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ECOLOGY OF THE EVENING BAT (*NYCTICEIUS HUMERALIS*) AT THE NORTHERN EDGE OF ITS RANGE

By

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Ecology of The Evening Bat (*Nycticeius humeralis*) at The Northern Edge of Its Range

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DEDICATION

This thesis is dedicated to two very special men in my life—my father and Brian. Thank you for all your support.

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ABSTRACT

Only a single colony of evening bats (*Nycticeius humeralis*) is known to occur in Michigan, and it is the northernmost colony on the North American continent. In mid-May, only female evening bats migrate to Michigan to raise their pups, and in late August, evening bats migrate to southern portions of their range, where they are ubiquitous. I studied the roosting and dietary ecology of the evening bat in southeastern Michigan. Evening bats roosted in cavities, crevices, and under exfoliating bark of older trees located in a bottomland forest, interlaced with waterways and surrounded by agricultural fields. These habitats play an important role in the diet of evening bats. Fourteen orders of insects and two orders of arachnids were found in fecal pellets of evening bats; Coleoptera, Diptera, Hymenoptera, and Hemiptera composed 94% of dietary volume. Several insects consumed by evening bats are economically important.

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ROOSTING ECOLOGY

INTRODUCTION

Guidelines for management of most species typically are based on studies conducted in the core of a species' range. This is because populations often are large and apparently stable in the center of an animal's distribution, making them easier to work with than groups on the periphery. Nevertheless, peripheral populations can be important. They are often thought to be under greater stress than the main population, and, consequently, declining health of an outlying group may be an early warning of potential problems for the central population (Kurta et al., 1996). Recent biogeographical analyses, however, indicate that peripheral sites often become critical refugia that allow peripheral populations to survive as the central population declines (Channell and Lomolino, 2000; Lomolino and Channell, 1995). For instance, some peripheral populations of the endangered Indiana bat (*Myotis sodalis*) are increasing, whereas populations in part of the core range are declining (Clawson, 2002). Hence, knowledge of ecological requirements for both peripheral and central populations is required for effective management and conservation.

Furthermore, knowledge of peripheral populations is important because the geographic distribution of many organisms is shifting northward (Cozier, 2004; Hughes, 2000; Lariviere, 2004; Parmesan and Yohe, 2003; Root et al., 2003; Thomas et al., 2001; Walther et al., 2002), possibly in response to anthropogenic factors, such as global climate change (Cozier, 2004; Humphries et al., 2002; Sheel et al., 1996; Willis and Brigham, 2003). The shorter summers and longer, colder winters of northern environments place physiological and distributional constraints on organisms (Boonstra, 2004). With global climate change, warmer temperatures that are now occurring in northern regions may change an organism's morphology, behavior, physiology (Bertreaux et al., 2004; Boonstra, 2004;

Root et al., 2003), and phenology (Bertreaux et al., 2004; Hughes, 2000; Root et al., 2003; Walther et al., 2002), which is the timing of life history events (e.g., migration, parturition, birth or hatching) that are regulated primarily by hormones (Bertreaux et al., 2004). As a result, ecological interactions within a community may change. For example, diet and foraging strategies of bats could be impacted by changes in seasonal and geographic distribution of their insect prey, as seen in insectivorous passerines (Stokke et al., 2005).

Other impacts on populations from global warming are that densities of a species in an area may change (Root et al., 2003), geographic ranges of species may adjust (Root et al., 2003; Walther et al., 2002), and warmer temperatures may reduce energetic expenditures by animals hibernating at the northern edge their range (Humphries et al., 2002). Suitable roosting sites limit tree-roosting populations of bats (Humphrey, 1975), and as nighttime temperatures in northern regions increase, thermoregulatory costs will be reduced and flying insects will become more abundant (Willis and Brigham, 2003), thus allowing bats to expand their ranges northward into areas of newly suitable habitat. Therefore, studying peripheral populations will help predict the types of habitats that will be colonized as global warming continues.

The evening bat (*Nycticeius humeralis*) is a medium-sized vespertilionid that is widely distributed from the Gulf Coast northward to the Great Lakes (Watkins, 1972). Although common in parts of the Southeast and central Midwest, the evening bat is rare to uncommon at the northern edge of its range. There are no records from the northern half of Ohio or the northern quarter of Indiana, and maternity colonies that were documented in buildings in Indiana by Cope et al. (1961) have vanished over the last several decades (Gottschang, 1981; Whitaker and Gummer, 1993, 2003). There is only one record from

Canada—an evening bat that was found at Pointe Pelee, Ontario, the southernmost point of mainland Canada, on 16 May 1911 (Peterson, 1966)—and only three records exist for Michigan prior to 2004. One pregnant female was found in Climax, Kalamazoo Co., on 23 May 1938 (Burt, 1946); one female, from Ann Arbor, Washtenaw Co., on 21 May 1956; and another female, from Harbert, Berrien Co., on 2 June 1969 (Kurta, 1982, 2008). These evening bats were thought to be vagrants or lost migrants (Kurta, 1995), because no maternity colonies were known from anywhere in the Great Lakes region, even though extensive surveys for bats had been conducted throughout northern Indiana (J. O. Whitaker, Jr., pers. comm.) and Michigan between 1980 and 2000 (e.g., Kurta, 1980; Kurta et al., 1987). Nevertheless, a maternity colony of evening bats was found in 2004 near Palmyra, in Lenawee Co., Michigan (Kurta et al., 2005; Winhold, 2007), and it is now the northernmost colony of evening bats on the continent. Because of its rarity, the evening bat is considered endangered in Indiana (Whitaker and Gummer, 1993, 2003), is listed as a species of special concern in Kentucky (T. Hemberger, pers. comm.), and is in the process of being classified as threatened in Michigan (Kurta, 2008). This proposed status in Michigan reflects decreasing populations in neighboring states, the small number of evening bats in Michigan, and their restricted distribution within the state.

Roosts are important for the survival and reproduction of bats (Kunz and Lumsden, 2003). Roosts provide protection from environmental conditions and predators and a site for pup-rearing, mating, hibernation-torpor, and social interaction. All roosts, however, are not created equal, and individual bats may differ in their selection of roosts based upon physiological or behavioral requirements. The energetic costs of pregnancy and lactation are high, and clustering of bats in a roost can reduce the cost of thermoregulation (Kurta, 1986), leaving more energy for production of a fetus or milk; therefore, microclimate of the roost can influence growth and development of pups (Altringham, 1996). Distribution and abundance of suitable roosts, distance to foraging areas, chiropteran physiology, and environmental conditions influence roost selection of individuals (Barclay and Kurta, 2007; Kunz and Lumsden, 2003).

Little research has been published on the roosting ecology of evening bats, compared with other species, such as the Indiana bat (*Myotis sodalis*—Kurta and Kennedy, 2002) or red bat (*Lasiurus borealis*—Carter and Menzel, 2007). Some early studies were conducted with colonies of evening bats that lived in buildings (e.g., Cope et al., 1991; Watkins, 1969; Wilkinson, 1992*a*, 1992*b*), but more recent projects have focused on the ecology of evening bats roosting in trees (Bowles et al., 1996; Boyles and Robbins, 2005; Hutchinson, 2001; Menzel et al., 1999, 2001; Miles et al., 2006). Nevertheless, published information is of limited use in understanding roost selection by reproductive females; most reports about evening bats in trees are anecdotal (Hutchinson, 2001), pertain to use of trees in winter (Boyles and Robbins, 2006), combine data from adult males and adult females, are plagued by small samples (Menzel et al., 1999, 2001), or involve data that were gathered incidental to other studies (Duchamp et al., 2004). The most comprehensive report to date is that of Miles et al. (2006), who studied evening bats over 2 years in an intensively managed pine forest in Georgia. However, the landscape over much of the range of evening bats, including southern Michigan, is dominated by agricultural land, with scattered blocks of deciduous woods. Furthermore, no information exists concerning evening bats on the northern edge of their range, where climate, vegetation, and potential competitors presumably differ from those at the core of their range.

Within the fragmented habitat in Lenawee Co., evening bats co-exist with other tree-roosting species, such as northern bats (*Myotis septentrionalis*) and Indiana bats (Stumpf, 2009; Winhold, 2007), and potential competition with these species for suitable roosting sites and prey may present challenges to the survival of this peripheral population of evening bats. Evening bats will also be faced with the ramifications of global warming, whether it is range expansion and/or changes in phenology. This study of the ecology of evening bats in Michigan will provide insight as to how a southern species copes with life in a fragmented landscape at the periphery of its range. Moreover, this multi-year study will assess the roosting requirements of evening bats in Michigan, which will provide land managers with information needed to protect this species.

METHODS

The study site is located ca. 6 km SE Palmyra, Lenawee Co., Michigan (T7S R4E Sections 33–35; T8S R4E Sections 1–5 and 8–9). The local landscape is part of the Maumee Subdistrict, of the Washtenaw District, of the Southern Lower Michigan Region (Albert et al., 1986). Thousands of years ago, this part of Michigan was under Lake Erie, and consequently, the landscape consists primarily of a lake plain, dominated by clay soils, although the plain is crossed by a number of broad drainages containing sandier soils. When Europeans arrived, the region was mostly wooded, and the land was poorly drained. Most of the plain, however, has been drained by humans and is used for growing primarily soy and corn. Forested areas that remain are predominantly isolated woodlots in sites with poor drainage or along the floodplains of modern streams that flow in the old glacial channels. This ecological study occurred along one such riparian network, consisting of the River Raisin and its tributaries, Black Creek, Grinnell Drain, and Bear Creek (Fig. 1.1).

Mist netting and radio tracking.—I netted (Kunz and Kurta, 1988) bats between 20 May and 14 September 2007 and from 8 May to 22 September 2007. Netting occurred typically 3–5 times per week, depending upon weather and the need to obtain bats for radio tracking. Nets were 9-m high and 6–18-m wide and placed along flyways, across streams, and near roost trees. Once captured, an evening bat was placed in a holding bag and weighed. Reproductive condition of females (pregnant, lactating, or postlactating) was determined by body mass, gentle palpation of the abdomen, morphology of the nipples, and ability to express milk from them (Racey, 1988). Because determining pregnancy by palpation is unreliable early in gestation (Nogueira and Peracchi, 2003) and 90% of females give birth each year (Watkins, 1972), I designated not palpably pregnant females caught during May and early June as pregnant. Degree of ossification of the metacarpal-phalangeal joint was used to place bats into categories of juvenile or adult (Anthony, 1988).

Each evening bat was banded with lipped bands (Model 1BR3521, Lambournes, Ltd., Leominster, England), stamped with a unique four-digit number and the letters "EMU YPSI MI," which refer to my university, city, and state, respectively. For 44 evening bats, a dorsal patch of fur was clipped and a radio transmitter weighing 0.4–0.6 g (Holohil Systems, Ltd., Carp, Ontario) was attached using a skin adhesive (Liquid Bonding Cement, Torbot Group, Inc., Cranston, Rhode Island).

I attempted to locate the roost site every day that the transmitter functioned, using three- and five-element Yagi antennas and an appropriate receiver (TRX-2000S, Wildlife Materials, Murphysboro, Illinois). Once a roost tree was discovered, its location was determined using a global-positioning unit (Etrex Legend, Garmin International, Inc., Olathe, Kansas). Number of bats using the roost and the type of roosting site (e.g., under bark, in a cavity, or in a crevice) was determined by watching bats leave the tree from 20 min prior to sunset to 50 min after sunset (Gardner et al., 1991). Time of emergence was recorded for the first and last bat, as well as the bat carrying a transmitter. Trees containing bats with transmitters were watched nightly, when possible, until the bat lost its transmitter or it ceased functioning. Up to three different trees were watched on any given night, including roosts previously occupied by bats carrying transmitters.

Roost fidelity and switching.—Tree-living bats commonly change roosts (Barclay and Kurta, 2007), and I examined patterns of roost switching by individual evening bats and by bats in different reproductive conditions. Some bats were radio tracked more than once, and to maintain independence, I combined data on number of roost switches and days spent in roosts for bats that were tracked multiple times. However, when conducting statistical analyses by reproductive condition, data from individuals that were radio tracked multiple times were analyzed separately if individuals were of different reproductive conditions during each tracking session (e.g., a bat first tracked while she was pregnant and tracked a second time when she was lactating).

With ArcGIS 9.1 (Environmental Systems Research Institute, Inc., Redlands, California), I measured the distance traveled by each bat between roost trees occupied on different days. On some days, I was not able to verify that evening bats were roosting in a specific tree by watching the roost at sunset, either because no bats were seen leaving the tree or because an observation could not be performed on that night. If I was unable to confirm the exact tree by observing emergence, I used the tree that evening bats were presumed to be roosting in, based upon daytime radio tracking, for calculating distance traveled between roosts. Roost trees were numbered systematically, based upon year and date of discovery;

for example roost 601 was the first roost discovered in 2006, whereas roost 709 referred to the ninth tree discovered in 2007. As a measure of the importance of the roost to the colony, I also calculated the number of bat-days that each tree was used in a given year by summing emergence counts for the entire year.

HABITAT ASSESSMENT

Roost trees.—Many factors potentially help explain why a bat does or does not use a particular tree as a roost (Barclay and Kurta, 2007; Kalcounis-Rüppell et al., 2005), and I recorded 25 variables of my roost trees and the surrounding vegetation for later analysis. I recorded the species of tree and measured the tree's diameter at breast height. I estimated percent of original bark remaining, percent of the current bark that was exfoliating, and the percent of the tree that was covered by loose and peeling bark under which a bat might roost (available bark). I assigned a stage of decay to each roost tree (Table 1.1), and roosting structures were classified as exfoliating bark, cavity, or crevice. Cavities were hollows formed either by a primary excavator or natural decay (Barclay and Kurta, 2007), whereas crevices were narrow, vertical or horizontal spaces in a tree caused by breakage due to high winds, lightning, or other natural events. Direction of the roost exit was obtained with a compass. Height of tree and height of emergence site were determined with a clinometer (Suunto, Vantaa, Finland). Percent canopy closure was obtained with a concave densiometer (Forest Densiometers, Bartlesville, Oklahoma) at the base of the roost tree and at 5-m from the base, in each cardinal direction, for a total of eight readings (Gardner et al., 1991). Number of hours that the roost site was exposed to sunlight was estimated, and each roost was classified as having high ($\geq$10 h), medium ($\geq$5 but <10 h), or low (<5 h) solar exposure. Foliage (clutter) around emergence sites was categorized as low (0–33% clutter), medium

(34–67% clutter), or high (68–100% clutter—Winhold, 2007). Characteristics of the nearest tallest and shortest trees sometimes are implicated in roost selection by bats (Barclay and Kurta, 2007; Kalcounis-Rüppell et al., 2005), so I also measured the distance from the roost tree to the nearest tallest and shortest trees, along with height, decay stage, and species of those trees.

Comparisons at the level of the plot and stand.—I measured variables for trees in the plot surrounding the roost tree and in the stand (Gardner et al., 1991) to assess the available habitat for evening bats within the immediate area. A circular plot of 0.1 ha (17.8-m radius) was delineated around each roost tree (Brigham et al., 1997; Kurta et al., 2002), and I recorded the species, decay stage, and diameter of all trees within the plot that were $\geq$10 cm in diameter. For each plot, I calculated Shannon's diversity index (H') and Pielou's measure of evenness (J'—Brower and Zar, 1984; Pielou, 1966), using the number of trees representing each genus that were present. The density (individuals/ha) and basal area of trees also was calculated for each plot (Brower and Zar, 1984). If plots from neighboring roost trees overlapped, I assessed only the plot from the roost tree that was discovered first to maintain independence of data.

To evaluate roost selectivity by evening bats at the level of the plot, I randomly selected a tree that had potential roosting characteristics (cavity, crevice, or exfoliating bark) from those in the plot surrounding the roost. A distance and a direction from the roost tree were determined using a table of random digits (Zar, 1999), and the tree closest to the random location was selected. For this randomly selected tree, I recorded the same characteristics that I did for the roost, except emergence height. For all other trees in the plot around the roost tree, I recorded the species, diameter, and decay stage.

To examine roost selectivity at the level of the stand, I used a tree that was located >36 m (twice the radius of the roost plot) from the roost tree but <200 m of the roost. A distance and a direction from the roost tree were selected using a table of random digits (Zar, 1999), and the tree nearest to this random location that appeared suitable for roosting was selected. I delineated a 0.1-ha circle around the new tree and recorded all characteristics of this randomly selected tree that I had noted for the roost tree and randomly selected tree in the roost plot, except emergence height. For all other trees in the stand plot, I recorded the species, diameter, and decay stage.

Comparisons at the level of the landscape.—Landcover can be important in determining distribution of bats and areas that potentially are biologically significant to specific species, such as open water, wetlands, or deciduous forests (Jaberg and Guisan, 2001). Coordinates (Universal Transverse Mercator) of my roost locations were downloaded into ArcGIS and overlaid on digital orthophoto quadrangles. I measured the distance to permanent water and open fields (croplands, conservation easements, or pastures) from roost trees and randomly selected trees because similar landscape features were found to be important habitat for evening bats in Indiana (Duchamp et al., 2004).

The National Oceanic and Atmospheric Agency (NOAA) digitally mapped 18 landcover types of Michigan in 2000 (NOAA, 2000). According to NOAA, 11 landcovers characterize the study area: deciduous forest, agricultural land, grassland-herbaceous, scrub-shrub, palustrine forested wetland, palustrine scrub-shrub, palustrine emergent wetland, water, palustrine aquatic bed, mixed forest, and development. To assess the influence of landscape structure on roost selection, I used ArcView GIS to delineate a circular buffer, which is a zone of a specified width around a point, around each roost tree. Following Miles

(2005), I set the radius of this buffer at the mean maximum distance between roosts used by all individual evening bats in my study, which is a measure of potential home range. I then determined the percent of each type of landcover within this home range.

Roosts of bats are often clustered in the landscape (Barclay and Kurta, 2007). Areas of high density of roosts in my study were determined using ArcGIS (Average Nearest Neighbor), and the proportion of each type of landcover in these areas was calculated. Also, Moran's *I* test of spatial autocorrelation (*Z* score—Loeb and O'Keefe, 2006) was utilized to evaluate the spatial distribution of roost trees used by evening bats in the project area. Moran's *I* test considers both the location of the point as well as its attributes (e.g., distance to water or height of tree) when detecting spatial patterns (Lee and Wong, 2001). I used eight attributes of the roost tree when applying this test: diameter, height, percent canopy cover, percent original bark, percent current bark that was exfoliating, and percent available loose bark, distance to water, and distance to open fields; categorical variables can not be used with Moran's test.

Statistical analyses.—Data were presented as $\overline{X} \pm 1$ *SE*, and an alpha of 0.05 was set as the significance level for statistical tests. Statistical analyses were performed primarily with Systat 11 (SYSTAT Software, Inc., Richmond, California) or Excel (Microsoft, Redmond, Washington), although VassarStats was used to conduct Fisher's exact or Chi-square tests (Lowry, 2008). Continuous variables were examined using analysis of variance, two-sample *t* tests, and Tukey's pairwise comparison test. To obtain normality of the data, I conducted logarithmic or square-root transformations for distances (i.e., distances to landscape characteristics and distances traveled); variables presented as percentages, such as canopy cover, were arcsine-transformed before analysis. Categorical or ordinal data were analyzed using chi-square or Fisher's exact tests (Zar, 1999).

The mean ± angular deviation of the direction that bats exited the roost was calculated using circular descriptive statistics, and to test whether the exits were oriented uniformly, I used a modification of Smirnov's test for circular distributions (Batschelet, 1965; Watson 1961, 1962; Zar, 1999). Values for diversity of genera of trees were compared using a *t*-test with infinite degrees of freedom (Brower and Zar, 1977; Zar, 1999).

RESULTS

Mist netting and radio tracking.—During the 2-year study, I captured 76 evening bats (Table 1.2); one individual flew away before the age-sex was determined, so it was not included in analyses based on reproductive condition or age. Of the evening bats that I captured, 45 were adult females, 12 were juvenile females, and 18 were juvenile males; no adult males were captured (Table 1.2). The first seasonal captures of evening bats were on 24 May 2006 and 18 May 2007, and both individuals were not palpably pregnant. The latest dates I captured a female classified as not palpably pregnant were 23 May 2006 and 7 June 2007, whereas the first palpably pregnant females were caught on 5 June 2006 and 7 June 2007. The first lactating females were captured on 18 June in both years, and the last were caught on 30 July 2006 and 23 July 2007. On 8 July 2007, I caught an adult with an attached youngster; the pup had a forearm length of 30 mm, weighed 6.0 g, and was covered in grayish-brown fur. The first volant juveniles, however, were not netted until 18 July 2006 and 19 July 2007. The last date on which an evening bat was known to occur in Michigan was 26 August 2006 and 15 August 2007, even though netting occurred into September in both years.

Adult evening bats weighed 12.7 ± 0.3 g, ranging from 9.5 to 19.0 g (Table 1.3). I included data from not palpably pregnant females with data from pregnant females because 90% of females give birth each year (Watkins, 1972) and preliminary analyses indicted no significant difference in mass between these conditions ($t_{18} = 1.87$; $P = 0.08$). Pregnant evening bats weighed more than lactating or post-lactating individuals ($F_{2, 42} = 14.63$; $P < 0.001$). Volant juveniles weighed 8.1 ± 0.3g, with a range of 5.0 to 11.5 g; body mass did not differ between female and male juveniles ($t_{25} = 1.08$; $P = 0.29$), yet a significant difference existed between juveniles and adults ($t_{69} = 9.90$; $P < 0.001$; Table 1.3).

Forearm length of adult evening bats was 36.3 ± 0.2 mm (Table 1.3). Compared to adults, volant juveniles had a shorter forearm (34.6 ± 0.3 mm; $t_{71} = 5.77$; $P < 0.001$). Female juveniles had a slightly longer forearm (35.3 ± 0.5 mm) than male juveniles (34.1 ± 0.3 mm; $t_{27} = 2.10$; $P = 0.04$). Although the mass of the nonvolant juvenile (6.0 g) captured with an adult was within the range of that of volant juveniles (5.0–11.5 g), the forearm length of the nonvolant juvenile (30 mm) was less than that of any juvenile capable of flight (31–38 mm).

Of the 76 bats captured, I radio tracked 44 (Table 1.2). Not all individuals captured were radio tracked because of a limited number of transmitters and assistants and attempts to evenly distribute samples among reproductive conditions. Eight individuals were radio tracked twice either within or between years. One reproductive female was tracked twice in 2006, and three females and one juvenile were radio tracked twice in 2007. Three reproductive females from 2006 were radio tracked during both years. Transmitters stayed attached for 7.7 ± 0.5 days, and the 44 individuals were radio tracked for a total of 346 transmitter-days.

Time of emergence and size of the colony.—Of the 190 roost observations conducted during the 2-year study, evening bats were observed exiting roosts during 152 of those observations (Fig. 1.2). Occasionally bats with transmitters did not leave the roost, usually because of bad weather. However, most observations of zero bats exiting the tree occurred when I watched a tree that did not shelter a bat with a transmitter on that particular night, but evening bats had previously occupied the tree. Eleven roost observations (7.2%) were of single bats emerging from trees; observations of single bats consisted of five pregnant, two lactating, one postlactating, two male juvenile, and one female juvenile. Approximately 66% of my observations were of 2–21 bats in a tree, whereas only 3.3% of observations were of >41 bats in a roost at the same time (Fig. 1.3). Number of evening bats observed during emergence from a single tree decreased slightly between pregnancy (20.2 ± 3.1; $n = 17$ observations; 25–31 May 2006 and 1–10 June 2006 and 19–31 May 2007 and 1–2 June 2007) and lactation (13.4 ± 1.7; $n = 16$; 4–8 July 2006 and 3–15 July 2007); group size was highest during the transition between lactation and postlactation, after juveniles had begun to fly (27.4 ± 3.5; $n = 21$; 14–16 July 2006 and 16–29 July 2007). The colony apparently fragmented into smaller groups in early August, when the average emergence count was 10.5 ± 1.3 bats ($n = 41$).

The colony of evening bats in Michigan discovered by Kurta et al. (2005) consisted of ca. 68 individuals, including juveniles, and they estimated the number of adults to be only 27. In my study, volant juveniles were never encountered before 18 July, so maximum number of adults in a single roost was 40 bats on 16 June 2006 (roost 601) and 46 bats on 16 June 2007 (roost 605; Fig. 1.2). The largest population at one tree in 2006 occurred after youngsters were flying, with 57 individuals leaving roost 604 on 24 July. In 2007, however, the largest count after young became volant was only 42 individuals on 22 July from roost 601. Although multiple roost trees were watched on some evenings, total number of bats emerging from all simultaneously observed roosts did not exceed the population size counted from these single roosts.

The first evening bat, the bat with a transmitter, and the last bat left the roost at 8.1 ± 0.6 (n = 152), 12.7 ± 0.7 (n = 119), and 16.8 ± 0.7 (n = 152) min after sunset, respectively. There were fewer records of bats with transmitters exiting the roost than first and last bats because either the transmitter fell off before the bat left or I did not have a functional receiver to document the time of emergence. First emergence ranged from 27 min prior to sunset to 27 min after sunset (8.1 ± 0.6; Fig. 1.4), with a strong correlation between time of first emergence and time of sunset ($r = 0.88$; $P < 0.001$). In some species, time of first emergence is more strongly correlated with time of civil twilight than with sunset (e.g., Viele et al., 2002). However, this was not true of evening bats, for which the correlation between times of emergence and end of civil twilight was similar ($r = 0.89$; $P < 0.001$; Fig. 1.5) to that between time of emergence and sunset. The first evening bats always departed before (-25 ± 0.6 min) the end of civil twilight. Not including single bats, duration of emergence of the colony (2–57 bats) was 9.1 ± 0.7 min (<1–37 min); number of bats leaving a tree and duration of emergence were moderately correlated ($r = 0.51$; $P < 0.001$; Fig. 1.6).

Fidelity and Switching.—Evening bats occupied 19 trees in 2006 and 29 trees in 2007. In most species of bats, some trees are used more often than others by a large number of bats and are termed primary roosts, whereas other trees are used less extensively and are called alternate roosts (Barclay and Kurta, 2007). The distinction between alternate and primary roosts often is arbitrary but empirically evident (Fig. 1.7). For my study, I used the term primary to describe roost trees that were occupied for >100 bat-days in a single season, and the remaining roosts were classified as alternate. Consequently, three trees were primary roosts in 2006 (roost 601, 604, 606), and five trees were primary roosts in 2007 (roost 601, 605, 606, 701, 709); two trees were primary roosts in both years (roost 601 and 606; Fig. 1.7). The six primary roosts accounted for 65.4% of all bat-days. Primary trees generally were not used in August of either year, when juveniles were no longer nursing, except roost 601, which was inhabited by eight bats on 5 August 2007.

At least some evening bats exhibited inter-annual fidelity to their home range near Palmyra. Four bats that I banded in 2006 were recaptured in the study area in 2007. All four bats were reproductive in 2006 (two pregnant and two postlactating) and again in 2007 (three pregnant and one postlactating).

Although evening bats exhibited inter-annual fidelity to their home range, I did not radio track any individual bats in 2007 to the same tree as in 2006. Only three bats, however, were radio tracked in both years. Nevertheless, the colony as a whole demonstrated inter-year fidelity to many roost trees. One of three roosts originally discovered in 2004 (Kurta et al., 2005) was occupied by up to 40 evening bats in 2006 and 46 bats in 2007 (roost 605 in my study). Fifteen of 19 roost trees (79%) that I discovered in 2006 were utilized to some degree in 2007, and 15 of 29 (52%) roosts used in 2007 also had been occupied in 2006.

Intra-year fidelity to roost trees by evening bats was also high; within each year, radio-tracked members of the colony roosted in 63% of trees used by other radio-tracked individuals. Individuals also exhibited intra-year fidelity; one bat re-used a primary tree (601) in two separate radio-tracking sessions in 2006. In 2007, eight bats returned to roosts used previously during the season, either in a different radio-tracking session ($n = 2$) or after

$\geq$ 1 night in another roost tree (n = 6). Five of these bats returned to primary roosts 601 and 701.

I examined whether or not fidelity to a roost tree was associated with roost structure; in other words, I analyzed whether or not evening bats spent more time in cavities or crevices or under bark. Data for different years and sex of juveniles were lumped because preliminary analyses indicated no significant differences in time spent in different types of roosts between years or sexes. A significantly higher proportion of radio-tracked individuals roosted on at least 1 day in cavities ($\chi^2_2 = 20.46$; $P < 0.05$; n = 29 bats; bats radio tracked twice in a season were only counted once) than under exfoliating bark (n = 9) or in crevices (n = 4; Fig. 1.8), even though cavities were not significantly more available than crevices or exfoliating bark in the surrounding forest (see *Comparison of trees in roost plots and stand plots*). Overall, bats were found in the same tree that they had used the previous day on 64% of days that they were radio tracked, and overall, 73% of consecutive days were in cavities. Maximum number of consecutive days that an evening bat spent in the same roost was 12. Evening bats of all reproductive conditions spent more time in cavities than other types of roosts ($\chi^2_6 = 69.23$; $P < 0.001$; Fig. 1.9).

Forty-four individuals were used for an analysis of roost switching and distance traveled between roost trees in 2006–2007; however, only 43 bats were used for comparisons of the effects of reproductive conditions and ages on roost switching, because one individual escaped before reproductive condition was recorded. Bats did not appear stressed by the experience of being captured and fitted with a transmitter. Number of switches and distance traveled the 1st night after capture were not significantly different from values for the 2nd night; therefore, I included the 1st night in the analysis (Table 1.4). Evening bats switched roosts 122 times during 2006–2007. Switches occurred every 2.9 days, and evening bats conducted 2.7 ± 0.3 changes/bat ($n = 44$ bats). Number of roost switches and number of days that individuals were tracked were correlated ($r = 0.59$; $P < 0.001$; Fig. 1.10). Frequency of switching (switches per days that the bat was radio tracked) did not differ significantly among pregnant, lactating, postlactating, and juvenile bats ($F_{3, 40} = 1.46$; $P = 0.24$), nor did it differ among juvenile males or females ($t_{14} = 0.35$; $P = 0.73$). Frequency of roost switching by all adults combined did not differ from that of all juveniles combined ($t_{42} = 1.25$; $P = 0.22$).

The distance that individual evening bats ($n = 44$) traveled between roosts ranged from 18 to 3,041 m, with a mean of 547 ± 102 m/switch. Distances moved for ca. 91% of roost switches were <1 km (Fig. 1.11). Three pregnant females and one male juvenile occupied roosts that were >2 km apart on consecutive days. Reproductive condition of evening bats did not influence distance traveled per switch ($F_{3, 35} = 2.00$; $P = 0.13$). The distance between roosts used by juveniles was not significantly different from all adult females combined ($t_{37} = 0.35$; $P = 0.73$).

ROOST AND HABITAT ASSESSMENT

Roost trees.—Thirty-three roost trees of 11 species were used by evening bats during the study (Table 1.5). Approximately 42% of trees were green ash (*Fraxinus pennsylvanica*). Other trees were three common hackberries (*Celtis occidentalis*), three silver maples (*Acer saccharinum*), three sugar maples (*Acer saccharum*), two American elms (*Ulmus americana*), two eastern cottonwoods (*Populus deltoides*), two shellbark hickories (*Carya laciniosa*), one American basswood (*Tilia americana*), one American sycamore (*Platanus occidentalis*), one boxelder (*Acer negundo*), and one honey locust (*Gleditsia triacanthos*).

