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THERMOREGULATION AND BEHAVIOR OF A PERIPHERAL POPULATION OF EVENING BATS

(*NYCTICEIUS HUMERALIS*)

By

Rachel Bricklin

Thesis

Submitted to the Department of Biology,

Eastern Michigan University

In partial fulfillment of the requirements

for the degree of

MASTER OF SCIENCE

in Ecology and Organismal Biology

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January 8, 2009

Ypsilanti, Michigan

DEDICATION

This thesis is dedicated to my partner in crime, M. Duane. His love and support during long nights of field work and thesis edits kept me sane. I also dedicate this thesis to my expanding family. D. Bricklin generously served as my technical advisor from day one. J. Duane immediately embraced my bat work with BCI newsletter subscriptions and the best bobble head doll. C. Bricklin and A. Duane provided great emotional support and bravely set aside their fear of flying mammals to accompany me on roost watches. A. Bricklin was always there on the other end of the phone when I needed a friend, and D. and B. Duane immortalized “my name is Rachel and I like to study bats, *STUDY BATS!*” Last but not least, to the newest member, Z. Duanklin. She has only been in my life for the last couple of months of the process, but I never met a more hilarious future field assistant.

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ABSTRACT

I used temperature-sensitive radio transmitters to measure body temperatures of tree-roosting evening bats (*Nycticeius humeralis*) at the northern edge of their range in Lenawee Co., Michigan. Temperature at sunset, diurnal temperature, and nocturnal temperature significantly correlated with use of torpor, whereas ambient temperature at sunset of the previous night, temperature at sunrise, amount of precipitation, abundance of insects, roost type, number of roost-mates, reproductive condition, and age did not. An analysis of individuals roosting in the same tree on the same day suggested that additional factors might determine exactly how low and for how long bats adjust their body temperatures. I also recorded nocturnal activity at the roost with a video recorder and receiver-logger and constructed an ethogram of seven behaviors associated with entering or emerging. Evening bats spent only 144 ± 114 (*SD*) min foraging each night, which is less than other species of bats.

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CHAPTER 1: USE OF TORPOR IN TREE-ROOSTING EVENING BATS

INTRODUCTION

Heat loss from an animal is proportional to the difference between ambient temperature (T_{ambient}) and body temperature (T_{body}), and all homeothermic endotherms must balance the energetic costs and benefits of maintaining a high, constant T_{body} (Hill et al., 2004). Insectivorous bats have high ratios of surface area to body mass due to their small size (typically <20 g) and membranous wings (Speakman and Thomas, 2003). Because animals lose heat from their surface, a high ratio of surface area to body mass means that it can be energetically taxing for bats to produce enough heat to compensate for heat lost at low T_{ambient} (Speakman and Thomas, 2003). For insectivorous bats in temperate areas, this problem is compounded by the negative effect of T_{ambient} on food availability. As T_{ambient} decreases, not only does heat loss increase, but energy intake, in the form of flying insects, typically decreases (Speakman and Thomas, 2003). In addition, reproduction, which is energetically costly, occurs during summer, when nights are shortest and thus foraging opportunities are restricted (Racey, 1982).

Metabolic rate is energy consumption per unit time and is equal to the sum of all energy released or stored by chemical reactions in the body. Metabolic rate can be measured as the amount of energy (food) an animal consumes, the amount of consumed food that an animal actually digests, or energy production (as growth or heat) per unit time (Hill et al., 2004). T_{body} is a measure of the average kinetic energy of molecules within the body, which is proportional to heat content, so T_{body} can be used as an index of metabolic rate at any particular T_{ambient} (Hill et al., 2004).

One strategy used by small bats to cope with the costs of maintaining a high T_{body} is torpor. Torpor is a controlled lowering of T_{body} below normothermic levels (Barclay et al.,

2001). Dropping T_{body} , however, lowers metabolic rate, thus slowing all physiological processes, including reproductive processes, such as fetal development and milk production (Racey, 1982; Speakman and Thomas, 2003). This slowing of physiological processes can be particularly significant in migratory species, because date of parturition and availability of milk during the first few weeks of life partly determines whether or not juveniles are of sufficient size and strength to fly to their wintering sites (Speakman and Thomas, 2003).

Until recently, most studies of use of torpor by bats occurred in the laboratory. A problem with laboratory studies is that animals often thermoregulate differently in captivity than in the wild (Kurta and Fujita, 1988). Thus, studies on free-living bats are critical to understanding use of torpor in the wild. Advances in technology over the past decade, particularly temperature-sensitive radio transmitters of increasingly smaller sizes, led to studies of use of torpor by bats under natural conditions (e.g., Grinevitch et al., 1995; Lausen and Barclay, 2003; Rambaldini and Brigham, 2008; Willis et al., 2006).

Previous studies on use of torpor in free-living bats found that both environmental variables (Willis et al., 2006) and individual condition (Lausen and Barclay 2003) affect thermoregulation. These environmental variables include T_{ambient} , precipitation, availability of food, type of roost, and size of a colony, whereas individual conditions include age, reproductive status, and body mass (Speakman and Thomas, 2003). World-wide threats to bats, such as loss of habitat for foraging, roosting, and hibernation, can force species to contend with sub-optimal environmental conditions (Fenton, 1997). Therefore, studying the relationship between ambient and individual variables and the use of torpor are critical to understanding how these losses might impact bats. In addition, as global temperatures warm, many mammals, including bats, are expanding their range northward (Humphries et al.,

2004). Physiological data on peripheral populations are critical to understanding the abiotic (environmental conditions) and biotic (individual condition) factors that determine the present and future range of these species (Humphries et al., 2004; McNab, 1982).

The evening bat (*Nycticeius humeralis*) is a small, migratory vespertilionid that ranges from northern Mexico to the Great Lakes region (Watkins, 1972). These bats are aerial insectivores that prey on various insects, including beetles, flies, flying ants, moths, and leafhoppers (Geluso et al., 2008; Münzer, 2009; Whitaker and Clem, 1992). Although males are solitary in summer, females form maternity colonies and typically give birth to twins in mid-to-late June (Watkins, 1972; Watkins and Shump, 1981; Wilkinson, 1992). Except when foraging, females remain close to their pups until youngsters are 2 weeks old (Watkins and Shump, 1981). Energetic costs of lactation are highest when pups are this age, because pups can not forage on their own, yet their larger body size results in higher caloric needs than at birth (Barclay, 1994; Hood et al., 2002; Wilkinson, 1992). Pups are able to fly and begin to forage on their own when they are about 3 weeks old, and they are weaned about 6 weeks after birth (Wilkinson, 1992).

A maternity colony of evening bats was discovered in Palmyra Township, Lenawee Co., Michigan, in August 2004, and it is the northernmost breeding colony of evening bats on the continent (Kurta et al., 2005). Though the evening bat roosts in both buildings and trees in other parts of its range (Wilkinson, 1992), members of the colony in Michigan invariably use trees, seeking shelter either in cavities and crevices in trunks and major branches or under exfoliating bark (Kurta et al., 2005; Münzer, 2009). Evening bats apparently arrive in Palmyra at the beginning of May and depart for their wintering grounds in mid-to-late August.

Thermoregulation by evening bats was studied in the laboratory using animals obtained in subtropical Florida (Genoud, 1993; McNab, 1974). However, no study examined thermoregulation in free-living evening bats or on evening bats in northern parts of their range, such as Michigan. In this study, I used temperature-sensitive radio transmitters to investigate thermoregulation in a population of tree-roosting evening bats at the northern edge of their range. I hypothesized that a combination of variables would determine use of torpor and that ambient conditions affect use of torpor more than individual reproductive condition or age.

METHODS

Study site.—Palmyra Township consists primarily of a flat lake plain that was formed when nearby Lake Erie once covered southeastern Michigan (Albert et al., 1986). Most of the plain has been drained and is used today for growing soy and corn. Forested areas that remain are mostly isolated woodlots in areas of poor drainage or along the floodplain of the River Raisin and its tributaries. The climate is continental but influenced by proximity to the Great Lakes; average maximum temperature in July at the nearby city of Adrian is 29°C and average minimum is 16°C (Keen, 1993).

Capture and marking.—From May through August of 2006 and 2007, bats were captured in 10-m-high mist-nets that were 9–12-m long. Nets were strung perpendicular to riparian corridors and other flyways. Age, sex, reproductive condition, weight, and forearm length of all captured evening bats were recorded. Bats were classified as either juveniles or adults based on the degree of fusion of the epiphyseal plates in the fingers of the wing (Anthony, 1988). Reproductive condition of adult bats (pregnant, lactating, or post-lactating) was determined by palpation of the abdomen, amount of fur surrounding the nipples, whether the nipples looked worn or fresh, and whether milk was visible when the nipples were gently squeezed (Racey, 1988). Temperature-sensitive (0.46-g) radio transmitters (Holohil Systems, Ltd., Carp, Ontario) were glued with surgical adhesive (SkinBond Cement, Smith and Nephew United, Inc., Largo, Florida) to the mid-dorsal region of all bats weighing ≥ 7 g (i.e., all but newly volant juveniles). These transmitters send out a signal that is heard as a series of clicks in an appropriate receiver, and the rate of clicks is proportional to temperature (Kurta and Fujita, 1988). The heat sensors in the transmitters respond to the temperature of the adjacent skin (T_{skin}), and studies have shown that T_{skin} is a reasonable estimate of T_{body} ,

particularly in small mammals such as bats (Audet and Thomas, 1996; Barclay et al., 1996; Willis and Brigham, 2003).

Recording skin temperature.—Bats were radio tracked to their day roosts the morning after they were fitted with transmitters. After finding the roost tree, I used an automated scanning receiver and data logger (Model SRX 400A, Lotek Wireless, Inc., Ontario, Canada) to record presence or absence of a signal from the transmitter. This instrument was capable of scanning for up to 10 different frequencies at predetermined intervals, allowing me to gather data on multiple animals on any given day. The receiver-logger was also capable of determining the rate at which the transmitter emitted clicks, and this pulse rate was converted to temperature using calibration equations provided by the manufacturer of the transmitters. Using the receiver-logger, I remotely monitored the T_{skin} of 1–6 bats every 0.25–3 min, depending on number of bats with transmitters in a tree.

The receiver-logger was connected to a 12-V, 12-A-h battery that was changed at least every 48 h to prevent gaps in data collection, and data were transferred regularly to a laptop computer in the field. Each day, bats with active transmitters were tracked to their respective day-roosting trees, and the receiver-logger was relocated if necessary. A weatherproof data logger that recorded T_{ambient} (Optic Stowaway, Onset Computer Corporation, Pocasset, Massachusetts) was moved with the receiver-logger. The receiver-logger was protected by a 46-l tub-like container (Latching Storage Container, Newell Rubbermaid, Sandy Springs, Georgia) during 2006. However, for better protection in 2007, I used a more rigid, 15-l waterproof case (1600 Case, Pelican Products, Inc., Torrance, California). I drilled holes in the sides of the latter for antenna wires, and then sealed everything with waterproof sealant. The bats often roosted in riparian forest that was subject

to sudden flooding; therefore, the case was elevated on a 0.7-m-high platform and locked to a nearby tree.

Definition of torpor.—Researchers often measure the frequency, duration, and depth of bouts of torpor when studying thermoregulation (Lausen and Barclay, 2003). To distinguish the torpid from the normothermic state, a minimum active temperature (T_{active}) must be defined. T_{active} is the lowest T_{skin} at which an animal is known to be active. Barclay et al. (2001) recommend determining a different T_{active} for each bat rather than using an average T_{active} for the population. This definition accounts for possible differences in individual T_{active} , as well as slight variations in amount of fur or adhesive between a bat's skin and its transmitter, which can affect how close transmitter readings are to actual T_{body} . Bats with T_{skin} below T_{active} are considered torpid, whereas bats with T_{skin} above T_{active} are considered normothermic.

