (*P*) for types of landcover around roosts of Indiana bats and randomly selected points. For all comparisons, sample size is 36.

Variable	Developed land	Open land	Upland deciduous forest	Lowland deciduous forest	Coniferous forest	Nonforested wetland	Open water
Developed land							
Open land	-0.64, < 0.001						
Upland deciduous forest	0.36, 0.03	-0.88, < 0.001					
Lowland deciduous forest	-0.01, 0.96	-0.52, 0.001	0.44, 0.01				
Coniferous forest	0.73, < 0.001	-0.83, < 0.001	0.71, < 0.001	0.28, 0.09			
Nonforested wetland	0.07, 0.70	-0.66, < 0.001	0.57, < 0.001	0.55, 0.001	0.35, 0.04		
Open water	0.34, 0.04	-0.58, < 0.001	0.40, 0.02	0.08, 0.66	0.34, 0.04	0.47, 0.004	

Table A12. Correlation coefficient (*r*) followed by probability (*P*) for types of landcover around roosts of little brown, northern, and Indiana bats. For all comparisons, sample size is 24.

Variable	Developed land	Open land	Upland deciduous forest	Lowland deciduous forest	Coniferous forest	Nonforested wetland	Open water
Developed land							
Open land	-0.24, 0.26						
Upland deciduous forest	0.24, 0.27	-0.95, < 0.001					
Lowland deciduous forest	-0.04, 0.86	-0.82, < 0.001	0.67, < 0.001				
Coniferous forest	0.06, 0.77	-0.83, < 0.001	0.80, < 0.001	0.70, < 0.001			
Nonforested wetland	0.02, 0.93	-0.90, < 0.001	0.76, < 0.001	0.77, < 0.001	0.73, < 0.001		
Open water	-0.05, 0.81	-0.74, < 0.001	0.60, 0.002	0.66, 0.001	0.52, 0.01	0.82, < 0.001	

Table A13. Correlation coefficient (*r*) followed by probability (*P*) for distances from landscape features to roosts of little brown bats and randomly selected points. For all comparisons, sample size is 20.

Feature	Water	Treeline/edge	Road	Building*	Town
Water					
Treeline/edge	-0.09, 0.70				
Road	-0.31, 0.19	0.10, 0.67			
Building*	-0.12, 0.62	0.08, 0.73	0.68, 0.001		
Town	-0.37, 0.11	-0.34, 0.14	-0.26, 0.28	-0.38, 0.09	

Table A14. Correlation coefficient (*r*) followed by probability (*P*) for distances from landscape features to roosts of northern bats and randomly selected points. For all comparisons, sample size is 22.

Feature	Water	Treeline/edge	Road	Building	Town
Water					
Treeline/edge	0.18, 0.42				
Road	-0.37, 0.09	-0.27, 0.23			
Building	-0.04, 0.86	-0.48, 0.02	0.18, 0.42		
Town	-0.47, 0.03	-0.03, 0.90	0.27, 0.22	0.48, 0.02	

Table A15. Correlation coefficient (*r*) followed by probability (*P*) for distances from landscape features to roosts of Indiana bats and randomly selected points. Unless indicated, sample size is 43.

Feature	Water	Treeline/edge	Road	Building*	Town
Water					
Treeline/edge	0.25,				
	0.11				
Road	0.33,	-0.34,			
	0.03	0.03			
Building*	0.36,	-0.22,	0.88,		
	0.02[a]	0.17[a]	< 0.001[a]		
Town	0.14,	-0.26,	0.49,	0.57,	
	0.36	0.09	0.001	< 0.001[a]	

[a] Sample size is 42.

Table A16. Correlation coefficient (*r*) followed by probability (*P*) for distances from landscape features to roosts of little brown, northern, and Indiana bats. For all comparisons, sample size is 37.

Feature	Water	Treeline/edge	Road	Building*	Town
Water					
Treeline/edge	0.20, 0.22				
Road	-0.29, 0.08	-0.47, 0.003			
Building*	-0.26, 0.11	-0.53, 0.001	0.55, < 0.001		
Town	-0.43, 0.01	-0.12, 0.50	0.31, 0.06	0.37, 0.02	

Appendix B. Locations and characteristics of roosts located in 2004–2006.

Table B1. Roosts of little brown bats.

Roost	County	Township	Other	Type	Usage	Type of roof	Orientation of roof	Maximum exit count	Landcover type
1	Lenawee	Ogden	Black Creek	barn	storage	shingles	north/ south & east/west	233	open land
2	Lenawee	Ogden	Black Creek	barn	storage	metal	east/ west	195	open land
3	St. Joseph	Burr Oak	Swan Creek	shed	storage	metal	north/ south	1	open land
4	Eaton	Vermontville	Thornapple River	barn	storage & livestock	metal	east/ west	104	open land
5	Eaton	Vermontville	Thornapple River	barn	storage & horse	metal	north/ south	85	open land
6	Washtenaw	Sharon	Sharon Hollow	barn	storage & livestock	shingles	north/ south & east/west	93	open land
7	Cass	Pokagon	Crystal Springs Camp	shelter	human social events	shingles	north/ south		lowland deciduous forest
8	Clinton	Eagle	Looking Glass River	barn	storage	metal	east/ west	305	open land

Table B2. Roosts of northern bats.