Roost trees were about equally distributed among decay stages, with 33% of trees alive, 30% of trees at stage 2, and 36% of trees dead (Table 1.5). Height of roost trees was 25.6 ± 1.4 m, and diameter was 57.6 ± 3.7 cm (Table 1.6). Mean height of emergence was 13.3 ± 0.7 m; height of emergence was correlated with height of the roost tree ($r = 0.56$; $P = 0.001$; Fig. 1.12). Even though ca. 50% of emergence sites were exposed to sunlight for >10 h, there was no statistical difference in distribution of roosts trees among the categories of solar exposure (Fisher's Exact; $P = 0.05$; Table 1.6). About 82% of trees had low amounts of clutter around the entrance of the roost (Fisher's Exact; $P = 0.9$; Table 1.6). Also, 67% of roost exits were in the south side of the roost tree with a mean direction of 159 ± 75 degrees (Fig. 1.13). Nevertheless, based on circular statistics (Batschelet, 1965), I found that the distribution of the directions of the exit did not differ from uniform ($U^2 = 0.08$; $P > 0.05$).

Overall, roost trees had 81.5 ± 3.6% of their bark remaining, and 22.4 ± 3.8 % of that remaining bark was apparently loose and available for roosting. Consequently, 17.7 ± 3.3% (81.5% x 22.4%) of the original bark was still present and available for bats to roost under. Trees with exfoliating bark as roost structures had a significantly higher percentage of current bark that was exfoliating (available exfoliating bark) than trees with cavities or crevices ($F_{2, 30} = 7.45$; $P = 0.002$; Table 1.6).

Fifty-five percent of roost structures used by evening bats were cavities, whereas exfoliating bark and crevices composed 27 and 18%, respectively. Cavities used by evening bats were located primarily in healthy or dying trees, as opposed to dead trees (79%; $\chi^2_1 = 5.26$; $P = 0.02$), and although the sample was too small for statistical analysis, crevices appeared evenly distributed among the three stages, with crevices occurring in two trees of each decay stage (Table 1.5). Roosts under exfoliating bark were mostly in dead trees

(67%); 22% were in trees of decay stage 2, and one tree (shellbark hickory) was healthy ($\chi^2_2 = 6.24$; $P = 0.04$; Table 1.5). All primary roosts were in cavities, except a crevice that was used for 129 bat-days in 2007; this roost tree (605) was initially discovered in 2004 (Kurta et al., 2005) and used in 2006 and 2007.

Comparison of trees in roost plots and stand plots.—Randomly selected trees within the roost plot were composed of fewer genera ($n = 7$) compared to randomly selected trees in the stand ($n = 11$; Table 1.7), but this difference was not significant ($\chi^2_1 = 0.89$; $P = 0.35$). Roost trees were taller and had more exfoliating bark than randomly selected trees (Table 1.8). Although roost trees were distributed evenly among decay stages, randomly selected trees in the plot and stand were healthier than roost trees ($\chi^2_4 = 10.41$; $P = 0.03$; Table 1.9). Roost trees also had significantly lower subcanopy clutter than randomly selected trees ($\chi^2_4 = 33.65$; $P < 0.001$), but amount of solar exposure did not significantly differ among roost trees and randomly selected trees (Table 1.9). I combined data for canopy cover from randomly selected trees in the roost plot and actual roost trees because these trees were in the same plot, and I compared canopy cover in roost plots ($n = 63$) to that surrounding randomly selected trees within the stand plots ($n = 36$). Canopy cover around trees in the stand was significantly denser than in the roost plot (Table 1.8; $t_{97} = 3.44$; $P = 0.001$).

Roost trees and randomly selected trees in the plot and stand did not differ in diameter; however, they varied significantly in height ($F_{2,\,96} = 4.09$; $P = 0.02$), available exfoliating bark ($F_{2,\,96} = 3.22$; $P = 0.04$), and canopy cover ($F_{2,\,96} = 6.56$; $P = 0.002$; Table 1.8). Roost trees were taller and had less canopy cover. Although the percent of exfoliating bark available for roosting was significantly different among roost and randomly selected trees, the conservative Tukey's test could not identify between which groups the differences occurred.

Of the categorical variables measured for roost and randomly selected trees (Table 1.9), decay stage ($\chi^2_4 = 10.41$; $P = 0.03$) and subcanopy clutter ($\chi^2_4 = 33.64$; $P < 0.001$) differed significantly. Clutter around roost trees was less and more roost trees were in decay stage 3. Solar exposure did not vary significantly between roost and randomly selected trees ($\chi^2_4 = 7.33$; $P = 0.12$). Last, roost trees and randomly selected trees in the plot and stand did not differ significantly ($\chi^2_4 = 2.4$; $P = 0.66$) in types of roosting structures (cavity, crevice, or exfoliating bark) potentially available to evening bats.

Distance to the nearest tallest tree was significantly greater from the roost tree than from randomly selected trees ($F_{2,\,94} = 8.93$; $P < 0.01$). However, distance to the nearest shortest tree did not vary significantly among the roost and randomly selected trees (Table 1.10). The nearest tallest and shortest trees were distributed equally among the three decay stages ($P = 0.66$).

Within plots, diversity of trees was numerically greater in the stand ($n = 20$; $H' = 0.98$) than around the roost tree ($n = 14$; $H' = 0.82$), but there was no significant difference ($t_\infty = 0.26$; $P > 0.05$); evenness of tree genera also was about the same in the plot ($J' = 0.73$) compared to the stand ($J' = 0.77$; Table 1.11). Trees within the roost plot (32.4 ± 0.8 cm) were significantly greater in diameter than stand trees (26.4 ± 0.5 cm; $t_{1699} = 6.84$; $P < 0.001$). At both the plot- and stand-level, ca. 80% of trees were alive and only ca. 6% of trees were dead; therefore, there was no significant difference between the decay class of stand and plot trees ($X^2_3 = 0.67$; $P = 0.72$; Table 1.11). Mean density of trees around the roost (225 ± 17 trees/ha) was significantly lower than around randomly selected trees in the stand (285 ± 18 trees/ha; $t_{65} = 2.51$; $P = 0.014$), but mean basal area around roost trees (1.12 ± 0.06 m^2/ha) was significantly greater than around stand trees (0.76 ± 0.04 m^2/ha; $t_{1699} = 5.23$; $P < 0.001$; Table 1.11).

Landscape level.—Evening bats roosted in a clustered rather than dispersed pattern in the project area (nearest neighbor analysis: $Z = -4.30$; $P = 0.01$). There were two areas of high density of roost trees, and they occurred where Black Creek meanders into a U-shape near the River Raisin (roost cluster 1) and along the River Raisin upstream of its confluence with Black Creek (roost cluster 2; Fig. 1.1 and 1.14). Density was 0.74 roosts/ha in Roost cluster 1 and 1.10 roosts/ha in roost cluster 2; density in the remaining study area was 0.02 roosts/ha.

Palustrine forested wetland was the dominant landcover within both roost cluster 1 and 2 (48 and 53%, respectively; Fig. 1.15). Other types of landcover in roost cluster 1 were water (27%), palustrine scrub-shrub (16%), palustrine aquatic bed (4%), agricultural (2%), grassland-herbaceous (2%), and deciduous forest (2%). In roost cluster 2, other landcovers consisted of water (19%), agricultural land (15%), palustrine scrub-shrub (8%), deciduous forest (3%), and palustrine aquatic bed (2%). Similarly, the remaining study area (ca. 212 ha) was composed primarily of palustrine forested wetland (51%), deciduous forest (15%), agricultural land (12%), palustrine scrub-shrub (9%), grassland-herbaceous (5%). Palustrine emergent wetland, palustrine aquatic bed, water, evergreen forest, mixed forest, and scrub-shrub each contribute < 2% each to the remaining study area. The largest difference between the roost clusters and the remainder of the study area was in the amount of water, which composed 19–27% of the area of the clusters but <2% outside the clusters (Fig. 1.15).

Roost trees were located significantly more often in palustrine forested wetland (85%) than in palustrine scrub-shrub (9%), deciduous forest (3%), and grassland-herbaceous habitats (3%; $X^2_3 = 63.36$; $P < 0.001$; Table 1.12). The single tree within deciduous forest was actually on a ridge surrounding palustrine forested wetlands, and the only tree that stood in a grassland-herbaceous area occasionally was inundated. Similarly, randomly selected trees in both plot (90%) and stand (72%) were found primarily in palustrine forested wetland; however, 25% of stand trees were located in deciduous forest, whereas roost (3%) or plot trees (0%) seldom were (Table 1.12).

The mean maximum distance between roosts used by all individual evening bats in my study was 687 m, so I delineated a circle with a 687-m radius around each roost tree for analysis of landscape structures in the potential home range of evening bats (Miles, 2005). Because roost trees of this colony were highly clustered in the landscape, there was overlap among the circles (Fig. 1.14). As a result, I used the outer boundaries of the non-overlapping areas to define the potential home range of the colony for my study (Fig. 1.14). The resulting area encompassed 707.2 ha. There were 13 landscape features (NOAA, 2000) within this potential home range. The most common habitat was agricultural land (68.3%), followed by palustrine forested wetland (14.9%) and deciduous forest (6.4%). Palustrine scrub-shrub (2.6%), grassland-herbaceous habitat (3%), and water (2.5%) composed a small proportion of available habitat. The remaining eight habitats composed <3.5 % of the total combined.

When considering landscape variables on the selection of roost trees, I found there was no significant difference in distance to water ($F_{1, 67} = 0.41$; $P = 0.52$) or open fields ($F_{1, 67} = 0.14$; $P = 0.71$) between roost and stand trees (Table 1.13). Statistical analysis using analysis of variance only considers the attributes of roost trees (e.g., distance to water), and nearest neighbor analysis takes into account only the spatial distribution of points relative to their neighbors. Conversely, Moran's *I* detects spatial patterns by considering both the location of the points and their attributes simultaneously (Lee and Wong, 2001). If a positive spatial autocorrelation occurs in a point distribution, then points with similar characteristics are distributed near one another. I used Moran's *I* to investigate if a positive spatial relationship exists due to eight attributes of roost trees. Of these attributes, only distance to open fields had a significantly positive spatial autocorrelation (Moran's $I = 0.23$, $Z = 3.10$; $P < 0.05$), indicating that the roost trees with similar distances to open fields are clustered in the landscape.

DISCUSSION

Mist netting and radio tracking.—In southern portions of the bat's range, such as southwestern Missouri, evening bats apparently do not migrate (Boyles and Robbins, 2006), but this is not true in northern areas. No evening bats, for example, are known to overwinter in Indiana or Ohio (Gottschang, 1981; Mumford and Cope, 1964; Whitaker and Gummer, 2003). The same appears to be true for Michigan, because I did not capture any evening bat after 26 August, despite netting into September.

Adult males are infrequently found with maternal colonies of evening bats in Indiana (Whitaker and Gummer, 2003), and males apparently do not migrate to Michigan. All evening bats captured during my study were female, as were all those mentioned in older records from Michigan and Ontario (Kurta, 2008; Peterson, 1966). In fact, the most northern records of males are from Posey County, Indiana (Whitaker and Gummer, 2003), and Boone County, Missouri (Easterla, 1965), which are >250 km southwest from Palmyra. The dearth of males in northern regions also is typical of some other species of bats that are migratory and colonial, such as the Indiana bat (Whitaker and Brack, 2002); male Indiana bats, for example, compose only 11% of the adult population in summer in Michigan, which also is at the northern edge of that species' range (Kurta and Rice, 2002). Presumably, female bats reduce competition for resources that they or their young need by migrating northward for the summer.

It is unknown how far females travel from their wintering grounds to southeastern Michigan. Humphrey and Cope (1968) document evening bats migrating from Indiana to Kentucky (ca. 300 km), and Watkins (1969) reports an individual flying ca. 550 km from Missouri to Arkansas. No evening bats are known to winter in Ohio or Indiana (Gottschang, 1981; Mumford and Cope, 1964; Whitaker and Gummer, 2003), so evening bats in Michigan presumably migrate at least as far as the Ohio River. The minimum distance from Palmyra to the Ohio River is ca. 309 km.

Little information is available as to when evening bats appear on their summer range, although Watkins and Shump (1981) indicated that these bats arrived at their maternity grounds in Missouri between 6 and 15 May, considerably earlier than in Michigan. Evening bats at the northernmost colony in Michigan also migrate southward earlier than evening bats in more southern parts of their range. In my study, the latest dates that evening bats occurred in Michigan were 26 August 2006 and 15 August 2007. Evening bats were found from early August until mid-November in Indiana, and they migrate from Nebraska by 21 September and from southeastern Illinois by 1 November (Clem, 1992; Geluso et al., 2004; Humphrey and Cope, 1968; Mumford and Cope, 1964; Smith and Parmalee, 1954). Earlier migration in the north also has been reported for little brown bats (Barbour and Davis, 1969). Evening bats probably leave Michigan at the end of August in response to decreasing photoperiod and decreasing nighttime temperatures (Weather underground, 2008; Fig. 1.16), which presumably limit foraging opportunities.

The reproductive cycle of evening bats in Michigan coincides with that of other populations of evening bats in the north. Female evening bats arrive in southeastern Michigan in mid-to-late May and give birth to two pups between mid-June and early July. In Nebraska, lactating females were captured from 16 June to 24 July (Benedict, 2004; Geluso et al., 2004; Kunz, 1965), indicating that evening bats give birth to their pups in approximately mid-June. In Missouri, female evening bats give birth between 14 and 17 June (Watkins and Shump, 1981). In the southern portion of their range, though, parturition occurs earlier, from mid-May to mid-June (Amelon and Burhans, 2006).

In my study, volant juveniles were not seen until 18 and 19 July; whereas in Nebraska, volant juveniles were captured as early as 30 June (Benedict, 2004; Geluso et al., 2004). In Missouri, juveniles left the roost to forage on 11 July; however, they were flying around the roost by 6 July (Watkins and Shump, 1981), much earlier than in Michigan. Generally, it takes ca. 3 weeks for young to become volant in the core of the species' range (Whitaker and Hamilton, 1998), but in Michigan, juveniles took ca. 4 weeks to become volant. Fujita (1986) found that postnatal growth rate in little brown bats was slower in Alberta than New Hampshire, indicating that lower ambient temperatures at higher latitudes decrease growth rate, and this phenomenon may explain the slower growth in Michigan compared with more southern sites.

Emergence from the roost.—Emergence time of bats varies from species to species, and it may depend upon foraging strategy, flight patterns, predation risk, and even barometric pressure (Jones and Rydell, 1994; Paige, 1995). First emergence of evening bats in Michigan

(8 min after sunset) was earlier than several other temperate bat species, such as the big brown bat (35 min—Jones and Rydell, 1994), Indiana bat (18 min—Viele et al., 2002), and cave myotis (37min; *Myotis velifer*—Jones and Rydell, 1994). Evening bats may have emerged early to take advantage of the activity of certain types of insects; dipterans, which accounted for 20% of the diet of evening bats in Michigan (Chapter 2), typically are active early in the evening, and bats that prey heavily on Diptera often depart their roosts early compared to other species (Jones and Rydell, 1994).

Overall, emergence of evening bats was strongly correlated with time of sunset (Fig. 1.4) and twilight (Fig. 1.5), similar to the emergence of Indiana bats and many other temperate species (Viele et al., 2002). Only on 13 occasions did evening bats leave prior to sunset, and the two earliest times were 17 and 27 min prior to sunset. Although a number of species vary their time of emergence over the season more closely with the end of twilight (Viele et al., 2002), this was not true of evening bats. Length of twilight presumably did not affect the timing of emergence by evening bats because they began departing early in the evening and total emergence was very rapid; consequently, all bats left the roost well before the end of twilight.

Size of the colony.—In both years, the size of the colony of evening bats in Michigan peaked in mid-June when bats were pregnant (>40 bats) and in mid-July after juveniles became volant (>42 bats), a temporal pattern seen in a few other tree-roosting species, such as the northern bat (Foster and Kurta, 1999; Barclay and Kurta, 2007). During pregnancy, which occurs during the coolest portion of the reproductive season, evening bats may cluster together in larger groups to help maintain a high body temperature (Foster and Kurta, 1999) and to avoid torpor, which can delay fetal development (Kunz, 1982); such behavior might be particularly important at the northern edge of their range. In August, number of bats in a single tree decreases to a mean of ca. 10 individuals, which suggests that the bats are dispersed among a number of different trees or that they have already started their southward migration. Whitaker and Gummer (2203:59) also qualitatively note that "after the young become volant, more trees are used [and] individual dusk counts are smaller" in Indiana. Use of a large number of trees in August may be a behavior that introduces young-of-the-year to potential roost trees that the bats might use the following spring, when they return after their first period of hibernation (Kurta et al., 2002).

Roost fidelity and switching.—Although I recaptured few banded individuals, evening bats apparently return each year to southeastern Michigan to raise their pups, as indicated by the predictable occurrence of evening bats in the study area and the use of numerous roost trees in multiple years. Such inter-annual site fidelity is common in other tree-living species, such as Indiana bats (Gumbert et al., 2002), eastern pipistrelles (*Perimyotis subflavus*—Veilleux and Veilleux, 2004), and big brown bats (*Eptesicus fuscus*—Willis and Brigham, 2004). Females return to Michigan in spring, when they are pregnant, when they are presumably stressed after a prolonged hibernation and long-distance migration, and when insects are scarce because of cool and wet weather. By returning to a familiar home area, these energetically strapped bats would not have to waste energy in finding suitable roosting sites or foraging areas (Barclay and Kurta, 2007; Lewis, 1995). Inter-annual site fidelity likely is important for sustaining healthy bat populations (Veilleux and Veilleux, 2004).

Reuse of specific trees in different years by members of the same species is known to occur in at least five other species in North America—big brown bat, California myotis (*M. californicus*), Indiana bat, northern bat (*Myotis septentrionalis*), and southeastern myotis (*M.*

austroriparius)—as well as 14 other species found throughout the world and from a diversity of ecological niches (Barclay and Kurta, 2007; Lewis, 1995). Only four trees discovered in 2006 were not used by evening bats in 2007, and two of these were damaged over the winter. One tree (roost 611) fell over, and the second tree (roost 614) lost the branch that evening bats were using as a roost.

Most species of tree-roosting bat appear to change trees every 2–3 days. For example, Indiana bats in Michigan and silver-haired bats (*Lasionycteris noctivagans*) in Oregon switched every 2.7 and 2.9 days, respectively (Kurta et al. 2002; Barclay and Kurta, 2007). Evening bats in Michigan switched roosts every 2.9 days, which is similar to studies in Missouri and South Carolina, where evening bats changed trees every 2.3 days (Menzel et al., 2001; Timpone et al., 2006). Kurta et al. (1996, 2002) reported a lower frequency of roost-switching by lactating compared to pregnant Indiana bats in Michigan, and O'Donnell and Sedgeley (1999) indicated that adult female long-tailed bats (*Chalinolobus tuberculatus*) in New Zealand moved more frequently than juveniles. However, evening bats in my study did not switch more during a particular reproductive period, nor did frequency of switching differ between adults and juveniles. A lack of differences among reproductive conditions or between age groups is commonly reported in the literature, although samples tend to be small, leading to low statistical power (Barclay and Kurta, 2007).

Changing roosts may be energetically costly and increase risk of predation (Lewis, 1995); however, Barclay and Kurta (2007) suggest that the energetic cost of roost switching is trivial and, therefore, this behavior is common among tree-living bats (Barclay and Kurta, 2007; Carter and Menzel, 2007). Three broad types of roost switching are documented: episodic, emergency, and recurrent (Barclay and Kurta, 2007). Episodic switching occurs as a response to changes in physiological condition (e.g., reproductive condition), changes in the population (e.g., when young begin to fly), or other predictable factors. Emergency switching occurs because of an unpredicted event, such as attempted predation or sudden destruction of a roost in a storm. Recurrent switching describes the repeated movement of individual bats between roost trees. This type of switching may provide familiarity with suitable roosts, facilitate information exchange, and maintain social bonds (Barclay and Kurta, 2007; Lewis, 1995; Willis and Brigham, 2004). Some roost switching by evening bats in Michigan may have been episodic; for example, fewer bats tended to occupy the same tree during lactation than during pregnancy, and the colony seemed to fragment in August after young became volant. Most roost changes, however, appear to be examples of recurrent roost switching, although the exact reasons for such changes were not apparent and are little understood for most species of bats (Barclay and Kurta, 2007).

Habitat assessment.—In Michigan, evening bats roosted in bottomland forest composed mostly of palustrine forested wetland that periodically floods. Trees within the roost plot were significantly greater in diameter than trees in the stand, and mean basal area of trees surrounding roost trees was also significantly higher than trees around randomly selected trees in the stand (Table 1.11). Furthermore, density of trees within the roost plot was considerably less than that in the stand plot (Table 1.11). This indicates that evening bats roost in stands of trees that are older, because stand density decreases via self-thinning as age of the stand increases (Kashian et al., 2005). Hence, roost trees of evening bats appeared to be more mature and taller and located in areas with a lower density of trees than randomly selected sites in the stand. Evening bats in other parts of their range also appear to select large trees in mature stands of low density (Miles et al., 2007; Perry et al., 2007), and these traits apparently are preferred by many species of bats (Barclay and Kurta, 2007; Kalcounis-Rüppell et al., 2005).

Roost trees were located in areas with more open canopy than randomly selected trees in the stand, and the nearest tallest trees were further away from the roost than from randomly selected trees in the stand (Tables 8 and 10). Furthermore, clutter around roosts typically was low compared with randomly selected trees in the stand (Table 1.9), which presumably facilitates safely getting in and out of the roosts. Some authors (e.g., Miller et al., 2002) have hypothesized that choosing roosts in areas with low canopy cover, low clutter, and greater distances to tall trees may permit more solar radiation to warm the tree, but I found no differences between roosts and randomly selected trees in amount of solar exposure (Table 1.9).

Evening bats roosted primarily in ash (*Fraxinus*) and maple (*Acer*) trees (Table 1.5), probably because those two genera dominate the area around the roost. Evening bats commonly roosted in silver maples in bottomland habitat in Indiana (Whitaker and Gummer, 2001), but in the core of their range, evening bats seem to prefer oak and pine (Amelon and Burhans, 2006; Menzel et al., 1999, 2001). Male evening bats in Arkansas primarily used shortleaf pine (*Pinus echinata*), followed by maples and oaks (Perry and Thill, 2008). In Florida, evening bats were documented roosting and foraging in a pine-oak coastal scrub habitat (Hutchinson, 2001). Indiana bats have been found roosting in >40 different species of trees (Kurta, 2005), and further work with evening bats may reveal a similar diversity across its range.

In my study, evening bats roosted in cavities (55%), exfoliating bark (27%) and crevices (18%; Table 1.5). Similarly, tree-roosting evening bats throughout their range sought shelter mostly in cavities and under exfoliating bark (Bowles et al., 1996; Boyles, 2004; Menzel et al., 2001, 3003; Miles, 2005; Whitaker and Gummer, 2001, 2003). Few studies, however, reported evening bats roosting in crevices (Boyles and Robbins, 2006; Hutchinson, 2001; Perry and Thill, 2008), although most biologists apparently did not discriminate between crevices and cavities (Barclay and Kurta, 2007). Therefore, use of crevices, as opposed to cavities, by evening bats may be underestimated in the literature.

Evening bats were somewhat eclectic in choice of roosting site (Table 1.5). Their roosting choices were much broader than those of Indiana bats, which almost invariably roosted under bark (Kurta, 2005), and more similar to those of northern bats and silver-haired bats, which used all three types of structures (Barclay and Kurta, 2007; Foster and Kurta, 1999). Characteristics of trees, such as diameter and height, were not significantly different among trees with cavities, crevices, or exfoliating bark, although the amount of exfoliating bark was understandably higher for trees on which bats roosted under loose bark (Table 1.6).

Despite occasional use of crevices and bark, all primary roosts were in cavities, except one crevice that was used for 129 bat-days in 2007 (roost 605; Fig. 1.7). Evening bats, and particularly pregnant females, spent a significantly greater proportion of time roosting in cavities than under exfoliating bark or in crevices (Fig. 1.8 and 1.9). However, once the pups stopped nursing, the proportion of time that evening bats roosted in these sites increased (Fig. 1.9). Cavities provide protection from predators and weather (Holloway, 2007) and are more durable than exfoliating bark (Altringham, 1996; Kunz and Lumsden, 2003). Cavities also may provide more microclimatic stability, particularly at the northern edge of their range, and protection during pregnancy and lactation, when energy and water conservation is important (Barclay and Kurta, 2007; Kunz and Lumsden, 2003). Cavities, in general, tend to be in larger, more mature trees that are either healthy or starting to decay (Holloway, 2007), and larger trees may have better insulative properties, as well as potential for bigger cavities that allow more individuals to cluster (Barclay and Kurta, 2007). Reproductive females likely roost more in cavities during cool weather (pregnancy), because cavities provide the space needed for bats to cluster, thereby maintaining a high body temperature (Foster and Kurta, 1999) and facilitating fetal development (Kurta, 1982).

Selection of roost trees by bats often is influenced by landscape characteristics and the proximity of roosts to various resources (Barclay and Kurta, 2007; Carter et al., 2002). Although evening bats use waterways as commuting paths, foraging sites (Menzel et al., 2001), and a source of drinking water (Kurta and Teramino, 1992), evening bats in Michigan did not select roosts according to distance to water (Table 1.12). Most likely this reflects the narrowness of the riparian forest, which results in all trees being close to the creeks and rivers. Despite the importance of water, other insectivorous species in temperate areas, such as eastern red bats and long-eared myotis (*Myotis evotis*), also did not choose roost trees that were closer to water than randomly chosen trees (Hutchinson and Lacki, 2000; Waldien et al., 2000). Similarly, agricultural fields appear to be important foraging sites for evening bats (Chapter 2—Duchamp et al., 2004), but the distance to open fields was not significantly different between roost trees and randomly selected trees (Table 1.12), likely because agricultural areas surround the narrow riparian corridor (Fig. 1.1). However, a Moran's *I* analysis, which takes into account the characteristics of roost trees and their location, indicated that distance to agricultural fields influences the clustered spatial distribution of roost trees in the landscape.

Future range expansion.—The range of the evening bat seems to be expanding westward and especially northward, with extralimital observations occurring recently in Texas, Kansas, Michigan, Nebraska, New York, and South Dakota (Benedict et al., 2000; Dowler et al., 1999; A. Hicks, pers. comm.; Kunz et al., 1980; Kurta et al., 2005; Lane et al. 2003; Sparks and Choate, 1996, 2000). The reason for this apparent expansion of the range is unknown. Possible factors include competition with other species (Duchamp et al., 2004; Whitaker and Gummer, 2003), destruction of preferred roosting or foraging habitats, particularly bottomland forests (Amelon and Burhans, 2006), or perhaps global warming. As global temperatures increase, many other species, ranging from the red fox (*Vulpes vulpes*) to the sachem butterfly (*Atalopedes campestris*), have extended their range northward (Crozier, 2004; Hersteinsson and Macdonald, 1992).

If global warming is responsible, one should be able to predict where in southeastern Michigan the evening bat might eventually be found, based upon apparent habitat preferences. Evening bats in Indiana and Michigan roost only in trees, presumably because competition with big brown bats prevents them from using buildings (Whitaker and Gummer, 2003). Roost trees in both states are most often found in bottomland forests, and the individual roost trees often are large. Diameter of roost trees of evening bats in Michigan, for example, was 58 cm (Table 1.6), which is considerably greater than those typically used by some other cavity- and bark-roosting bats in the area. In contrast, average diameter of roost trees of Indiana and northern bats along Black Creek are only 46 and 44 cm, respectively (Stumpf, 2009).

Areas of mature bottomland forest are uncommon in southeastern Michigan, probably due to the small number and size of rivers in the Great Lakes region. This habitat does occur in a thin strip along the Rouge River, in Wayne Co.; however, the surrounding land is highly urbanized (Kurta and Teramino, 1992), which likely precludes evening bats from establishing a colony there (Duchamp et al., 2004). Suitable habitat also exists along upper portions of the River Raisin, especially near the Ives Road Fen, in Lenawee Co. (Kurta and Foster, 2001), along the lower reaches of the Huron River, and perhaps the upper portion of the Grand River in Jackson Co. (A. Kurta, pers. comm.) These older riparian forests are largely surrounded by agricultural land and would be the most likely areas to find evening bats if they are expanding their range northward into the state.

LITERATURE CITED

Altringham, J. D. 1996. Bats: biology and behaviour. Oxford University Press, New York, 262 pp.

Amelon, S., and D. Burhans. 2006. Conservation assessment: *Nycticeius humeralis* (evening bat) in the Eastern United States. Pp. 31–42, *in* Conservation assessments for five forest bat species in the Eastern United States (F. R. Thompson III, ed.). General Technical Report NC-260:1–89.

Anthony, E. L. P. 1988. Age determination of bats. Pp. 47–58, *in* Ecological and behavioral methods for the study of bats (T. H. Kunz, ed.). Smithsonian Institution Press, Washington, D.C., 533 pp.

Barclay, R. M. R., and A. Kurta. 2007. Ecology and behavior of bats roosting in tree cavities and under bark, Pp. 17–59, *in* Bats in forests: conservation and management (M. J. Lacki, J. P. Hayes, and A. Kurta, eds.). Johns Hopkins University Press, Baltimore, Maryland, 329 pp.

Batschelet, E. 1965. Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. American Institute of Biological Sciences, Washington, D.C, 226 pp.

Benedict, R. A. 2004. Reproductive activity and distribution of bats in Nebraska. Western North American Naturalist, 64:231–248.

Benedict, R. A., H. H. Genoways, and P. W. Freeman. 2000. Shifting distributional patterns of mammals in Nebraska. Transactions of the Nebraska Academy of Sciences, 26: 55–84.

Boonstra, R. 2004. Coping with changing northern environments: the role of the stress axis in birds and mammals. Integrated and Comparative Biology, 44:95–108.

Bowles, J. B., D. Howell, J. W. Van Zee, and G. M. Wilson. 1996. Use of alternate roost trees by the evening bat, *Nycticeius humeralis*, in Iowa. Pp. 217–224, *in* Contributions in mammalogy: a memorial volume honoring Dr. J. Knox Jones, Jr. (H. H. Genoways and R. J. Baker, eds.). Museum of Texas Tech University, Lubbock, Texas.

Boyles, J. G. 2004. A comparison of summer and winter roosting habitat and behavior of evening bats (*Nycticeius humeralis*) in Missouri. M.S. thesis, Southwest Missouri State University, Springfield, 55 pp.

Boyles, J. G., and L. W. Robbins. 2006. Characteristics of summer and winter roost trees used by evening bats (*Nycticeius humeralis*) in southwestern Missouri. American Midland Naturalist, 155:210–220.

Brigham, R. M., M. J. Vonhof, R. M. R. Barclay, and J. C. Gwilliam. 1997. Roosting behavior and roost-site preferences of forest-dwelling California bats (*Myotis californicus*). Journal of Mammalogy, 78:1231–1239.

Brower, J. E., and J. H. Zar. 1984. Field and laboratory methods for general ecology. Second ed. Wm. C. Brown Publishers, Dubuque, Iowa, 226 pp.

Burt, W. H. 1946. Mammals of Michigan. University of Michigan Press, Ann Arbor, Michigan, 288 pp.

Carter, T. C., and J. M. Menzel. 2007. Behavior and day-roosting ecology of North American foliage-roosting bats. Pp. 61–81, *in* Bats in forests: conservation and Management (M. J. Lacki, J. P. Hayes, and A. Kurta, eds.). Johns Hopkins University Press, Baltimore, Maryland, 329 pp.