To find each bat's T_{active} , I first compiled all measurements of T_{skin} that were recorded for each bat just prior to its leaving the roost to forage at dusk. At the time of evening emergence, all bats were assumed to be active and normothermic (Barclay et al., 2001). Previous studies (Chruszcz and Barclay, 2002; Lausen and Barclay, 2003) recorded T_{skin} at intervals of 10 min and used the last measurement before emergence to represent T_{active} . However, I recorded T_{skin} with much greater frequency, so I chose to use the second-to-last T_{skin} measured before emergence to represent T_{active} , to ensure that the bat was not flying when that value was recorded.

The unit of measure for amount or use of torpor was °C-h, because this unit describes both depth and duration of torpor (Lausen and Barclay, 2003). To calculate use of torpor (the amount of °C-h in torpor), I plotted T_{active} and T_{skin} on the y-axis against time on the x-axis

and then measured the area below the line for T_{active} but above the line for T_{skin} , that is, the area between T_{active} and T_{skin} when T_{skin} is less than T_{active} (Fig. 1.1). I measured the amount of torpor that occurred from the last time that the bat entered the roost in the morning, usually close to sunrise, to the first time that the bat emerged from the roost in the evening, usually close to sunset. Torpor is often separated into two categories: shallow torpor and deep torpor. Following Lausen and Barclay (2003), I defined shallow torpor as occurring when T_{skin} was $<10^{\circ}\text{C}$ below T_{active} . Deep torpor was defined as $T_{\text{skin}} \geq 10^{\circ}\text{C}$ below T_{active} . When investigating minimum T_{skin} for each bat, I called the largest difference between T_{skin} and T_{active} “minimum T_{skin} ” and measured this value in $^{\circ}\text{C}$ below T_{active} . Minimum T_{skin} indicates the maximum depth of torpor.

Analysis of use of torpor.—Because the evening bat is at the northern edge of its range in southern Michigan, I wanted to determine if environmental or individual factors played a larger role in use of torpor and then compare the bats’ thermoregulatory responses to these factors with results from other populations of tree-roosting bats. I looked for both inter- and intraspecific differences in use of torpor. The environmental variables that I considered were T_{ambient} , amount and duration of precipitation, availability of food, type of roost, and number of bats in the tree. I used the term “number of roost-mates” to refer to the number of volant bats in a single tree on any given day.

The individual variables that I considered were reproductive condition and age. Though body mass also can affect use of torpor (Speakman and Thomas, 2003), I did not include mass because body mass in the field changes by 10–40%, depending on time of capture (low near sunset and higher after the animal has obtained food and water—

Wilkinson, 1992) and seasonal factors, such as reproductive condition (e.g., pregnancy versus lactation—Kurta et al., 1990).

All data for T_{skin} , T_{active} , and T_{ambient} were graphed in both Excel (Microsoft, Redmond, Washington) and SigmaPlot (Systat Software Inc., Richmond, California). I used formulas within Excel to calculate the area between T_{skin} and T_{active} , which yielded measurements of torpor bouts in °C-h. All statistics, however, were calculated using Systat 11 (Systat Software Inc., Richmond, California) and Excel.

To determine the relationship between T_{ambient} and use of torpor, I used regression analysis with several measures of T_{ambient} . I examined the relationship between amount of torpor and T_{ambient} at sunset on the previous day, T_{ambient} at sunset on the day of measurement, and T_{ambient} at sunrise on the day of measurement. I also calculated indices to temperature that were related to T_{ambient} over the entire previous night or the entire day of measurement. These indices were calculated by measuring the area between 0°C and T_{ambient} and then dividing by the total number of hours in the night or day. Measures of T_{ambient} at sunset on the previous day, the all-night T_{ambient} , and T_{ambient} at sunrise presumably would be related to foraging success (Kurta, 1986; Wilkinson, 1992), whereas T_{ambient} at sunrise and sunset on the day of measurement, as well as the all-day index, presumably reflected the potential magnitude of heat loss by a roosting bat. All values analyzed were means for each bat to ensure that data were independent.

I obtained data on precipitation recorded at the Adrian airport (ca. 16 km from my study site) for each night from <http://www.wunderground.com/history/>. Because amount of precipitation was reported hourly (or more often) on this website, I was able to calculate both total amount of precipitation from sunset to sunrise as well as the percent of the total time

from sunset to sunrise during which precipitation occurred. I arcsine transformed the percentages and then used regression analysis to look at the relationships between use of torpor and total precipitation, as well as the percent of the night with precipitation. I also used regression analysis to look at number of roost-mates versus amount of torpor. Colony size was determined by emergence counts at the roost from sunset to 50 min after sunset on the day of measurement. For regressions, I computed the extra sum of squares due to the addition of a second-order term to determine if polynomial equations were significant improvements in explaining relationships between variables over simple first-order equations (Kleinbaum et al., 1988).

Each night that I watched a roost tree, I qualitatively estimated insect abundance at sunset as high, medium, or low based on the number of flying insects observed. I used one-way analysis of variance to identify significant differences in use of in torpor after nights of differing insect abundances. I also used one-way analysis of variance to identify differences in use of in torpor by bats that spent the day in different types of roost (i.e., cavity, crevice, or exfoliating bark).

To identify individual differences in use of torpor and investigate combined effects of environmental and individual variables on use of torpor, I examined amount of torpor of different bats roosting in the same tree on the same day and amount of torpor, minimum T_{skin} (calculated by subtracting each bat's lowest T_{skin} on any particular day from its overall T_{active}), and number of days that bats used deep versus shallow torpor. For statistical analyses, I divided the individual radio-tagged bats into three reproductive groups: pregnant females, lactating females, and juveniles of either sex. Two bats captured at the beginning of the season were not palpably pregnant, but they were included in the pregnant group. This

lumping is justified because two other not-palpably-pregnant bats, captured on 6 June 2007, were later recaptured while lactating, and because all adult females captured after 6 June in both 2006 and 2007 were either lactating or post-lactating.

I also analyzed the data by the “season” or reproductive periods during which the radio-tagged bat was captured. Reproductive periods (pregnancy, lactation, and post-lactation), were determined by the reproductive condition of the majority of adult females in the colony that were most recently mist netted at the time that the radio-tagged bat was monitored, rather than the specific condition of the radio-tagged individual (after Lausen and Barclay, 2003). In both 2006 and 2007, pregnancy lasted from 3 to 23 June; lactation, from 24 June to 27 July; and post-lactation, from 28 July to 22 August.

I chose to group bats by reproductive period, as well as by individual reproductive condition, because significant differences by reproductive period might suggest an interplay between environmental and individual factors in use of torpor. For example, significant differences in use of torpor by bats between the reproductive periods of pregnancy and lactation might suggest that both month-to-month differences in T_{ambient} as well as reproductive condition affect use of torpor. I looked at reproductive period and differences among reproductive groups in number of days that deep torpor ($\geq 10^{\circ}\text{C}$ below T_{active}) versus shallow torpor ($<10^{\circ}\text{C}$ below T_{active}) was used. I analyzed these differences with chi-squared using a correction for continuity (Zar, 1999). I then used one-way analysis of variance to look at differences in minimum T_{skin} (the greatest difference between T_{skin} and T_{active}) and number of $^{\circ}\text{C}\cdot\text{h}$ in torpor among reproductive groups and periods of the season. For multiple comparisons after a significant analysis of variance, I used Tukey’s Honestly Significant

Difference test. If necessary, data were square-root or rank transformed (Conover and Iman, 1981) to meet the assumption of normality. All means are given as ± 1 *SD*.

RESULTS

Sample size.—I recorded T_{skin} , from about sunrise to sunset, for 23 bats. One bat was monitored while post-lactating in both years, so I have data for five bats from 2006 and 19 bats from 2007. During this study, I monitored five pregnant, six lactating, and two post-lactating adults, including the individual that was monitored in both 2006 and 2007; in addition, I obtained data from nine juveniles and one bat that was released before reproductive condition was noted. Data on lactating bats were only recorded during summer 2007, but data on the other reproductive groups were obtained during both summers. Number of days recorded per bat ranged from 1 to 8. Data were obtained on 54 calendar-days, with a grand total of 92 bat-days; a bat-day is defined as one bat being monitored for one day.

Overall, use of torpor on the 92 bat-days ranged from 0 to 294.8°C-h ($53.5 \pm 55.9^\circ\text{C-h}$). There was no significant difference in use of torpor between adults and juveniles when pregnant and lactating bats were lumped together ($F_{1,20} = 1.39$; $P = 0.25$). Similarly, there were no significant differences in amount of torpor among reproductive groups (pregnant, lactating, or juvenile; $F_{2,17} = 0.87$; $P = 0.44$).

Sample size and T_{active} .—For the 23 bats for which full-day data were obtained, I recorded T_{active} on 3–11 days per bat (6.1 ± 2.5 days). Minimum T_{active} for each bat ranged from 28.3 to 39.1° ($33.3 \pm 2.6^\circ\text{C}$). Number of days that T_{active} was recorded had no statistical effect on minimum T_{active} , although the relationship approached significance ($r^2 = 0.13$; $F_{1,22} = 3.24$; $P = 0.09$).

Ambient temperature and use of torpor.—From June through August 2006 and 2007, T_{ambient} at sunrise ranged from 10.9 to 24.2°C, and T_{ambient} at sunset varied from 13.9 to 28.9°C (Table 1.1). T_{ambient} calculated over the entire day ranged from 14.4 to 29.2°C, and

T_{ambient} over the whole night varied from 13.7 to 25.6°C (Table 1.1). Mean T_{ambient} at sunset, mean daily T_{ambient} , and mean nightly T_{ambient} showed significant negative relationships with mean use of torpor by each bat ($F_{1,20} = 18.89, P < 0.001$; $F_{1,20} = 13.27, P < 0.001$; and $F_{1,20} = 4.4, P = 0.049$, respectively; Fig. 1.2). That is, as these temperatures decreased, °C-h in torpor increased. However, mean T_{ambient} at sunset of the previous night and mean T_{ambient} at sunrise did not show significant relationships with mean use of torpor by each bat ($F_{1,18} = 3.75, P = 0.07$; and $F_{1,20} = 2.72, P = 0.11$, respectively). Second-order regression analysis did not explain significantly more variation than did first-order analysis. Thus, simple linear regressions were used.

Precipitation and use of torpor.—On 6 calendar-days (13 bat-days), precipitation was >0 cm during the previous night. Total precipitation on these nights ranged from 0.2 to 12.0 cm, and the proportion of the night with precipitation ranged from 1.3 to 79.2%. Amount of torpor after nights with precipitation ranged from 0.7 to 124.1°C-h, whereas use of torpor on all days, with and without precipitation, ranged from 0.3 to 294.8°C-h. Use of torpor was greatest following the night with the highest proportion of precipitation and lowest following the night with the lowest proportion of precipitation (Fig. 1.3). However, there was no statistical relationship between proportion of the night with precipitation and use of torpor the next day or between amount of precipitation and use of torpor the next day (both $P > 0.15$). Nine bats were monitored on days following nights with and without rainfall, and seven of the nine bats showed higher use of torpor after nights without precipitation than after nights with precipitation (Table 1.2).

Insect abundance and torpor.—I recorded abundance of insects at sunset on 43 of the 54 calendar-nights (76 bat-nights) prior to recording T_{skin} , and I obtained temperature at

sunset for 40 of these calendar-nights. All 23 bats in my sample had abundance recorded for ≥ 1 night prior to recording T_{skin} . Fourteen calendar-nights had low abundance; 16, medium abundance; and 10, high abundance. One-way analysis of variance showed significant differences in sunset temperature among nights with low ($20.0 \pm 2.9^\circ\text{C}$), medium ($21.4 \pm 1.8^\circ\text{C}$), or high ($22.8 \pm 2.4^\circ\text{C}$) abundance of insects ($F_{2,37} = 4.16$; $P = 0.02$). However, Tukey's test was unable to show where the difference was. Mean use of torpor was $65.9 \pm 54.8^\circ\text{C-h}$ after nights with low abundance of insects, $45.5 \pm 37.9^\circ\text{C-h}$ after nights with medium abundance, and $29.2 \pm 43.7^\circ\text{C-h}$ after nights with high abundance. However, one-way analysis of variance did not show significant differences in use of torpor among nights of varying insect abundance ($F_{2,35} = 1.79$; $P = 0.18$; Fig. 1.4).