Roost	County	Township	Other[a]	Tree species	Decay class	Location on tree	Roost type	Maximum exit count	Landcover type
1	Washtenaw	Pittsfield	Pittsfield Preserve	silver maple	1	major lateral branch	crevice	7	lowland deciduous forest
2	Washtenaw	Pittsfield	Pittsfield Preserve	silver maple	2			1	lowland deciduous forest
3	Livingston	Putnam	near Pinckney	American elm	5	trunk	loose bark	12	lowland deciduous forest
4	Livingston	Putnam	near Pinckney	maple	6.5	trunk	crevice	17	lowland deciduous forest
5	Washtenaw	Lyndon	Waterloo SRA	red maple	2	lateral branch	crevice	1	nonforested wetland
6	Lenawee	Ogden	Black Creek	box elder	5	trunk	loose bark	5	lowland deciduous forest
7	Lenawee	Ogden	Black Creek	green ash	1	trunk	crevice or loose bark	1	lowland deciduous forest
8	Lenawee	Ogden	Black Creek	American elm	3	trunk	loose bark	1	lowland deciduous forest
9	Calhoun	Convis	Big Marsh Lake	red maple	2	trunk	loose bark	1	nonforested wetland
10	Eaton	Vermontville	Thornapple River	silver maple	2	trunk	loose bark	5	nonforested wetland

[a] SRA = State Recreation Area

Table B3. Roosts of Indiana bats.

Roost	County	Township	Other[a]	Tree species	Decay class	Location on tree	Roost type	Maximum exit count	Landcover type
1	Jackson	Norvell	near Norvell	American elm	5	trunk	loose bark	3	upland deciduous forest
2	Jackson	Norvell	near Norvell	Green ash	6	trunk	loose bark	14	nonforested wetland
3	Lenawee	Ogden	Black Creek	American elm	4.5	trunk	loose bark	4	lowland deciduous forest
4	Lenawee	Palmyra	Black Creek	American elm	4.5	trunk	loose bark	34	lowland deciduous forest
5	Lenawee	Palmyra	Black Creek	American elm	4.5	trunk	loose bark	33	lowland deciduous forest
6	Cass	Newberg	Crane Pond SGA	American elm	5.5	major lateral branch	loose bark	30	lowland deciduous forest
7	Cass	Newberg	Crane Pond SGA	American elm	5	trunk	loose bark	27	lowland deciduous forest
8	Calhoun	Convis	Big Marsh Lake	American elm	7	trunk	loose bark	18	nonforested wetland
9	Calhoun	Convis	Big Marsh Lake	American elm	6	trunk	loose bark	10	nonforested wetland
10	Calhoun	Convis	Big Marsh Lake	American elm	6		loose bark		nonforested wetland
11	St. Joseph	Burr Oak	Swan Creek	American elm	4.5	trunk	loose bark	92	lowland deciduous forest
12	Jackson	Henrietta	near Munith	American elm	6	trunk	loose bark	1	lowland deciduous forest
13	Jackson	Henrietta	near Munith	American elm	6	trunk	loose bark		lowland deciduous forest
14	Barry	Woodland	Mud Creek	American elm	5.5	major lateral branch	loose bark	3	lowland deciduous forest

[a] SRA = State Recreation Area; SGA = State Game Area

Appendix C. Location of 83 sites netted throughout southern Lower Michigan in 2004–2006, along with nearest roads and bodies of water.