Carter, T. C., S. K. Carroll, J. E. Hofmann, J. E. Gardner, and G. A. Feldhamer. 2002. Landscape analysis of roosting habitat in Illinois. Pp. 160–164, *in* The Indiana bat: biology and management of an endangered species (A. Kurta and J. Kennedy, eds.). Bat Conservation International, Austin, Texas, 253 pp.

Channell, R., and M. V. Lomolino. 2000. Dynamic biogeography and conservation of endangered species. Nature, 403:84–86.

Clawson, R. L. 2002. Trends in population size and current status. Pp. 2–8, *in* The Indiana bat: biology and management of an endangered species (A. Kurta and J. Kennedy, eds.). Bat Conservation International, Austin, Texas, 253 pp.

Clem, P. D. 1992. Seasonal population variation and emergence patterns in the evening bat, *Nycticeius humeralis*, at a west-central Indiana colony. Proceedings of the Indiana Academy of Science, 101:33–44

Cope, J. B., W. Baker, and J. Confer. 1961. Breeding colonies of four species of bats of Indiana. Proceedings of the Indiana Academy of Science, 70:262–266.

Cope, J. B., J. O. Whitaker, Jr., and S. L. Gummer. 1991. Duration of bat colonies in Indiana, USA. Proceedings of the Indiana Academy of Science, 99:199–202.

Crozier, L. 2004. Warmer winters drive butterfly range expansion by increasing survivorship. Ecology, 85:231–241.

Dowler, R. C., R. C. Dawkins, and T. C. Maxwell. 1999. Range extensions for the evening bat (*Nycticeius humeralis*) in west Texas. Texas Journal of Science, 51:193–195.

Duchamp, J. E., D. W. Sparks, and J. O. Whitaker, Jr. 2004. Foraging-habitat selection by bats at an urban-rural interface: comparison between a successful and a less successful species. Canadian Journal of Zoology, 82:1157–1164.

Easterla, D. A. 1965. A nursery colony of evening bats in southern Missouri. Journal of Mammalogy, 46:498.

Foster, R. W., and A. Kurta. 1999. Roosting ecology of the northern bat (*Myotis septentrionalis*) and comparisons with the endangered Indiana bat (*Myotis sodalis*). Journal of Mammalogy, 80:659–672.

Fujita, M. S. 1986. A latitudinal comparison of growth and development in the little brown bat, *Myotis lucifugus*, with implication for geographic variation in adult morphology. Ph.D. dissertation. Boston University, Boston, Massachusetts, 261 pp.

Gardner, J. E., J. D. Garner, and J. E. Hofmann. 1991. Summer roost selection and roosting behavior of *Myotis sodalis* (Indiana bat) in Illinois. Unpublished report. Illinois Natural History Survey, Champaign, Illinois, 14 pp.

Geluso, K. N., R. A. Benedict, and F. L. Kock. 2004. Seasonal activity and reproduction in bats of east-central Nebraska. Transactions of the Nebraska Academy of Sciences, 29:33–44.

Gottschang, J. L. 1981. A guide to the mammals of Ohio. Ohio State University Press, Columbus, 176 pp.

Gumbert, M. W. J. M. O'Keefe, and J. R. MacGregor. 2002. Roost fidelity in Kentucky. Pp. 143–152. *in* The Indiana bat: biology and management of an endangered species (A. Kurta and J. Kennedy, eds.). Bat Conservation International, Austin, Texas, 253 pp.

Hersteinsson, P., and D. W. Macdonald. 1992. Interspecific competition and the geographical distribution of red and arctic foxes *Vulpes vulpes* and *Alopex lagopus*. Oikos, 64:505–515.

Holloway, G. L., J. P. Caspersen, M. C. Vanderwel, and B. J. Naylor. 2007. Cavity tree occurrence in hardwood forests of central Ontario. Forest Ecology and Management, 239:191–199.

Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? Trends in Ecology and Evolution, 15:56–61.

Humphries, M. M., D. W. Thomas, and J. R. Speakman. 2002. Climate-mediated energetic constraints on the distribution of hibernating mammals. Nature, 418:313–316.

Humphrey, S. R. 1975. Nursery roosts and community diversity of neartic bats. Journal of Mammalogy, 56:321–346.

Humphrey, S. R., and J. B. Cope. 1968. Records of migration of the evening bat, *Nycticeius humeralis*. Journal of Mammalogy, 49:329.

Hutchinson, J. T. 2001. Observations on use of coastal scrub habitat by evening bats (*Nycticeius humeralis*) in Florida. Bat Research News, 42:44–46.

Hutchinson, J. T., and M. J. Lacki. 2000. Selection of day roosts by red bats in mixed mesophytic forests. Journal of Wildlife Management, 64:87–94.

Jaberg, C., and A. Guisan. 2001. Modeling the distribution of bats in relation to landscape structure in a temperate mountain environment. Journal of Applied Ecology, 38:1169–1181.

Jones, G., and J. Rydell. 1994. Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. Philosophical Transactions of the Royal Society of London: Biological Sciences, 346:445–455.

Lewis, S. E. 1995. Roost fidelity of bats: a review. Journal of Mammalogy, 76:481–496.

Kalcounis-Rüppell, M. C., J. M. Psyllakis, and R. M. Brigham. 2005. Tree roost selection by bats: an empirical synthesis using meta-analysis. Wildlife Society Bulletin, (33):1123–1132

Kashian, D. M., M. G. Turner, W. H. Romme, and C. G. Lorimer. 2005. Variability and convergence in stand structural development on a fire-dominated subalpine landscape. Ecology, 86:643–654.

Kunz, T. H. 1965. Notes on some Nebraskan bats. Transactions of the Kansas Academy of Science, 68:201–203.

Kunz, T. H., and A. Kurta. 1988. Capture methods and holding devices. Pp. 1–30, *in* Ecological and behavioral methods for the study of bats (T. H. Kunz, ed.). Smithsonian Institution Press, Washington, D.C., 533 pp.

Kunz, T. H., and L. F. Lumsden. 2003. Ecology of cavity and foliage roosting bats. Pp. 3–89, *in* Bat ecology (T. H. Kunz and M. B. Fenton, eds.). University of Chicago Press, Chicago, Illinois, 779 pp.

Kunz, T. H., J. R. Choate, and S. B. George. 1980. Distributional records for three species of mammals in Kansas. Transactions of the Kansas Academy of Science, 83:74–77.

Kurta, A. 1980. The bats of southern Lower Michigan. M. S. thesis, Michigan State University, East Lansing, Michigan, 147 pp.

———. 1982. A review of Michigan bats: seasonal and geographic distribution. Michigan Academician, 14:295–312.

———. 1986. Factors affecting the resting and postflight body temperature of little brown bats, *Myotis lucifugus*. Physiological Zoology, 59:429–438.

———. 1995. Mammals of the Great Lakes region. University of Michigan Press, Ann Arbor, 376 pp.

———. 2005. Roosting ecology and behavior of Indiana bats (*Myotis sodalis*) in summer. Pp. 29–38, *in* Proceedings of the Indiana bat and coal mining: a technical interactive Forum (K. C. Vories and A. Harrington, eds.). U.S. Department of the Interior, Office of Surface Mining, Alton, Illinois, 14 pp.

———. 2008. Bats of Michigan. Indiana State University Center for North American Bat Research and Conservation, Terra Haute, Indiana, 72 pp.

Kurta, A., and R. Foster. 2001. Ecology of the endangered Indiana bat (*Myotis sodalis*): what is necessary, typical, and acceptable? Unpublished report. Michigan Department of Natural Resources, Lansing, Michigan, 31 pp.

Kurta, A., and J. Kennedy. 2002. The Indiana bat: biology and management of an endangered species. Bat Conservation International, Austin, Texas, 253 pp.

Kurta, A., and H. Rice. 2002. Ecology and management of the Indiana bat in Michigan. Michigan Academician 34:175–190.

Kurta, A., and J. A. Teramino. 1992. Bat community structure in an urban park. Ecography, 15:257–261.

Kurta, A., K. A. Johnson, and T. H. Kunz. 1987. Oxygen consumption and body temperature of female little brown bats (*Myotis lucifugus*) under simulated roost conditions. Physiological Zoology, 60:386–397.

Kurta, A., K. J. Williams, and R. Mies. 1996. Ecological, behavioural, and thermal observations of a peripheral population of Indiana bats (*Myotis sodalis*). Pp. 102–117, *in* Bats and forests symposium (R. M. R. Barclay and R. M. Brigham, eds.). Research Branch, British Columbia Ministry of Forests, Victoria, British Columbia, 292 pp.

Kurta, A., S. W. Murray, and D. H. Miller. 2002. Roost selection and movements across the summer landscape. Pp. 118–129, *in* The Indiana bat: biology and management of an endangered species (A. Kurta and J. Kennedy, eds.). Bat Conservation International, Austin, Texas, 253 pp.

Kurta, A., R. Foster, E. Hough, and L. Winhold. 2005. The evening bat (*Nycticeius humeralis*) on the northern edge of its range—a maternity colony in Michigan. American Midland Naturalist, 154:264–267.

Lane, J. E., C. L. Buck, and R. M. Brigham. 2003. The bat fauna of southeast South Dakota. Prairie Naturalist, 35:246–256.

Lariviere, S. 2004. Range expansion of raccoons in the Canadian prairies: review of hypotheses. Wildlife Society Bulletin, 32:955–963.

Lee, J., and D. W. S. Wong. 2001. Statistical analysis with ArcView GIS. John Wiley & Sons, Inc., New York, New York, 192 pp.

Loeb, S. C., and J. M. O'Keefe. 2006. Habitat use by forest bats in South Carolina in relation to local, stand, and landscape characteristics. Journal of Wildlife Management, 70:1210–1218.

Lomolino, M. V., and R. Channell. 1995. Splendid isolation: patterns of geographic range collapse in endangered mammals. Journal of Mammalogy, 76:335–347.

Lowry, R. 2008. VassarStats: website for statistical computation. Vassar College, Poughkeepsie, New York. URL http://faculty.vassar.edu/lowry/VassarStats.html Accessed May 2008.

Menzel, M. A., D. M. Krishon, T. C. Carter, and J. Laerm. 1999. Notes on tree roost characteristics of the northern yellow bat (*Lasiurus intermedius*), the Seminole bat (*L. seminolus*), the evening bat (*Nycticeius humeralis*), and the eastern pipistrelle (*Pipistrellus subflavus*). Florida Scientist, 62:185–193.

Menzel, M. A., T. C. Carter, W. M. Ford, and B. R. Chapman. 2001. Tree-roost characteristics of subadult and female adult evening bat (*Nycticeius humeralis*) in the upper coastal plain of South Carolina. American Midland Naturalist, 145:112–119.

Miles, A. C. 2005. Bat community structure, foraging activity, and evening bat roost site selection in loblolly pine and longleaf pine forests of Georgia. M.S. thesis, University of Georgia, Athens, 79 pp.

Miles, A. C., S. B. Castleberry, D. A. Miller, and L. M. Conner. 2007. Multi-scale roost-site selection by evening bats on pine-dominated landscapes in southwest Georgia. Journal of Wildlife Management, 70:1191–1199.

Miller, N. E., R. D. Drobney, R. L. Clawson, and E. V. Callahan. 2002. Summer habitat in northern Missouri. Pp. 165–171, *in* The Indiana bat: biology and management of an endangered species (A. Kurta and J. Kennedy, eds.). Bat Conservation International, Austin, Texas, 253 pp.

Mumford, R. E., and J. B. Cope. 1964. Distribution and status of the Chiroptera of Indiana. American Midland Naturalist, 72:473–489.

National Oceanic and Atmospheric Agency. 2000. Land cover analysis: coastal Great Lakes landcover—Michigan Lower Peninsula 2000 land cover data. NOAA Coastal Services Center. Charleston, South Carolina. URL http://www.csc.noaa.gov/crs/lca/greatlakes.html. Accessed July 2007.

Nogueira, M. R., and A. L. Peracchi. 2003. Fig-seed predation by 2 species of *Chiroderma*: discovery of a new feeding strategy in bats. Journal of Mammalogy, 84:225–233.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature, 421:37–42.

Perry, R. W., and R. E. Thill. 2008. Diurnal roosts of male evening bats (*Nycticeius humeralis*) in diversely managed pine-hardwood forests. American Midland Naturalist, 160:374–385.

Perry, R. W., R. E. Thill, and D. M. Leslie, Jr. 2007. Selection of roosting habitat by forest bats in a diverse forested landscape. Forest Ecology and Management, 238:156–166.

Pielou, E. C. 1966. The measurement of diversity in different types of biological collections. Journal of Theoretical Biology, 13:131–144.

Racey, P. A. 1988. Reproductive assessment in bats. Pp. 31–46, *in* Ecological and behavioral methods for the study of bats (T.H. Kunz, ed.). Smithsonian Institution Press, Washington, D.C., 533 pp.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature, 421:57–60.

Sedgeley, J. A., and C. F. J. O'Donnell. 1999. Roost selection by the long-tailed bat, *Chalinolobus tuberculatus*, in temperate New Zealand rainforest and its implications for the conservation of bats in managed forests. Biological Conservation, 88:261–276.

Smith, P. W., and P. W. Parmalee. 1954. Notes on distribution and habits of some bats from Illinois. Transactions of the Kansas Academy of Science, 57:200–205.

Sparks, D. W., and J. R. Choate. 1996. New distributional records for mammals in Kansas. Prairie Naturalist, 27:185–192.

———. 2000. Distribution, natural history, conservation status, and biogeography of bats in Kansas. Pp. 173–228, *in* Reflections of a naturalist: papers honoring Professor Eugene D. Fleharty (J. R. Choate, ed.). Fort Hays Studies, 1:1–241.

Stokke B. G., A. P. Møller, B. E. Sæther, G. Rheinwald, and H. Gutscher. 2005. Weather in the breeding area and during migration affects the demography of a small long-distance passerine migrant. Auk, 122:637–647.

Stumpf, J. 2009. Resource partitioning among three syntopic species of *Myotis* in southeastern Michigan. M.S. thesis, Eastern Michigan University, Ypsilanti, Michigan.

Thomas, C. D., E. J. Bodsworth, R. J. Wilson, A. D. Simmons, Z. G. Davies, M. Musche, and L. Conrad. 2001. Ecological and evolutionary processes at expanding range margins. Nature, 411:577–580.

Timpone, J. C., J. G. Boyles, and L. W. Robbins. 2006. Potential for niche overlap in roosting sites between *Nycticeius humeralis* (evening bats) and *Eptesicus fuscus* (big brown bats). Northeastern Naturalist, 13:597–602.

Veilleux, J. P., and S. L. Veilleux. 2004. Intra-annual and interannual fidelity to summer roost areas by female eastern pipistrelles, *Pipistrellus subflavus*. American Midland Naturalist, 152:196–200.

Viele, D. P., A. Kurta, and J. A. Kath. 2002. Timing of nightly emergence. Pp. 199–207, *in* The Indiana bat: biology and management of an endangered species (A. Kurta and J. Kennedy, eds.). Bat Conservation International, Austin, Texas, 253 pp.

Waldien, D. L., J. P. Hayes, and E. B. Arnett. 2000. Day-roosts of female long-eared myotis In western Oregon. Journal of Wildlife Management, 64:785–796.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature, 416:389–395.

Watkins, L. C. 1969. Observations on the distribution and natural history of the evening bat (*Nycticeius humeralis*) in northwestern Missouri and adjacent Iowa. Transactions of the Kansas Academy of Science, 72:330–336.

———. 1972. *Nycticeius humeralis*. Mammalian Species, 23:1–4.

Watkins, L. C., and K. A. Shump, Jr. 1981. Behavior of the evening bat *Nycticeius humeralis* at a nursery roost. American Midland Naturalist, 105:258–268.

Watson, G. S. 1961. Goodness-of-fit tests on a circle. Biometrika, 48:109–114.

———. 1962. Goodness-of-fit tests on a circle, II. Biometrika, 49:57–63.

Weather underground. 2008. History. URL http://www.wunderground.com/history/. Accessed September 26, 2008.

Whitaker, J. O., Jr. 1988. Food habits analysis of insectivorous bats. Pp. 171–189, *in* Ecological and behavioral methods for the study of bats (T.H. Kunz, ed.). Smithsonian Institution Press, Washington, D.C., 533 pp.

Whitaker, J.O., Jr., and V. Brack, Jr. 2002. Distribution and summer ecology in Indiana. Pp. 48–54, *in* The Indiana bat: biology and management of an endangered species (A. Kurta and J. Kennedy, eds.). Bat Conservation International, Austin, Texas, 253 pp.

Whitaker, J. O., Jr., and S. L. Gummer. 1993. The status of the evening bat, *Nycticeius humeralis*, in Indiana. Proceedings of the Indiana Academy of Science, 102:283–291.

———. 2003. Current status of the evening bat, *Nycticeius humeralis*, in Indiana. Proceedings of the Indiana Academy of Science, 112:55–60.

Whitaker, J. O., Jr., and W. J. Hamilton. 1998. Mammals of the eastern United States. Cornell University Press, Ithaca, New York, 583 pp.

Wilkinson, G. S. 1992*a*. Communal nursing in the evening bat, *Nycticeius humeralis*. Behavioral Ecology and Sociobiology, 31:225–235.

———. 1992*b*. Information transfer at evening bat colonies. Animal Behaviour, 44:501–518.

Willis, C. K. R., and R. M. Brigham. 2003. New records of the eastern red bat, *Lasiurus borealis*, from Cypress Hills Provincial Park, Saskatchewan: a response to climate change? Canadian Field-Naturalist, 117:651–654.

Willis, C. K. R., and R. M. Brigham. 2004. Roost switching, roost sharing and social cohesion: forest-dwelling big brown bats, Eptesicus fuscus, conform to the fission–fusion model. Animal Behaviour, 68:495–505.

Winhold, L. 2007. Community ecology of bats in southern Lower Michigan, with emphasis on roost selection by *Myotis*. M.S. thesis, Eastern Michigan University, Ypsilanti, Michigan, 144 pp.

Zar, J. H. 1999. Biostatistical analysis. Fourth ed. Prentice Hall, Upper Saddle River, New Jersey, 663 pp.

Table 1.1. Decay-stage classification of trees within the study area, near Palymra, Michigan. Modified from Boyles and Robbins (2006).

Decay Stage	Description
1	Live, usually healthy, no or few defects (hollows or cracks), no or few dead branches, and no or little exfoliating bark.
2	Live but dying tree, unhealthy, portions or most of the canopy defoliated, many defects (hollow, cracks, or broken top), and usually exfoliating bark.
3	Dead with usually > 50% exfoliating bark, abundant defects, typically extensive internal and external decay, and often < 4m in height.

Table 1.2. Number of evening bats captured (number radio tracked) according to reproductive condition, near Palmyra, Michigan, during 2006–2007.

Reproductive Condition	2006	2007	Total
Not palpably pregnant	1 (1)	3 (2)	4 (3)
Pregnant	11 (3)	5 (3)	16 (6)
Lactating	4 (2)	12 (10)	16 (12)
Post-lactating	8 (6)	1 (1)	9 (7)
Female Juvenile	4 (3)	8 (4)	12 (7)
Male Juvenile	5 (3)	13 (5)	18 (8)
Unknown		1 (1)	1 (1)
Total	33 (18)	43 (26)	76 (44)

Table 1.3. Mass and forearm length of adult and volant juvenile evening bats, near Palmyra, Michigan, during 2006–2007. Data were presented as $\overline{X} \pm SE$ (range) *n*. One male and female juvenile bat did not have their mass measured.

Reproductive Condition	Mass (g)	Forearm Length (mm)
Adult	12.7 ± 0.3 (9.5–19.0) 46	36.3 ± 0.2 (34–38) 46
Not palpably pregnant	12.9 ± 1.0 (10.5–15.5) 4	36.8 ± 0.9 (34–38) 4
Pregnant	14.2 ± 0.4 (10.5–19.0) 20	36.4 ± 0.3 (34–38) 20
Lactating	11.3 ±0.4 (9.5–14.5) 16	36.1 ± 0.2 (34–37) 16
Post-lactating	12.0 ± 0.6 (10–15) 9	36.9 ± 0.3 (35–38) 9
Juvenile	8.1 ± 0.3 (5–11.5) 27	34.6 ± 0.3 (30–38) 29
Females	8.5 ± 0.5 (5.5–11.5) 11	35.3 ± 0.5 (32–38) 12
Males	7.8 ± 0.4 (5.0–11.0) 16	34.1 ± 0.3 (31–36) 17

Table 1.4. The mean distance traveled and number of switches conducted by evening bats in the first day (0–1) and second day (1–2) after capture.

	Day 0–1	Day 1–2	Statistics	
			t_{88}	P
Distance traveled	232.2 ± 85	267.4 ± 45	0.36	0.72
Number of switches	0.51 ± 0.08	0.51 ± 0.08	0.00	1.00

Table 1.5. The tree species and type of roost used by evening bats near Palmyra, Michigan, during 2006–2007.

Roost	Years used	Species of tree	Type of roost	Decay stage
601	2006, 2007	American elm	Cavity	1
602	2006, 2007	American basswood	Exfoliating bark	3
603	2006, 2007	Eastern cottonwood	Cavity	1
604	2006	Green ash	Cavity	2
605[a]	2006, 2007	Green ash	Crevice	2
606	2006, 2007	Green ash	Cavity	2
607	2006, 2007	Shellbark hickory	Cavity	3
608	2006, 2007	American sycamore	Cavity	3
609	2006, 2007	Green ash	Exfoliating bark	3
610	2006	Green ash	Exfoliating bark	3
611	2006	American elm	Exfoliating bark	2
612	2006, 2007	Silver maple	Cavity	2
613	2006, 2007	Shellbark hickory	Exfoliating bark	1
614	2006	Green ash	Crevice	1
615	2006, 2007	Green ash	Cavity	1
616	2006, 2007	Green ash	Crevice	3
617	2006, 2007	Silver maple	Cavity	2
618	2006, 2007	Common hackberry	Cavity	1
619	2006, 2007	Silver maple	Crevice	2
701	2007	Common hackberry	Cavity	1
702	2007	Sugar maple	Cavity	3
703	2007	Honey locust	Cavity	1
704	2007	Boxelder	Exfoliating bark	3
705	2007	Green ash	Cavity	2
706	2007	Green ash	Cavity	3
707	2007	Eastern cottonwood	Cavity	1
708	2007	Green ash	Exfoliating bark	3
709	2007	Green ash	Cavity	1
710	2007	Sugar maple	Exfoliating bark	3
711	2007	Common hackberry	Crevice	1
712	2007	Green ash	Crevice	3
713	2007	Green ash	Cavity	2
714	2007	Sugar maple	Cavity	2

[a] Roost tree originally discovered in 2004.

Table 1.6. The characteristics of roost trees and the trees with cavities, available exfoliating bark, and crevices near Palmyra, Michigan, during 2006–2007. Statistical comparisons were conducted among types of roost structure. Continuous variables are presented as $\overline{X} \pm SE$ (range) n.

	Height of tree (m)	Diameter of tree (cm)	Height of emergence (m)	Canopy cover (%)	Available exfoliating bark (%)	Subcanopy clutter (high, medium, low)	Solar exposure (high, medium, low)
Roost	25.6 ± 1.4 (11–41) 33	57.6 ± 3.7 (24–121) 33	13.3 ± 0.7 (6–21) 33	85.8 ± 2.1 (58–99) 33	17.7 ± 3.3 (0–90) 33	1, 5, 27	16, 11, 6
Roosting structure							
Cavity	28.0 ± 2.1 (12–41) 18	60.2 ± 5.7 (24–121) 18	14.1 ± 1.0 (6–21) 18	87.6 ± 2.6 (66–99) 18	10.3 ± 3.1^{a} (0–55) 18	0, 4, 14	8, 7, 3
Exfoliating bark	20.6 ± 2.2 (11–32) 9	49.6 ± 5.3 (28–77) 9	11.2 ± 1.3 (6–17) 9	83.8 ± 4.4 (62–98) 9	34.8 ± 8.0^{a} (8–90) 9	1, 1, 7	4, 3, 2
Crevice	26 ± 2.2 (19–34) 6	61.9 ± 7.7 (30–84) 6	13.9 ± 0.7 (12–14) 6	83.5 ± 5.8 (58–96) 6	14.0 ± 4.3 (1–33) 6	0, 0, 6	4, 1, 1
Statistics	$F_{2,30} = 2.79$; $P = 0.08$	$F_{2,30} = 0.88$; $P = 0.42$	$F_{2,30} = 1.91$; $P = 0.17$	$F_{2,30} = 0.44$; $P = 0.65$	$F_{2,30} = 7.45$; $P = 0.002$	Fisher's exact; $P = 0.5$	Fisher's exact; $P = 0.9$

Table 1.7. The percent (*n*) of of roost trees in each genera, randomly selected trees within roost plots, and randomly selected trees within stand plots, and trees at the plot- and stand-level.

Genus	Roost Tree	Plot		Stand	
		Randomly selected tree	All trees	Randomly selected tree	All trees
Fraxinus (ash)	43 (14)	33 (10)	30 (205)	11 (4)	20 (201)
Acer (maple)	21 (7)	27 (8)	26 (175)	25 (9)	17 (178)
Celtis (hackberry)	9 (3)	17 (5)	7 (50)	11 (4)	10 (103)
Carya (hickory)	6 (2)		4 (25)	14 (5)	3 (28)
Ulmus (elm)	6 (2)		8 (51)	8 (3)	12 (119)
Populus (cottonwood)	6 (2)	3 (1)	2 (11)		4 (44)
Other genera	9 (3)	20 (6)	23 (157)	31 (11)	34 (354)
Total	33	30	674	36	1,027

Table 1.8. Continuous characteristics of roost trees used by evening bats in 2006–2007 and randomly selected trees in the same plot and stand, near Palmyra, Michigan. Variables are presented as $\overline{X} \pm SE$ (range) *n*. Statistical analysis of canopy cover was conducted between roost and plot versus stand trees.

	Diameter (cm)	Height (m)	Available exfoliating bark (%)[a]	Canopy cover (%)
Roost	57.6 ± 3.7 (24–121) 33	25.6 ± 1.4[b] (11–41) 33	17.7 ± 3.3 (0–90) 33	85.8 ± 2.1[b] (58–99) 33
Plot	44.2 ± 4.0 (15–107) 30	19.9 ± 1.4[b] (7–39) 30	8.6 ± 2.3 (0–50) 30	88.8 ± 1.3 (62–98) 30
Stand	53.1 ± 3.9 (21–112) 36	23.1 ± 1.3 (8–38) 36	18.1 ± 4.0 (0–100) 36	93.5 ± 0.8[b] (79–100) 36
Statistics	$F_{2, 96} = 2.91$; $P = 0.06$	$F_{2, 96} = 4.09$; $P = 0.02$	$F_{2, 96} = 3.22$; $P = 0.04$	$t_{97} = 3.44$; $P = 0.001$

[a] Conservative Tukey's test could not indicate where the differences occur.

Table 1.9. Categorical characteristics of roost trees used by evening bats in 2006–2007 and randomly selected trees in the same plot and stand, near Palmyra, Michigan

	Decay stage (1, 2, 3)	Subcanopy clutter (high, medium, low)	Solar exposure (high, medium, low)
Roost	11, 10, 12	1, 5, 27	16, 11, 6
Plot	19, 5, 6	14, 9, 7	9, 16, 5
Stand	16, 15, 5	17, 17, 11	7, 20, 9
Statistics	$\chi^2_4 = 10.41$; $P = 0.03$	$\chi^2_4 = 33.64$; $P < 0.001$	$\chi^2_4 = 7.33$; $P = 0.12$

Table 1.10. The distance to the nearest tallest and shortest trees from roost trees and randomly selected plot and stand trees and the decay stage of the nearest tallest and shortest trees. Variables are presented as $\overline{X} \pm SE$ (range) *n*.

	Nearest tallest tree		Nearest shortest tree	
	Distance (m)	Decay stage (1, 2, 3)	Distance (m)	Decay stage (1, 2, 3)
Roosts	$11.7 \pm 4.5^{a, b}$ (0.7–150) 33	31, 1, 0	4.5 ± 0.6 (0–15.3) 33	26, 7, 0
Plot	4.4 ± 0.5^{a} (1.2–14) 33	26, 3, 1	4.2 ± 0.5 (0.7–13) 33	23, 4, 0
Stand	4.3 ± 0.7^{b} (0.3–21) 33	29, 5, 1	3.5 ± 0.5 (0.2–14) 33	30, 5, 1
Statistics	$F_{2, 94} = 8.93$; $P < 0.01$	$\chi^2_4 = 3.66$; $P = 0.45$	$F_{2, 94} = 1.04$; $P = 0.36$	$\chi^2_4 = 2.46$; $P = 0.65$

Table 1.11. Comparisons of characteristics of trees in the roost (*n* = 674 trees) and stand (*n* = 1026) plots. Continuous variables other than diversity and evenness are presented as $\overline{X} \pm SE$. The number of genera is in parentheses. No statistical test is available to compare evenness of genera between roost and stand plots.

	Diversity of trees	Evenness of genera of trees	Diameter of tree (cm)	Decay stage (1, 2, 3)	Density of trees (trees/ha)	Mean basal area (m^2/ha)
Roost	0.98 (20)	0.73 (20)	32.4 ± 0.8	537, 98, 39	225 ± 17	1.12 ± 0.06
Stand	0.82 (14)	0.77 (14)	26.4 ± 0.5	802, 164, 60	285 ± 18	0.76 ± 0.04
Statistics	$t_{\infty} = 0.26$; $P > 0.05$		$t_{1699} = 6.84$; $P < 0.001$	$X^2_3 = 0.67$; $P = 0.72$	$t_{65} = 2.51$; $P = 0.014$	$t_{1699} = 5.23$; $P < 0.001$

Table 1.12. Distribution and statistical analysis of roost trees and randomly selected trees within landcover type. Data are presented as % (*n*).

	Palustrine Forested Wetland	Palustrine Scrub-Shrub	Deciduous Forest	Grassland-Herbaceous	Statistic
Roost	85 (28)	9 (3)	3 (1)	3 (1)	$X^2_3 = 63.36$; $P < 0.001$
Plot	90 (27)	7 (2)		3 (1)	$X^2_2 = 48.60$; $P < 0.001$
Stand	72 (26)	3 (1)	25 (9)		$X^2_2 = 30.17$; $P < 0.001$
Statistics	$X^2_2 = 0.02$; $P = 0.99$				

Table 1.13. Distances to water and open fields from roost, plot, and stand trees within the study area. Variables are presented as $\overline{X} \pm SE$ (range) *n*. Statistical comparisons were conducted between roost and stand trees.