Type of roost and use of torpor.—Most roosts that were utilized during days on which torpor occurred were cavities (8 of 14 roosts). Of the remainder, two were crevices, two were exfoliating bark, one was both a cavity and exfoliating bark, and one was both a cavity and a crevice. I included only the first three categories (cavity, crevice, and exfoliating bark) in my analysis. Mean amount of torpor was $55.4 \pm 44.4^\circ\text{C-h}$ while roosting in cavities, $20.1 \pm 25.5^\circ\text{C-h}$ in crevices, and $7.0 \pm 6.2^\circ\text{C-h}$ under exfoliating bark. However, there was no significant difference in amount of torpor among roost types, though the difference among roost types approached significance ($F_{2,23} = 3.0$; $P = 0.07$).

Number of roost-mates and use of torpor.—I recorded emergence counts for 36 of the 54 calendar-nights (66 total bat-nights for 22 bats). Number of bats emerging from the roost at sunset was 2–57, with a mean of 21.1 ± 12.5 bats. On all nights that I recorded emergence counts, a radio-tagged bat roosted with <10 other bats on only 3 days (4%), all in mid-to-late

August. However, mean emergence count was not correlated with mean amount of torpor for each bat ($F_{1,20} = 0.53$; $r = 0.16$; $P = 0.47$; Fig. 1.5).

Deep versus shallow torpor.—Bats used torpor on 87 (94.6%) of the 92 bat-days. Shallow torpor occurred on 65 bat-days, and deep torpor was used on 22 bat-days. On 74 of the bat-days during which torpor occurred, bats that went into torpor were of known reproductive condition, and sample sizes of that group were large enough to analyze. My sample size of post-lactating bats was too small to analyze, and female juveniles and male juveniles were lumped because these bats were not yet sexually mature.

Adult bats overall used deep torpor significantly more often than juveniles bats ($X^2 = 5.45$; $P < 0.03$; Table 1.3). When pregnant and lactating bats were compared, I found no significant differences in the frequency of deep and shallow torpor ($X^2 = 0.31$; $P > 0.5$). Pregnant bats did show more frequent use of deep torpor than juvenile bats ($X^2 = 4.33$; $P < 0.05$), though lactating bats did not ($X^2 = 1.77$; $P > 0.1$). A chi-squared test also did not show any significant differences in the frequency of deep and shallow torpor among the three reproductive periods (pregnancy, lactation, and post-lactation; all $P > 0.25$).

Trends in T_{skin} through the day.—Times that bats entered the roost for the last time were highly variable and ranged from 8.6 h before sunrise to 0.8 h after sunrise (Fig. 1.6). On most bat-days (51 of 92; 55%), bats entered the roost for the last time in the hour before sunrise. However, 26% (24 of 92 bat-days) of last entrances occurred >6 h before sunrise. On the remaining bat-days, seven entrances occurred 2.5–5.5 h before sunrise, five happened after sunrise (the latest entrance time was 0.8 h after sunrise), and five occurred 1–1.5 h before sunrise.

After entering the roost on days when deep torpor was used, T_{skin} tended to decrease until late-morning (ca. 1000 h), and then bats passively re-warmed as T_{ambient} increased. On eight (36%) of these 22 deep-torpor days, T_{skin} remained close to T_{ambient} until a few hours prior to emergence, when T_{skin} then rose above T_{active} (Fig. 1.7a). On the rest of these deep-torpor bat-days, T_{skin} either rose above T_{active} about mid-day (ca. 1200 h; 7 of 22 days) or mid-afternoon (ca. 1500–1800 h; 7 of 22 days) and then fluctuated around T_{active} until emergence (Fig. 1.7b). On days that bats did not use deep torpor, T_{skin} tended to fluctuate around T_{active} throughout the day (Fig. 1.7c).

Minimum T_{skin} .—Overall, the lowest T_{skin} I recorded for a bat was 16.1°C and the highest minimum was 32.3°C (mean $22.4 \pm 4.2^\circ\text{C}$). The greatest difference between T_{skin} and T_{active} for each bat ranged from 2.8 to 23.0°C below T_{active} , with a mean of $10.9 \pm 4.6^\circ\text{C}$ below T_{active} (Table 1.4). Differences in mean minimum T_{skin} (°C below T_{active}) among pregnant, lactating, and juvenile bats approached significance ($F_{2,17} = 3.40$; $P = 0.057$). When minimum T_{skin} (°C below T_{active}) was analyzed by period, there was no significant difference ($F_{2,89} = 0.76$; $P = 0.47$; Table 1.5).

Intraspecific differences in use of torpor on the same day.—On 17 of the 54 calendar-days, two or more bats with transmitters roosted in the same tree for ≥ 2 days. Days with multiple bats in the same tree presented unique opportunities to examine intra-specific differences in use of torpor, because these bats presumably experienced similar environmental conditions. Amount of torpor on the same day by different bats, even individuals of the same reproductive condition, varied greatly. For example, on 9 June 2007, there was a difference of $>100^\circ\text{C}\cdot\text{h}$ in use of torpor between two pregnant bats roosting in the same tree. Although the extent of torpor varied greatly between individuals, the relative use

of torpor was identical on 15 of the 17 days during which multiple bats with transmitters roosted in the same tree for multiple days. For example, bats 781 and 822 both showed the most °C-h in torpor on 9 June, second most on 12 June, and least on 8 June (Table 1.6). These results suggest that there was not an interactive effect of environmental and individual conditions on use of torpor.

DISCUSSION

These results support my hypothesis that a combination of variables determines use of torpor in the evening bat. Three different measures of T_{ambient} showed significant relationships with amount of torpor, though these measures are correlated with other variables as well. Adult (pregnant and lactating females) and juvenile bats showed significant differences in use of deep versus shallow torpor, with adults using deep torpor more often than juveniles, perhaps due to the higher energetic needs of the adults. However, pregnant and lactating bats did not differ in their overall use of torpor or frequency of deep versus shallow torpor. These results also support my hypothesis that ambient conditions appear to affect use of torpor more than individual reproductive condition and age, particularly the similar thermoregulatory patterns in bats of different ages and reproductive conditions roosting in the same tree on the same day.

Genoud (1993) found that evening bats from Florida that were exposed to moderate T_{ambient} (20–30°C) maintained normothermy, as evidenced by high levels of oxygen consumption; mean normothermic T_{body} was $33.6 \pm 1.2^{\circ}\text{C}$. Between 5 and 20°C, evening bats either became torpid or remained normothermic, and below 5°C, they always became torpid. The mean T_{active} (minimum normothermic temperature) for bats in my study was $33.3 \pm 2.6^{\circ}\text{C}$. T_{ambient} in my study was usually between 15–30°C (Table 1.1), and my evening bats appeared to use torpor more frequently than the bats from Florida (Table 1.3). The bats that Genoud (1993) used, however, were well fed and laboratory acclimated, which may explain the lower use of torpor by his bats (Kurta and Fujita, 1988).

Thermoregulatory patterns of the evening bat were similar to those of other temperate species recorded during the reproductive season. In field studies of big brown bats (*Eptesicus*

fuscus) and western long-eared bats (*Myotis evotis*), researchers also found that individuals entered torpor soon after returning to the roost, and then passively warmed as T_{ambient} increased (Chruszcz and Barclay, 2002; Lausen and Barclay, 2003; Solick and Barclay, 2006), a pattern similar to that reported for freshly captured little brown bats (*Myotis lucifugus*) monitored in the laboratory under simulated roost conditions (Kurta, 1991; Kurta et al., 1987). No bats in my study used torpor for >24 h as Willis et al. (2006) found in pregnant hoary bats (*Lasiurus cinereus*) during extreme conditions (T_{ambient} near 0°C). However, temperatures never fell below 10°C during the time that I monitored evening bats (the lowest sunrise temperature recorded during my study was 10.9°C on 18 August 2007), and on only two occasions did a bat (a juvenile male) miss a complete night of foraging due to weather conditions (Chapter 2).

Jacobs et al. (2007) also found that subtropical bats in different types of roosts (building, tree cavity, and foliage) all used torpor, but noted differences in use of torpor between bats in tree cavities and foliage. They described longer, shallower bouts of torpor by bats roosting in cavities, and shorter, deeper bouts of torpor by bats roosting in foliage. In the bats they studied, the African yellow bat (*Scotophilus dinganii*) and the recently-discovered *S. mhlangani*, depth and duration of torpor were greater when roosting in foliage than in cavities. Though my sample sizes of use of torpor by bats in crevices and exfoliating bark were small, I did not find significant differences in use of torpor among these different roost types, which presumably differ in the amount of insulation that they provide.

The 23 bats in my sample always roosted communally, similar to big brown bats roosting in tree cavities (Willis and Brigham, 2007). Willis and Brigham (2007) found that occupied roosts of big brown bats had higher maximum temperatures than unoccupied roosts,

and proposed that roosting with other bats provides individuals with substantial energy savings over roosting alone. If roosting with others decreases the need for torpor, then individuals from social species would be expected to always roost with others. In a laboratory study that simulated conditions in the roost and used freshly captured animals, Kurta (1986) found that communally-housed little brown bats of different reproductive conditions had similar T_{body} , but solitary bats had higher T_{body} during pregnancy and post-lactation than during lactation, perhaps due to the high energetic cost of lactation. Solitary bats had lower T_{body} than bats taken from the center of a cluster, and date also affected the T_{body} of bats housed alone, presumably reflecting seasonal acclimatization to changing T_{ambient} . Kurta's (1986) results suggest that both reproductive condition and body heat from other bats have significant effects on an individual's T_{body} . Group living can help maintain a high T_{body} , particularly by reducing the ratio of surface area to body mass of individual bats and increasing the cumulative amount of heat produced inside a roost. Consequently, group living should facilitate increased fetal development, milk production, and juvenile growth. Even though the bats in my study showed a high frequency of use of torpor, group living might shorten the depth and duration of each bout of torpor.

No other studies provide information on free-living bats roosting in the same tree on the same day, though Dietz and Kalko (2006) graphically compared thermoregulation of reproductive and non-reproductive Daubenton's bats (*Myotis daubentonii*) under similar ambient temperatures. They found that reproductive individuals did not use torpor, while non-reproductive bats did. These results do not agree with my findings that bats under the same conditions (i.e., same roost and same day) exhibit similar thermoregulatory patterns despite differences in age or reproductive condition. However, Dietz and Kalko (2006) compared

thermoregulation of bats recorded on different days, so perhaps other factors played a role in use of torpor by their bats as well. Perhaps individual factors more specific than general reproductive condition determine the amount of time spent in torpor.

I was most surprised by the lack of significant differences in use of torpor among evening bats of different reproductive conditions, particularly because evening bats in Michigan were at the northernmost edge of their range and perhaps exposed to lower ambient temperatures than anywhere else on the continent. I expected lactating bats to show a higher use of torpor than pregnant bats because more energy is required to produce milk than to support a fetus (Kurta et al., 1989). Speakman and Thomas (2003) noted that there are many contradictions in the literature on use of torpor by bats. Although my sample was small, my results added to these contradictions, finding some aspects of torpor that agree with previous studies and some that do not. However, these contradictions made sense in light of torpor resulting from so many different variables. In a survey of use of torpor in birds, Brigham et al. (2006) did not find any one variable that consistently explained thermoregulatory patterns and suggested that multiple factors explain use of torpor. Also, one must keep in mind that torpor is considered an example of phenotypic plasticity (Humphries et al., 2003). Plastic traits vary based on ambient and individual conditions and are not always easily modeled or predicted. Perhaps so many studies find such conflicting results because many environmental and individual variables determine use of torpor, and some of these variables might not even have been examined yet in bats, such as hereditary effects. For example, thermoregulatory behaviors, such as nesting and temperature preferences in house mice (*Mus musculus*), are known to be influenced by genetics (Lacy and Lynch, 1979; Lynch and Hegmann, 1972).