Site	Dates	Net	County	Township	Road	Water body	Other[a]	Latitude	Longitude
1	24-25 May 2004	A	Washtenaw	Pittsfield	Textile		Central Area Rural Preserve	42.20284	-83.71651
	24-25 May 2004	B	Washtenaw	Pittsfield	Textile		Central Area Rural Preserve	42.20483	-83.71597
2	27 May 2004	A-C	Jackson	Norvell	Austin	Norvell Manchester Drain	Fenceline	42.14265	-84.15736
3	3-4 Jun 2004	A	Washtenaw	Lynden	N. Territorial	Green Lake	Right-of-way for pipeline	42.37945	-84.07543
	3-4 Jun 2004	B	Washtenaw	Lynden	N. Territorial	Green Lake	Right-of-way for pipeline	42.37890	-84.07550
4	7-8 Jun 2004	A	Livingston	Putnam	Kelly	Honey Creek	near George Preserve	42.45670	-83.99040
	7-8 Jun 2004	B	Livingston	Putnam	Kelly	Honey Creek	near George Preserve	42.45570	-83.98720
5	12-13 Jun 2004	A	Jackson	Waterloo	Moeckel	Portage Lake Swamp	Waterloo SRA	42.36610	-84.20350
	12-13 Jun 2004	B	Jackson	Waterloo	Moeckel	Portage Lake Swamp	Waterloo SRA	42.36890	-84.20180
6	14 Jun 2004	A	Lapeer	Mayfield	Five Lakes	Fish Lake	Lapeer SGA	43.12120	-83.23250
7	21-23 Jun 2004	A	Oakland	Rose	Munger	Fish Lake	Right-of-way for pipeline near Clyde	42.70486	-83.63768
	21-23 Jun 2004	B	Oakland	Rose	Munger	Fish Lake	Right-of-way for pipeline near Clyde	42.70593	-83.63791
8	23,25,26,28 Jun 2004	A	Oakland	Springfield	Shaffer	Huron Swamp	Indian Springs Metropark	42.71499	-83.50321
8	23,25,26,28 Jun 2004	B	Oakland	Springfield	Shaffer	Huron Swamp	Indian Springs Metropark	42.71513	-83.50120
	26,28 Jun 2004	C	Oakland	Springfield	Shaffer	Huron Swamp	Indian Springs Metropark	42.71680	-83.50257
9	29-30 Jun 2004	A	Oakland	Brandon	Allen	lake S of Long Lake	Ortonville	42.80430	-83.43110

Site	Dates	Net	County	Township	Road	Water body	Other[a]	Latitude	Longitude
9	29-30 Jun 2004	B	Oakland	Brandon	Allen	lake S of Long Lake	Ortonville		
	29-30 Jun 2004	C	Oakland	Brandon	Allen	lake S of Long Lake	Ortonville		
10	30 Jun-1 Jul 2004	A	Washtenaw	Lyndon	Embury	Sullivan Lake	near Chelsea	42.38985	-84.05449
	30 Jun-1 Jul 2004	B	Washtenaw	Lyndon	Embury	Sullivan Lake	near Chelsea	42.39126	-84.05444
11	2-3 Jul 2004	A	Washtenaw	Lyndon	Cassidy	Hankard Lake	Waterloo SRA	42.37310	-84.10894
	2-3 Jul 2004	B	Washtenaw	Lyndon	Cassidy	Hankard Lake	Waterloo SRA	42.37336	-84.10805
12	7-8 Jul 2004	A	Livingston	Cohoctah	Dean	Hidden Lake	Oak Grove SGA	42.72048	-83.92897
	7-8 Jul 2004	B	Livingston	Cohoctah	Dean	Hidden Lake	Oak Grove SGA	42.72217	-83.92862
13	8-9 Jul 2004	A	Livingston	Deerfield	Cohoctah	South Branch Shiawassee River	Oak Grove SGA	42.76334	-83.91522
	8-9 Jul 2004	B	Livingston	Deerfield	Cohoctah	South Branch Shiawassee River	Oak Grove SGA	42.76411	-83.91463
14	11-12 Jul 2004	A	Ingham	Ingham	Dexter Trail	Hewes Lake	Dansville SGA	42.52460	-84.33680
	11-12 Jul 2004	B	Ingham	Ingham	Dexter Trail	Hewes Lake	Dansville SGA	42.52390	-84.33770
15	11-12 Jul 2004	A	Jackson	Grass Lake	Katz		Waterloo SRA	42.31968	-84.19738
	11-12 Jul 2004	B	Jackson	Grass Lake	Katz		Waterloo SRA	42.32046	-84.19606
16	14-15 Jul 2004	A	Jackson	Grass Lake	List	Portage Lake	Waterloo SRA	42.32102	-84.23889
	14-15 Jul 2004	B	Jackson	Grass Lake	List	Portage Lake	Waterloo SRA	42.32198	-84.23889
17	15-16 Jul 2004	A	Washtenaw	Saline	Heartman	Saline River	Saline Mills	42.14521	-83.78111
	15-16 Jul 2004	B	Washtenaw	Saline	Heartman	Saline River	Saline Mills	42.14293	-83.78098
18	19-20 Jul 2004	A	Monroe	Summerfield	Lulu	Stacy Drain	Petersburg SGA	41.87983	-83.68432