	Roost	Plot	Stand	Statistics
Distance to water (m)	36.4 ± 5.5 (1–128) 33	40 ± 6.0 (1–125) 30	41.5 ± 6.5 (3–149) 36	$F_{1,67} = 0.41$; $P = 0.52$
Distance to open fields (m)	86.0 ± 10.3 (0–200) 33	87.1 ± 10.5 (0–212) 30	78.7 ± 10.2 (6–244) 36	$F_{1,67} = 0.14$; $P = 0.71$

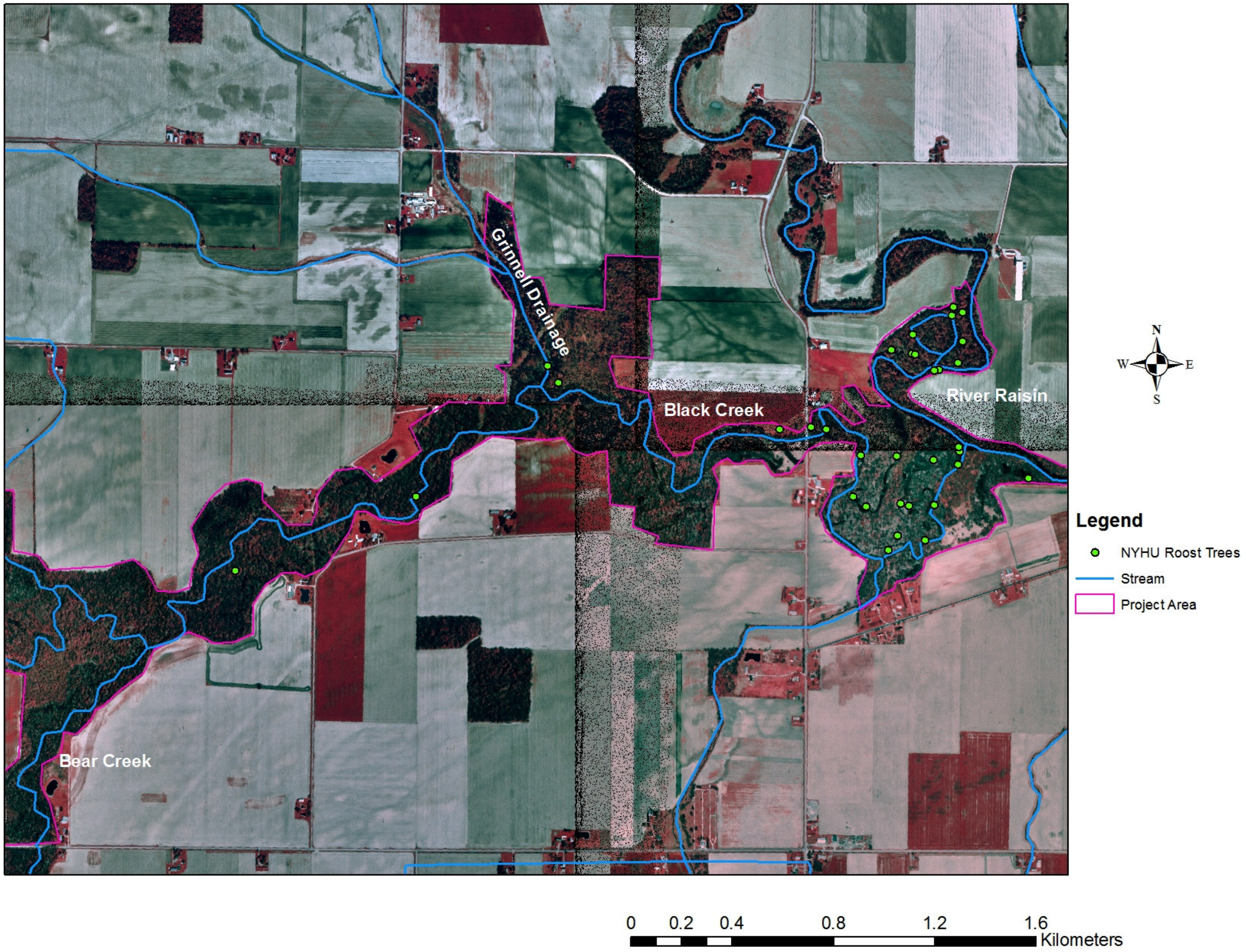


Figure 1.1. Aerial photo of study area near Palmyra, Michigan. Roost trees discovered in 2006–2007 are indicated by dots.

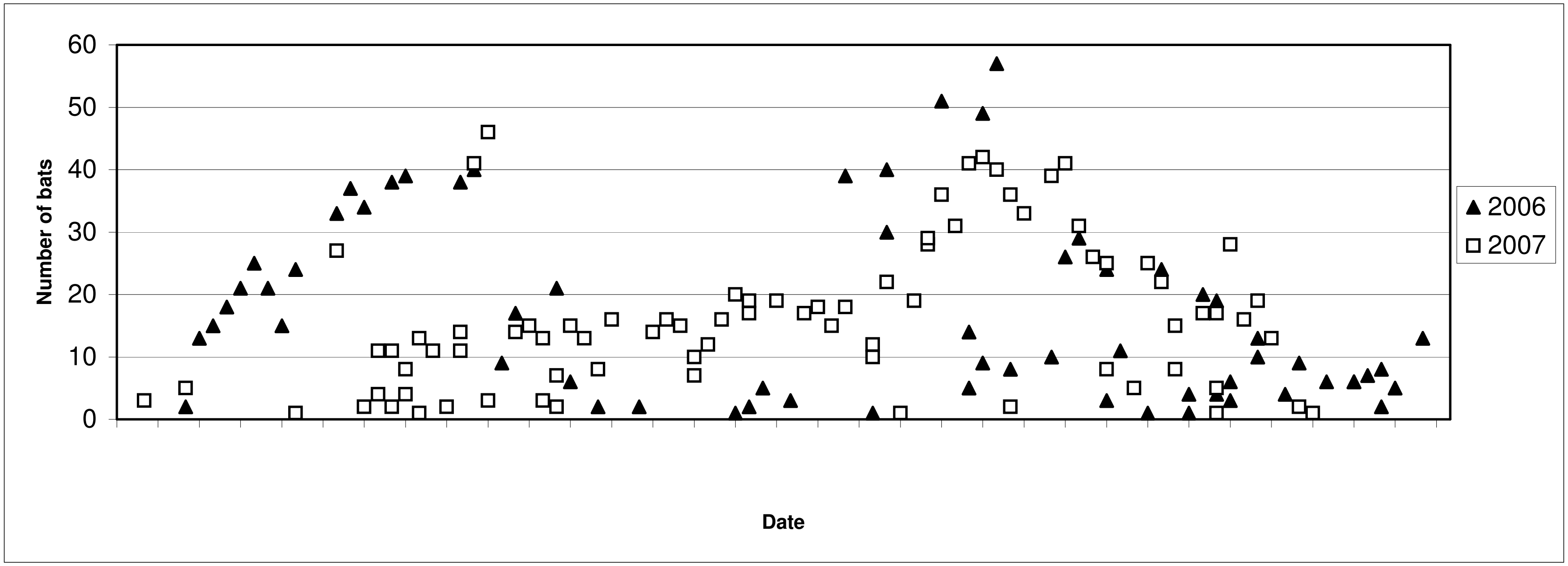


Figure 1.2. The number of evening bats observed exiting roost trees near Palmyra, Michigan, from May through August 2006–2007. Colony size peaked during the end of pregnancy (mid-June) and once juveniles became volant (mid-July). Evening bats were seen leaving the tree during 152 of 190 roost watches. I did not include data for 38 occasions during which no bats were seen.

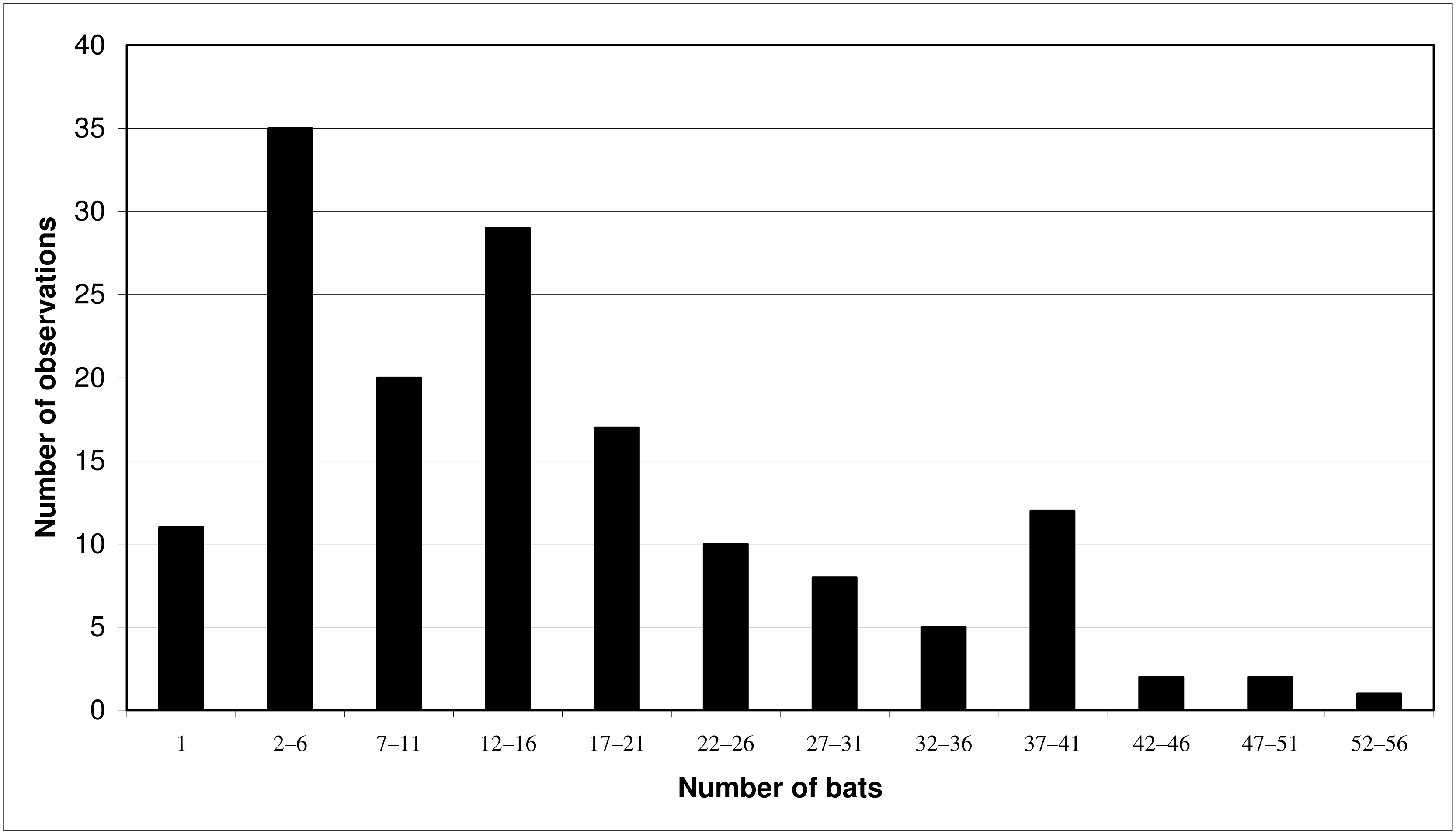


Figure 1.3. Histogram of the number of bats exiting a roost tree near Palmyra, Michigan, during 2006–2007. At least one evening bats left the roost during 152 observations of evening emergence.

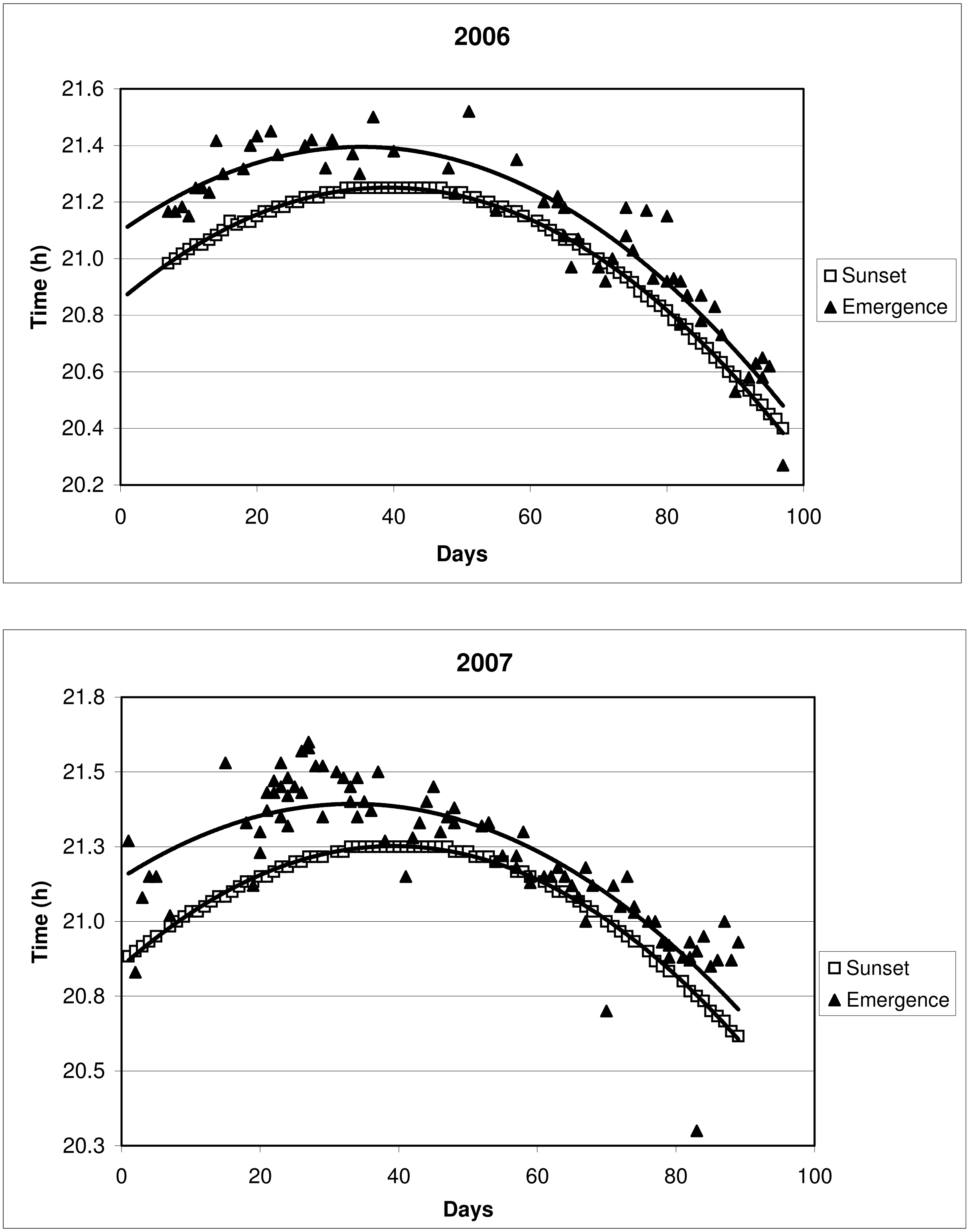


Figure 1.4. Emergence time of evening bats from roosts compared to times of sunset, near Palmyra, Michigan, between 19 May (Day 0) and 23 August (Day 97) 2006–2007. Evening bats first emerged at 8.1 ± 0.6 min after sunset (*n* = 152), ranging from 27 min prior to 27 min after sunset. Time is Eastern Standard.

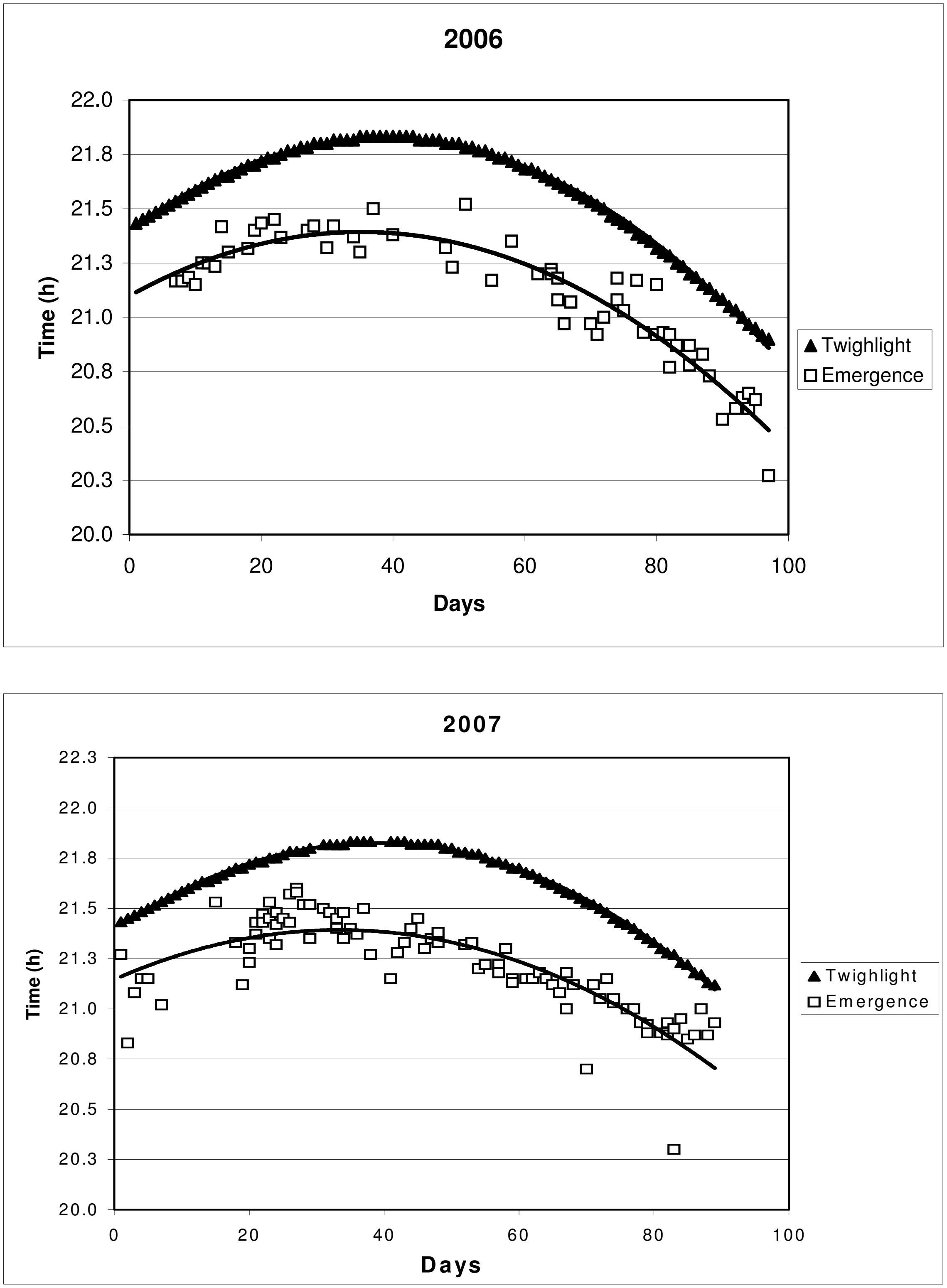


Figure 1.5. Emergence time of evening bats from roosts compared to times of twilight, near Palmyra, Michigan, between 19 May (Day 0) and 23 August (Day 97) 2006–2007. Evening bats first emerged at 25 ± 0.6 min prior to twilight (*n* = 152). Time is Eastern Standard.

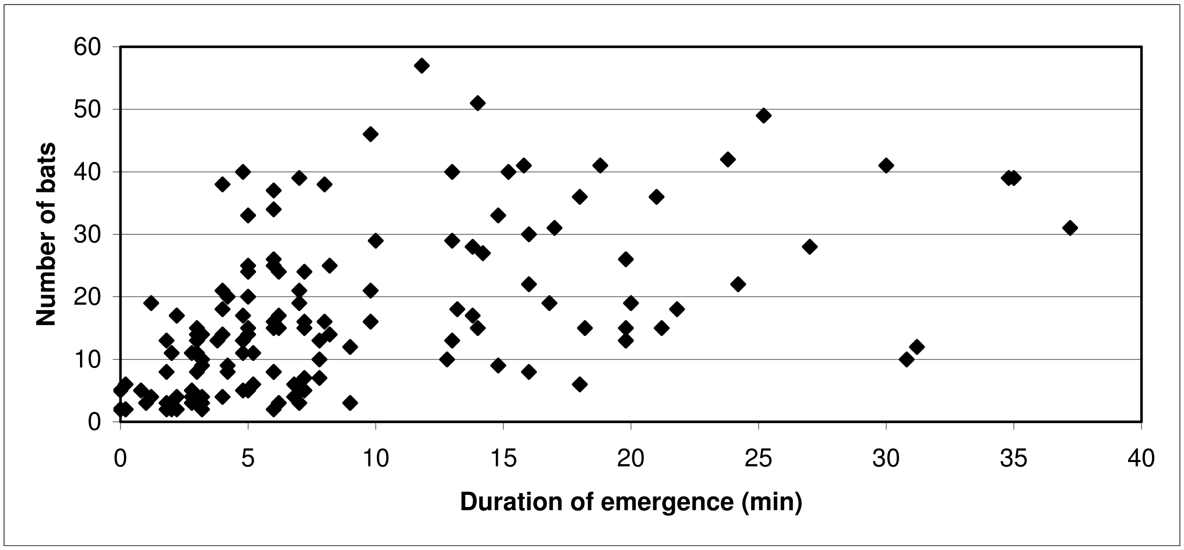


Figure 1.6. Relationship between number of bats and length of time (min) for all bats to exit the roost (n = 136; r = 0.51; P < 0.001). Only observations of ≥2 bats are included.

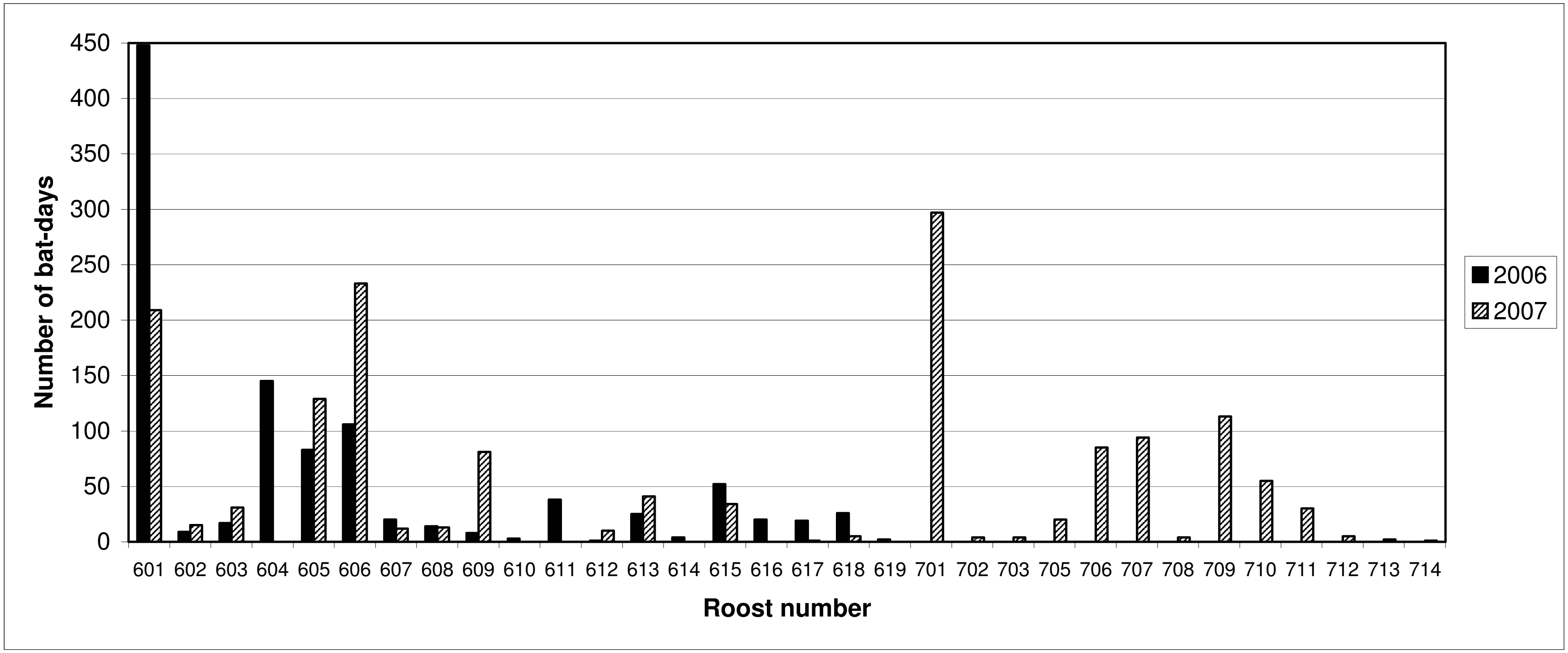


Figure 1.7. Number of bat-days in roost trees near Palmyra, Michigan, during 2006–2007. Bat-days are the sum of emergence counts of evening bats from each roost tree. The total number of roost observations during which at least one bat emerged was 152.

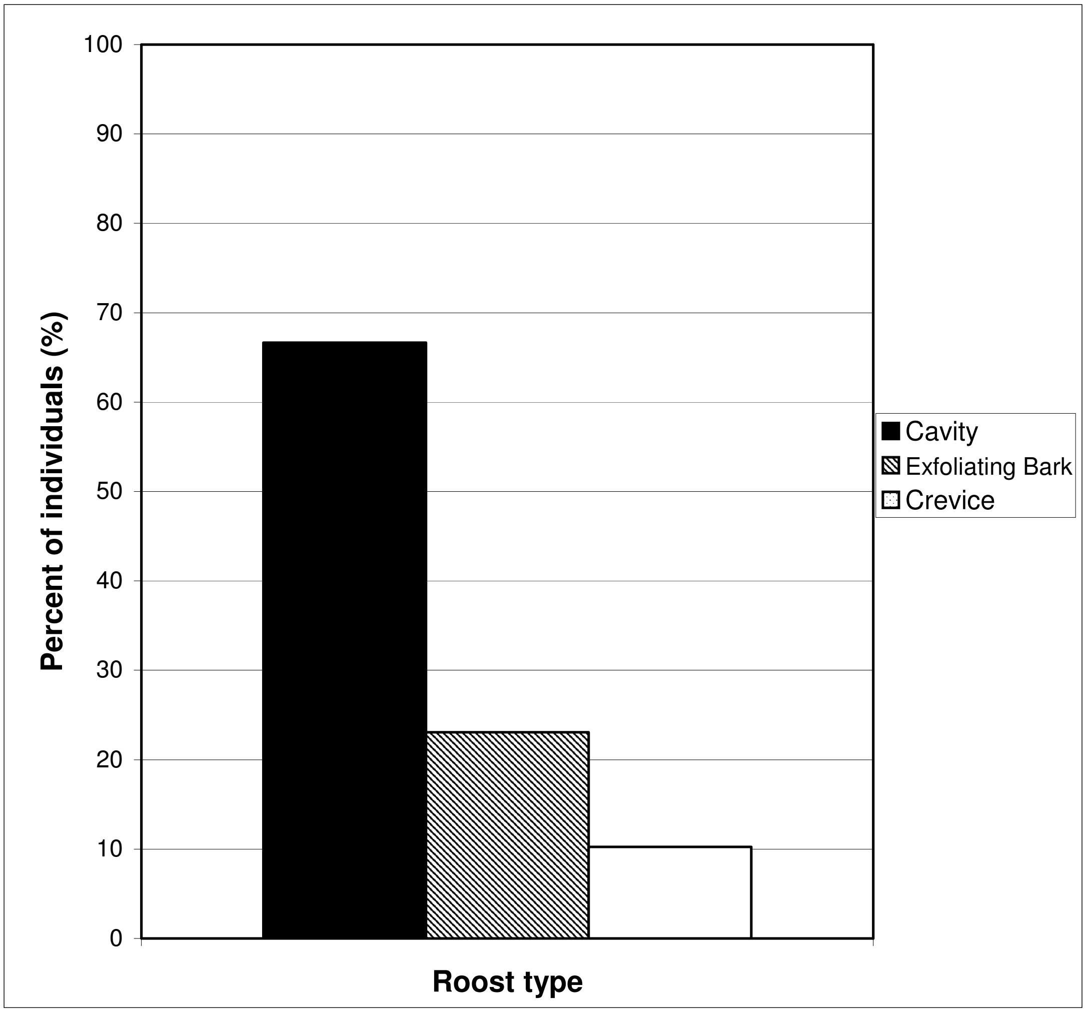


Figure 1.8. The percent of radio-tracked individuals that roosted in cavities ($n = 29$ bats), exfoliating bark ($n = 9$), or in crevices ($n = 4$) near Palmyra, Michigan, during 2006–2007.

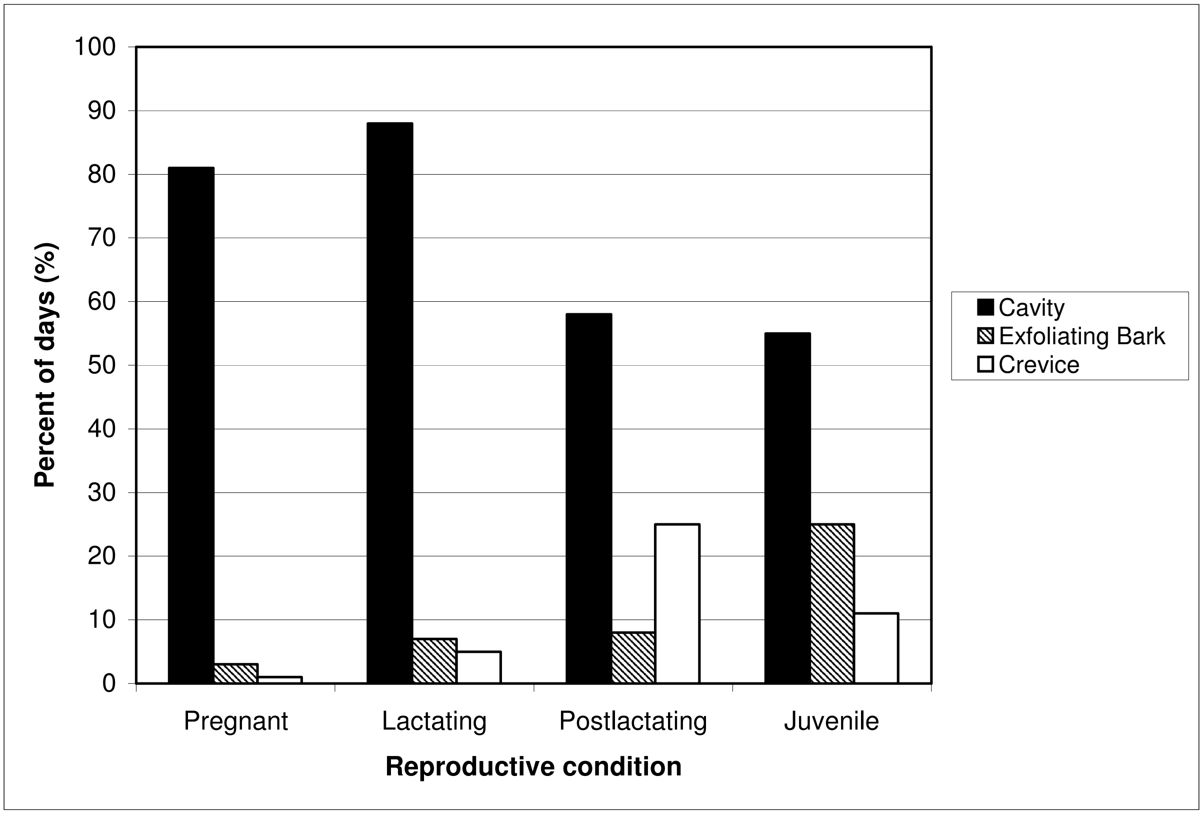


Figure 1.9. Percent of days that radio-tracked pregnant (*n* = 9), lactating (*n* = 12), postlactating (*n* = 7), and juvenile (*n* = 16) evening bats spent in cavities, or crevices or under exfoliating bark. Females that were not palpably pregnant during May and early June were included with pregnant females. Time spent was total number of days that a particular type of roost structure was occupied of all days that the individual was radio tracked.