Both laboratory and field studies over the past 40 years have answered many questions about use of torpor in reproductive female bats. However, there is still much to discover. Species-specific differences in use of torpor during the reproductive season, as well as differences between captive and wild bats, caution against drawing definite conclusions about use of torpor in reproductive female bats from only a few case studies. Researchers must consider the results of multiple studies and look for patterns across species and geographic regions. There is a need for more field studies on use of torpor by different populations of the same species (e.g., Solick and Barclay, 2007). Comparative studies of use of torpor and reproductive rates in the same species at different parts of its range are also critical to assess potential impacts of climate change.

Because environmental factors such as T_{ambient} and precipitation can affect the timing of reproduction in temperate bats (Grindal et al., 1992), as well as reproductive rates (Barclay et al., 2004), changes in these environmental factors potentially can have large population-level consequences. With warmer temperatures, reproductive rates of bats might increase due to decreased use of torpor, leading to earlier parturition, higher fetal and juvenile survivorship, and/or greater litter size (Tuttle and Stevenson, 1982). My findings that use of torpor by evening bats at the northern edge of their range correlates with environmental conditions, such as T_{ambient} , but not individual conditions, such as reproductive state, suggest that a warmer climate might allow evening bats at Palmyra to decrease use of torpor and increase their reproductive success. A warmer climate also might allow the evening bat to move farther north, into areas that currently may be too cold for successful reproduction by this essentially southern species.

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Table 1.1.—Variables that summarize differences in T_{ambient} among reproductive periods. Dates apply to both 2006 and 2007.

Period	Dates	Minimum / maximum T_{ambient} at sunrise (°C)	Mean T_{ambient} at sunrise (°C)	Minimum / maximum T_{ambient} at sunrise (°C)	Mean T_{ambient} at sunset (°C)	Minimum / maximum diurnal T_{ambient} (°C)	Mean diurnal T_{ambient} (°C)	Minimum / maximum nocturnal T_{ambient} (°C)	Mean nocturnal T_{ambient} (°C)
Pregnancy	3–23 June	12.2 / 23.3	16.8 ± 3.5	13.9 / 24.4	19.7 ± 3.3	14.4 / 26.1	21.8 ± 3.3	14.8 / 24.8	18.6 ± 3.5
Lactation	24 June–27 July	11.4 / 21.9	15.5 ± 3.1	16.5 / 25.5	21.1 ± 2.5	19.3 / 28.3	22.3 ± 2.5	13.7 / 22.3	17.1 ± 2.3
Post-lactation	28 July–22 August	10.9 / 24.2	17.8 ± 3.4	16.3 / 28.9	22.2 ± 3.0	15.6 / 29.2	23.2 ± 3.4	13.9 / 25.6	19.6 ± 2.9
All	3 June–22 August	10.9 / 24.2	16.6 ± 3.5	13.9 / 28.9	21.2 ± 2.9	14.4 / 29.2	22.5 ± 3.0	13.7 / 25.6	18.3 ± 3.0

Table 1.2.—Use of torpor by nine bats with T_{skin} recorded after nights with and without precipitation.

Bat transmitter frequency	Number of nights with precipitation prior to recording T_{skin}	Mean precipitation (cm)	Mean portion of night with precipitation	Mean amount of torpor after no precipitation ($^{\circ}\text{C}\cdot\text{h}$)	Mean amount of torpor after precipitation ($^{\circ}\text{C}\cdot\text{h}$)
099	2	6.3	0.2	67.2	1.4
147	2	6.3	0.2	69.0	1.7
219	1	1.3	0.1	17.8	4.0
440	1	1.3	0.1	0.4	7.6
478	1	1.3	0.1	27.6	1.5
059	1	12.0	0.3	77.4	11.0
701	2	6.3	0.2	107.2	12.0
862	1	2.7	0.1	294.8	68.2
940	2	2.7	0.4	40.1	66.6

Table 1.3.—Number of days in torpor and deep torpor by reproductive group. One bat (of unknown age) was not included.

Reproductive condition	Number of bats	Number of bat-days	Number of bat-days in torpor	Number of bat-days in deep torpor
Pregnant	5	14	13	5
Lactating	6	29	25	6
Post-lactating	2	5	5	3
Juvenile	9	36	36	3
All	22	84	79	17

Table 1.4.—Minimum T_{skin} (greatest difference between T_{skin} and T_{active}) for reproductive groups.

Group	Number of bats	Minimum T_{skin} of group (°C below T_{active})	Mean minimum T_{skin} of each bat (°C below T_{active})
Pregnant	5	23.0	15.2 ± 7.1
Lactating	6	13.8	10.8 ± 2.3
Juvenile	9	10.2	8.1 ± 2.9
All bats ^a	23	23.0	10.9 ± 4.6

^aIncludes bats of unknown reproductive condition and post-lactating females.

Table 1.5.—Minimum T_{skin} (greatest difference between T_{skin} and T_{active}) for reproductive periods.

Period	Number of bat-days	Minimum T_{skin} of period ($^{\circ}\text{C}$ below T_{active})	Mean minimum T_{skin} of each bat-day ($^{\circ}\text{C}$ below T_{active})
Pregnancy	16	23.0	9.5 ± 6.4
Lactation	48	13.8	6.6 ± 4.5
Post-lactation	28	13.9	6.6 ± 3.7
All days	92	23.0	7.1 ± 4.7

Table 1.6.— Sample of days with multiple bats in the same roost. The first three numbers are the transmitter frequency of the bat, reproductive condition is in parentheses, and the last number is amount of torpor in °C-h. Reproductive conditions listed are pregnant (PG), lactating (LA), and juvenile (J).

8 June	9 June	12 June	9 July	12 July	13 July	20 July	21 July	22 July	23 July
781 (PG): 1.5	781 (PG): 123.6	781 (PG): 25.5							
822 (PG): 44.0	822 (PG): 228.5	822 (PG): 114.6							
			440 (LA): 0.0	440 (LA): 38.9	440 (LA): 77.1	440 (LA): 32.9	440 (LA): 78.3		
			901 (LA): 0.6	901 (LA): 98.0	901 (LA): 159.3				
						059 (LA): 98.8	059 (LA): 124.4	059 (LA): 93.5	059 (LA): 72.6
						099 (J): 83.3	099 (J): 111.0	099 (J): 80.5	099 (J): 69.3
						147 (J): 81.0	147 (J): 121.0	147 (J): 78.0	147 (J): 55.5

Figure 1.1.—Illustration of the area between T_{skin} and T_{active} . The black shaded region represents $^{\circ}\text{C}\cdot\text{h}$ in torpor.

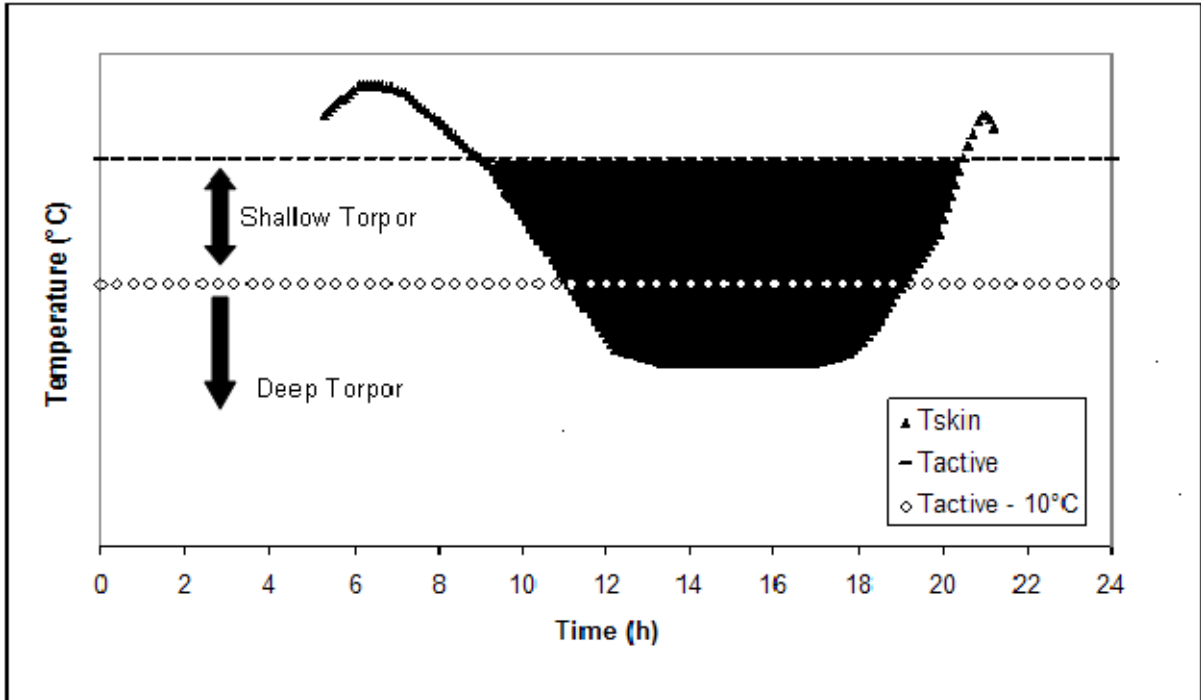


Figure 1.2a-c.—Sunset, diurnal, and nocturnal T_{ambient} and use of torpor.

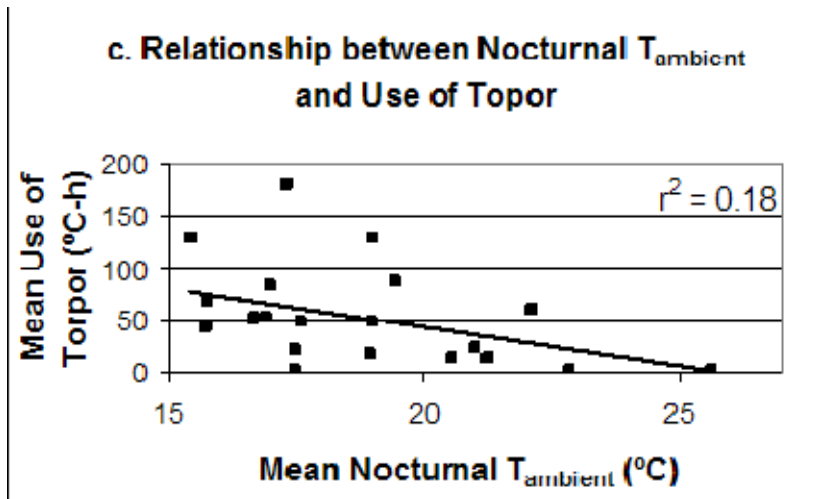
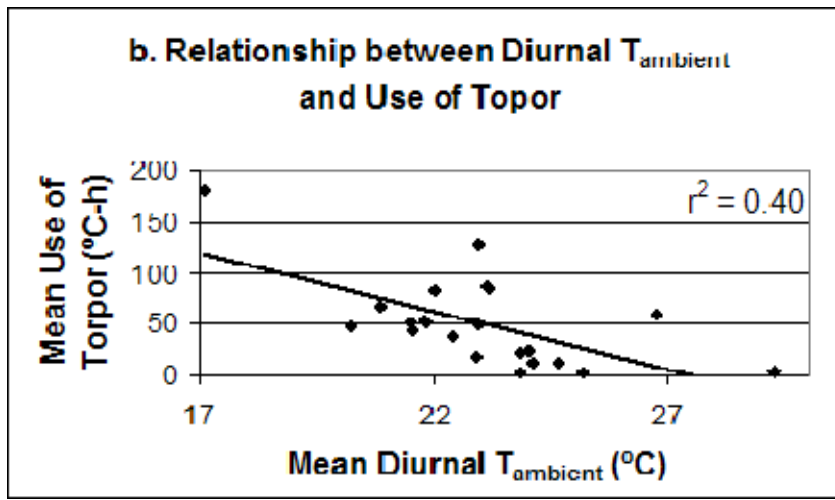
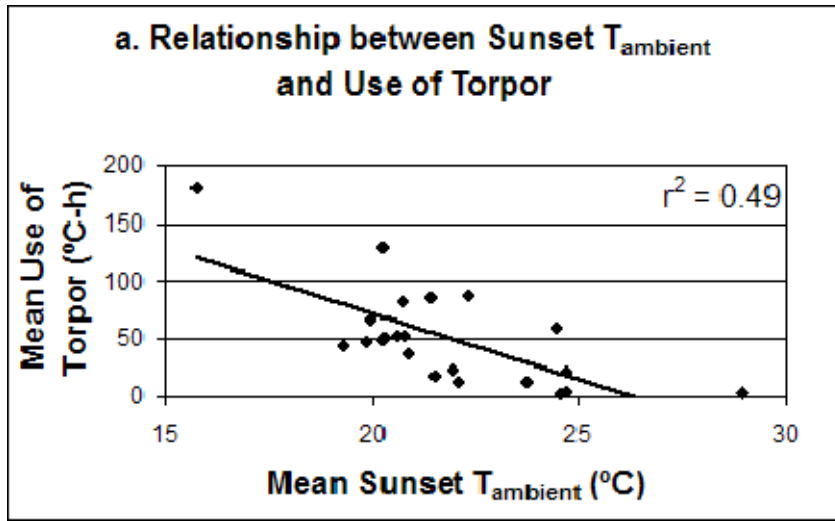