Site	Dates	Net	County	Township	Road	Water body	Other[a]	Latitude	Longitude
18	19-20 Jul 2004	B	Monroe	Summerfield	Lulu	Stacy Drain	Petersburg SGA	41.87922	-83.68471
19	22-23 Jul 2004	A	Washtenaw	Superior	Dixboro	Fleming Creek	Matthaei Botanical Gardens	42.29930	-83.65990
	22-23 Jul 2004	B	Washtenaw	Superior	Dixboro	Fleming Creek	Matthaei Botanical Gardens		
20	22,24 Jul 2004	A	Washtenaw	Lyndon	Boyce	Joslin Lake	near Kaiserville	42.40733	-84.07342
	22,24 Jul 2004	B	Washtenaw	Lyndon	Boyce	Joslin Lake	near Kaiserville	42.41172	-84.07126
21	29 Jul, 2-Aug 2004	A	Lenawee	Ogden	Bruce	Black Creek	near Palmyra	41.80551	-83.96480
	29 Jul, 2-Aug 2004	B	Lenawee	Ogden	Bruce	Black Creek	near Palmyra	41.80562	-83.96689
22	5,12 Aug 2004	A	Lenawee	Palmyra	Gorman	Big Meadow Drain	Downstream of Indiana bat roost	41.81943	-83.93607
23	6-7 Aug 2004	A	Lenawee	Ogden	Crockett	Black Creek	Sheldon property	41.81611	-83.92069
	6-7 Aug 2004	B	Lenawee	Ogden	Crockett	Black Creek	Sheldon property	41.81572	-83.92042
24	12-13 Aug 2004	A	Lenawee	Franklin	M-50	Hidden Lake	Hidden Lake Gardens	42.03520	-84.11119
	12-13 Aug 2004	B	Lenawee	Franklin	M-50	Hidden Lake	Hidden Lake Gardens	42.03326	-84.11559
25	2-3 Jun 2005	A	Kalamazoo	Ross	42nd	Augusta Creek	W. K. Kellogg Forest	42.36676	-85.35580
	2-3 Jun 2005	B	Kalamazoo	Ross	42nd	Augusta Creek	W. K. Kellogg Forest	42.36793	-85.35473
26	3-4 Jun 2005	A	Kalamazoo	Ross	43rd	Augusta Creek	Augusta Creek Fish and Wildlife Area	42.40379	-85.35469
	3-4 Jun 2005	B	Kalamazoo	Ross	43rd	Augusta Creek	Augusta Creek Fish and Wildlife Area	42.40472	-85.35394
27	6 Jun 2005	A	Cass	Porter	Norton	Mill Creek	Three Rivers SGA	41.86779	-85.76512
	6 Jun 2005	B	Cass	Porter	Norton	Mill Creek	Three Rivers SGA	41.86754	-85.76431

Site	Dates	Net	County	Township	Road	Water body	Other[a]	Latitude	Longitude
27	7 Jun 2005	C	Cass	Porter	Norton	Mill Creek	Three Rivers SGA	41.86730	-85.76310
	7 Jun 2005	D	Cass	Porter	Norton	Mill Creek	Three Rivers SGA	41.86800	-85.76480
28	7-8 Jun 2005	A	St. Joseph	Constantine	Preston	Mill Creek	Three Rivers SGA	41.87395	-85.74500
	7-8 Jun 2005	B	St. Joseph	Constantine	Preston	Mill Creek	Three Rivers SGA	41.87370	-85.74400
29	8 Jun 2005	A	St. Joseph	Constantine	Preston	Mill Creek	Three Rivers SGA	41.87150	-85.73440
	8 Jun 2005	B	St. Joseph	Constantine	Preston	Mill Creek	Three Rivers SGA	41.87260	-85.73600
	9 Jun 2005	C	St. Joseph	Constantine	Preston	Mill Creek	Three Rivers SGA	41.87055	-85.73547
	9 Jun 2005	D	St. Joseph	Constantine	Preston	Mill Creek	Three Rivers SGA	41.87047	-85.73413
30	13,17 Jun 2005	A	St. Joseph	Constantine	Williams	Mill Creek Swamp	Three Rivers SGA	41.88689	-85.73790
	13,16 Jun 2005	B	St. Joseph	Constantine	Williams	Mill Creek Swamp	Three Rivers SGA	41.88530	-85.74100
	16-17 Jun 2005	C	St. Joseph	Constantine	Williams	Mill Creek Swamp	Three Rivers SGA	41.88745	-85.73617
31	18-19 Jun 2005	A	Cass	Newberg	Bald Hill		Crane Pond SGA	41.94117	-85.81620
	18-19 Jun 2005	B	Cass	Newberg	Bald Hill		Crane Pond SGA	41.94197	-85.81572
32	18-19 Jun 2005	A	Cass	Newberg	Mann		Crane Pond SGA	41.95492	-85.80993
	18-19 Jun 2005	B	Cass	Newberg	Mann		Crane Pond SGA	41.95591	-85.81013
33	21-22 Jun 2005	A	Cass	Newberg	Mann		Crane Pond SGA	41.95506	-85.85548
	21-22 Jun 2005	B	Cass	Newberg	Mann		Crane Pond SGA	41.95500	-85.85409
34	25-26 Jun 2005	A	Cass	Newberg	Bald Hill	Forked Lake	Crane Pond SGA	41.93660	-85.83803
	25-26 Jun 2005	B	Cass	Newberg	Bald Hill	Forked Lake	Crane Pond SGA	41.94050	-85.83913
35	28-29 Jun 2005	A	St. Joseph	Flowerfield	Delong	Rocky River	near Moore Park	42.01742	-85.70254