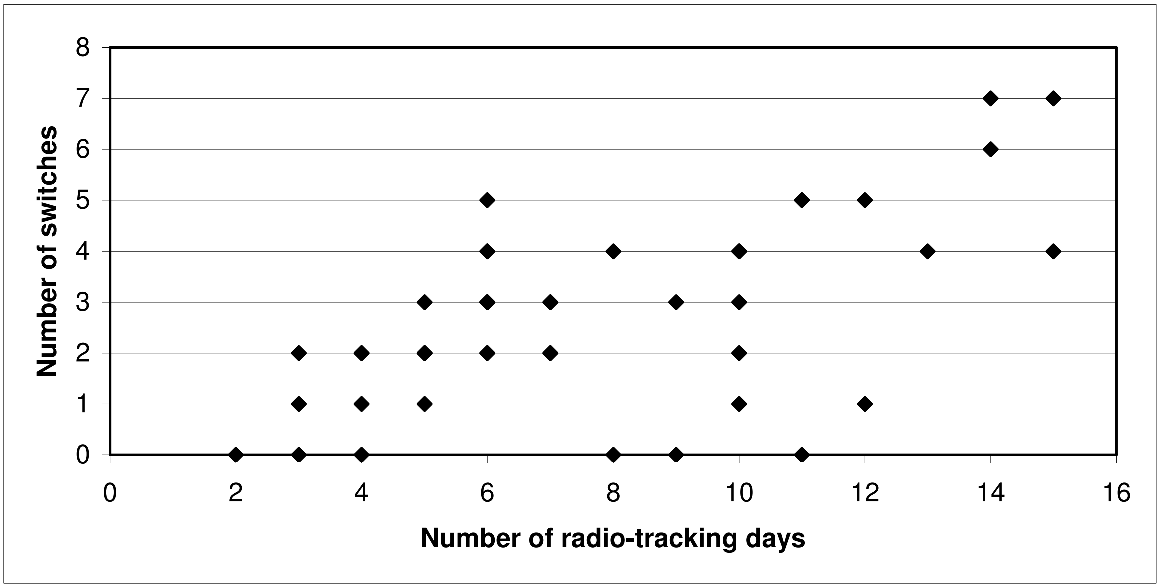


Figure 1.10. Relationship between number of switches and number of days that a bat was radio tracked ($n = 45$; $r = 0.59$; $P < 0.001$).

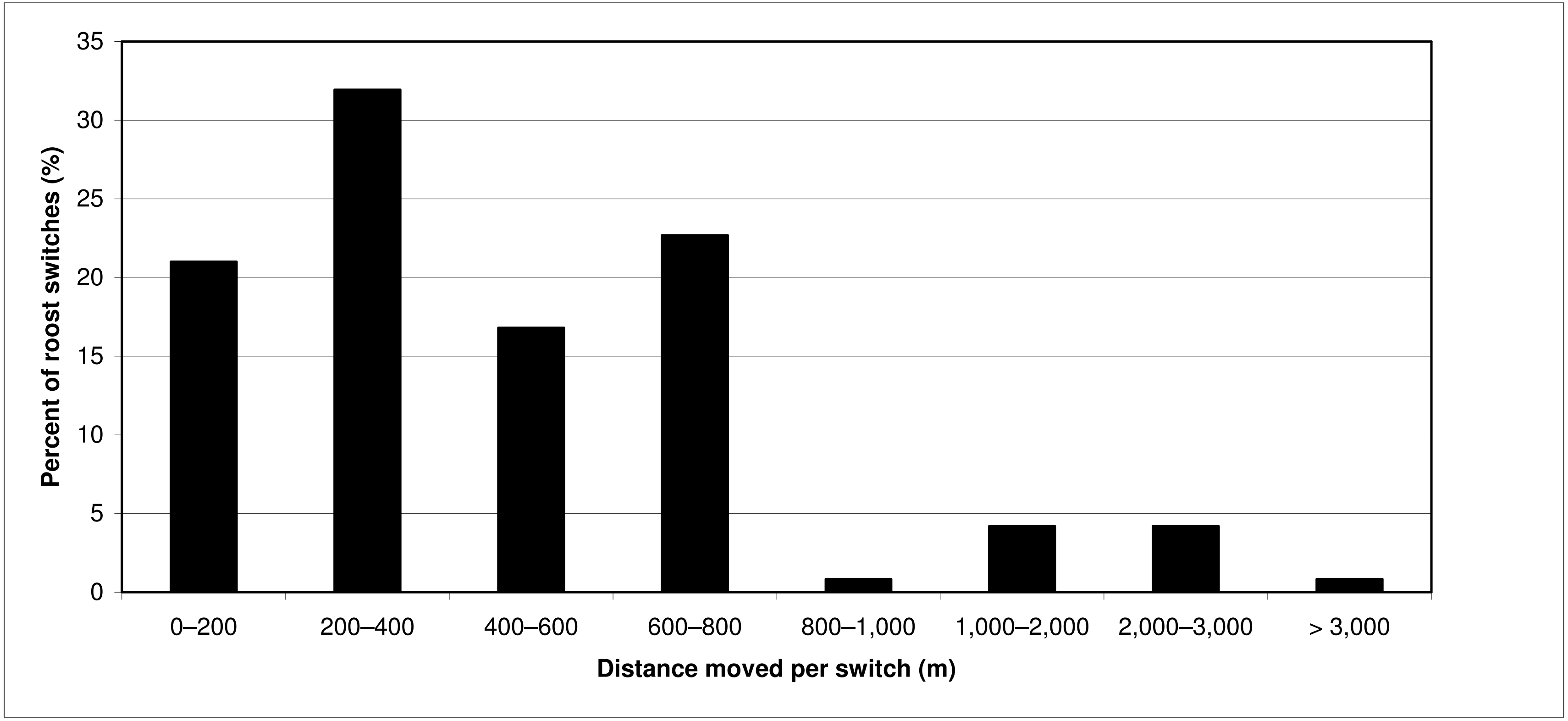


Figure 1.11. Percent of roost switches that resulted in movements of varying distances near Palmyra, Michigan, during 2006–2007. Evening bats conducted a total of 122 switches.

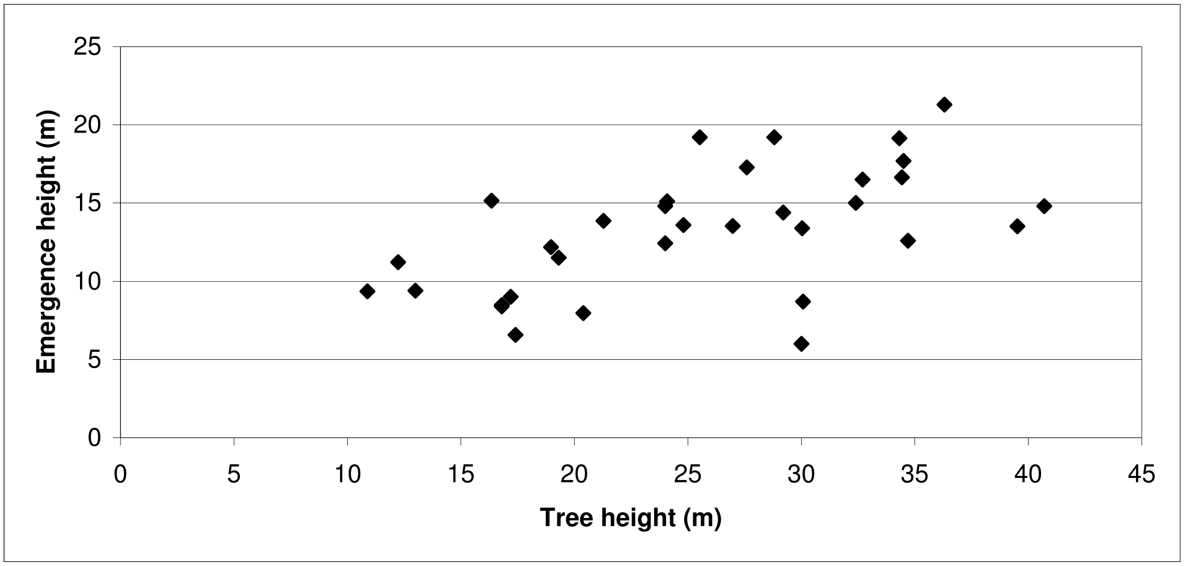


Figure 1.12. Relationship between the height of the emergence site and height of the tree ($n = 33$; $r = 0.56$; $P = 0.001$).

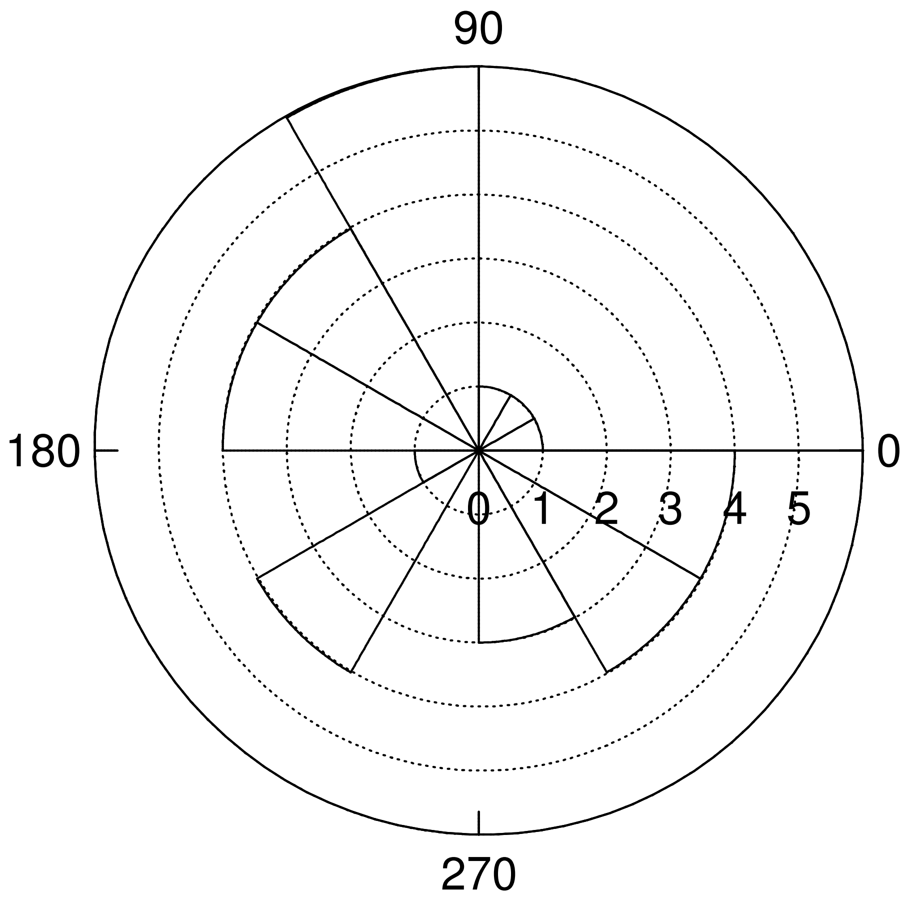


Figure 1.13. A circular histogram illustrating the density of roost exits (*n* = 33) facing in different directions (0–360º). The length of each bar indicates the number of roosts. Roost exits faced primarily south (159 ± 75º).

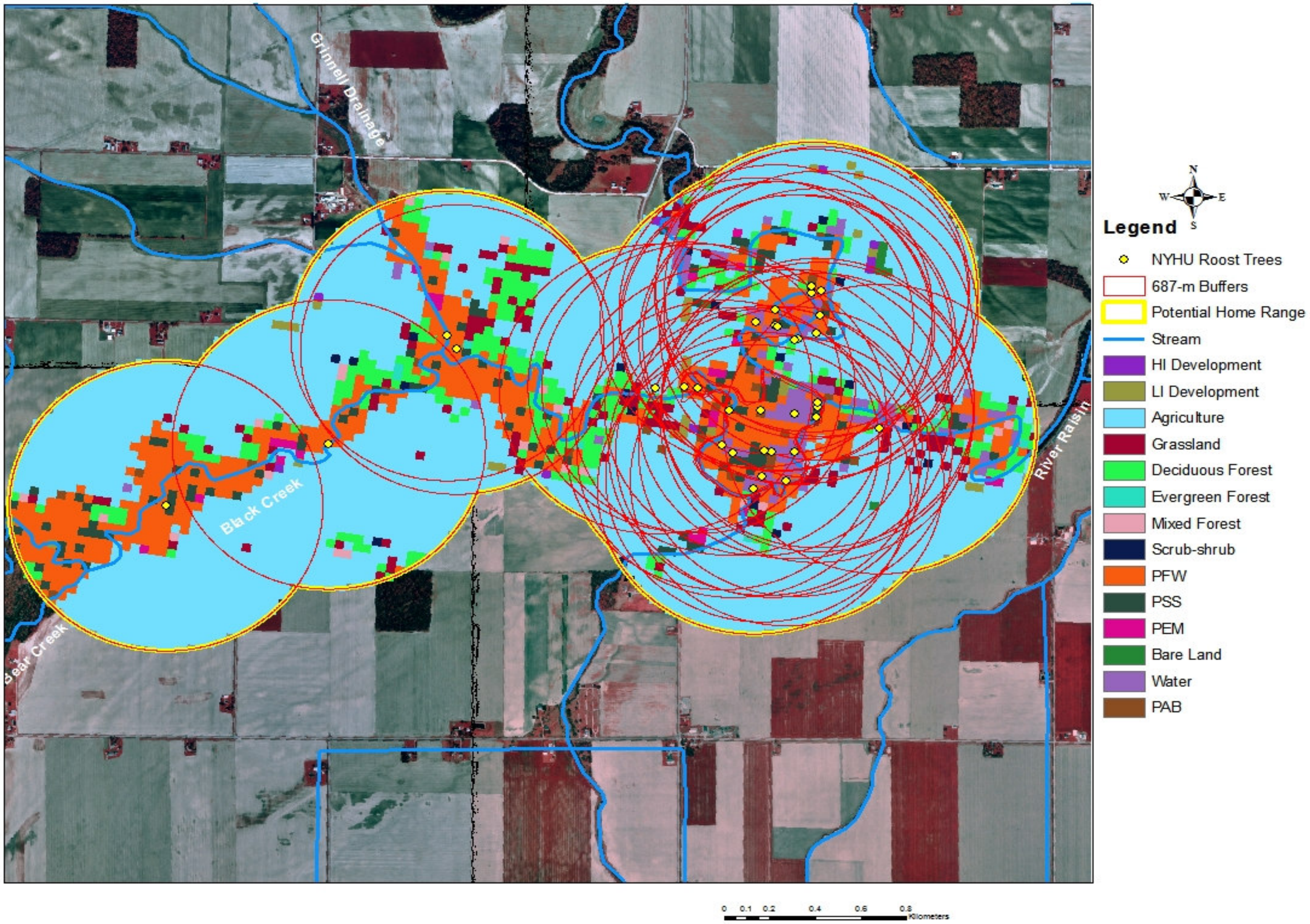


Figure 1.14. Circular buffers (687–m radius) surrounding each roost tree and the landcovers within each. The outer boundaries of all circles delineate the potential home range of the colony in Palmyra, Michigan. Abbreviations are: HI development = high-intensity development; LI development = low-intensity development (combined with HI as "development" in the text); PFW = palustrine forested wetland; PSS = palustrine scrub-shrub; PEM = palustrine emergent wetland; and PAB = palustrine aquatic bed.

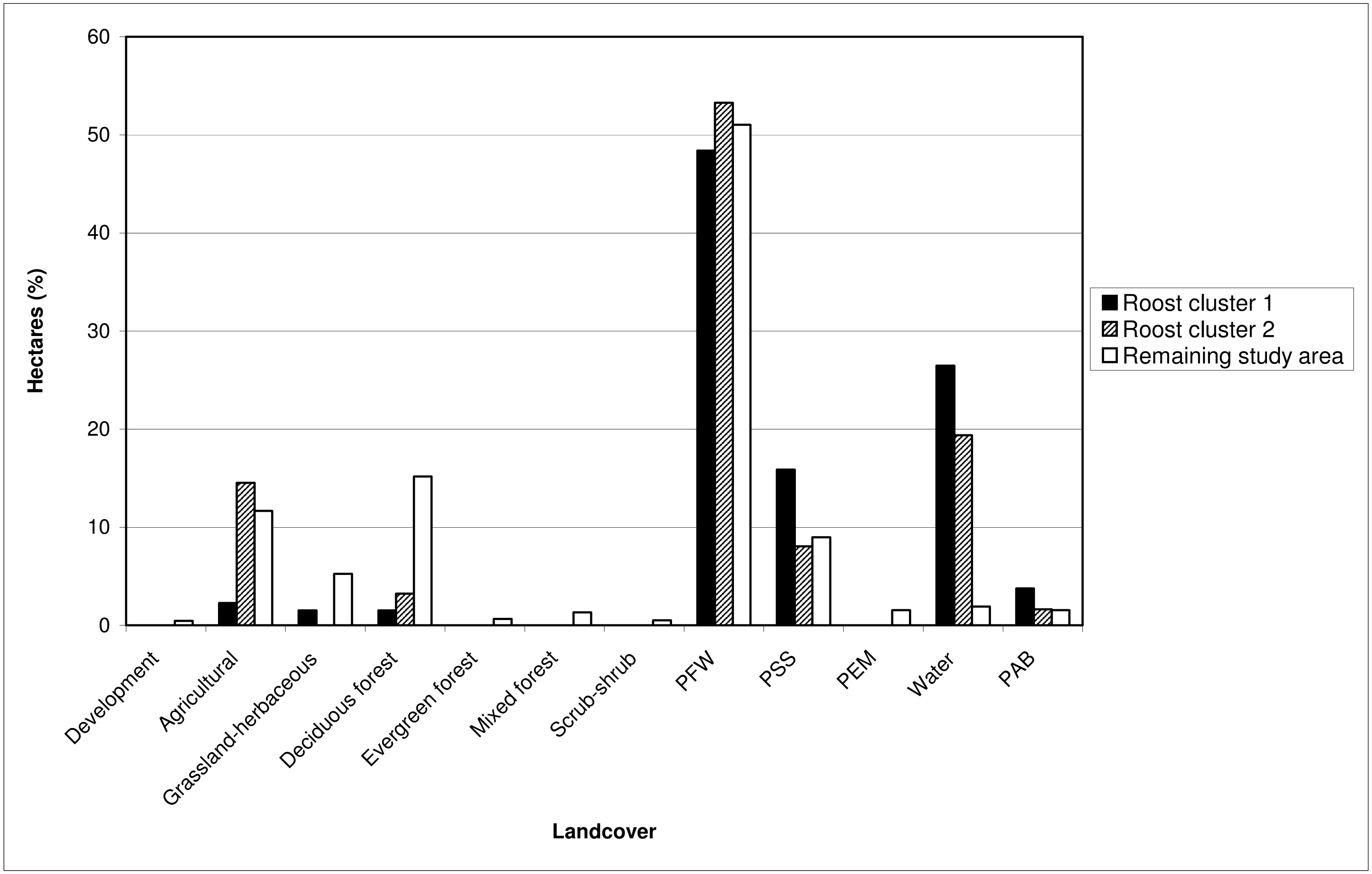


Figure 1.15. The distribution of landcover in roost cluster 1 and 2, and the remainder of the study area. Roost cluster 1 is located at the confluence of Black Creek and River Raisin, and roost cluster 2 is upstream of the confluence (Fig. 1.1). Abbreviations are: PFW = palustrine forested wetland; PSS = palustrine scrub-shrub; PEM = palustrine emergent wetland; and PAB = palustrine aquatic bed.

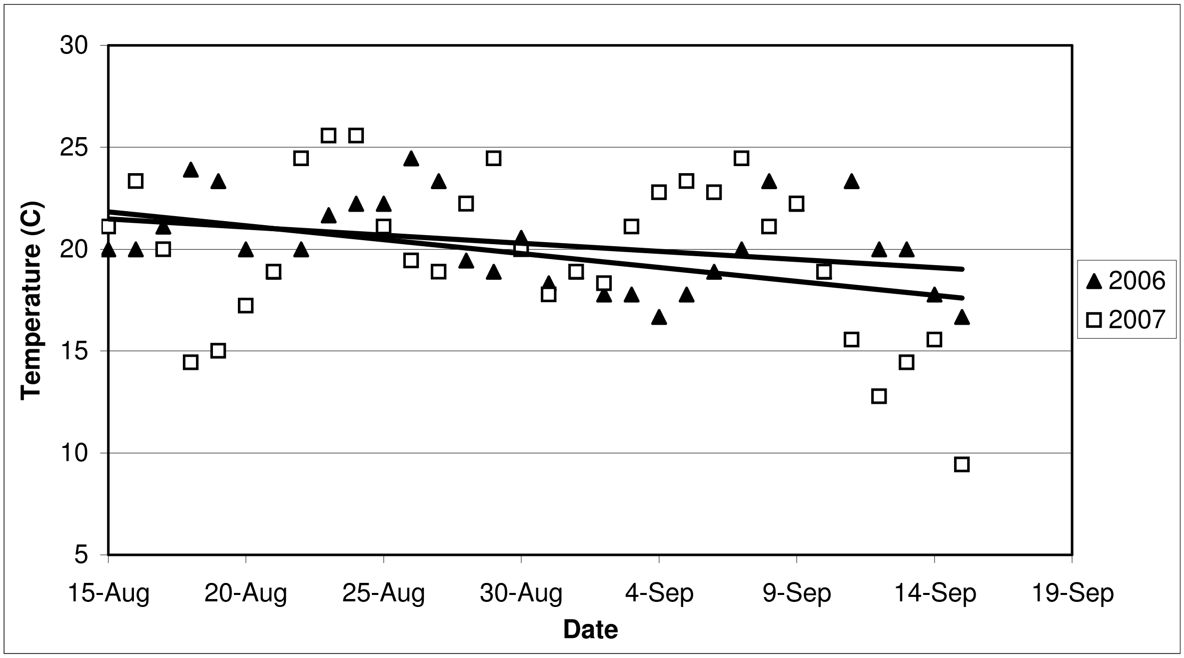


Figure 1.16. Mean ambient temperature in Adrian, Michigan, near the study area, from 15 August until 15 September 2006 and 2007 (Weather underground, 2008).

CHAPTER 2

DIETARY ECOLOGY

INTRODUCTION

Foraging method and diet vary among different species of animals (Pierson, 1998), and for insectivorous bats, diet often results from an interplay between jaw morphology and wing shape (Altringham, 1996). Size and shape of the mandible, for example, can determine whether hard-bodied insects, such as beetles, are commonly eaten, or whether the bat specializes on soft-bodied species, such as dipterans (Freeman, 1981; Soto-Centeno and Kurta, 2006). Wing shape, in contrast, often determines how fast and how maneuverable a bat is (Norberg and Rayner, 1987), which, in turn, determine the types of habitat that the animal can forage in and, therefore, the types of insects that it might encounter. Understanding what an animal eats is crucial to its management and can help elucidate aspects of an animal's natural history, such as foraging habitat (Murray and Kurta, 2002), temporal patterns of activity (Jones and Rydell, 1994), metabolic rate (McNab, 2003), and even their proclivity to use torpor (Schalk and Brigham, 1995).

Although morphology has a great effect on the types of food eaten, varying energetic costs during different reproductive stages may alter the foraging strategies and diet of bats (Anthony and Kunz, 1977). Pregnant bats, for instance, have a higher wing loading and reduced feeding efficiency because of the added mass of the fetus, which may alter the habitats in which they can forage (Anthony and Kunz, 1977; Kunz, 1974). In northern regions during May, when females are pregnant, availability of insects often is limited due to environmental conditions, such as rainfall and low ambient temperatures; consequently, foraging success is more variable, average daily consumption is lower, and bats are less selective than later in summer (Anthony and Kunz, 1977).

Energetic costs during lactation are much higher than during pregnancy, due to milk production, maternal care of the young, greater alertness by the mother, and increased duration of foraging needed to obtain the necessary food (Barclay, 1989; Anthony and Kunz, 1977). As a result, lactating females greatly increase their consumption of insects. As an example, little brown bats (*Myotis lucifugus*) eat an average of 5.5 g/day of insects during pregnancy versus 6.7 g/day in lactation, a 22% increase. During peak lactation, however, food consumption rises to 9.9 g/day—an 80% increase over average daily intake during pregnancy, and the amount of insects consumed daily represents 129% of the mother's body mass (Kurta et al., 1989). These higher costs are somewhat offset by the greater abundance and predictability of insects that lactating females encounter in June and July (Anthony and Kunz, 1977).

In addition to reproductive condition, age also may affect the diet of bats. Newly volant juveniles often leave the roost later than adults (e.g., Kurta et al., 1993), and different types of insect are most active at different times of the night (Jones and Rydell, 1994); this temporal difference in foraging may expose young bats to prey populations that differ from those that adults encounter. Spatial differences in behavior between young and their parents also occur and could lead to differences in diet. Very young bats, for example, make only short flights close to the maternity colony (Hamilton and Barclay, 1998), and even older juveniles often forage in less cluttered environments than do the adults (Adams, 1997). These differences in foraging behavior result from youngsters having less-developed echolocation abilities (Gould, 1955, 1971), they are less experienced at foraging and maneuvering (Adams, 1997; Hamilton and Barclay, 1998), and it can also reduce competition.

Species of bats typically have large geographic ranges, often spanning the length and/or breadth of North America (Wilson and Reeder, 1993). Availability of specific types of insects, however, varies with latitude (Kunz, 1974), so it is not reasonable to assume that the diet of a wide-ranging species will be identical throughout its range. Indiana bats (*Myotis sodalis*), for instance, consume mostly beetles and moths in Missouri (Brack and La Val, 1985), but caddisflies and true flies are a large part of the diet in Michigan (Kurta and Whitaker, 1998; Murray and Kurta, 2002). Populations that are on the periphery of their range especially might be liable to show differences in diet. Types of species and number of individuals in prey populations on the periphery of a predator's range are likely different from those in the core of the range. Furthermore, energetic demands on a bat should differ greatly in different parts of their range, especially northern versus southern populations, and this too could influence dietary choices. Thus, it is important for wildlife biologists to base management decisions on dietary information that is locally derived.

As global warming continues, many species of animals are moving northward (Cozier, 2004; Hughes, 2000; Lariviere, 2004; Parmesan and Yohe, 2003; Root et al., 2003; Thomas et al., 2001; Walther et al., 2002), including bats (Humphries et al., 2002; Sheel et al., 1996; Willis and Brigham, 2003). Warmer temperatures now occurring in northern regions may alter patterns of allocation, assimilation, and acquisition of food by resident populations that have developed over many generations. Additionally, global climate change may alter the phenology (i.e., the timing of migration, parturition, and other life-history events) of both predators and prey (Bertreaux et al., 2004; Hughes, 2000; Root et al., 2003; Walther et al., 2002), and if changes in the phenology of a predator do not match those of its prey, the predator may suffer individual- and population-level consequences. In Holland, Netherlands, for example, the laying date for great tits (*Parus major*) has not changed much in recent decades, but the hatching date of caterpillars used as food has become earlier. Thus, the birds are experiencing decreased reproductive success because they are not producing young at a time when prey is abundant (Visser et al., 1998). It is, therefore, important to understand the diet of animals on the northern edge of their range now so that we can understand potential problems in a warmer world.

The evening bat (*Nycticeius humeralis*) is a medium-sized (10–19-g) vespertilionid that is common throughout the Southeast and central Midwest of the United States (Watkins, 1972). Despite the ubiquity of the evening bat in the core of its range, research on diet of this species is surprisingly limited. Most studies have relied on small samples that were collected during a single field season or only part of a season (Carter et al., 1998, 2004; Feldhamer et al., 1995; Geluso et al., 2008; Whitaker, 2004; Whitaker and Clem, 1992; Wilkinson, 1992), and there has been no thorough study of diet in any peripheral population of the species. Although common in some parts of its range, the evening bat currently is considered endangered in Indiana (Whitaker and Gummer, 1993, 2003) and is in the process of being classified as threatened in Michigan (Kurta, 2008).

In the present study, I examined diet of the evening bat in Michigan over 2 years, using animals from the northernmost maternity colony of the species in North America (Kurta et al., 2005). I hypothesized that diet would vary throughout the season, among adults in different reproductive condition, and between adults and juveniles. I also predicted that diet of evening bats in the north would differ from diet of those in the south, as shown with other species, such as little brown bats (Anthony and Kunz, 1977) and Indiana bats (Murray and Kurta, 2002).

METHODS

Study area—The project area is located ca. 6 km SE Palmyra, Lenawee Co., Michigan (T7S R4E Sections 33–35; T8S R4E Sections 1–5, and 8–9). The local landscape is part of the Maumee Subdistrict, of the Washtenaw District, of the Southern Lower Michigan Region (Albert et al., 1986). At one time, this part of Michigan was under nearby Lake Erie, and consequently, the landscape consists primarily of a lake plain, dominated by clay soils, although the plain is crossed by a number of broad glacial drainages containing sandier soils. At the time of European settlement, the region was heavily forested, and the land was poorly drained. Most of the plain, however, is now drained and primarily is used for growing crops, such as soy and corn. Forested areas that remain are predominantly isolated woodlots in sites with poor drainage or along the floodplains of modern streams that occupy the old glacial channels. This dietary study occurred along one such riparian network, consisting of the River Raisin and its tributaries, Black Creek, Grinnell Drain, and Bear Creek (Fig. 2.1).

The evening bat in Palmyra.—The colony of evening bats that I studied was discovered in 2004 and is the only one known in Michigan (Kurta et al., 2005; Winhold, 2007). Extensive monitoring of this population, through mist-netting and radio tracking in 2006 and 2007 (Chapter 1), indicates that only females migrate to Michigan each year, with the first captures of the season occurring on 18–24 May. Births, as indicated by presence of lactating females, began on 18 June, and young are capable of flight about 30 days later. All youngsters are volant, and lactation ceases by the last week in July. Evening bats apparently migrate south by late August, with the latest date of capture being 26 August.

The colony consists of 40–50 adults, as well as young of the year (Chapter 1). The bats roost in cavities and crevices and under the exfoliating bark of trees, and like other tree-living species (Barclay and Kurta, 2007), evening bats use multiple roost trees and switch roosts every 2–3 days (Chapter 1). Most roost trees that I studied were located in riparian forest near the junction of the River Raisin and Black Creek (Fig. 2.1).

Dietary analysis.—Diet of the evening bat was ascertained by fecal analysis (Whitaker, 1988). I obtained samples by placing collectors made from nylon screen, at breast height, under the entrance/exit to roost trees that had been located by radio tracking (Chapter 1). To minimize disturbance, collectors were placed only after bats left to forage. Fecal pellets were collected at least four times per week when pellets were available. If no evening bats emerged at sunset from a roost with a collector, then any pellets on the collector were not used. Samples were stored in vials and frozen until they could be dried in an oven at 50°C for ≥24 h.

I also supplemented my analysis of diet based on fecal samples obtained from roosts with pellets gathered from individuals caught in mist nets. These animals were placed in holding bags for ca. 30 min or until the bat defecated. Pellets were frozen, dried, and stored for later analysis.