Figure 1.3.—Amount of precipitation (in both percent of the night and total cm) and °C-h in torpor the next day.

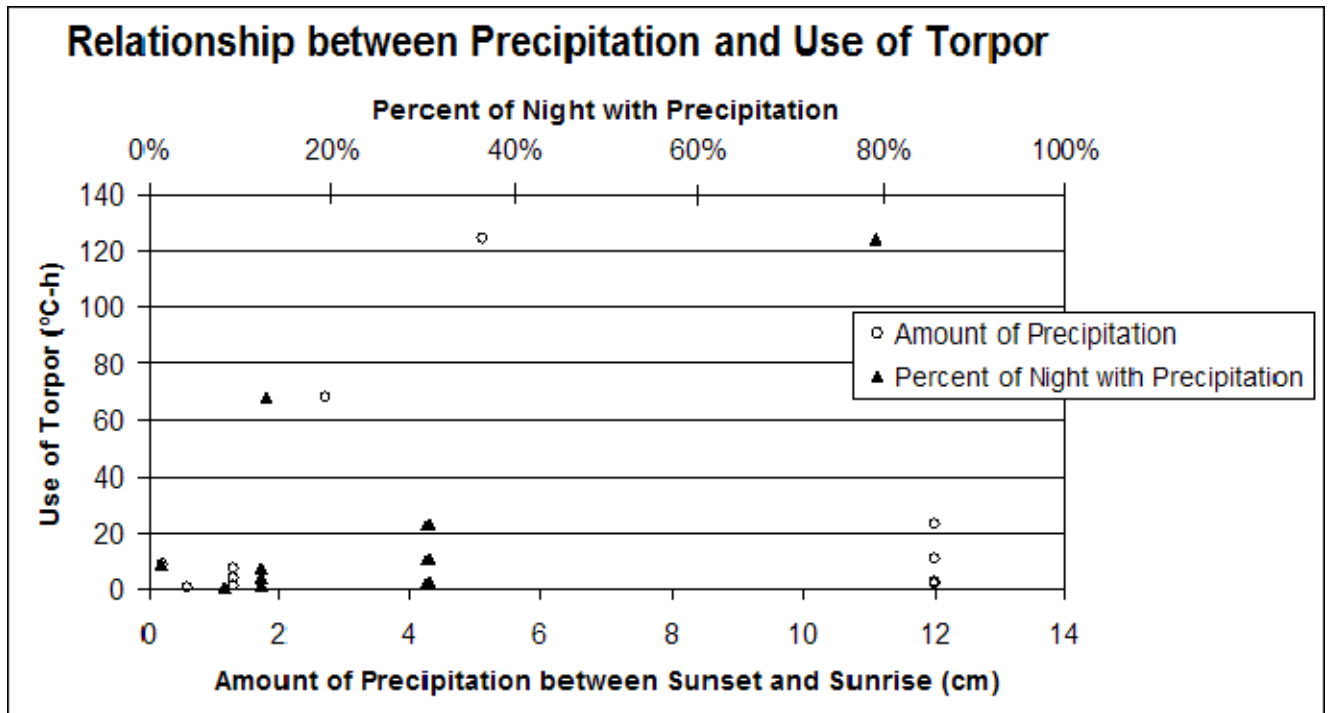


Figure 1.4.—Relationship between abundance of insects and mean use of torpor the next day.

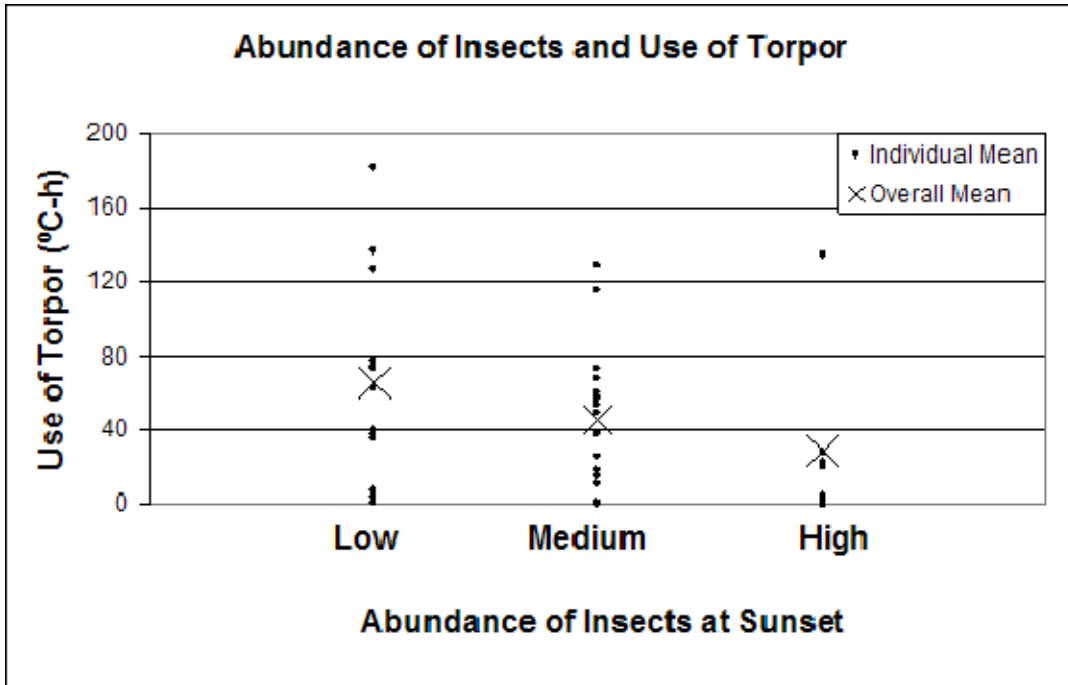


Figure 1.5.—Relationship between mean emergence count for each bat and °C-h in torpor.

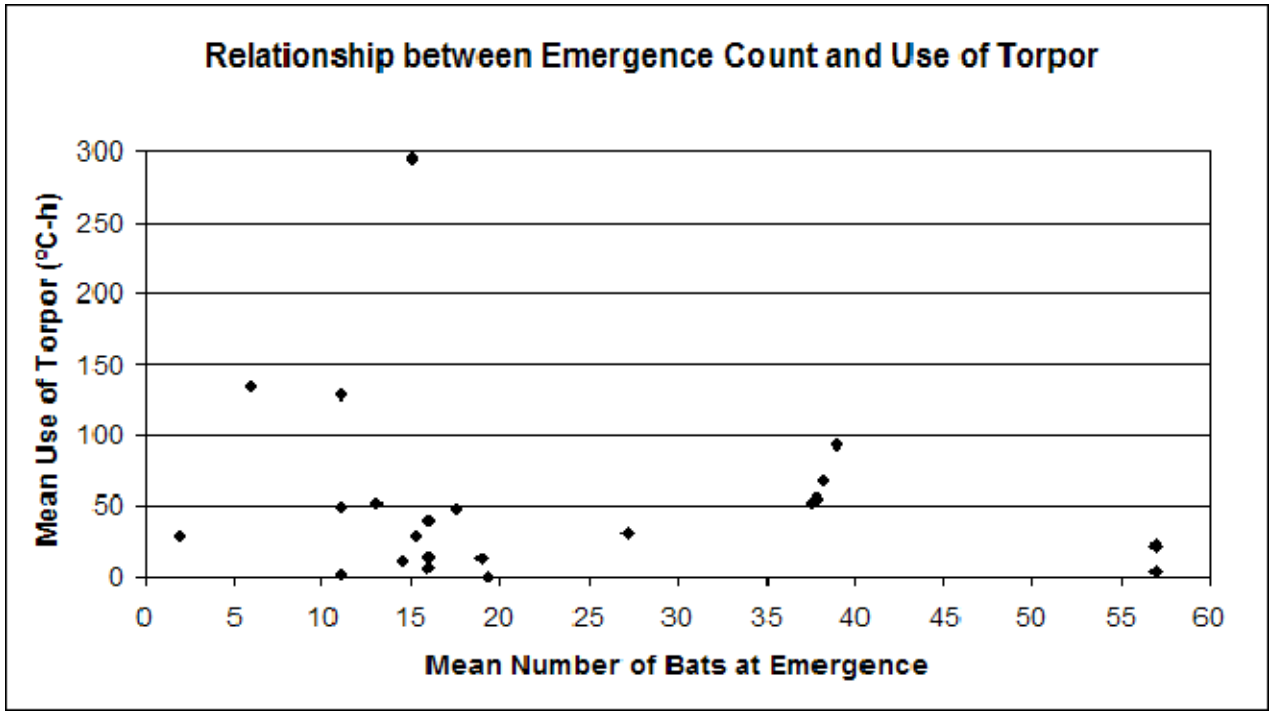


Figure 1.6.—Histogram of final times bats entered the day roost tree each morning.