Site	Dates	Net	County	Township	Road	Water body	Other[a]	Latitude	Longitude
35	28-29 Jun 2005	B	St. Joseph	Flowerfield	Delong	Rocky River	near Moore Park	42.01577	-85.70166
36	1-2 Jul 2005	A	St. Joseph	Flowerfield	Pulver	Rocky River	near Moore Park	42.01779	-85.66336
	1-2 Jul 2005	B	St. Joseph	Flowerfield	Pulver	Rocky River	near Moore Park	42.01730	-85.66276
37	6 Jul 2005	C	St. Joseph	Flowerfield	Pulver	Rocky River	near Moore Park	42.01838	-85.66579
	6 Jul 2005	D	St. Joseph	Flowerfield	Pulver	Rocky River	near Moore Park	42.01846	-85.66587
38	7-8 Jul 2005	A	Kalamazoo	Brady	W	Portage River	Fink Farm	42.10953	-85.48825
	7-8 Jul 2005	B	Kalamazoo	Brady	W	Portage River	Fink Farm	42.10894	-85.48744
39	9 Jul 2005	A	Branch	Sherwood	Ralston	St Joseph River	Hawken property	41.99132	-85.27975
	9 Jul 2005	B	Branch	Sherwood	Ralston	St Joseph River	Hawken property	41.99131	-85.28129
40	10 Jul 2005	C	Branch	Sherwood	Ralston	St Joseph River	Hawken cabin	41.99205	-85.28747
	10 Jul 2005	D	Branch	Sherwood	Ralston	St Joseph River	Hawken cabin	41.99198	-85.28787
41	11,13 Jul 2005	A	Kalamazoo	Alamo	Hart	Sand Creek	Kal-haven Trail	42.36197	-85.69593
	11,13 Jul 2005	B	Kalamazoo	Alamo	Hart	Sand Creek	Kal-haven Trail	42.36277	-85.69673
42	14-16 Jul 2005	A	Calhoun	Convis	15 1/2 Mile	Big Marsh Lake	Baker Sanctuary	42.37855	-85.00440
	14-16 Jul 2005	B	Calhoun	Convis	15 1/2 Mile	Big Marsh Lake	Baker Sanctuary	42.37842	-85.00323
43	18-19 Jul 2005	A	Kalamazoo	Cooper	Westnedge	Kalamazoo River	Kalamazoo Nature Center	42.36042	-85.58734
	18-19 Jul 2005	B	Kalamazoo	Cooper	Westnedge	Kalamazoo River	Kalamazoo Nature Center	42.36037	-85.58372
44	20,24 Jul 2005	A	Calhoun	Athens	1 1/2 Mile	Pine Creek	Pine Creek Indian Reservation	42.10535	-85.25812
	20,24 Jul 2005	B	Calhoun	Athens	1 1/2 Mile	Pine Creek	Pine Creek Indian Reservation	42.10484	-85.25891
45	22-23 Jul 2005	A	St. Joseph	Burr Oak	Needham	Swan Creek	Eaton property	41.88958	-85.34908
	22-23 Jul 2005	B	St. Joseph	Burr Oak	Needham	Swan Creek	Eaton property	41.89061	-85.34915