To aid in identification of the chitinous fragments in the pellets, I gathered a reference sample of insects from the study area, using insect light traps and a butterfly sweep net. Although it is useful to know whether bats are selecting from insects that are present in the environment, I did not sample “availability” of insects for two reasons. First, all insect-trapping procedures are intrinsically biased, attracting some types of insects more than others (Kunz, 1988; Whitaker et al., 1999). Second, proper sampling of insects would require trapping at the same height and in the same habitats that the bats are actually foraging in (Whitaker, 1994); such sampling, however, is not feasible because bats typically have numerous foraging areas that occur kilometers apart and are used to varying degrees on any given night (e.g., Murray and Kurta, 2004).

In the laboratory, all pellets obtained from individuals were examined. However, all pellets obtained from roosts during each week were combined into a single weekly sample. If ≤30 pellets were in a weekly sample, all pellets were analyzed. If >30 pellets were present, I randomly selected 30 pellets for examination; selection occurred by placing each pellet in a square on a numbered grid and using Excel (Microsoft Corporation, Redmond, Washington) to generate 30 random numbers. Whitaker et al. (1999) indicated that examining 20 pellets would identify all major foods eaten by an insectivorous bat and that 30 pellets likely would detect >85% of food items in the diet.

Pellets were soaked in 70% ethanol and teased apart under a dissecting scope (Murray and Kurta, 2002). I visually estimated percent volume, in 5% increments, of each order of arthropods in each pellet. Since proficiency of identification of insects increases with experience, I examined each pellet a second time, starting with pellets I looked at in the beginning of the dietary analysis, until the number of new identifications began to plateau. The average percent volume (sum of individual volumes/number of pellets x 100) of each order of insect was calculated per week (Feldhamer et al., 1995; Whitaker and Clem, 1992). When possible, I documented the presence of families or species of insects and I calculated their percent frequency of occurrence (i.e., the percentage of pellets that contained that type of insect). I did not calculate percent volume for families or species because volume was often minute. Other items, such as hair, wood, or vegetation were identified but not included in statistical analyses.

Weekly samples of pellets from beneath roosts were compared between years (2006 and 2007) and among reproductive conditions (pregnant, lactating, and postlactating-juvenile). Because pellets from postlactating and volant juvenile bats occur at the same time of year and are impossible to distinguish, I combined them into a period labeled as postlactating-juvenile. Pellets from roosts were assigned to a particular reproductive condition based on the reproductive condition of individuals that were captured during that week. For example, if all bats that were caught in a particular week were pregnant, then I assigned all pellets from that week to the pregnant group. Pregnancy in bats normally is determined by palpation of the abdomen (Chapter 1—Racey, 1988), but this method is unreliable during the first two thirds of pregnancy. Because rates of pregnancy in temperate bats often exceed 90% (Watkins, 1972), I assumed that all females caught early in the season before palpably pregnant bats were noted were actually pregnant. During periods when reproductive stages of captured individuals overlapped (e.g., when both pregnant and lactating individuals were present), I categorized those periods as transitional.

During 1 week, 18 June to 1 July 2006, netting was not possible because of extensive flooding in the study area, but I was able to obtain pellets from beneath some roosts, except during 26 June to 1 July 2006. To assign these pellets to the appropriate category, I relied on the capture of six pregnant bats and one lactating female that occurred on 17 June. As a result of my data and the literature (Chapter 1—Whitaker and Hamilton, 1998), I assumed that the females during this week were in transition from pregnancy to lactation.

Statistical analysis.—Statistical analyses were performed with Systat 11 (SYSTAT Software, Inc., Richmond, California) or Excel. Data were presented as $\overline{X} \pm 1$ *SE*, and alpha was set at 0.05 for all statistical tests. Data given in units of percent volume were arcsine transformed to attain normally distributed data (Zar, 1999). Analysis of variance and Tukey's pairwise comparison test were utilized to examine variation in percent volume of items in the diet between years, among reproductive conditions, and among weekly samples. For roost and individual samples, only orders comprising $\geq$5% of the diet were included in any statistical analysis (Murray and Kurta, 2002). The frequency of occurrence was calculated for order, family, and species of insects for overall diet and year, and chi-square analysis was performed on the number of pellets with and without a particular taxon. I performed the chi-square analysis on orders that comprised $\geq$5% of the overall diet, on families that occurred within pellets at a frequency of $\geq$15%, and for all identified species.

To examine dietary diversity, I used the reciprocal of Simpson's Index (*D*): $D = 1/\sum p_i^2$, where p_i represented the proportion of each order of prey (Beals et al., 1999; Brower and Zar, 1984; Murray and Kurta, 2002). Simpson's Index denotes the likelihood that two randomly selected individuals from a sample belong to the same taxon, or alternatively it can be interpreted as an indication of how many equally abundant orders would have a diversity equivalent to that detected in the sample (Brack, 1983; Brower and Zar, 1999; Murray and Kurta, 2002). Dietary diversity among reproductive conditions and year were compared using analysis of variance and Tukey's pairwise comparison test.

RESULTS

Overall diet from roosts.—I analyzed 594 pellets collected from under roost trees during a 13-week period in 2006 and a 14-week period in 2007 (Table 2.1). Diet of evening bats included 14 orders of insects and two orders of arachnids (Table 2.2). Four orders—Coleoptera, Diptera, Hymenoptera, Hemiptera—composed 85% of the volume of the diet. Coleoptera contributed most to the volume (40.0%), followed by Diptera (19.6%), Hymenoptera (13.6%), and Hemiptera (12.8%; Table 2.2). Similarly, Coleoptera occurred with the highest frequency in pellets from roosts (98.0%), followed by Diptera (94.3%), Hymenoptera (73.6%), and Hemiptera (68.5%; Table 2.3).

I assigned 406 pellets collected from under the roosts of evening bats to the three reproductive conditions—pregnancy ($n = 61$ pellets), lactation (141), and postlactation-juvenile (204). The percent volume of Coleoptera did not vary significantly among the diets of pregnant, lactating, and postlactating-juvenile bats ($F_{2,403} = 0.86$; $P = 0.42$; Table 2.4). The percent volume of Diptera differed significantly among reproductive conditions ($F_{2,403} = 11.09$; $P < 0.001$), with lactating females (16.1%) consuming less than pregnant (23.9%) and postlactating-juvenile (19.7%) bats. Hemiptera also was eaten in varying amounts by different reproductive conditions ($F_{2,403} = 9.23$; $P < 0.001$); lactating (13.4%) and postlactating-juvenile (13.8%) bats consumed a greater percent volume of Hemiptera than pregnant individuals (8.2%; Table 2.4). A difference was also detected in the percent volume of Hymenoptera ($F_{2,403} = 15.98$; $P < 0.001$); significant variation occurred among all the reproductive conditions, with pregnant bats eating the least amount (5.2%) and lactating bats, the most (17.0%; Table 2.4).

I identified 11 orders of arthropods in the diet of pregnant bats, 12 in pellets of lactating bats, and 14 in the diet of postlactating-juvenile bats (Table 2.4). I compared diversity of orders in the diet of pregnant, lactating, and postlactating-juvenile bats among 18 weeks (Table 2.1), excluding transitional weeks. Dietary diversity differed among reproductive conditions ($F_{2,\,15} = 5.43$; $P = 0.02$); diversity for postlactating-juvenile bats (4.20 ± 0.19) was higher than that of pregnant bats (3.03 ± 0.33) but statistically equal to that of lactating bats (4.09 ± 0.30). Diversity of diet did not differ between pregnant and lactating evening bats. The dietary diversity of orders in pellets from the entire study was 4.34.

Four of the 31 families identified in pellets from roosts occurred at a frequency ≥15% of pellets from 2006 and 2007—Carabidae (36.9%), Curculionidae (35%), Chrysomelidae (19.4%), and Corixidae (18%; $\chi^2_3 = 94.10$; $P < 0.001$; Table 2.3). I was able to identify a few species as well: spotted cucumber beetle (*Diabrotica undecimpunctata*), green stink bug (*Acrosternum hilare*), and emerald ash borer (*Agrilus planipennis*). These insects were found in 15.3, 12.0, and 0.8%, respectively, of the pellets from roosts of evening bats throughout the study (Table 2.3). I also observed hair, presumably from bats, fragments of plants and wood, and strands from mist nets in fecal pellets of evening bats.

Variation within 2006.—Fecal pellets were gathered under roost trees for 12 of 13 weeks between 29 May and 27 August; during week 7 (26 June–2 July), no pellets were collected because roost trees were inaccessible due to flooding along the River Raisin. In the 320 pellets analyzed, I found two orders of arachnids and 13 orders of insects. Dietary diversity was 4.20.

I analyzed 230 pellets that were assigned to the three reproductive conditions to test whether differences occurred in the diet among reproductive conditions in 2006. The volume of the four most common orders—Coleoptera ($F_{2,\,227} = 4.79$; $P = 0.009$), Diptera ($F_{2,\,227} = 4.96$; $P = 0.008$), Hemiptera ($F_{2,\,227} = 9.70$; $P < 0.001$), and Hymenoptera ($F_{2,\,227} = 6.58$; $P = 0.002$)—varied among reproductive conditions in 2006. Tukey's tests indicated that pregnant bats consumed significantly more Coleoptera than postlactating-juveniles (Fig. 2.2), whereas Diptera was eaten significantly less during lactation than by pregnant or postlactating-juveniles. Hemiptera formed less of the diet of pregnant bats than postlactating-juveniles, and lactating and postlactating-juvenile bats ate more Hymenoptera than pregnant bats (Fig. 2.2).

I also examined composition of the diet of evening bats by week, including weeks that were transitional between reproductive conditions. There was a significant difference among weeks in volume of Coleoptera ($F_{11, 308} = 3.01$; $P = 0.001$), Diptera ($F_{11, 308} = 3.75$; $P < 0.001$), Hemiptera ($F_{11, 308} = 5.92$; $P < 0.001$), and Hymenoptera ($F_{11, 308} = 5.68$; $P < 0.001$) consumed by evening bats. The amount of Coleoptera and Diptera eaten by evening bats differed by ca. 18% (30–48%) and 13% (15–28%) within the year, respectively (Fig. 2.3). The volume of Hemiptera varied between 6 and 21%, and Hymenoptera fluctuated between 0 and 22% in weekly samples during 2006 (Fig. 2.3).

I was able to identify 29 families and the three species (spotted cucumber beetle, green stink bug, and emerald ash borer) of insects in the fecal pellets of evening bats in 2006 (Table 2.3). Curculionidae (47%), Carabidae (40%), Corixidae (24%), and Chrysomelidae (21%) were the families most frequently detected in pellets from roosts (Table 2.3). Spotted cucumber beetles (17%) and green stink bugs (13%) often were detected, but the emerald ash borer was uncommon (0.6%).

In general, the frequency occurrence of Corixidae, Curculionidae, and Chrysomelidae was high during the postlactating-juvenile period (after week 10; Fig. 2.5); however, Carabidae fluctuated throughout the season, with frequency occurrence >60% during lactation (week 6), the first week of postlactation-juvenile (week 8), and prior to migration (week 15). Spotted cucumber beetles, which were the most common member of the

Chrysomelidae, also peaked late in the season, prior to migration (50%; Fig. 2.5). The frequency occurrence of the green stink bug was variable; nonetheless, it was found at the greatest frequency prior to migration (25%; week 15) and during lactation (23%; week 6) and postlactation-volancy (17%; week 12). The emerald ash borer was detected in only a few pellets during pregnancy (12–18 June) and prior to migration (Fig. 2.5).

Variation within 2007.—I collected feces from under roosts for 13 of 14 weeks beginning 14 May and ending 19 August; no feces were collected during week 3 (28 May–3 June) because of thunderstorms, a local emergency (police manhunt), and no evening bats emerging from trees thought to contain radio-tracked bats. Thirteen orders were identified in 274 pellets analyzed in 2007. Dietary diversity was 4.44.

A total of 170 pellets from 2007 were assigned to reproductive conditions; I deleted pregnant females from my analysis of reproductive conditions in 2007 because my sample size was low ($n = 6$ pellets). The statistical analysis indicated a significant difference between the percent volume of Coleoptera in the diet of lactating and postlactating-juvenile bats ($F_{1,\,168} = 5.58$; $P = 0.02$), with postlactating-juveniles consuming greater amounts of Coleoptera than lactating bats (Fig. 2.5). However, no statistical differences were found in the percent volume of Diptera ($F_{1,\,168} = 0.08$; $P = 0.78$), Hemiptera ($F_{1,\,168} = 1.16$; $P = 0.28$), nor Hymenoptera ($F_{1,\,168} = 1.15$; $P = 0.29$) consumed by lactating and postlactating-juvenile bats (Fig. 2.2).

Percent volume among weeks for Coleoptera ($F_{10,\,257} = 1.80$; $P = 0.061$), Hemiptera ($F_{10,\,257} = 1.18$; $P = 0.31$), and Hymenoptera ($F_{10,\,257} = 1.71$; $P = 0.08$) did not vary, but there were significant differences among weeks for Diptera ($F_{10,\,257} = 2.25$; $P = 0.02$). The amount of Diptera consumed during week 2 was 63.3%, but during the remainder of the season, Diptera fluctuated from 12 to 22 % (Fig. 2.3).

Evening bats consumed 21 families of insects that were identified in 2007, and four families had a frequency occurrence $\geq$15% (Table 2.3). Carabidae (34%) and Curculionidae (21%) were most frequently observed in the diet of evening bats, although Formicidae (12%) was consumed at a higher frequency than Corixidae (10%), which was the third most common family in 2006. Two species of Coleoptera (spotted cucumber beetle and emerald ash borer) and one species of Hemiptera (green stink bug) were identified in the diet of evening bats; these insects were found in 14, 1, and 16% of the pellets, respectively (Table 2.3).

Similar to 2006, the frequency occurrence of Curculionidae and Chrysomelidae spiked during postlactation-juvenile (Fig. 2.5). Conversely, Carabidae was found at a high frequency during lactation (63%), and Corixidae fluctuated between 0 and 20% throughout the year. Spotted cucumber beetles peaked during postlactation-juvenile, as in 2006, and fragments of green stink bugs were found at a greater frequency during lactation; green stink bugs did not increase prior to migration, as they had in 2006 (Fig. 2.5). The emerald ash borer was detected during only week 12 (30 July–5 August).

Variation between years.—The percent volume of Coleoptera did not vary between 2006 and 2007 ($F_{1, 592} = 3.04$; $P = 0.08$). Diptera, however, was more common in 2006 than 2007 ($F_{1, 592} = 12.33$; $P < 0.001$), whereas Hymenoptera ($F_{1,592} = 16.80$; $P < 0.001$) and Hemiptera ($F_{1, 592} = 4.32$; $P = 0.04$) were more abundant during 2007 than 2006 (Table 2.2). The frequency occurrence of orders varied significantly between years for Coleoptera ($\chi^2_1 = 4.11$; $P = 0.04$) and Diptera ($\chi^2_1 = 5.01$; $P = 0.03$), but evening bats did not vary the frequency at which they consumed Hemiptera ($\chi^2_1 = 2.14$; $P = 0.14$) or Hymenoptera ($\chi^2_1 = 0.01$; $P = 0.91$). Dietary diversity for 2007 (4.44) was ca. 4% higher than in 2006 (4.20), but this difference was not significant ($F_{1, 23} = 0.04$; $P = 0.84$).

Eight more families of insects were identified in 2006 than 2007 (Table 2.3). Of the families that composed ≥15%, there was no significant difference between years in the frequency of Carabidae ($\chi^2_1 = 2.37$; $P = 0.12$) or Chrysomelidae ($\chi^2_1 = 1.16$; $P = 0.28$), but there was significant difference in the frequency occurrence of Curculionidae ($\chi^2_1 = 41.93$; $P < 0.001$), Corixidae ($\chi^2_1 = 20.63$; $P < 0.001$), and Pentatomidae ($\chi^2_1 = 3.17$; $P < 0.01$) between 2006 and 2007 (Table 2.3). In 2006, Curculionidae and Corixidae were found at a higher frequency in pellets than in 2007. The frequency of green stink bugs in the diet was higher in 2006 than 2007 ($\chi^2_1 = 3.17$; $P < 0.01$), yet the proportion of pellets containing spotted cucumber beetles ($\chi^2_1 = 1.29$; $P < 0.26$) and emerald ash borers ($\chi^2_1 = 0.39$; $P < 0.53$) did not differ significantly between years (Table 2.3).

Diet of individual evening bats.—Fifty-seven pellets were collected from 31 individual evening bats captured in mist nets. Seventeen individuals defecated more than one pellet, and all pellets from the same individual were combined into one sample to maintain statistical independence. I collected 18 fecal pellets from 10 pregnant females, 17 from 8 lactating adults, 15 from 5 postlactating females, and 17 from 8 juveniles. Diet of individuals was composed of 11 orders of insects (Table 2.5). Arachnids were not found in any pellets from individuals. Eighty-nine percent of the volume of the diet consisted of four orders: Coleoptera, Hemiptera, Diptera, and Hymenoptera. Coleoptera occurred at a frequency of 100% in pellets of individuals, followed by Diptera (83.3%), Hemiptera (80.4%), and Hymenoptera (64.8%; Table 2.6). Dietary diversity for individuals was 3.16.

In the diet of individuals, there was no significant difference between years in the percent volume of Coleoptera ($F_{1, 29} = 0.01$; $P = 0.91$), Diptera ($F_{1, 29} = 1.51$; $P = 0.23$), Hemiptera ($F_{1, 29} = 0.00$; $P = 0.99$), or Hymenoptera ($F_{1, 29} = 0.13$; $P = 0.73$) or among reproductive conditions—Coleoptera ($F_{3, 27} = 1.88$; $P = 0.16$), Diptera ($F_{3, 27} = 2.63$; $P = 0.07$), Hemiptera ($F_{3, 27} = 0.31$; $P = 0.82$), and Hymenoptera ($F_{3, 27} = 1.46$; $P = 0.25$). However, the sample sizes of bats in each reproductive condition were small (Table 2.7). Also, there was no significant difference between years in the frequency occurrence of orders in pellets of individuals (Table 2.6).

Fifteen families of insects were identified within the diet of individuals; however, only five families occurred at a frequency $\geq$15%— Carabidae (61.3%), Curculionidae (58.1%), Chrysomelidae (35.5%), Corixidae (19.4%), and Scarabaeidae (16.1%; Table 2.6). I compared the frequency occurrence of families and species among years, and only Curculionidae ($\chi^2_1 = 5.56$; $P = 0.02$; Table 2.6) was significantly different between years, with more Curculionidae detected in 2006 than 2007. Three species (spotted cucumber beetle, emerald ash borer, and green stink bug) were also identified in the diet of individual evening bats at a frequency occurrence of 32.3%, 3.2%, and 19.4%, respectively (Table 2.6). There were no significant differences between years for species detected in pellets from individual bats (Table 2.6).

DISCUSSION

Differences in diet among species of bat often are related to different strategies of echolocation and differences in morphology of the jaws and wing (Altringham, 1996). As an aerial hawking bat with low aspect ratio and high wing loading, evening bats typically forage for flying insects in uncluttered areas (Jones and Rydell, 1994; Norberg and Rayner, 1987), and the diet of evening bats in Michigan exemplified this foraging strategy. Evening bats consumed primarily aerial insects (e.g., Coleoptera, Diptera, and Hemiptera), although they occasionally (<1% volume) fed on terrestrial arthropods, such as Araneida, Blattodea, or Orthoptera (primarily Gryllotalpidae: mole cricket). Evening bats likely consumed these terrestrial arthropods during occasional bouts of gleaning, or when these arthropods were flying, ballooning, or in a web. Acari and Phthiraptera most likely were ectoparasites that were ingested while bats were grooming themselves. Furthermore, the skull of evening bats is of intermediate robustness, allowing them to eat a range of insects from hard beetles to soft flies (Freeman, 1981).

The wing morphology of evening bats is adapted for foraging in open habitats with low clutter (Fleming and Eby, 2003; Menzel et al., 2005; Norberg and Rayner, 1987), such as agricultural fields (Clem, 1993; Duchamp et al., 2004) and riparian corridors (Menzel et al, 2005). Evening bats in Michigan inhabited bottomland forest that was interlaced with waterways and standing pools of varying duration and surrounded by agricultural fields (Chapter 1). Waterways and stagnant pools are excellent habitats for some Diptera (e.g., Culicidae and Chironomidae) and Hemiptera (e.g., Corixidae). Corixidae, an aquatic family, was frequently found in the diet of evening bats (18% of pellets). These insects were not likely gleaned from the surface of a pond or stream but probably were captured while in flight (Adams, 1993), as they dispersed to other aquatic habitats (Stevens et al., 2007). Other aquatic insects (e.g., Ephemeroptera; 3% volume) also were found, suggesting that evening bats occasionally foraged over the streams and sloughs or that they opportunistically consumed these insects while commuting to upland sites. Some families of Coleoptera (e.g., Curculionidae and Chrysomelidae) are common in agricultural fields, and the presence of multiple crop pests in the diet (see *Prey of economic interest*) indicated that these bats commonly foraged over cropland.

Prey of economic interest.—Bats, in general, are extremely important in regulating the number of insects in forests and reducing herbivory (Kalka et al., 2008; Wilson and Barclay, 2006), and some species provide an important insect-control service for farmers (Williams-Guillén et al., 2008). Mexican free-tailed bats (*Tadairida brasiliensis*), for instance, consume the adults of destructive pests of cotton, including the cotton bollworm (*Helicoverpa zea*). The value of this pest-control service in just an eight-county region of Texas is estimated at $741,000 annually, which includes the value of the increased production of cotton and the decreased need for chemical insecticides (Cleveland et al., 2007).

Evening bats in Illinois and Indiana consume a number of agricultural pests (Feldhamer et al., 1995; Whitaker and Clem, 1992), and the same appears true of evening bats in Michigan. For example, fragments of spotted cucumber beetles occurred at frequencies of ca. 30% and 15% in pellets taken from individuals and roosts, respectively (Table 2.3 and 2.6). The larval stage of the spotted cucumber beetle is also known as the corn rootworm, which tunnels through and feeds on the roots of soybean and corn, the two most common crops in the study area, whereas the adult beetles damage leaves and flowers of these plants (Lazarus and Swanson, 1983; Meinke et al., 1985). Adult cucumber beetles emerge in spring, feed on the foliage of new plants, and lay their eggs at the base of plants. In late July and early August, the larvae of cucumber beetles pupate and ultimately become adults (Jess and Zandstra, 1999; Sorenson and Baker, 2008). After week 11 (end of July), evening bats in Michigan ate greater amounts of spotted cucumber beetles than in previous weeks (Fig. 2.6), and this increase in consumption probably coincides with the onset of activity by the new generation of beetles.

Like the cucumber beetle, the green stink bug often feeds on crops, such as the pods of soybeans, causing irreversible damage (Panizzi and Slanski, 1985). Fragments of green stink bug were found at a frequency of 12–15% in pellets from individuals and roosts (Table 2.3 and 2.6). Mating of green stink bugs occurs during the first warm days of spring. Throughout May and early June, a few adults may be active, but they become more common in mid-to-late June. A life cycle takes 30–45 days and depending upon ambient temperature, a second generation may occur in July and August (Gomez and Mizell, 2008). Green stink bugs were much less common in the diet than were cucumber beetles, and consequently, distinct trends are less apparent. Nevertheless, in 2006, green stink bugs occurred in the diet of evening bats primarily in mid-to-late June and in August, and during 2007, these bugs were detected most frequently in early July (Fig. 2.6). These dates of higher consumption roughly correspond with the expected life cycle of green stink bugs.

Although I could not identify any to species, beetles of the family Curculionidae (snout beetles and true weevils) occurred at a frequency of 35 and 58% in pellets from roosts and individuals, respectively (Table 2.3 and 2.6). Members of this family are plant feeders (phytophagous), and some are serious agricultural pests (Triplehorn and Johnson, 2005). Adult weevils feed on buds, flowers, and fruit of various crops (e.g., alfalfa, peppers, and potato), and the larvae develop within and feed upon the plants, thereby reducing yield (Toapanta et al., 2005). These beetles were most common in the diet during late July and August, and this may coincide with appearance of a new generation of adults.

Although not an agricultural pest, emerald ash borers also were found in the diet of evening bats. Emerald ash borers are exotic beetles from Asia that have killed or wounded more than 5 million ash trees (*Fraxinus*) in southeastern Michigan (Poland and McCullough, 2006). Depending upon ambient temperature, adult beetles begin to emerge in early June and are present until mid-August; they generally live for 3 weeks (McCullough and Katovich, 2004). As adults, emerald ash borers eat the foliage of ash trees, and the larvae feed upon the phloem and cambium. Emerald ash borers were only a small component of the diet of evening bats (≤1%), probably because this insect is diurnal (European and Mediterranean Plant Protection Organization, 2005). Evening bats either gleaned emerald ash borers off foliage at night or more likely consumed them as the beetles flew during periods of twilight near sunset and sunrise.

Mosquitoes (Culicidae) occurred in a notable portion of the diet of evening bats, with a frequency occurrence of 6 and 3% in pellets from roosts and individuals, respectively (Table 2.3 and 2.6). Mosquitoes rarely are a principal component in the diet of bats, except at high latitudes. For example, mosquitoes were found at a frequency occurrence of 17% in the diet of little brown bats in Alaska (Whitaker and Lawhead, 1992), and 77.4% in New Hampshire (Anthony and Kunz, 1977). Other studies at lower latitudes have reported mosquitoes much less frequently (Buchler, 1976; Whitaker, 2004; Whitaker et al., 1977). In general, North American bats seldom consume many mosquitoes because mosquitoes are small, only some species swarm, and they tend to fly close to vegetation rather than above it where bats are foraging (Kurta, 2008; Whitaker and Lawhead, 1992). Although mosquitoes are not major prey of evening bats, their consumption by bats is important because mosquitoes are a nuisance to humans and can be a vector of diseases to mammals and birds, such as the West Nile Virus.

Variation between years.—My study was the first to compare diet of evening bats between years. Dietary diversity (Simpson's Index) was the same between years, and the major components (orders) of the diet remained the same between years, although the exact proportions differed slightly and sometimes significantly for various groups. Coleoptera dominated the diet of evening bats in both 2006 and 2007 and clearly was the most important food, in terms of both volume and frequency (Table 2.2 and 2.3). Although inter-year variation did not occur among orders in the pellets from individuals (Table 2.5), differences in percent volume of some insects were found in pellets gathered from roosts (Table 2.2 and 2.5). In 2006, evening bats consumed greater volumes of Diptera and lesser amounts of Hemiptera and Hymenoptera than in 2007 (Table 2.2).

Although it is possible that some of these differences are adaptive, they most likely are related to differences in availability. Flying ants, for example, often occur in large swarms at unpredictable times (Kunz et al., 1995; Kurta, 2005; Whitaker and Rodríguez-Durán, 1999), which may help explain the greater abundance of Hymenoptera in one year compared to the other. Furthermore some inter-annual differences likely are due to weather-related factors. In 2006, the project area was subjected to extensive flooding at the end of June, with water extending $\geq$3 m above the ordinary high-water mark. Such conditions presumably allowed aquatic species to flourish in the following weeks, leading to higher frequencies of Corixidae and Culicidae in 2006 than 2007 (Table 2.3 and 2.6). Culicidae, for instance, was detected in >10% of pellets taken from roosts in 2006 but <1% in 2007.

Variation within years.—I found no variation among reproductive conditions in the diet of individual evening bats, although samples were small (5–10 bats per group). In pellets gathered from roosts, Coleoptera consistently dominated the diet throughout each year, but there were minor differences among reproductive periods and weeks for some taxa (Table 2.4; Fig. 2.4). Individual pregnant bats consumed at least twice as much Diptera than juvenile, lactating, or postlacting bats (Table 2.7). Similarly, I found that pellets from roosts had a higher percent volume of Diptera during the pregnancy (23.9%) and postlactation-juvenile periods (19.7%) than during lactation (16%; Table 2.4). The high percentage of Diptera during pregnancy may be related partly to small samples in 2007; however, insect abundance is generally lower early in the season, when bats are pregnant, and to increase foraging success, many bats consume insects that swarm, such as certain Diptera (e.g., Chironomidae—Anthony and Kunz, 1977). Increased use of Diptera in the postlactation-juvenile period may reflect the inexperience of young bats. Juveniles soon after volancy are less efficient foragers than adults (Adams, 1996; Anthony and Kunz, 1977; Gould, 1955, 1971), and swarming insects may be easier to detect and capture.

The percent volume of Hymenoptera was greatest during lactation, and the amount of Hemiptera was lowest during pregnancy (Table 2.4). In South Carolina, Carter et al. (2004) found that evening bats consumed the greatest percent volume of Coleoptera and Hymenoptera in early summer (mid-June) and the highest amount of Hemiptera late in summer (mid-August). These trends are similar to those of the evening bat in Michigan. These patterns may be attributed to the life cycle of the insect, as seen with the cucumber beetle, or perhaps be related to energetic or nutritional demands during various reproductive stages, because caloric and nutritional values vary among insects (Ramos-Elorduy, 1997).

Geographic variation in diet.—Overall, diet of evening bats in Michigan was diverse, with a total of 14 orders of insects and two orders of arachnids, although the combined amount of Acari, Araneida, Blattodea, Neuroptera, Odonata, Orthoptera, and Phthiraptera composed <2% of the diet (Table 2.2). Coleoptera was the most important food for evening bats in Michigan (39% volume; 98% frequency occurrence), followed by Diptera (19.6%; 94.3%), Hymenoptera (13.6%; 73.6%), and Hemiptera (12.8%; 68.5%). Results from six dietary studies in Georgia, Illinois, Indiana, Nebraska, and South Carolina were generally similar to Michigan in that diet in each state was dominated by Coleoptera, with beetles composing 39–60% of the volume (Table 2.8).

Most reports indicated that evening bats also consumed Diptera, Hemiptera, Homoptera, Hymenoptera, and Lepidoptera, but the magnitude of the contribution by each order to the overall diet differed greatly (Table 2.8). Hymenoptera, for example, varied from 0% in Illinois to 36% in Georgia. Lepidoptera varied from 3 to 20% in two studies in Indiana, whereas Homoptera ranged from 3% in Georgia to 20% in Indiana. Such large variation in secondary components does not appear related to latitude and may be a result of site-specific factors. Although the major orders present in the diet were similar among studies, each report identified fewer total orders than in Michigan (Table 2.8); however, these studies also had much smaller samples, and as the number of pellets examined is increased, the potential of detecting minor food items becomes greater (Whitaker et al., 1999).

The largest difference in dietary composition between Michigan and other states is in the amount of Diptera. At the northern edge of their range, evening bats consumed a higher amount of Diptera (19.6% volume) compared to other studies that generally indicated <6% (Carter et al., 1998, 2004; Feldhamer et al., 1995; Geluso et al., 2008; Whitaker, 2004;

Whitaker and Clem, 1992; Table 2.8). Large amounts of Diptera in the diet in Michigan may reflect the abundance of aquatic habitats near the roost trees (Chapter 1), although another study performed on evening bats in an apparently similar bottomland forest yielded only 2.5% Diptera (Whitaker, 2004). As indicated earlier, evening bats in Michigan consume the most Diptera early in the season (Table 2.4; Figure 2.2 and 2.3), when ambient temperatures are cool, perhaps taking advantage of swarming insects when others are scarce.