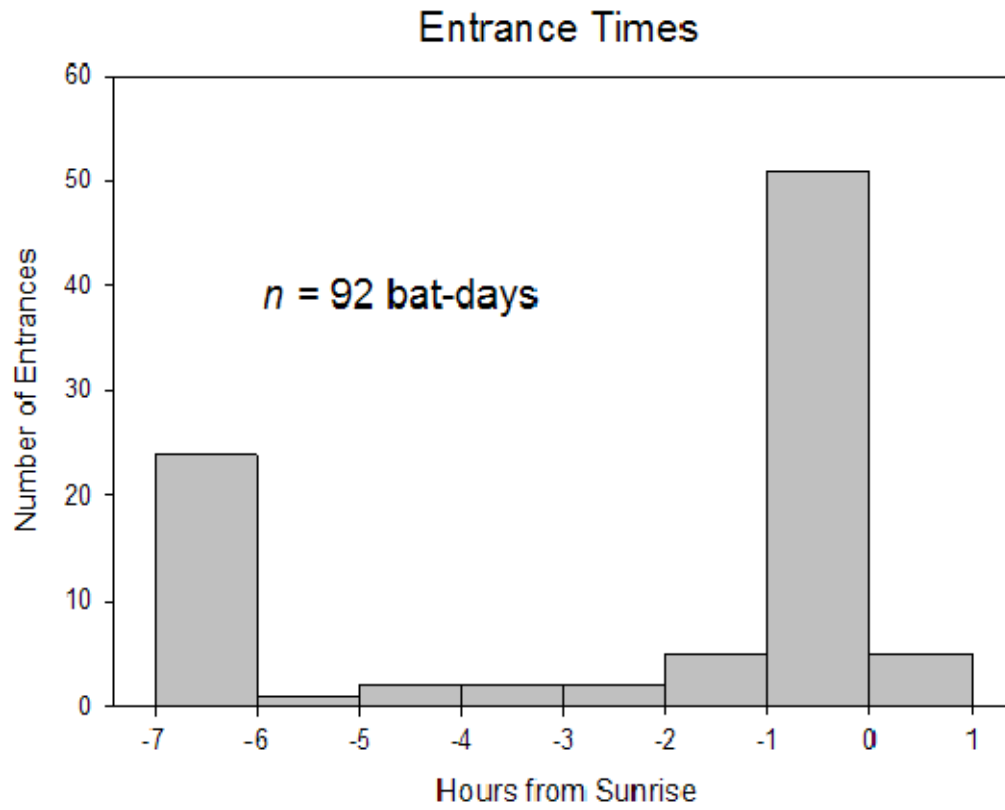
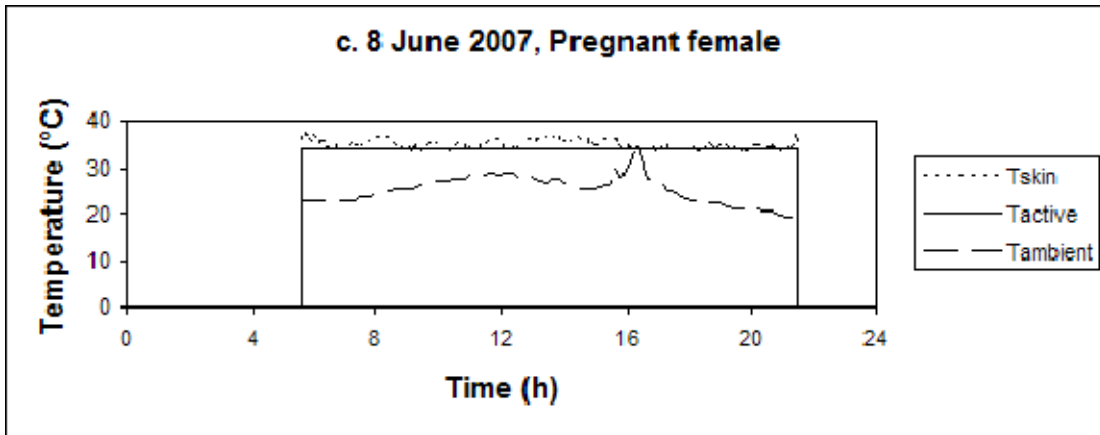
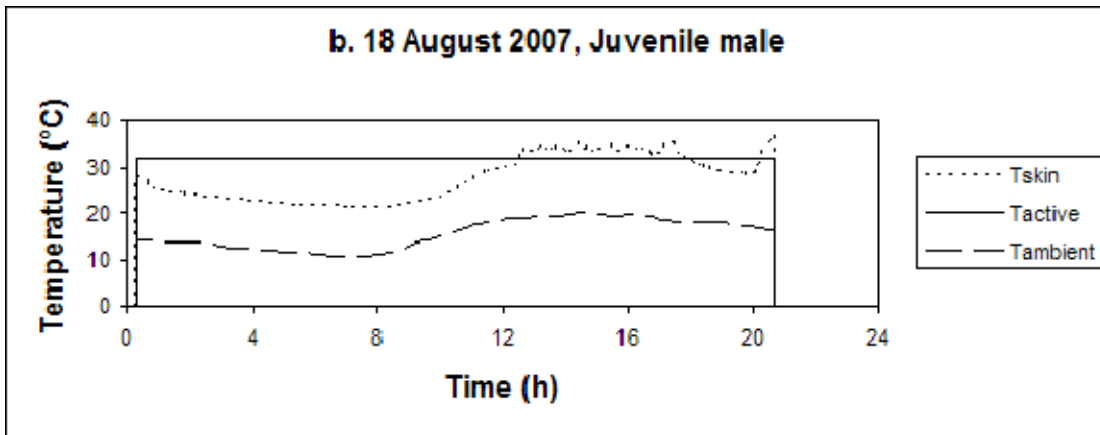
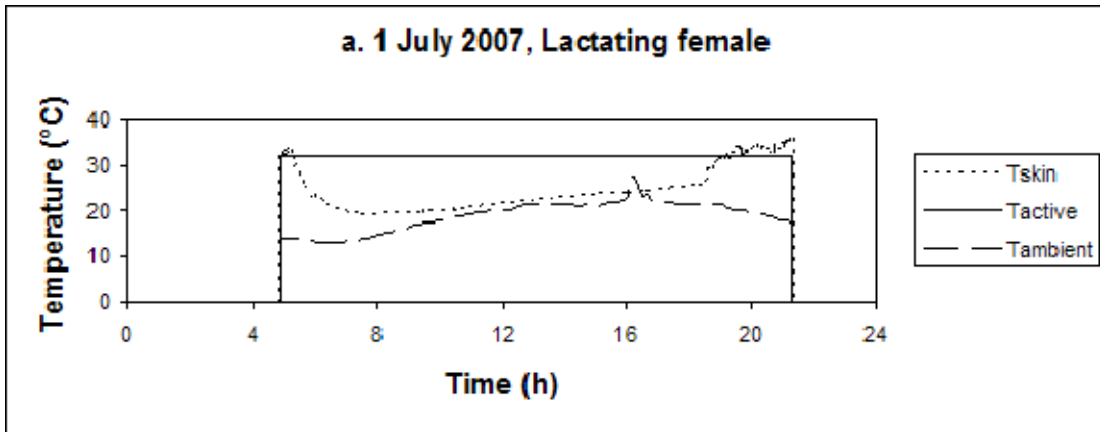


Figure 1.7a-c.—Representative patterns of torpor.



CHAPTER 2: NOCTURNAL ACTIVITY AND BEHAVIOR AT THE DAY ROOST

INTRODUCTION

Through natural selection, animals have evolved strategies to conserve energy, because conserving energy means that more energy is available for reproductive purposes (Shoener, 1971). According to optimal foraging theory, the most efficient foragers maximize energy consumed while minimizing feeding effort (Shoener, 1971; Stephens and Krebs, 1986). This feeding effort generally consists of energy used to search for and then handle food (Altringham, 1996). Individual condition and environmental conditions both affect the energetic needs of an animal and thus impact foraging strategy.

Another factor that animals must consider when searching for food is how to avoid becoming food themselves (Altringham, 1996). For many animals, any time that they leave a safe resting spot in search of food, they must behave in ways that minimize their risk of depredation. These behaviors can be both preventative, such as concentrating feeding into times of the day when predators are not active, and reactionary, such as rushing back to safety once predators are spotted.

Most insectivorous bats exhibit characteristic foraging and roosting patterns. Both optimal foraging theory and avoidance of predators have been used to explain when, where, and how often bats forage (Altringham, 1996). Near sunset, bats emerge from their day roost to search for insects and often rest at night for varying amounts of time between foraging bouts; night roosting, as it is called, can occur in the same structure that the bats used before sunset, a different roost that they will occupy the next day, or a separate night roost that they will abandon before sunrise (Ormsbee et al., 2007). If bats utilize the same day roost for consecutive days and food is available near the day roost, optimal foraging theory predicts that a bat should rest at the day roost between foraging bouts because doing so would require

the least energy. If food is not available near the day roost and a bat does not have pups to nurse, a separate night roost might be more efficient. The time that bats emerge from their roost is usually close to sunset, when abundance of food is still high yet predation risk is low (Sparks et al., 2000).

Understanding the behavior of bats at roosts, particularly tree roosts (Barclay and Kurta, 2007), and motivations behind these behaviors is crucial to conservation of these flying mammals. Ormsbee et al. (2007) recently surveyed the existing literature on night roosting in bats and note that many aspects of nocturnal behavior are still unknown. In this study, I used a video camera and an automatic scanning receiver-datalogger to record activity patterns and behaviors of a tree-roosting colony of evening bats (*Nycticeius humeralis*), a species that tends to forage closer to its day roost than other species (Duchamp et al., 2004). The goals of this study were to discover if individual condition, environmental conditions, or a combination of factors influence the behavior of these bats, and how evening bats at the northern edge of their range compare to other populations and species. I looked for evidence of bats interacting with each other at the roost entrance and identified other animals that utilized roost trees. I also described all behaviors observed and determined if certain behaviors were more common than others.

METHODS

Study species and location.—In August 2004, a maternity colony of evening bats was discovered in Palmyra Township, Lenawee Co., Michigan, which is the northernmost breeding colony of this species on the continent (Kurta et al., 2005). The evening bat is a small (6–12 g) insectivorous species that ranges from northern Mexico to southern Michigan (Watkins, 1972). These bats migrate seasonally, with adult males and females often separating for the summer (Watkins, 1972). In Palmyra Township, only adult females and juveniles are present during the breeding season. Most females give birth during June to twins that are weaned after ca. 6 weeks (Wilkinson, 1992). Though the evening bat roosts in both buildings and trees in other parts of its range (Wilkinson, 1992), members of the colony in Michigan invariably use trees, roosting either in cavities and crevices in trunks and major branches or under exfoliating bark (Kurta et al., 2005; Münzer, 2009).

Recording activity patterns and behavior.—Bats were captured, identified, and fitted with miniature radio transmitters, between May and August 2006 and 2007 (Chapter 1). During the morning after capture, bats were radio tracked to their day roosts, and the most likely emergence sites were determined for each tree. I then placed an automatic scanning receiver-datalogger (Model SRX 400A, Lotek Wireless, Inc., Ontario, Canada) near this tree to record presence or absence of a signal from up to 10 transmitters at predetermined intervals throughout the night. This receiver-logger allowed me to monitor the nocturnal activity patterns of individual bats at the roost tree.

I also video-recorded the emergence site from sunset to sunrise using a system modeled on one described by Rodrigues and Palmeirim (1995) that consisted of an infrared light, video camera, and recorder. Infrared lights are ideal for observing behavior of bats

because they illuminate areas without disturbing the animals (Boldogh et al., 2007). The 20-degree infrared light that I used (Model IRLamp6, Wildlife Engineering, Tuscon, Arizona) was field rugged. The light was designed to be powered by 12-V, sealed, lead-acid batteries and vented in back to prevent overheating. A 9-A-h battery sold with the light did not last through the night, but a 12-A-h battery provided the amount of power necessary. For a camera, I chose a black-and-white video camera (Model SSC-M383, Sony Electronics Inc., San Diego, California) that was very sensitive in low light. I paired the camera with a 100-Gb digital video recorder (Model AV500, with extended battery, Archos, Greenwood Village, Colorado). This recorder was replaced with another model (AV504) in the middle of 2007. The latter camera had less memory (30 Gb), but it was sufficient to record through the night because each hour of video only required ca. 1 Gb of memory.

The camera was elevated on a tripod on the ground. I placed the tripod within ca. 10 m of the base of a roost tree and focused the camera as closely as possible on the entrance to the roost. The camera usually was located ca. 15–20 m from the entrance to the roost and ca. 1–3 m² were visible in the field of view.

Bats of different species occasionally utilized the same day-roosting tree, although not on the same date (Stumpf, 2009). Thus, I am assuming that bats using a day-roosting tree as a night roost are usually the same species as well. Close-up views during certain nights of video anecdotally confirmed that the bats were in fact evening bats.

Analysis.—An evening bat has multiple day-roosting trees, and each bat switches between trees somewhat unpredictably throughout the season (Münzer, 2009). Consequently, absence of a bat on any given night could reflect the bat's normal pattern of being away from the day roost (foraging or night-roosting in another structure) or it could

reflect the fact that the bat had changed to a different day roost. To standardize my analysis, I examined data recorded by the receiver-logger or the video system only if the animal returned for the following day to the same tree that it had left at sunset. Behavior on any single night actually occurred on two calendar dates, one from sunset to midnight and another after midnight, but to simplify reporting, all nights are referred to in this chapter by the date when the night began.