Site	Dates	Net	County	Township	Road	Water body	Other[a]	Latitude	Longitude
46	25,27 Jul 2005	A	Berrien	Benton	Benton Center	Paw Paw River	Lew Sarett Sanctuary	42.15447	-86.38175
	25,27 Jul 2005	B	Berrien	Benton	Benton Center	Paw Paw River	Lew Sarett Sanctuary	42.15452	-86.38020
47	28,31 Jul 2005	A	Barry	Yankee Springs	Gun Lake	Hall Lake	Yankee Springs SRA	42.61615	-85.49049
	28,31 Jul 2005	B	Barry	Yankee Springs	Gun Lake	Hall Lake	Yankee Springs SRA	42.61773	-85.49031
48	31 Jul-1 Aug 2005	A	Barry	Rutland	Upton	Hill Creek	Barry SGA	42.66778	-85.46269
	31 Jul-1 Aug 2005	B	Barry	Rutland	Upton	Hill Creek	Barry SGA	42.66773	-85.45981
49	1 Aug 2005	A	Barry	Rutland	Gun Lake	Otis Lake	Barry SGA	42.61758	-85.42184
	1 Aug 2005	B	Barry	Rutland	Gun Lake	Otis Lake	Barry SGA	42.61836	-85.42310
50	2 Aug 2005	A	Allegan	Manlius	126th	Big Dailey Bayou	Allegan SGA - Hoffman landing	42.61652	-86.05477
	2 Aug 2005	B	Allegan	Manlius	126th	Big Dailey Bayou	Allegan SGA - Hoffman landing	42.61784	-86.05254
51	2 Aug 2005	A	Allegan	Heath	130th	Kalamazoo River	Allegan SGA	42.62528	-86.00643
	2 Aug 2005	B	Allegan	Heath	130th	Kalamazoo River	Allegan SGA	42.62551	-86.00604
52	4 Aug 2005	A	Van Buren	Almena	Fish Hatchery	Wolf Lake Fish Hatchery	Wolf Lake Fish Hatchery	42.28903	-85.79109
	4 Aug 2005	B	Van Buren	Almena	Fish Hatchery	Wolf Lake Fish Hatchery	Wolf Lake Fish Hatchery	42.29012	-85.79005
53	8 Aug 2005	A	Berrien	Chikaming	Warren Woods	Galien River	Warren Woods	41.84080	-86.62210
	8 Aug 2005	B	Berrien	Chikaming	Warren Woods	Galien River	Warren Woods		
54	8 Aug 2005	A	Cass	Pokagon	Frost St	Dowagiac River	Dowagiac Woods	41.97212	-86.18977
	8 Aug 2005	B	Cass	Pokagon	Frost St	Dowagiac River	Dowagiac Woods	41.97220	-86.18983
55	9 Aug 2005	A	Van Buren	Covert	44th	Brandywine Creek	The Nature Conservancy	42.25894	-86.32972
	9 Aug 2005	B	Van Buren	Covert	44th	Brandywine Creek	The Nature Conservancy	42.25965	-86.32919
56	12 Aug 2005	A	Branch	Union	Girard	Coldwater River	near Union City	42.02612	-85.10515

Site	Dates	Net	County	Township	Road	Water body	Other[a]	Latitude	Longitude
56	12 Aug 2005	B	Branch	Union	Girard	Coldwater River	near Union City	42.02812	-85.10567
57	13 Aug 2005	A	Allegan	Clyde	116th	Ely Lake	Allegan SGA	42.52561	-86.03452
	13 Aug 2005	B	Allegan	Clyde	116th	Ely Lake	Allegan SGA	42.52606	-86.03401
	14 Aug 2005	C	Allegan	Clyde	116th	Ely Lake	Allegan SGA	42.52587	-86.03390
	14 Aug 2005	D	Allegan	Clyde	116th	Ely Lake	Allegan SGA	42.52604	-86.03394
58	15 Aug 2005	A	Allegan	Heath	126th	Kalamazoo River	Allegan SGA	42.61133	-86.00152
	15 Aug 2005	B	Allegan	Heath	126th	Kalamazoo River	Allegan SGA	42.61066	-86.00100
	15 Aug 2005	C	Allegan	Heath	126th	Kalamazoo River	Allegan SGA	42.61002	-86.00161
59	22 Jul 2005	A	Jackson	Henrietta	Fitchburg	Cahaogan Creek	near Munith	42.40040	-84.26940
60	2 Aug 2005	A	Eaton	Vermontville	Vermontville	Thornapple River	Vermontville	42.62530	-84.96360
61	8 Aug 2005	A	Washtenaw	Sharon	Sharon Valley	River Raisin	Sharon Hollow	42.16820	-84.12330
62	1-2 Jun 2006	A	Barry	Irving	Coldwater	Coldwater River	Middleville SGA	42.76658	-85.38807
	1-2 Jun 2006	B	Barry	Irving	Coldwater	Coldwater River	Middleville SGA	42.76584	-85.38854
63	4 Jun 2006	A	Barry	Yankee Springs	Chief Noonday	Turner Creek	Barry SGA	42.64340	-85.45590
	4 Jun 2006	B	Barry	Yankee Springs	Chief Noonday	Turner Creek	Barry SGA	42.64260	-85.45590
64	6-8 Jun 2006	A	Barry	Woodland	Barnum	Mud Creek	near Woodland	42.71150	-85.10130
	6-8 Jun 2006	B	Barry	Woodland	Barnum	Mud Creek	near Woodland	42.71040	-85.10080
65	12-13 Jun 2006	A	Eaton	Sunfield	St. Joe	Tamarack Lake	near Woodbury	42.72831	-85.05432