Opportunist or specialist?—Researchers have investigated whether insectivorous bats are opportunistic or selective feeders. Whitaker (1995) argues that if all insectivorous bats consumed whatever insects were available, all bats would have more or less the same diet, and because they do not, bats must specialize to some degree on available insects. Such specialization may be active, in the sense that a bat detects and pursues only specific types of prey. However, the speed of a flying bat coupled with the rapid attenuation of high-frequency sound make it unlikely that most bats are able to discern much detail about a flying insect before it is intercepted (Barclay and Brigham, 1994). Bats most likely demonstrate selectivity by choosing a particular habitat for foraging (dependent on wing morphology) and then pursue whatever insect is present and within the abilities of the bat to detect (dependent on properties of the bat's echolocation calls) and to consume (dependent on the bat's jaw morphology—Brigham et al., 1992; Whitaker, 1995). The evening bat consistently eats beetles, so it might be called a specialist. However, it is perhaps better described as an opportunistic specialist—always consuming beetles but also taking advantage of other types of prey that vary within or between years or as geography changes.

My study was limited in its ability to identify species and even families that contribute to the diet of evening bats, so it is difficult to predict whether global warming will affect the phenology of the evening bat's prey. However, given the apparent broadness of the bat's diet, compared with more narrow diets of certain birds, such as golden plovers (*Pluvialis apricaria*) and puffins (*Fratercula artica*—Visser and Both, 2005), I predict that global warming will not have a negative impact on evening bats in Michigan. It is possible, though, that the composition of the diet of the colony in Michigan might change; for example, the amount of Diptera in the diet may decrease if ambient temperatures increase earlier in the season and allow other insects to become more active.

LITERATURE CITED

Adams, R. A. 1993. Consumption of water boatmen (Hemiptera: Corixidae) by little brown bats, *Myotis lucifugus*. Bat Research News, 3:66–67.

———. 1996. Site-specific resource use in juvenile little brown bats, *Myotis lucifugus* (Chiroptera: Vespertilionidae): is there an ontogenetic shift? Canadian Journal of Zoology, 74:1204-1210.

———. 1997. Onset of volancy and foraging patterns of juvenile little brown bats, *Myotis lucifugus*. Journal of Mammalogy, 78:239–246.

Altringham, J. D. 1996. Bats: biology and behaviour. Oxford University Press, New York, 262 pp.

Anthony, E. L. P., and T. H. Kunz. 1977. Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. Ecology, 58:775–786.

Barclay, R. M. R. 1989. The effect of reproductive condition on the foraging behavior of female hoary bats, *Lasiurus cinereus*. Behavioral Ecology and Sociobiology, 24:31–37.

Barclay, R. M. R., and R. M. Brigham. 1994. Constraints on optimal foraging: a field test of prey discrimination by echolocating insectivorous bats. Animal Behaviour, 48:1013-1021.

Barclay, R. M. R., and A. Kurta. 2007. Ecology and behavior of bats roosting in tree cavities and under bark. Pp. 17–59, *in* Bats in forests: conservation and management (M. J. Lacki, J. P. Hayes, and A. Kurta, eds.). Johns Hopkins University Press, Baltimore, Maryland, 57 pp.

Beals, M., L. Gross, and S. Harrell. 1999. Diversity indices: Simpson's *D* and *E*. http://www.tiem.utk.edu/~gross/bioed/bealsmodules/simpsonDI.html. Accessed June 2008.

Brack, V., Jr. 1983. The non-hibernating ecology of bats in Indiana with emphasis on the endangered Indiana bat, *Myotis sodalis*. Ph.D. dissertation, Purdue University, West Lafayette, Indiana, 279 pp.

Brack, V., Jr., and R. K. LaVal. 1985. Food habits of the Indiana bat in Missouri. Journal of Mammalogy, 66:308–315.

Brower, J. E., and J. H. Zar. 1984. Field and laboratory methods for general ecology. Second Ed. Wm. C. Brown Publishers, Dubuque, Iowa, 226 pp.

Buchler, E. R. 1976. Prey selection by *Myotis lucifugus* (Chiroptera: Vespertilionidae). American Naturalist, 110:619–628.

Carter, T. C, M. A. Menzel, D. M. Krishon, and J. Laerm. 1998. Prey selection by five species of vespertilionid bats on Sapelo Island, Georgia. Brimleyana, 25:158–170.

Carter, T. C., M. A. Menzel, B. R. Chapman, and K. V. Miller. 2004. Partitioning of food resources by syntopic eastern red (*Lasiurus borealis*), Seminole (*L. seminolus*) and evening (*Nycticeius humeralis*) bats. American Midland Naturalist, 151:186–191.

Clem, P. D. 1993. Foraging patterns and the use of temporary roosts in female evening bats, *Nycticeius humeralis*, at an Indiana maternity colony. Proceedings of the Indiana Academy of Sciences, 102:201–206.

Cleveland, C. J., M. Betke, P. Federico, J. D. Frank, T. G. Hallam, J. Horn, et al. 2007. Economic value of the pest control service provided by Brazilian free-tailed bats in south-central Texas. Frontiers in Ecology and the Environment, 4:238–243.

Crozier, L. 2004. Warmer winters drive butterfly range expansion by increasing survivorship. Ecology, 85:231–241.

European and Mediterranean Plant Protection Organization. 2005. Data sheets on quaratine pests: *Agrilus planipennis*. OEPP/EPPO Bulletin, 35:436–438.

Feldhamer, G. A., J. O. Whitaker, Jr., J. K. Krejca, and S. J. Taylor. 1995. Food of the evening bat (*Nycticeius humeralis*) and red bat (*Lasiurus borealis*) from southern Illinois. Transactions of the Illinois State Academy of Science, 88:139–143.

Fleming, T. H., and P. Eby. 2003. Ecology of bat migration. Pp. 156-208, *in* Bat ecology (T. H. Kunz and M. B. Fenton, eds.). University of Chicago Press, Chicago, Illinois, 779 pp.

Freeman, P. W. 1981. Correspondence of food habits and morphology in insectivorous bats. Journal of Mammalogy, 62:166–173.

Geluso, K. N., J. P. Damm, and E. W. Valdez. 2008. Late-seasonal activity and diet of the evening bat (*Nycticeius humeralis*) in Nebraska. Western North American Naturalist, 68:21-24.

Gomez, C., and R. F. Mizell, III. 2008. Featured creatures: green stink bug, *Acrosternum hilare* (Say) (Insecta: Hemiptera: Pentatomidae). Publication EENY-431. Accessed December 8, 2008. http://creatures.ifas.ufl.edu/veg/bean/green_stink_bug.htm.

Gould, E. 1955. The feeding efficiency of insectivorous bats. Journal of Mammalogy, 36:399–407.

———. 1971. Studies of maternal-infant communications and development of vocalizations in the bats *Myotis* and *Eptesicus*. Communications in Behavioral Biology (Part A), 5:263–313.

Hamilton, I. M., and R. M. R. Barclay. 1998. Ontogenetic influences on foraging and mass accumulation by big brown bats (*Eptesicus fuscus*). Journal of Animal Ecology, 67:930–940.

Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? Trends in Ecology and Evolution, 15:56–61.

Humphries, M. M., D. W. Thomas, and J. R. Speakman. 2002. Climate-mediated energetic constraints on the distribution of hibernating mammals. Nature, 418:313–316.

Jess, L. J., and B. Zandstra. 1999. Crop Profile for cucumbers (fresh market) in Michigan. Accessed December 8, 2008. http://www.ipmcenters.org/cropprofiles/docs/micucumbers-freshmarket.pdf

Jones, G., and J. Rydell. 1994. Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. Philosophical Transactions of the Royal Society of London: Biological Sciences, 346:445–455.

Kunz, T. H. 1974. Feeding ecology of a temperate insectivorous bat (*Myotis velifer*). Ecology, 55:693–711.

———. 1988. Methods of assessing the availability of prey to insectivorous bats. Pp. 191–210, *in* Ecological and behavioral methods for the study of bats (T.H. Kunz, ed.). Smithsonian Institution Press, Washington, D.C., 533 pp.

Kunz, T. H., J. O. Whitaker, Jr., and M. D. Wadanoli. 1995. Dietary energetics of the insectivorous Mexican free-tailed bat (*Tadarida brasiliensis*) during pregnancy and lactation. Oecoogia, 101:407–415.

Kurta, A. 2008. Bats of Michigan. Indiana State University Center for North American Bat Research and Conservation, Terra Haute, Indiana, 72 pp.

Kurta, A., and J. O. Whitaker, Jr. 1998. Diet of the endangered Indiana bat (*Myotis sodalis*) on the northern edge of its range. American Midland Naturalist, 140:280–286.

Kurta, A., G. P. Bell, K. A. Nagy, and T. H. Kunz. 1989. Energetics of pregnancy and lactation in free-ranging little brown bats (*Myotis lucifugus*) in summer. Physiological Zoology, 62:804–818.

Kurta, A., J. Kath, E. L. Smith, R. Foster, M. W. Orick, and R. Ross. 1993. A maternity roost of the endangered Indiana bat (*Myotis sodalis*) in an unshaded, hollow, sycamore tree (*Platanus occidentialis*). American Midland Naturalist, 130:405–407.

Kurta, A., R. Foster, E. Hough, and L. Winhold. 2005. The evening bat (*Nycticeius humeralis*) on the northern edge of its range—a maternity colony in Michigan. American Midland Naturalist, 154:264–267.

Lariviere, S. 2004. Range expansion of raccoons in the Canadian prairies: review of hypotheses. Wildlife Society Bulletin, 32:955–963.

Lazarus, W. F., and E. R. Swanson. 1983. Insecticide use and crop rotation under risk: rootworm control in corn. American Journal of Agricultural Economics, 65:738–747.

McCullough, D. G. and S. A. Katovich. 2004. Pest alert: emerald ash borer. United States Department of Agriculture, Forest Service, State and Private Forestry, Northeastern Area. NA–PR–02–04.

McNab, B. K. 2003. The physiological ecology of vertebrates: a view from energetics. Journal of Mammalogy, 84:774–775.

Meinke, L. J., F. Gould, and J. W. Van Duyn. 1985. Soybean: a larval host for the southern corn rootworm (Coleoptera: Chrysomelidae). Florida Entomologist, 68:496–498.

Menzel, J. M, M. A. Menzel, J. C. Kilgo, W. M. Ford, J. W. Edwards, and G. F. McCracken. 2005. Effect of habitat and foraging height on bat activity in the coastal plain of South Carolina. Journal of Wildlife Management, 69:235–245.

Murray, S. W., and A. Kurta. 2002. Spatial and temporal variation in diet. Pp. 182–192, *in* The Indiana bat: biology and management of an endangered species (A. Kurta and J. Kennedy, eds.). Bat Conservation International, Austin, Texas, 253 pp.

Norberg, U., and J. M. V. Rayner. 1987. Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy, and echolocation. Philosophical Transactions of the Royal Society of London B, 316:335–427.

Panizzi, A. R., and F. Slanski, Jr. 1985. Review of phytophagous pentatomids (Hemiptera: Pentatomidae) associated with soybean in the Americas. Florida Entomologist, 68:184–214.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature, 421:37–42.

Pierson, E. D. 1998. Tall trees, deep holes, and scarred landscapes: conservation biology of North American bats. Pp. 309–325, *in* Bat biology and conservation (T. H. Kunz and P. A. Racey, eds.). Smithsonian Institution Press, Washington, D.C., 365 pp.

Poland, T. M., and D. G. McCullough. 2006. Emerald ash borer: invasion of the urban forest and the threat to North America's ash resource. Journal of Forestry, 104:118–124.

Racey, P. A. 1988. Reproductive assessment in bats. Pp. 31–45, *in* Ecological and behavioral methods for the study of bats (T. H. Kunz, ed.). Smithsonian Institution Press, Washington, D.C., 533 pp.

Ramos-Elorduy, J., J. M. P. Moreno, E. E. Prado, M. A. Perez, J. L. Otero, and O. L. de Guevara. 1997. Nutritional value of edible insects from the state of Oaxaca, Mexico. Journal of Food Composition and Analysis, 10:142–157.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature, 421:57–60.

Schalk, G., and R. M. Brigham. 1995. Prey selection by insectivorous bats: are essential fatty acids important? Canadian Journal of Zoology, 73:1855–1859.

Sorenson, K. A., and J. R. Baker. 2008. Insects and related pests of vegetables: some important, common and potential pests in southeastern United States. Accessed December 8, 2008. http://ipm.ncsu.edu/AG295/html/index.htm

Soto-Centeno, J. A., and A. Kurta. 2006. Diet of two nectarivorous bats, *Erophylla sezekorni* and *Monophyllus redmani* (Phyllostomidae), on Puerto Rico. Journal of Mammalogy, 87:19–26.

Stevens, L. E., J. T. Polhemus, R. S. Durfee, and C. A. Olson. 2007. Large mixed-species dispersal flights of predatory and scavenging aquatic Heteroptera and Coleoptera, Northern Arizona, USA. Western North American Naturalist, 67:587–592.

Thomas, C. D., E. J. Bodsworth, R. J. Wilson, A. D. Simmons, Z. G. Davies, M. Musche, and L. Conradt. 2001. Ecological and evolutionary processes at expanding range margins. Nature, 411:577–580.

Toapanta, M. A., D. J. Schuster, and P. A. Stansly. 2005. Development and life history of *Anthonomus eugenii* (Coleoptera: Curculionidae) at constant temperatures. Environmental Entomology, 34:999–1008.

Triplehorn, C. A., and N. F. Johnson. 1005. Borror and DeLong's introduction to the study of insects, Seventh ed. Thomson Brooks/Cole, Belmont, California, 864 pp.

Visser, M. E., A. J. van Noordwijk, J. M. Tinebergen, and C. M. Lessells. 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). Proceedings of the Royal Society, London B, 265:1867–1870.

Visser, M. E., and C. Both. 2005. Shifts in phenology due to global climate change: the need for a yardstick. Proceedings of the Royal Society, London B, 272:2561–2569.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature, 416:389–395.

Whitaker, J. O., Jr. 1988. Food habits analysis of insectivorous bats. Pp. 171–189, *in* Ecological and behavioral methods for the study of bats (T. H. Kunz, ed.). Smithsonian Institution Press, Washington, D.C., 533 pp.

———. 1995. Food availability and opportunistic versus selective feeding in insectivorous bats. Bat Research News, 35:75–77.

———. 2004. Prey selection in a temperate zone insectivorous bat community. Journal of Mammalogy, 85:460-469.

Whitaker, J.O., Jr., and P. Clem. 1992. Food of the evening bat, *Nycticeius humeralis*, from Indiana. American Midland Naturalist, 127:211–214.

Whitaker, J.O., Jr., and B. Lawhead. 1992. Foods of *Myotis lucifugus* in a maternity colony in central Alaska. Journal of Mammalogy, 73:646–648.

Whitaker, J. O., Jr., and W. J. Hamilton. 1998. Mammals of the eastern United States. Cornell University Press, Ithaca, New York, 583 pp.

Whitaker, J. O., Jr., and S. L. Gummer. 1993. The status of the evening bat, *Nycticeius humeralis*, in Indiana. Proceedings of the Indiana Academy of Science, 102:283–291.

———. 2003. Current status of the evening bat, *Nycticeius humeralis*, in Indiana. Proceedings of the Indiana Academy of Science, 112:55–60.

Whitaker, J. O., Jr., and A. Rodríguez-Durán. 1999. Seasonal variation in the diet of Mexican free-tailed bats, *Tadarida brasiliensis antillularum* (Miller) from a colony in Puerto Rico. Caribbean Journal of Science, 35:23–28.

Whitaker, J. O., Jr., C. Maser, and L. E. Keller. 1977. Food habits of bats of western Oregon. Northwest Science, 51:46–55.

Whitaker, J. O., Jr., S. S. Issac, G. Marimuthu, and T. H. Kunz. 1999. Seasonal variation in the diet of the Indian pygmy bat, *Pipistrellus mimus*, in southern India. Journal of Mammalogy, 80:60–70.

Wilkinson, G. S. 1992. Information transfer at evening bat colonies. Animal Behaviour, 44:501–518.

Williams-Guillén, K., I. Perfecto, and J. Vandermeer. 2008. Bats limit insects in a neotropical agroforestry system. Science, 320:70.

Willis, C. K. R., and R. M. Brigham. 2003. New records of the eastern red bat, *Lasiurus borealis*, from Cypress Hills Provincial Park, Saskatchewan: a response to climate change? The Canadian Field-Naturalist, 117:651–654.

Wilson, D. E., and D. A. M. Reeder. 1993. Mammal species of the world: a taxonomic and geographic reference. Smithsonian Institution Press, Washington, D.C., 1206 pp.

Wilson, J. M., and R. M. R. Barclay. 2006. Consumption of caterpillars during an outbreak of western spruce budworm. American Midland Naturalist, 155:244–249.

Zar, J. H. 1999. Biostatistical analysis. Fourth ed. Prentice Hall, Upper Saddle River, New Jersey, 663 pp.

Table 2.1. The number of pellets, reproductive condition, and dietary diversity index for weekly samples gathered near Palmyra, Michigan, during 2006–2007.

	Week[a]														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
2006															
Number of pellets			30	25	30	30		30	30	17	23	30	30	29	16
Reproductive condition[b]			PG	PG	T	T		LA	T	PL-J	PL-J	PL-J	PL-J	PL-J	PL-J
Dietary diversity index			3.62	3.52	4.16	4.52		3.48	3.76	4.88	4.47	3.53	3.92	5.15	4.12
2007															
Number of pellets	3	3		8	30	21	30	30	30	30	30	30	14	15	
Reproductive condition[b]	PG	PG		T	T	LA	LA	LA	T	T	PL-J	PL-J	PL-J	PL-J	
Dietary diversity index	2.69	2.26		5.28	4.53	4.62	4.59	3.69	4.31	4.65	4.80	4.06	3.71	3.38	

[a] Week 1 began on 15 May 2006 and 14 May 2007, and week 15 ended on 27 August 2006 and 26 August 2007.

[b] PG = pregnancy; L = lactation; T = transition; and PL-J = postlactation-juvenile.

Table 2.2. Percent volume of arthropods contained in fecal pellets from roosts of evening bats gathered near Palmyra, Michigan, during 2006–2007. Statistical analysis was conducted only on taxa that contributed $\geq$5% of the overall diet. Number of pellets is given in parentheses.

Taxon	Overall (*n* = 594)	2006 (*n* = 320)	2007 (*n* = 274)	Statistics for comparisons between years	
				$F_{1,\ 592}$	*P*
Coleoptera	40.0	40.2	37.6	3.04	0.08
Diptera	19.6	21.0	17.8	12.33	<0.001
Hymenoptera	13.6	10.9	16.7	16.80	<0.001
Hemiptera	12.8	11.9	14.0	4.32	0.04
Lepidoptera	4.7	6.2	3.0		
Trichoptera	4.1	4.2	3.9		
Ephemeroptera	3.0	2.7	3.3		
Homoptera	1.6	1.6	1.7		
Neuroptera	0.8	0.7	0.9		
Orthoptera	0.2	0.3	0.1		
Psocoptera	0.2	0.2	0.1		
Odonata	0.2	0.0	0.3		
Phthiraptera	0.1	<0.1	0.1		
Acari	0.1	0.2	<0.1		
Araneida	<0.1	<0.1	0.0		
Blattodea	<0.1	<0.1	0.0		
Unknown	<0.1	0.0	<0.1		

Table 2.3. Percent occurrence of families and species of insects identified in fecal pellets gathered from roosts near Palmyra, Michigan, during 2006–2007, and statistical comparisons between years. Number of pellets is given in parentheses.

Taxon	Overall (n = 594)	2006 (n = 320)	2007 (n = 274)	Statistics for comparisons between years[a]	
				χ^2_1	P
Coleoptera	98.0	99.1	96.7	4.11	0.043
Anobiidae	4.0	3.8	4.4		
Buprestidae	2.9	0.8	4.1		
Agrilus planipennis	0.9	0.6	1.1	0.39	0.53
Carabidae	36.9	39.7	33.6	2.37	0.12
Cerambycidae	0.5	0.3	0.7		
Chrysomelidae	19.4	20.6	17.9	1.16	0.28
Diabrotica undecimpunctata	15.3	16.9	13.5	1.29	0.26
Cleridae	0.2	0.3			
Coccinellidae	7.9	10.4	4.4		
Curculionidae	34.9	46.6	21.2	41.93	<0.001
Dermestidae	0.5	0.9			
Dysticidae	0.8	1.3	0.4		
Elateridae	0.2	0.3			
Heteroceridae	0.3	0.6			
Histeridae	4.0	3.8	4.4		
Hydrophilidae	2.0	1.9	2.2		
Lucanidae	0.5	0.9			
Nitidulidae	1.4	1.3	1.5		
Passalidae	0.2	0.3			
Scarabaeidae	5.4	5.6	5.1		
Staphylinidae	4.0	3.8	4.4		
Tenebrionidae	0.3	0.3	0.4		
Diptera	94.3	96.3	92.0	5.01	0.03
Chironomidae	0.2	0.3			
Culicidae	5.9	10.3	0.7		
Dolichopodidae	0.2	0.0	0.4		
Hymenoptera	68.5	65.9	71.5	0.01	0.91
Ichneumonidae	0.2	0.3			
Formicidae	6.4	1.6	12.0		
Hemiptera	73.6	73.8	73.4	2.14	0.14
Corixidae	17.5	24.1	9.9	20.63	<0.001
Pentatomidae	12.0	8.7	15.7	6.76	<0.01
Acrosternum hilare	12.0	8.7	15.7	6.76	<0.01
Homoptera					
Cercopidae	2.7	3.1	2.2		
Cicadellidae	7.58	10.3	4.4		
Delphacidae	0.2	0.3			

Taxon	Overall (n = 594)	2006 (n = 320)	2007 (n = 274)	Statistics for comparisons between years[a]	
				χ^2_1	P
Neuroptera					
Chrysopidae	0.2		0.4		
Orthoptera					
Gryllotalpidae	0.5	0.9			

[a] Analysis of the percent frequency occurrence of insects was conducted on the number of pellets with and without each taxon.

Table 2.4. Percent volume of insect orders found in pellets from roosts during periods of pregnancy, lactation, or postlactation-juvenile. Pellets were gathered near Palmyra, Michigan, during 2006–2007. A total of 406 pellets were analyzed for comparisons among reproductive condition, and statistical comparisons were conducted for the four dominant orders of insects. Number of pellets is given in parentheses.

Taxon	Pregnant (n = 61)	Lactating (n = 141)	Postlactating and juvenile (n = 204)	Statistics for comparisons among reproductive conditions	
				$F_{2, 403}$	P
Coleoptera	44.3	39.8	40.0	0.86	0.42
Diptera	23.9^{a}	$16.1^{a, b}$	19.7^{b}	11.09	<0.001
Hymenoptera	5.2^{a}	17.0^{a}	10.2^{a}	15.98	<0.001
Hemiptera	8.2^{a}	13.4^{b}	$13.8^{a, b}$	9.23	<0.001
Lepidoptera	4.5	5.1	6.0		
Trichoptera	4.7	4.2	3.1		
Ephemeroptera	7.8	1.5	2.8		
Homoptera	0.7	1.5	2.2		
Neuroptera	0.4	0.4	1.2		
Orthoptera			0.5		
Psocoptera	0.2	0.1	0.4		
Odonata		0.6			
Phthiraptera		0.2	<0.1		
Acari	<0.1	<0.1	0.1		
Araneida			<0.1		
Blattodea			<0.1		
Unknown		0.1			

Table 2.5. Percent volume of arthropods consumed by individual evening bats, that were caught near Palmyra, Michigan, during 2006–2007. Statistical analysis was conducted only on taxa that contributed $\geq$5% to the overall diet. Number of pellets is given in parentheses

Taxon	Overall (n = 31)	2006 (n = 16)	2007 (n = 15)	Statistics for comparisons between years	
				$F_{1,29}$	P
Coleoptera	51.0	50.6	51.3	0.01	0.9
Diptera	11.7	12.5	10.9	1.51	0.2
Hymenoptera	8.6	7.3	10.0	0.13	0.7
Hemiptera	16.6	15.6	17.7	0.00	1.0
Lepidoptera	2.1	2.3	1.8		
Trichoptera	4.0	6.1	1.9		
Ephemeroptera	0.5	0.4	0.6		
Homoptera	3.0	2.0	4.0		
Neuroptera	1.5	1.9	1.0		
Orthoptera	0.9	0.6	1.1		
Psocoptera	0.2	0.3	<0.1		
Unknown	0.2	0.3			

Table 2.6. Percent occurrence of families and species of insects in the diet of individual evening bats, that were caught near Palmyra, Michigan, during 2006–2007. Statistical comparisons were made between years of orders and families that occurred at a frequency >5% in the overall diet of individuals. Number of pellets is given in parentheses.

Taxon	Overall (n = 31)	2006 (n = 16)	2007 (n = 15)	Statistics for comparisons between years[a]	
				χ^2_1	P
Coleoptera	100.0	100.0	100.0	0.03	0.86
Anobiidae	3.2	6.3			
Buprestidae	3.2	6.3			
Agrilus planipennis	3.2	6.3			
Carabidae	61.3	68.8	53.3	0.47	0.49
Chrysomelidae	35.5	37.5	33.3	0.09	0.76
Spotted cucumber beetle	32.3	31.3	33.3		1.00
Cleridae	3.2	6.3			
Coccinellidae	6.5	12.5			
Curculionidae	58.1	87.5	26.7	5.56	0.02
Hydrophilidae	3.2		6.7		
Scarabaeidae	16.1	25.0	6.7	1.80	0.18
Staphylinidae	3.2	6.3			
Diptera	83.3	100.0	66.7	1.39	0.24
Culicidae	3.2	6.3			
Hymenoptera	64.8	68.8	60.0	0.20	0.66
Formicidae	3.2	6.3			
Hemiptera	80.4	87.5	73.3	0.36	0.55
Corixidae	19.4	25.0	13.3	0.67	0.41
Pentatomidae	19.4	6.3	33.3		
Acrosternum hilare	19.4	6.3	33.3	2.67	0.10
Homoptera					
Cicadellidae	3.2	6.3			
Cercopidae	3.2		6.7		
Orthoptera					
Gryllotalpidae	12.9	12.5	13.3		

[a] Analysis of the percent frequency occurrence of insects was conducted on the number of pellets.

Table 2.7. Percent volume of orders of insects in the diet of individual evening bats according to reproductive condition. Pellets were gathered near Palmyra, Michigan, during 2006–2007. Statistical comparisons were made among reproductive conditions when percent volume was $\geq$15% in the overall diet of individuals. Number of pellets is given in parenthesis.

Taxon	Pregnant (n = 10)	Lactating (n = 8)	Postlactating (n = 5)	Juvenile (n = 8)	Statistics for comparisons among reproductive conditions	
					$F_{3, 27}$	P
Coleoptera	41.4	60.3	61.4	47.0	1.88	0.16
Diptera	20.7	6.3	5.5	9.8	2.63	0.07
Hymenoptera	11.7	11.6	3.9	4.7	1.46	0.25
Hemiptera	13.8	14.3	21.3	4.7	0.31	0.82
Lepidoptera	1.5	1.5	3.2	2.7		
Trichoptera	9.4		1.8	0.3		
Ephemeroptera	0.2	1.7				
Homoptera	1.6	1.0	1.5	7.7		
Neuroptera	0.1	2.1	0.3	3.3		
Orthoptera		1.3	1.3	1.3		
Psocoptera				0.8		

Table 2.8. Percent volume of orders of insects identified in the fecal pellets from the evening bat in other parts of its range. Number of pellets is given in parentheses

Taxon	Georgia Carter et al., 1998 (*n* = 99)	Illinois Feldhamer et al., 1995 (*n* = 13)	Indiana Whitaker and Clem, 1992 (*n* = 60)	Indiana Whitaker, 2004 (*n* = 154)	Nebraska Geluso et al., 2007 (*n* = 14)	South Carolina[a] Carter et al., 2004 (*n* = 49)
Coleoptera	45.0	68.1	59.9	60.1	40.7	39.0
Diptera	0.07	5.8	5.5	2.5	0.6	0.3
Hymenoptera	36.0		0.2	3.9	23.3	20.3
Hemiptera	11.0	8.0	5.7	5.7	10.7	2.0
Lepidoptera	7.0	5.4	19.7	3.2	6.4	5.3
Trichoptera			0.2	2.2		1.3
Homoptera	0.03	12.7	7.0	20.4	7.2	13.3
Neuroptera			0.7	1.2		0.3
Orthoptera			0.6	0.7		
Acari			0.1			
Unidentified					11.3	

[a] Percent volume for this study was averaged among three arbitrary seasons (early summer, middle summer, and late summer).

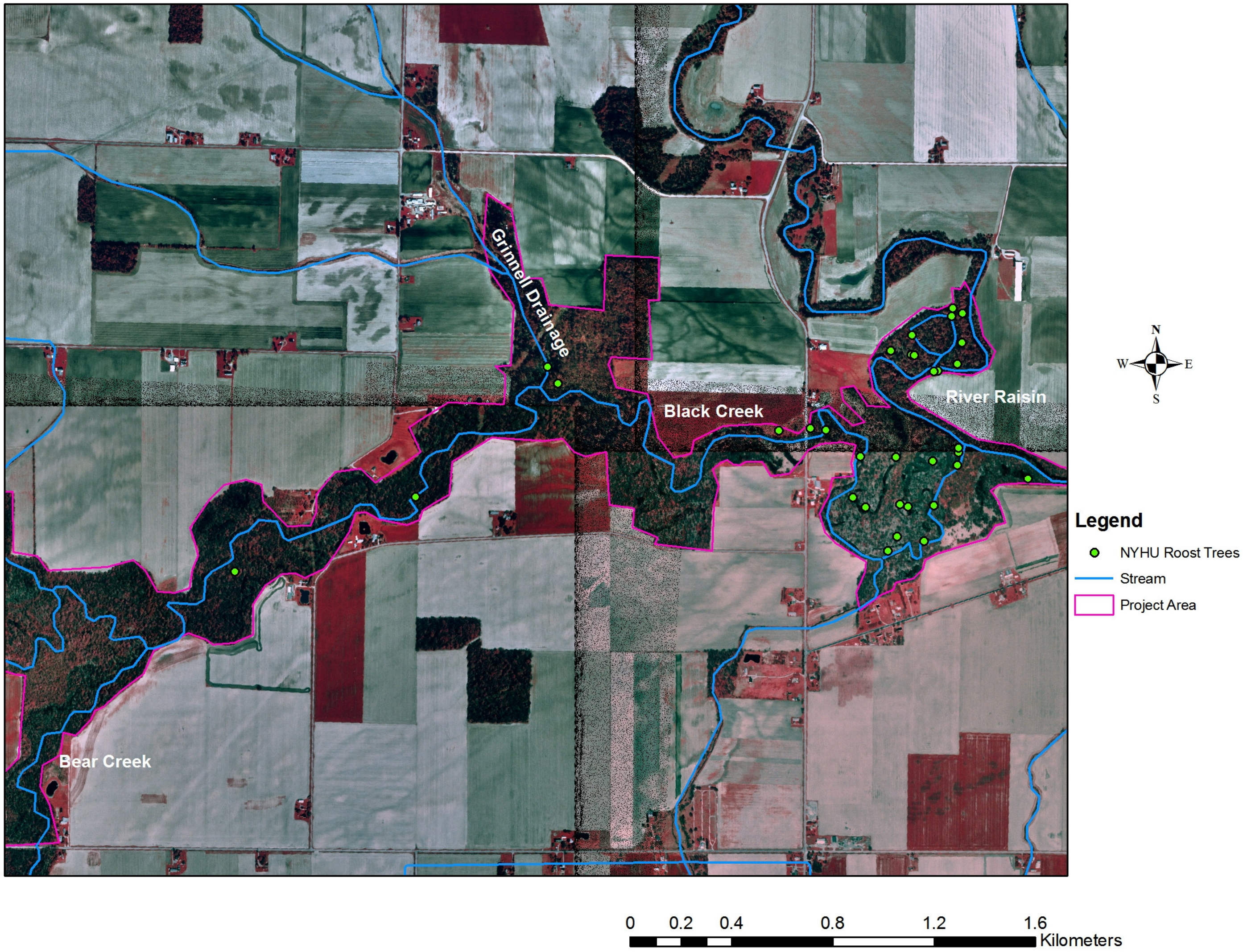


Figure 2.1. Aerial photo of study area near Palmyra, Michigan. Roost trees discovered in 2006–2007 are indicated by dots.