After downloading files from the receiver-logger onto a computer, I graphed all data concerning presence/absence versus time of night. I defined a gap in signal presence to be any amount of time >10 min. Although arbitrary, a minimum duration of 10 min was similar to the sampling frequency used in other studies of activity patterns at bat roosts (Table 2.3). By this definition, trips away from the roost and visits to the roost each had to be >10 min to be counted. From these data, I was able to calculate emergence times, entrance times, number and duration of visits, and the percent of the night spent in the day roost. To calculate the latter, I defined the night as the time between sunset and sunrise.

Though all components were protected by weatherproof cases, I did not analyze video from nights with rain or high humidity because the quality of the image was too poor to observe behaviors. For the analysis, I wanted to focus on behaviors between emergence and final entrance because these behaviors have not been well-studied in tree-roosting bats, so I eliminated recordings from the hour following sunset and the hour prior to sunrise. I divided the remainder of the night into thirds, and labeled these periods as early, middle, and late. Then I randomly chose a 15-min sample of video from each period to analyze. To choose samples, I used the random number function in Excel (Microsoft, Redmond, Washington) to generate a number between zero and one. I multiplied this random number by the duration of

a nightly period (135.3–168.0 min) and then added this value to the start time of the nightly period to obtain the starting time of my 15-min sample.

An ethogram is “a set of comprehensive descriptions of the characteristic behavior patterns of a species,” and construction of an ethogram is the initial step in describing behavior of any species (Lehner, 1996:90). Ethograms are particularly useful when comparing behaviors of populations or species. I wanted to create a reference to help future studies distinguish between common and unusual behaviors in other populations of evening bats, as well as other tree-roosting species. To construct an ethogram, I recorded each behavior that I observed in the 15-min samples and the time at which it occurred. I did not include bats that flew past the far side of the tree, because these distant bats were not seen clearly and might have been a different species, and because this area was not always visible. Following Lausen and Barclay (2003), I defined reproductive periods by the reproductive condition of the majority of adult females that were captured as part of other studies (Chapter 1; Münzer, 2009). For my study, pregnancy lasted from 3 to 23 June; lactation, from 24 June to 27 July, and post-lactation, from 28 July to 22 August.

To document patterns of activity, I counted the number of nightly periods that I observed any activity by bats during each 15-min sample. To document behaviors, I constructed an ethogram, listing and describing all behaviors. I used continuous individual recording to code all behaviors and amount of time performing each behavior (Martin and Bateson, 1993). Each behavior was brief, not lasting >1 s, so for the purpose of time-budget analyses, I considered the duration of each behavior to be 1 s.

Statistics.—Entrance and emergence times were graphed in Excel to look for patterns and outliers. I used one-way analysis of variance, with data transformed as necessary to meet

the assumptions of normality, to look for differences among reproductive groups in mean time of entrance, number and length of visits, and percent of the night in the roost. A chi-squared test was used to look for significant differences in activity patterns and behaviors. Chi-squared values and means were calculated using Excel, with probabilities obtained from Zar (1999). All other statistical analyses were done using Systat 11 (Systat Software Inc., Richmond, California). When looking at the population as a whole (e.g., time of emergence), I included all bat-nights in my analysis ($n = 94$ bat-nights, unless indicated otherwise). When looking at differences among groups, however, I calculated a mean value for each bat ($n = 27$ bats, unless indicated otherwise) to maintain statistical independence. Means are presented $\pm 1 SD$.

RESULTS

Sample size.—Using the receiver-logger, I recorded data on presence/absence on 65 different calendar-nights for a total of 94 bat-nights. Each bat-night represented data on one bat that was recorded from sunset to sunrise, and multiple bat-nights were often recorded on the same calendar-night. Nine of the bats were pregnant, six were lactating, and three were post-lactating; eight were juveniles, and one was of unknown age.

Times of emergence and entrance.—On all but four of the 94 bat-nights, bats emerged from their day roost within 1 h after sunset (Fig. 2.1). On one occasion, two bats did not emerge for the first time until close to sunrise, and on two occasions, the same bat (a juvenile male) never left, though he emerged on subsequent nights. These unusual emergences coincided with low ambient temperature and/or precipitation, as described later. The 2 bat-nights that the juvenile male never left were not included in calculating the duration of first flights away from the roost, the number of trips away from the roost each night, total time away from the roost each night, or final entrance times. Thus, my sample size for these analyses was 92 rather than 94 bat-nights.

The first trip away from the roost lasted 1.5 ± 1.5 h. Bats left the roost 2.5 ± 1.2 times each night (range: 1–6 trips), for a total of 2.4 ± 1.9 h away from the roost. Final entrance times were much more haphazard (-2.6 ± 3.3 h from sunrise), and ranged from ca. 8.6 h before sunrise to 0.8 h after sunrise, with three main clumps at the beginning, middle, and end of the night, respectively (Fig. 2.1). However, most (59 of 92 or 64.1%) final entrances were within 2 h of sunrise, including those that occurred after sunrise, and 55 (59.8%) entrances occurred within 1 h of sunrise. Pregnant, post-lactating, and juvenile bats returned to the roost for the last time throughout the night, but lactating bats did so either within 2 h of

sunset (>7 h before sunrise) or within 1.5 h of sunrise (Fig. 2.1). Relative to sunrise, juveniles had the earliest final entrance (4.0 ± 3.2 h before sunrise; Figure 2.2), whereas post-lactating bats had the latest final entrance (1.3 ± 1.9 h before sunrise). However, there was no significant difference in mean entrance time among pregnant, lactating, post-lactating, and juvenile bats ($F_{3, 22} = 1.79$, $P = 0.18$).

Number and duration of visits.—Evening bats returned to the roost 1.5 ± 1.2 times between first emergence and final entrance. The mean number of visits each night did not differ among reproductive groups ($F_{3, 22} = 0.91$, $P = 0.45$; Fig. 2.3), but mean duration of a visit did vary ($F_{3, 22} = 3.14$, $P = 0.046$; Fig. 2.4). Lactating bats had the longest mean duration of visit (3.5 ± 1.9 h), and visits by post-lactating bats had the shortest duration (0.9 ± 0.8 h), although a Tukey post-hoc test failed to differentiate these groups.

Duration of night varied seasonally, so I also examined duration of visits in terms of the proportion of the entire night that bats night-roosted in a tree. There was a significant difference among groups in percent of the night that was spent in the day roost ($F_{3, 22} = 4.0$, $P = 0.02$; Fig. 2.5). A Tukey test showed significant differences in the proportion of the night that lactating and post-lactating bats spent in the roost each night ($80.0 \pm 7.7\%$ and $43.3 \pm 33.4\%$ of time from sunset to sunrise, respectively).

Environmental conditions on nights with unusual activity patterns.—Bats did not leave or left for the first time just before sunrise on only 2 calendar-nights. On 21 July 2007, a male juvenile (bat 099) never emerged, though three other bats roosting in the same tree (a lactating female, female juvenile, and female of unknown reproductive condition) emerged within 30 min of sunset. This male juvenile (099) also did not leave the roost on the night of 26 July 2007. On this night, two other radio-tagged bats in the roost, a lactating female and a

female juvenile, did not depart until 0553 and 0544 h, respectively, though a fourth bat (the female of unknown reproductive condition) departed from the roost 45 min after sunset.

The night of 21 July 2007 had the third lowest mean nocturnal temperature (Chapter 1) of all nights; mean temperature from sunset to sunrise was 14.1°C, compared with 18.3 ± 3.0°C for nights overall). Ambient temperature dropped to 10.8°C in the early hours of 22 July, and evening bats, like most other bat species, do not usually forage below 10°C (Watkins, 1972). The night of 26 July 2007 was warmer, with a mean nocturnal temperature of 18.6°C and a minimum temperature of 17.7°C close to midnight. Although there was no rain on the night of 21 July, 12 cm of rain fell on the night of 26 July, the most precipitation of any night. Between sunset on 26 July and sunrise on 27 July, rain fell during 31% of the night.

Ethogram, frequency of behaviors, and other observations.—I analyzed data from 22 calendar-nights of video recorded at eight different roost trees. Three of these nights were recorded in August 2006, and the rest were recorded from May to August 2007. Four nights of behavior were recorded during pregnancy; 12, during lactation; and six, during post-lactation.

I recorded seven different behaviors exhibited by evening bats at the entrance to the roost at night (Table 2.1). Most behaviors that I observed seemed associated with entering or emerging from the roost, rather than clinging to or crawling on the tree outside the roost. The most common behaviors that I observed were what I defined as pass, dip, land, and take-off (Table 2.2, Fig. 2.6). These behaviors often were part of a sequence, with multiple passes, dips, and lands, and then the bat either left the area or entered the roost. The least common

behavior was crawl. After bats landed on a tree, they almost always resumed flight or entered the roost immediately after landing.

On 30 June and 11 and 12 July 2007, during lactation, I observed behaviors that indicated possible interactions between bats that might have included following others to roosts on 57 occasions. One bat would fly by the roost entrance, and then another would be visible in the screen flying directly behind and at the same angle as the first bat. Alternately, one bat would land on the tree, often after repeatedly passing the entrance to the roost with another bat following, and then the second bat would land on the tree and enter the roost just after the first bat.

Anecdotal observations of other animals at the roost.—Bats were not the only animals observed near roost entrances. Spiders, ants, and other invertebrates were often seen crawling on the tree, and moths, lightning beetles, and other insects were often seen flying by. While watching evening emergence at a roost in May 2006, I observed a young raccoon climbing in a branch of the roost tree, though always at least a few meters from the entrance. I again observed a raccoon in video recorded during August 2007, though this was not one of the nights that I analyzed. This raccoon also did not venture closer than a few meters from the roost entrance. Though I did not observe any raccoons directly interacting with a roost entrance or evening bat, raccoons are known to be potential predators (Sparks et al., 2003).

The only other non-bat vertebrates in the video that I analyzed were mice. According to their appearance, known range, and nesting habits, the mice were most likely white-footed mice (*Peromyscus leucopus*—Kurta, 1995). I saw mice near roost entrances during 3 nights at three separate trees. All three trees had large scars with small cavities along the edges of the scar. The first mouse I observed on video was on roost tree 116 at 2305 h on 21 August

2006. The mouse was visible for ca. 10 sec. During this time, it ran to the roost entrance, turned around, ran from the entrance, then back to the entrance, then left. When the mouse was near the roost entrance, it sniffed the air, perhaps checking whether anything was inside the roost. The second mouse was observed on roost tree 106 at 0106 h on 20 July 2007. This mouse ran down the tree and was visible only long enough to be identified. The final mouse that I saw was on roost tree 150 at 0431 h on 1 August 2007. This mouse ran along the scar and was visible for a total of ca. 90 seconds. In addition to mice recorded by the camera, I observed mice on two other occasions while watching evening emergence at roost tree 106 and roost tree 150.

DISCUSSION

My results suggest that reproductive condition impacts activity patterns and behavior of evening bats in Michigan. The duration of each nocturnal visit and proportion of the night spent in the day roost showed significant differences among reproductive groups, with lactating bats spending a greater proportion of the night in the roost than post-lactating bats. However, mean number of visits did not differ among reproductive or age groups. Perhaps length of each visit and proportion of the night in the roost are more important to evening bats in maximizing opportunities for both foraging and care of offspring.

My results also support the concept of the ambient environment influencing activity patterns, because bats did not forage, or foraged little, on the night of 21 July 2007, when temperatures dropped close to 10.0°C, and on the night of 26 July 2007, when 12 cm of precipitation fell. Ambient temperature appears to explain why bat 099 did not emerge on the night of 21 July, and precipitation appears to explain abnormal emergence patterns of bat 009 and two other individuals on 26 July. Bat 099 weighed only 7 g when captured, the lowest body mass of all 27 bats in my study. His forearm length was also the shortest at 32 mm, and the shortest forearm of any volant juvenile caught in Michigan was only 31 mm. Bat 099 likely was the youngest bat in my sample and probably an inexperienced forager, which may have influenced his activity.