Site	Dates	Net	County	Township	Road	Water body	Other[a]	Latitude	Longitude
65	12-13 Jun 2006	B	Eaton	Sunfield	St. Joe	Tamarack Lake	near Woodbury	42.72825	-85.05481
66	14,19,22 Jun 2006	A	Kent	Vergennes	McPherson	Flat River	Fallasburg Park	42.98444	-85.32942
	14,19,22 Jun 2006	B	Kent	Vergennes	McPherson	Flat River	Fallasburg Park	42.98372	-85.32975
67	20-21 Jun 2006	A	Barry	Woodland	Velte	Mud Creek	Mary's Farm - MS6-1 roost	42.71504	-85.11036
	20-21 Jun 2006	B	Barry	Woodland	Velte	Mud Creek	Mary's Farm - MS6-1 roost	42.71486	-85.11093
68	24-26 Jun 2006	A	Allegan	Manlius	133rd	Rabbit River	near New Richmond	42.66210	-86.07060
	25-26 Jun 2006	B	Allegan	Manlius	133rd	Rabbit River	near New Richmond	42.66420	-86.06900
69	27 Jun 2006	A	Clinton	Victor	Babcock Lake	Looking Glass River	near Bath	42.86880	-84.45180
	28-29 Jun 2006	B	Clinton	Victor	Babcock Lake	Looking Glass River	near Bath	42.87060	-84.45440
	29 Jun 2006	C	Clinton	Victor	Babcock Lake	Looking Glass River	near Bath		
70	27-28 Jun 2006	A	Ionia	Danby	Towner	Grand River	Portland SGA	42.82109	-84.93069
	27-28 Jun 2006	B	Ionia	Danby	Towner	Grand River	Portland SGA	42.82150	-84.93091
71	18-19 Jul 2006	A	Gratiot	Fulton	Grafton	Maple River	Maple River SGA	43.12349	-84.65022
	18-19 Jul 2006	B	Gratiot	Fulton	Grafton	Maple River	Maple River SGA	43.12250	-84.65321
72	18-19 Jul 2006	A	Clinton	Lebanon	Tallman	Maple River	Maple River SGA	43.08950	-84.76069
	19 Jul 2006	B	Clinton	Lebanon	Tallman	Maple River	Maple River SGA	43.08969	-84.76160
73	21-22 Jul 2006	A	Clinton	Eagle	Herbison	Looking Glass River	near Eagle	42.82612	-84.79463
	21 Jul 2006	B	Clinton	Eagle	Herbison	Looking Glass River	near Eagle	42.82614	-84.79377
74	22 Jul 2006	C	Clinton	Eagle	Herbison	Looking Glass River	near Eagle	42.82495	-84.79384

Site	Dates	Net	County	Township	Road	Water body	Other[a]	Latitude	Longitude
75	21,24 Jul 2006	A	Clinton	Watertown	Forest Hill	Looking Glass River	near Wacousta	42.82867	-84.68269
	21,24 Jul 2006	B	Clinton	Watertown	Forest Hill	Looking Glass River	near Wacousta	42.82871	-84.68367
76	25,30 Jul 2006	A	Kent	Tyrone	20 Mile	Spring Lake	Rogue River SGA	43.25715	-85.66857
	25,30 Jul 2006	B	Kent	Tyrone	20 Mile	Spring Lake	Rogue River SGA	43.25794	-85.66800
77	30 Jul 2006	A	Muskegon	Egelston	Maple Island	Mosquito Creek	Muskegon SGA	43.28445	-86.07945
	30-31 Jul 2006	B	Muskegon	Egelston	Maple Island	Mosquito Creek	Muskegon SGA	43.28491	-86.07819
78	1-2 Aug 2006	A	Muskegon	Cedar Creek	Crocker	Cedar Creek	Manistee NF	43.37460	-86.12770
	2 Aug 2006	B	Muskegon	Cedar Creek	Crocker	Cedar Creek	Manistee NF	43.37840	-86.12750
79	4-5 Aug 2006	A	Ottawa	Crockery	Taft	Crockery Creek	near Nunica	43.10410	-86.03960
	4-5 Aug 2006	B	Ottawa	Crockery	Taft	Crockery Creek	near Nunica	43.10360	-86.04130
80	6-7 Aug 2006	A	Ottawa	Robinson	N. Cedar	Grand River	near Bass River SRA	43.02450	-86.03520
	6-7 Aug 2006	B	Ottawa	Robinson	N. Cedar	Grand River	near Bass River SRA	43.02530	-86.03540
81	8-9 Aug 2006	A	Muskegon	Ravenna	Patterson	Crockery Creek	near Ravenna	43.14800	-85.96680
	8-9 Aug 2006	B	Muskegon	Ravenna	Patterson	Crockery Creek	near Ravenna	43.14530	-85.96620
82	10-11 Aug 2006	A	Muskegon	Cedar Creek	River	Little Cedar Creek	Muskegon SGA	43.30520	-86.09180
	10-11 Aug 2006	B	Muskegon	Cedar Creek	River	Little Cedar Creek	Muskegon SGA	43.30410	-86.09100
83	12-13 Aug 2006	A	Ottawa	Crockery	132nd	Bruce Bayou	Grand Haven SGA	43.04730	-86.11640
	13 Aug 2006	B	Ottawa	Crockery	132nd	Bruce Bayou	Grand Haven SGA		

[a] SRA = State Recreation Area; SGA = State Game Area

Appendix D. Bats captured at each site that was listed in Appendix C. Some sites were netted specifically because *Myotis* had been captured there in previous studies and were considered biased; these sites are indicated with an asterisk. A question mark in the net column indicates that the specific net in which bats were captured was not recorded.