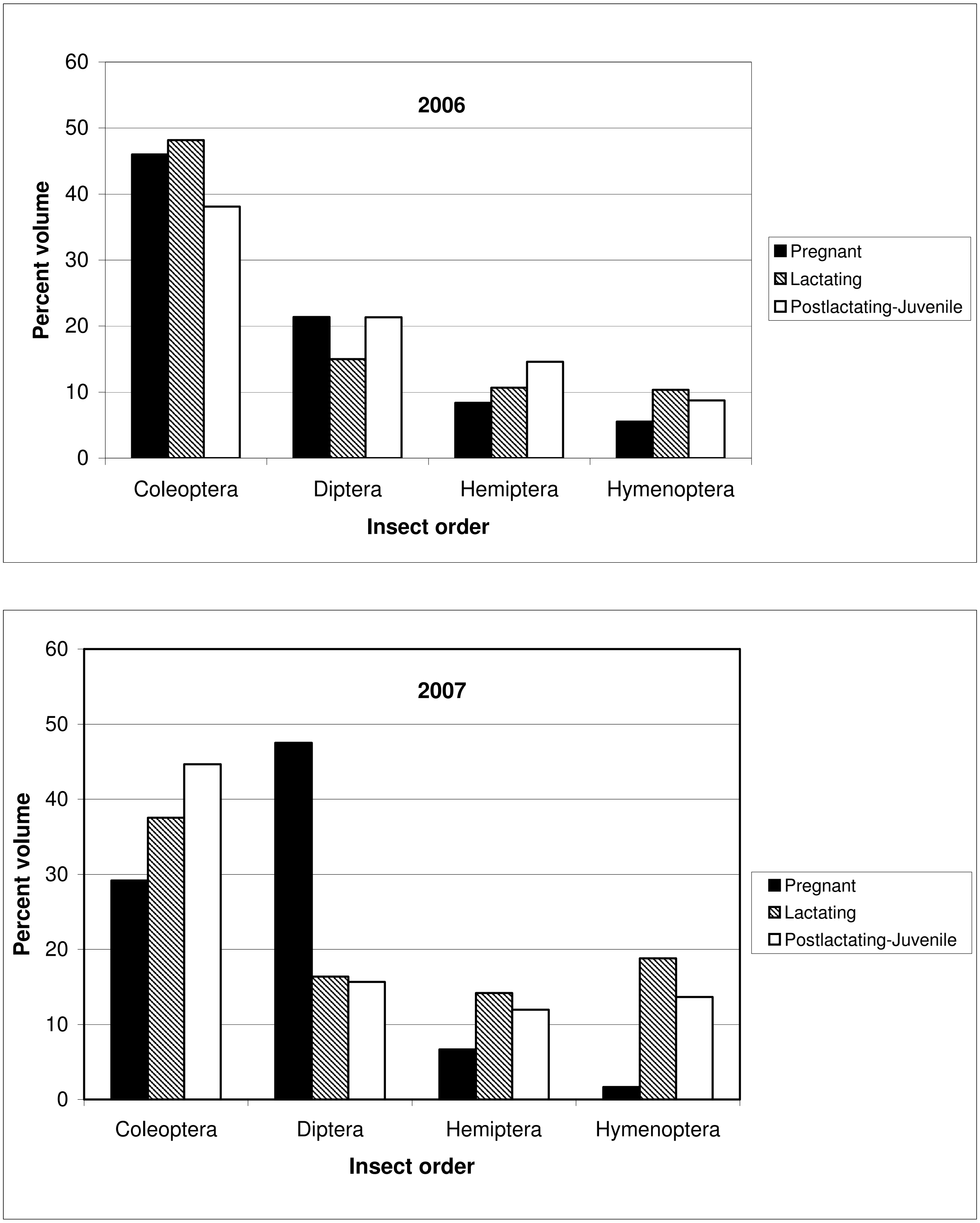
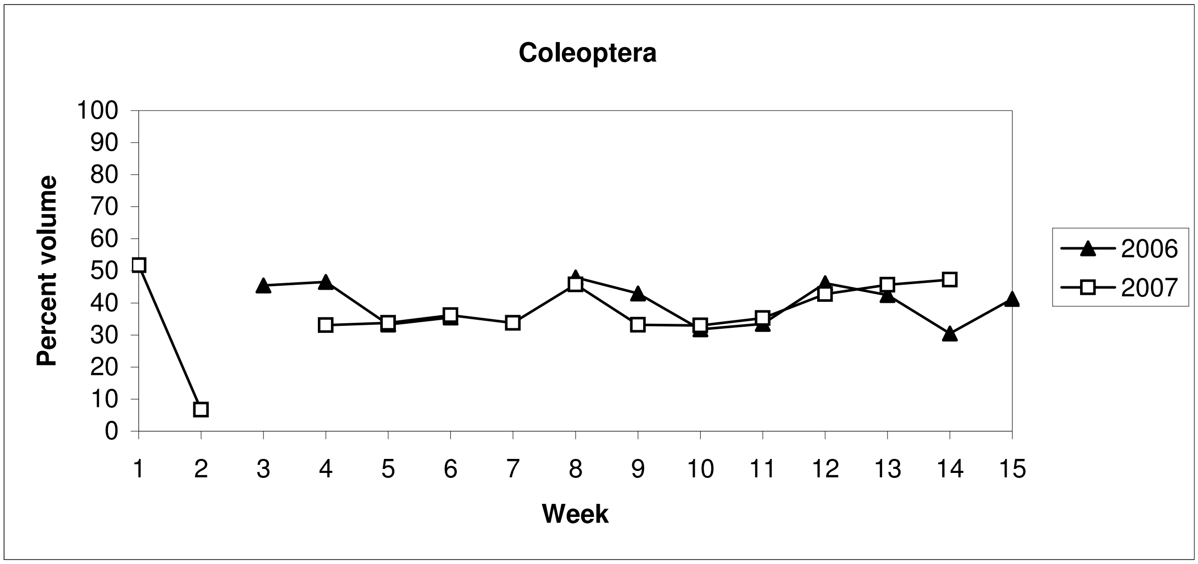
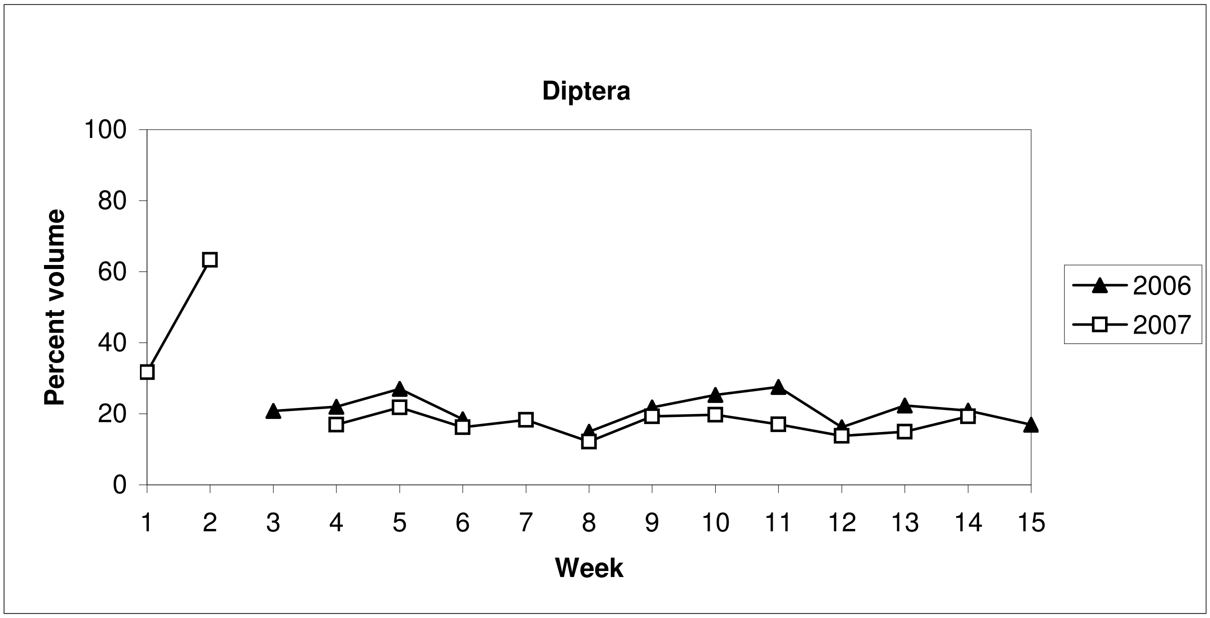
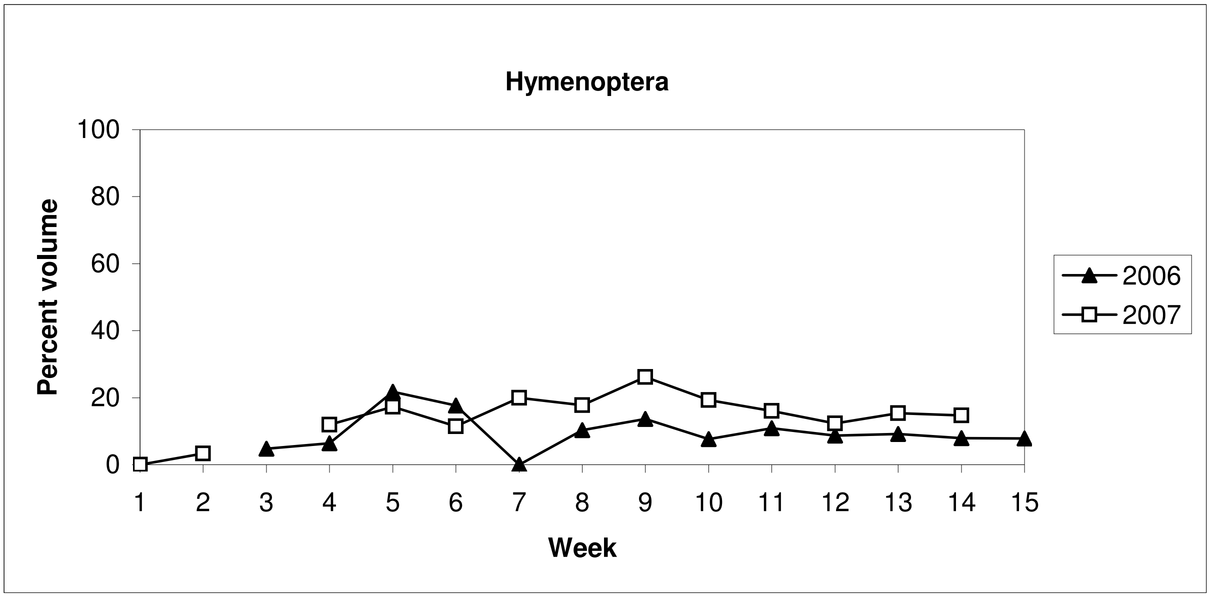


Figure 2.2. Percent volume of insect orders found in fecal pellets that were obtained during the periods of pregnancy, lactation, and postlaction-juvenile. Pellets were gathered from roosts near Palmyra, Michigan, during 2006–2007.


Coleoptera
Percent volume
100
90
80
70
60
50
40
30
20
10
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Week
2006
2007


Diptera
Percent volume
100
80
60
40
20
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Week
2006
2007



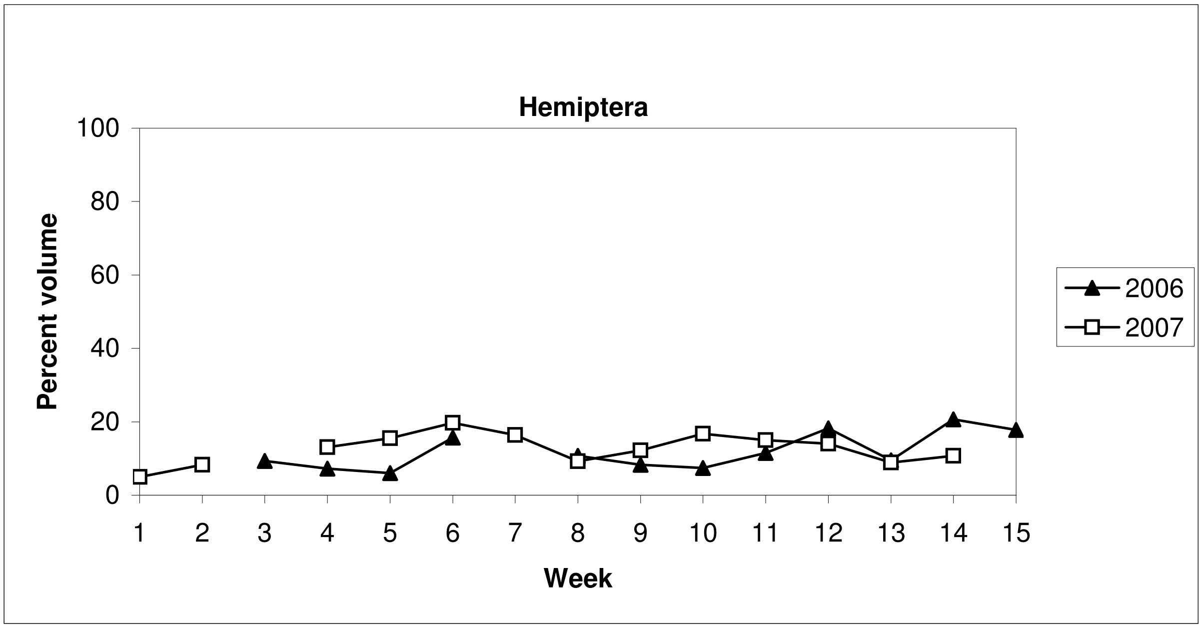
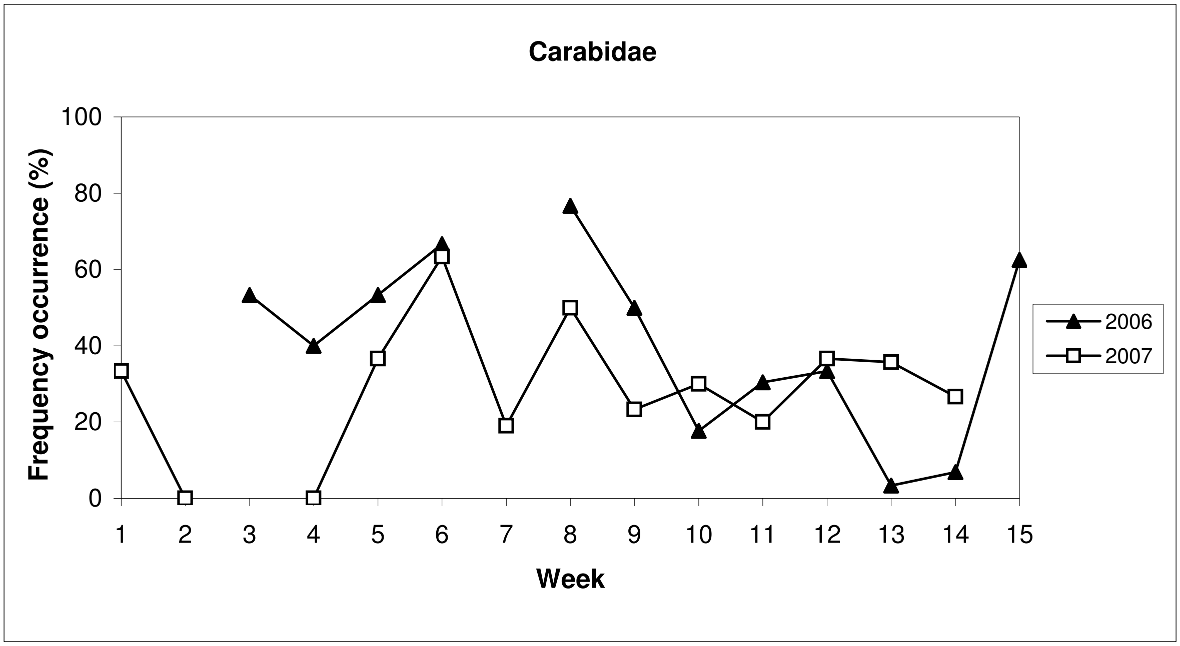
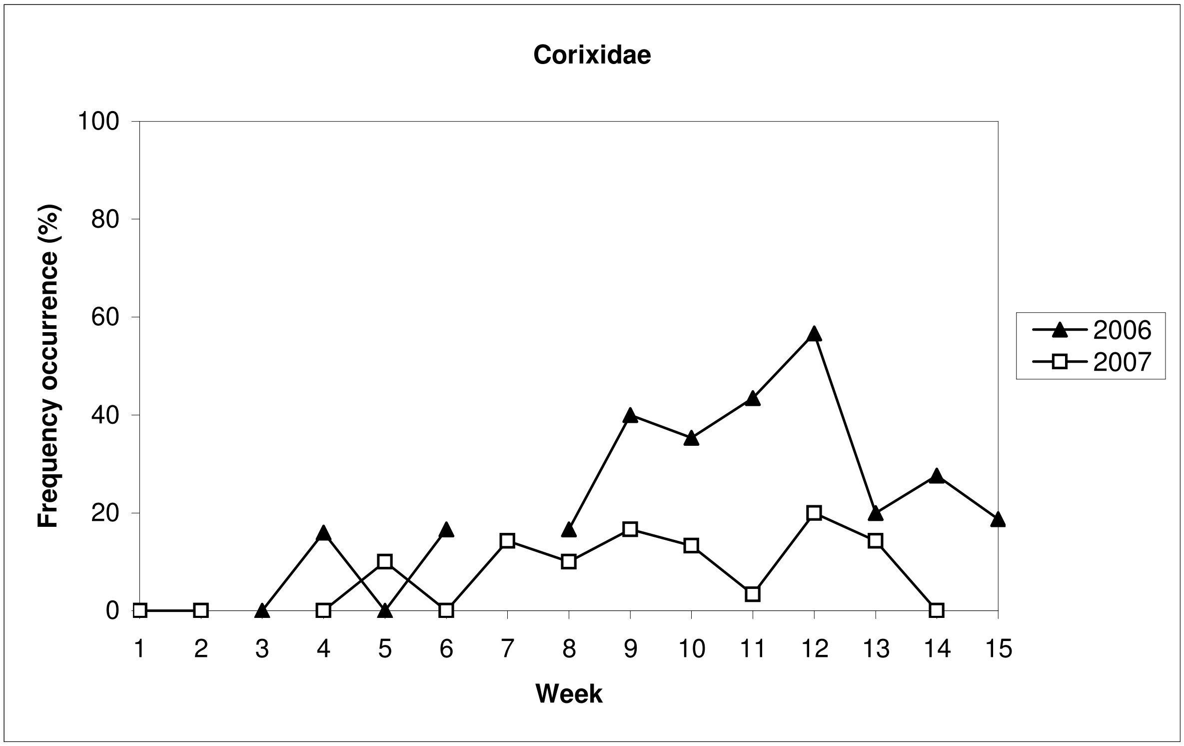


Figure 2.3. Weekly summary of percent volume of the six most prevalent orders of insects detected in the diet of evening bats during 2006–2007. Pellets were obtained from roosts near Palmyra, Michigan. Fecal pellets were not collected during weeks 1, 2, and 7 of 2006, and weeks 3 and 15 of 2007. Week 1 began on 15 May 2006 and 14 May 2007, and week 15 ended on 27 August 2006 and 26 August 2007.


Carabidae
Frequency occurrence (%)
0
20
40
60
80
100
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Week
2006
2007


Corixidae
Frequency occurrence (%)
0
20
40
60
80
100
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Week
2006
2007

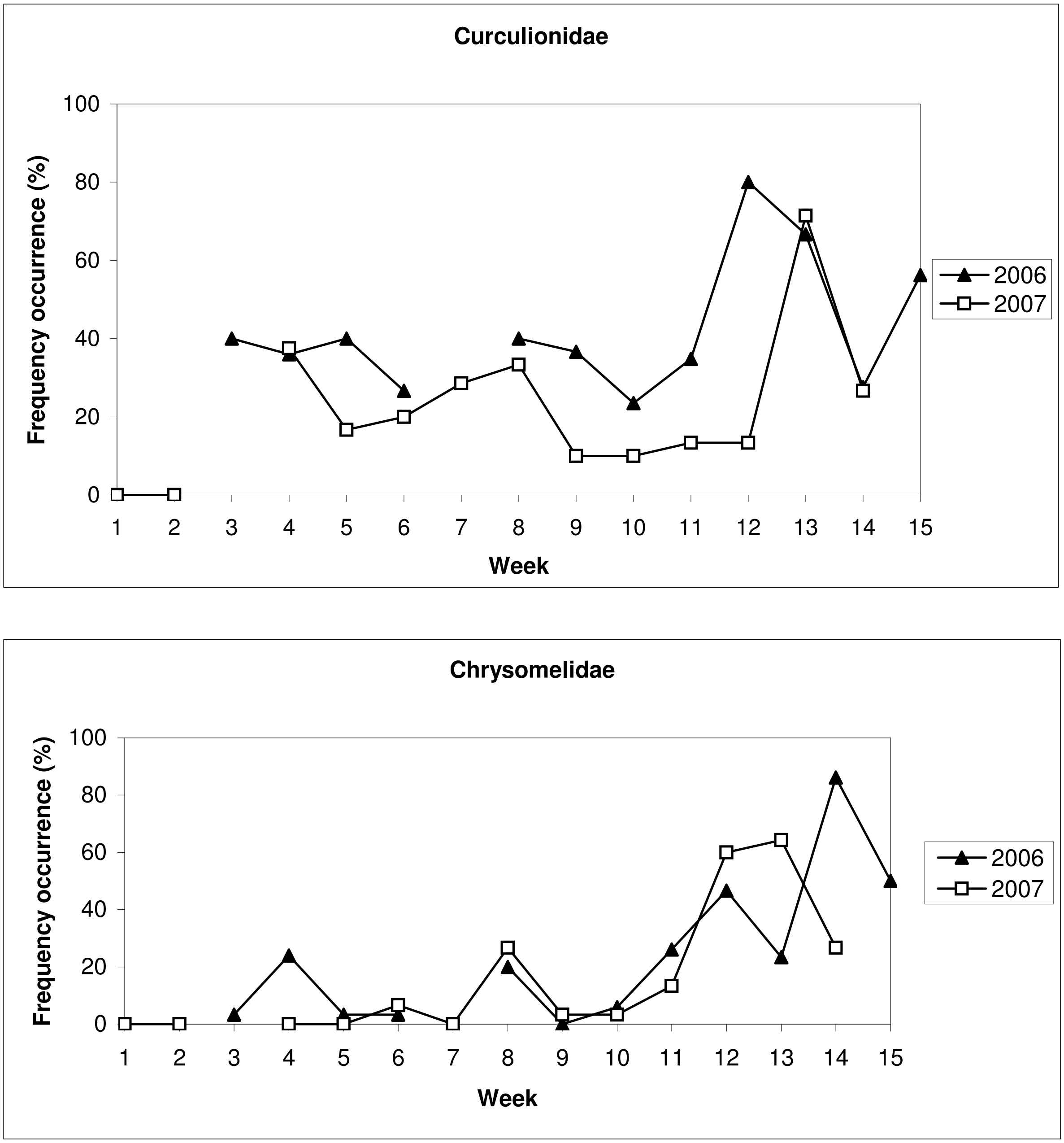
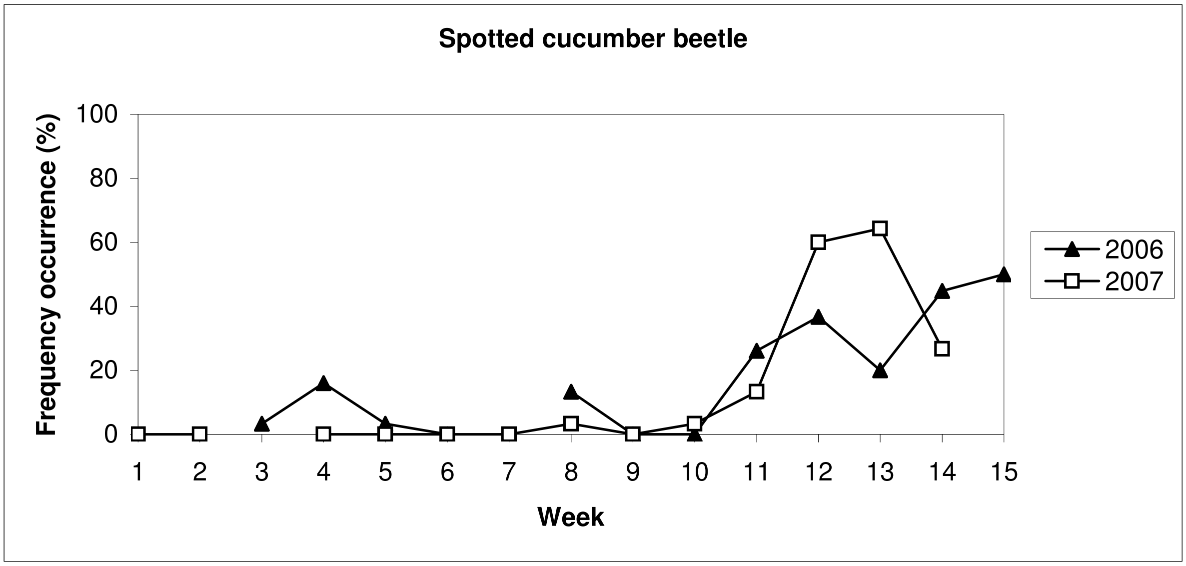
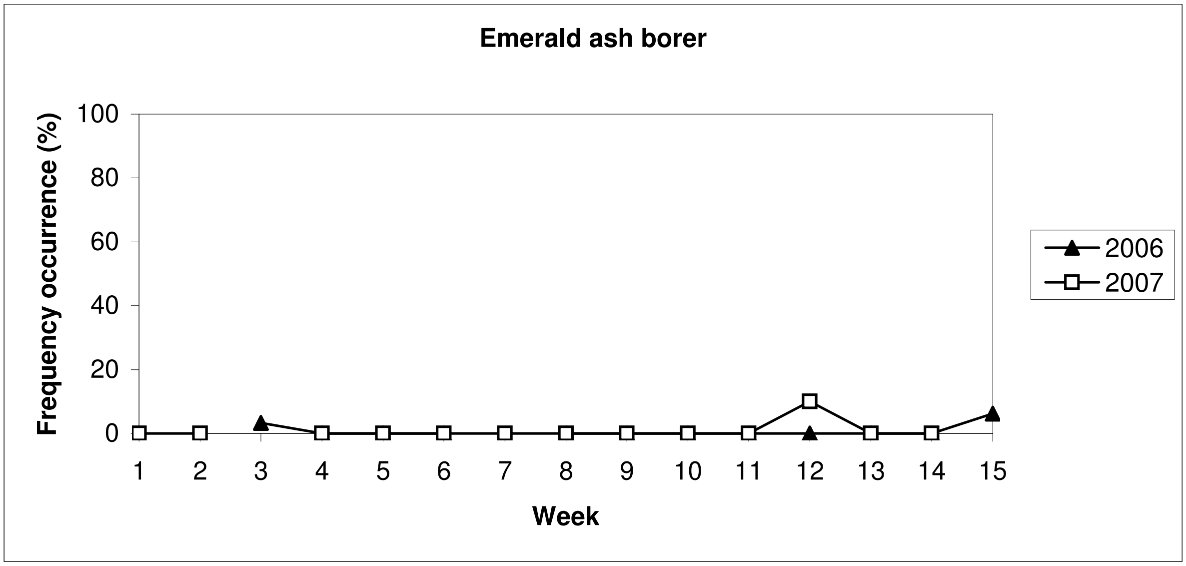


Figure 2.4. Weekly summary of percent frequency occurrence of the four most prevalent families of insects detected in the diet of evening bats during 2006–2007. Pellets were obtained from roosts near Palmyra, Michigan. Fecal pellets were not collected during weeks 1, 2, and 7 of 2006, and weeks 3 and 15 of 2007. Week 1 began on 15 May 2006 and 14 May 2007, and week 15 ended on 27 August 2006 and 26 August 2007.


Spotted cucumber beetle
Frequency occurrence (%)
100
80
60
40
20
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Week
2006
2007


Emerald ash borer
Frequency occurrence (%)
100
80
60
40
20
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Week
2006
2007

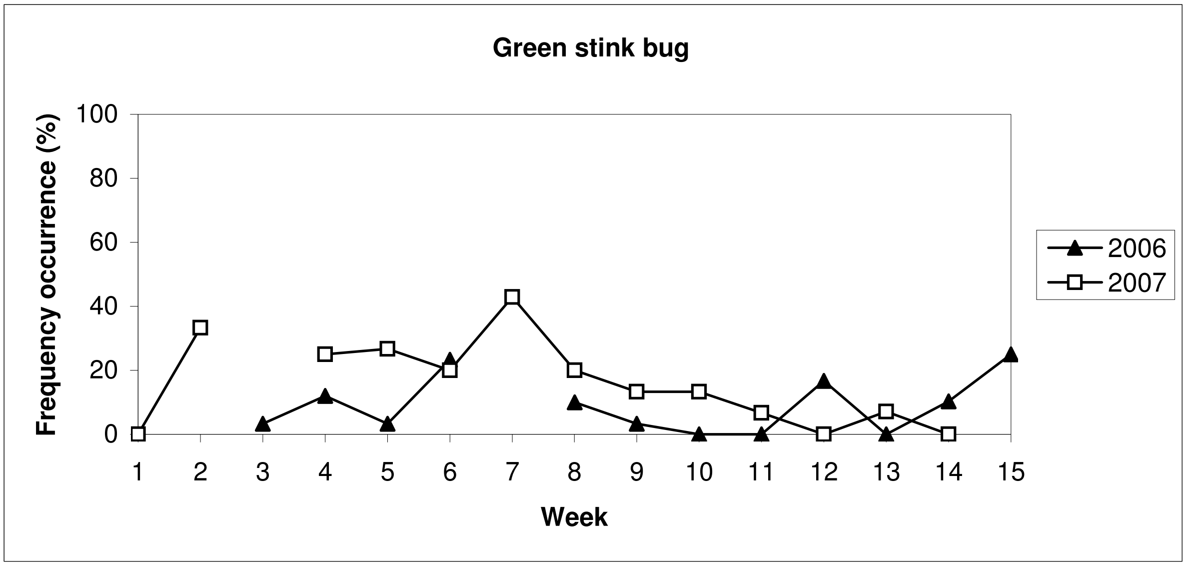


Figure 2.5. Weekly summary of percent frequency occurrence of the three species of insects detected in the diet of evening bats during 2006–2007. Pellets were obtained from roosts near Palmyra, Michigan. Fecal pellets were not collected during weeks 1, 2, and 7 of 2006, and weeks 3 and 15 of 2007. Week 1 began on 15 May 2006 and 14 May 2007, and week 15 ended on 27 August 2006 and 26 August 2007.