Site	Net	Big brown bat	Red bat	Hoary bat	Silver-haired bat	Little brown bat	Northern bat	Indiana bat	Evening bat	Total
1	A	1					1			2
	B				1					1
2*	A-C	1						5		6
3	A	8	2							10
	B	4	2							6
4	A									0
	B						1			1
5	A	16	1							17
	B	14	2							16
6	A	11	5							16
7	A									0
	B	2								2
	?	1								1
8	A	11	1							12
	B	4	1							5
	C									0
9	A									0
	B	1								1
	C	1	1							2
	?	1								1
10	A	7	1							8
	B	2	2							4
11	A	3					1			4
	B	13								13
12	A									0
	B									0
	?	10	3							13
13	A									0
	B	5								5
14	A									0
	B	6								6
	?	9	1							10
15	A	22	1							23
	B	20	1							21
16	A	32	3	1						36
	B	14	3							17
17	A	7								7
	B	22	2							24
18	A									0
	B									0

Site	Net	Big brown bat	Red bat	Hoary bat	Silver-haired bat	Little brown bat	Northern bat	Indiana bat	Evening bat	Total
19	A	3								3
	B	4								4
20	A	6	1	1						8
	B	14								14
21	A									0
	B									0
	?	3				28	1	1		33
22	A	1	1			5		5		12
23	A									0
	B									0
	?	5	2			3	1		1	12
24	A	3								3
	B	5	4							9
25	A	1								1
	B	6								6
26	A	3								3
	B	5	1							6
27	A	3	1							4
	B									0
	C	2	1							3
	D									0
28	A	8	1							9
	B	5	2							7
29	A									0
	B									0
	C									0
	D	2	1							3
30	A	3								3
	B	15	3							18
	C									0
31	A	1								1
	B									0
32	A	1	1					1		3
	B	1	2					1		4
33	A	4	1							5
	B	6								6
34	A	1	2							3
	B	2	1					2		5
35	A	18	2							20
	B	5		1						6
36	A	7								7
	B	2								2
37	C	4	2							6
	D	1								1

Site	Net	Big brown bat	Red bat	Hoary bat	Silver-haired bat	Little brown bat	Northern bat	Indiana bat	Evening bat	Total
38	A	21								21
	B	7								7
39	A	1								1
	B									0
40	C									0
	D									0
41	A	8								8
	B	7								7
42	A						1			1
	B	5						1		6
43	A	12	2							14
	B	4								4
44	A	1	1	1						3
	B	6								6
45	A	26	2	1						29
	B	28				2		2		32
46	A	10	3							13
	B									0
47	A	5	2							7
	B		1							1
	?	2								2
48	A	17	3							20
	B	14	1							15
49	A									0
	B	3								3
50	A	5	1							6
	B	5	1							6
51	A	2	1							3
	B									0
52	A	9	1					2		12
	B	2								2
53	A									0
	B									0
	?	1								1
54	A	7	4							11
	B									0
55	A									0
	B									0
56	A									0
	B									0
57	A	1								1
	B									0
	C									0
	D									0

Site	Net	Big brown bat	Red bat	Hoary bat	Silver-haired bat	Little brown bat	Northern bat	Indiana bat	Evening bat	Total
58	A	2	1							3
	B		1							1
	C									0
59	A	5						1		6
60*	A	5	5			5	1			16
61*	A	3	2			1		1		7
62	A	6	2							8
	B									0
63	A									0
	B									0
64	A	10						1		11
	B	2						1		3
65	A									0
	B									0
66	A		1							1
	B	7								7
67*	A	11	1							12
	B	1								1
68	A									0
	B	8	5	1						14
69	A									0
	B	4								4
	C	11								11
70	A	10	4							14
	B		1							1
71	A	20	2	1						23
	B	12								12
72	A									0
	B									0
73	A	8	3							11
	B	1								1
74	C	7				2				9
75	A	15				2				17
	B	2								2
76	A	5								5
	B	10	1							11
77	A	10	1							11
	B	1								1
78	A	7	4							11
	B		2							2
79	A	15	3							18
	B									0
80	A		1							1
	B	1								1

Site	Net	Big brown bat	Red bat	Hoary bat	Silver-haired bat	Little brown bat	Northern bat	Indiana bat	Evening bat	Total
81	A									0
	B	1	2							3
82	A									0
	B	2	1							3
83	A	1								1
	B									0
Total		810	127	7	1	48	7	24	1	1,025