Other studies have found that individual evening bats utilized numerous day-roosting trees that typically are only 687 m apart (Münzer, 2009), and evening bats foraged in more condensed areas than similar species, such as big brown bats (Duchamp et al., 2004). Evening bats in Indiana did not use an alternate night roost before returning to their day roost after the first foraging flight (Duchamp et. al., 2004), and foraging evening bats marked with

light tags did not venture far from their site of capture in Missouri (LaVal et al., 1977).

Duchamp et al. (2004) suggested that evening bats are poorer flyers than many other species due to their higher wing loading. My bats spent very little time outside the roost, which also suggests that they foraged close to their roosts and traveled only short distances between day-roosting trees.

I found evidence of possible following behavior around the time that juveniles were about to fly. Video images of two bats flying in the same direction and entering the roost in close succession could have been bats following each other. Vaughan and O'Shea (1976) noted that pallid bats (*Antrozous pallidus*) tended to enter roosts in pairs or groups when juveniles had just become volant (from late June to early July), and Brigham and Brigham (1989) described a mother big brown bat and her single offspring consistently foraging and roosting close to one another, suggesting that youngsters were learning from their mothers. Juveniles, however, were not volant when I recorded apparent following behavior in evening bats, so mother-offspring interactions can not explain my observations. Juvenile evening bats in Missouri followed adults to alternate roosts when excluded from a building (Wilkinson, 1992), and evening bats in Michigan changed trees frequently, every 2.9 days (Münzer, 2009); perhaps my observations of following behavior represented adults leading (or being followed by) other adults to a different roost. Nevertheless, the reason that this behavior occurred only between 30 June and 12 July is unknown, though following behavior might have occurred on other dates or times on the video that I did not watch.

Although I did not observe white-footed mice attacking evening bats, these rodents were observed five times, on video or through personal observation, close to the entrance to roosts of evening bats and may represent potential predators or competitors. The omnivorous

white-footed mouse and the closely-related deer mouse (*Peromyscus maniculatus*) are known to feed occasionally on *Myotis* (Fenton, 1970; Hitchcock, 1965; Sparks et al., 2000), and because evening bats are only slightly larger than *Myotis* (Barbour and Davies, 1969; Kurta, 1995), predation by these mice seems feasible. In addition, the white-footed mouse often nests in tree cavities and may be a potential competitor of evening bats for suitable roosting/nesting sites. Dolan and Carter (1977) mentioned that southern flying squirrels (*Glaucomys volans*) occasionally built their own nest after evicting songbirds from a tree cavity, and Vaughan and O'Shea (1976) found fecal evidence of cactus mice (*Peromyscus eremicus*) and wood rats (*Neotoma albigula*), living in former bat roosts.

Several previous studies looked at nocturnal activity patterns in bats (Table 2.3). Similar to my results, lactating evening bats in Indiana spent less time away from the roost than post-lactating bats each night (Clem, 1993). Although evening bats overall did not typically spend >200 min outside the day roost at night (Clem, 1993; Wilkinson, 1992; this study), greater mouse-eared bats (*Myotis myotis*), Hodgson's bats (*Myotis formosus*), long-tailed bats (*Chalinolobus tuberculatus*), and Indiana bats (*Myotis sodalis*) spent >300 min outside the roost each night (Audet, 1990; Murry and Kurta, 2004; O'Donnell, 2002; Shen and Lee, 2000), perhaps due to larger foraging areas.

Lactating evening bats in Indiana and Missouri left the roost more often than pregnant bats, which usually foraged only once per night (Clem 1993; Duchamp et al, 2004; Wilkinson, 1992). However, I did not find significant differences between pregnant and lactating bats in the number of trips away from the roost each night. In contrast to evening bats, both pregnant and lactating big brown bats (*Eptesicus fuscus*) did not leave the roost after returning from initial foraging flights (Duchamp et al., 2004) and, at the other end of the

spectrum, long-tailed bats of different reproductive conditions showed a mean of four active periods each night (O'Donnell, 2002). In greater mouse-eared bats, Hodgson's bats, and little brown bats, lactating females returned to the roost more often than pregnant individuals, presumably to feed pups, and thus showed a greater number of trips away from the roost than pregnant bats (Audet et al., 1990; Henry et al., 2002; Lee and Shen, 2000). Indiana bats in Michigan are similar to evening bats in Michigan and foraged about 2.5 times each night overall. Durations of first trips away from the roost were similar for tree-roosting evening bats in Michigan and Indiana (ca. 90 min), though they were considerably shorter than those of Hodgson's bats (148 ± 49.4 min in 1st week after parturition, then increasing in duration—Shen and Lee, 2000), long-tailed bats (140 min—O'Donnell, 2002), and big brown bats (135 ± 29.8 min—Duchamp et al., 2004).

Most quantitative descriptions of behavior by bats are related to activities at the day roost (Burnett and August, 1981; Codd et al., 2003; Munoz-Romo, 2006; Winchell and Kunz, 1996), and published accounts containing nocturnal time budgets are mainly for bats living in buildings (Anthony et al., 1982; Barclay, 1982; Shen and Lee, 2000) and mines (Fleming et al., 1998). To the best of my knowledge, my study includes the first ethogram of nocturnal behavior in tree-roosting bats. The passing, dipping, and landing behaviors that I observed throughout the night match the descriptions of checking behavior in pallid bats returning to cliff roosts close to sunrise, though the frequencies of these behaviors were not quantified (Vaughan and O'Shea, 1976). Vaughan and O'Shea (1976) suggested that the function of this behavior was to determine whether a roost was safe by identifying familiar scents. Because tree roosts are often small and narrow, these behaviors might also be multiple attempts of bats trying to enter narrow spaces, particularly pregnant bats with additional weight to carry

or juvenile bats just learning to fly (Barclay, 1982). Despite tree roosts being difficult to enter, evening bats did not crawl along the outside of the tree very often or for very long. Crawling was also the least-common behavior observed inside a building roost of eastern pipistrelles (*Perimyotis subflavus*—Winchell and Kunz, 1996). Perhaps crawling is an awkward movement for bats that makes them vulnerable to predation or injury.

Activity patterns and behaviors of evening bats in Michigan were generally similar to those of other species. Evening bats consistently emerged close to sunset and left and re-entered the roost most often during the first third of the night. Emergence times close to sunset are common among bats and tend to correlate more with time of sunset than other environmental variables, such as temperature (Viele et al., 2002). Greatest activity by bats, including the evening bat, early in the night likely occurs because insect abundance is near its daily peak during this time, while predation risk from many aerial predators, such as hawks, is minimal (Duverge et al., 2000).

Evening bats left their roost very late or not at all in apparent response to low ambient temperatures and rain, which also was similar to the behavior of other species. For example, on windy nights with minimum temperatures below 13°C, black mastiff bats (*Molossus ater*) often did not leave the roost to forage (Fenton et al., 1998). Rain and low ambient temperatures reduced the number of flying insects, making it energetically prudent to remain in the roost (Ormsbee et al., 2007).

Results from this study and previous studies support the idea that evening bats most likely forage near their day roosts. These bats prefer roosting and foraging areas with smaller amounts of urban development more so than similar species such as big brown bats, which tend to thrive around human-dominated landscapes (Duchamp et al., 2004). Because

behavior can influence success in a given habitat, effective conservation and management plans require information about many aspects of a species' life history, which include ecology, physiology, and behavior.

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Table 2.1.—Ethogram of nocturnal behaviors by evening bats at roost trees.

Behavior	Number	Description
Pass	1	Fly by roost entrance side of tree
Take Off	2	Fly off tree
Dip	3	Between pass and land
Land	4	Land on tree
Crawl	5	Crawl along tree
Emerge	6	Emerge from roost entrance
Enter	7	Enter roost entrance

Table 2.2.—Frequency of nocturnal behaviors (described in Table 2.1) by evening bats at roost trees overall, by nightly period, and by reproductive period.

Period	Behavior (number of observations)								Statistics		
	Pass	Take-off	Dip	Land	Crawl	Emerge	Enter	All	X^2	df	P
Nocturnal period											
Early	80	51	52	82	17	9	41	332	521.3	6	<0.001
Middle	69	44	51	46	8	15	17	250	85.8	6	<0.001
Late	60	78	123	68	14	31	22	396	153.4	6	<0.001
Reproductive period											
Pregnancy	11	12	4	14	4	3	5	53	16.6	6	<0.025
Lactation	128	101	174	117	21	40	58	639	193.1	6	<0.001
Post-lactation	70	60	48	65	14	12	17	286	97.2	6	<0.001
Total	209	173	226	196	39	55	80	978	267.7	6	<0.001

Table 2.3—Comparison of nocturnal activity patterns in populations of bats that include reproductive females. Species are evening bats unless indicated otherwise. All error terms converted to ± 1 *SD*. If three means are listed, then values are for pregnant, lactating, and post-lactating bats, respectively.

Species, reference	Location (roost type), sample size	Sampling effort	Time away from day roost from sunset to sunrise	Trips away from day roost per night	Duration of first trip away from day roost
This study	Michigan (trees), 27 bats	Continuous at roost	71.7 \pm 49.5, 123.6 \pm 54.7, and 209.0 \pm 135.8 min (144 \pm 114 min for all bats)	1.7 \pm 0.8, 2.6 \pm 0.9, and 2.7 \pm 1.0 (2.5 \pm 1.2 for all bats)	90 \pm 90 min
Clem, 1993	Indiana (buildings), 19 bats	Continuous at roost	78.3 \pm 35.0, 107.2 \pm 43.4, and 127.4 \pm 43.7 min	1.0, 1.3, and 1.0	
Duchamp et al., 2004	Indiana (trees), 11 bats	Every 3–30 min for first third of night		Only lactating bats left after first flight	94 \pm 19.2 min
Wilkinson, 1992	Missouri (buildings), 105 nights	Continuous at roost	100–300 min	one foraging trip by pregnant bats, >3 by lactating bats	
Greater mouse-eared bat (<i>Myotis myotis</i>); Audet, 1990	Germany (buildings), 27 bats	Continuous	387 \pm 32.5, 301.4 \pm 64.7, 306 min	More trips by lactating bats than pregnant bats	
Big brown bat (<i>Eptesicus fuscus</i>); Duchamp et al., 2004	Indiana (buildings), 11 bats	Every 3–30 min for first third of night		No foraging flights detected in 2 hours after returning from first foraging flight	135 \pm 29.8 min
Little brown bat (<i>Myotis lucifugus</i>);	Canada (buildings), 28	Every 15 min		More trips by lactating bats than	

Henry et al., 2002	bats			pregnant bats	
Indiana bat (<i>Myotis sodalis</i>); Murry and Kurta, 2004	Michigan (trees), 12 bats	Every 10– 30 min	375 ± 55.4 min in flight	2.5 ± 1.4 foraging bouts	
Long-tailed bat (<i>Chalinolobus tuberculatus</i>); O'Donnell, 2002	New Zealand (trees), 37 bats	Continuous	354 ± 64.5 min active	4 ± 1.2 active periods	Approximately 140 min for first foraging flight, then progressively shorter
Hodgson's bat (<i>Myotis formosus</i>); Shen and Lee, 2000	Taiwan (buildings), 15 bats	Continuous	563.9 ± 47.3 min before parturition, 401.8 ± 46.2 to 553.8 ± 23.6 min from 1 st to 4 th week after parturition	One trip before parturition, 2–4 trips after parturition	148.0 ± 49.4 min to 447.7 ± 100.7 min from 1 st to 4 th week after parturition

Figure 2.1.—Times of first emergence and final entrance for all 92 bat-nights that bats emerged. Emergences are indicated by triangles; entrances are shown by X's.

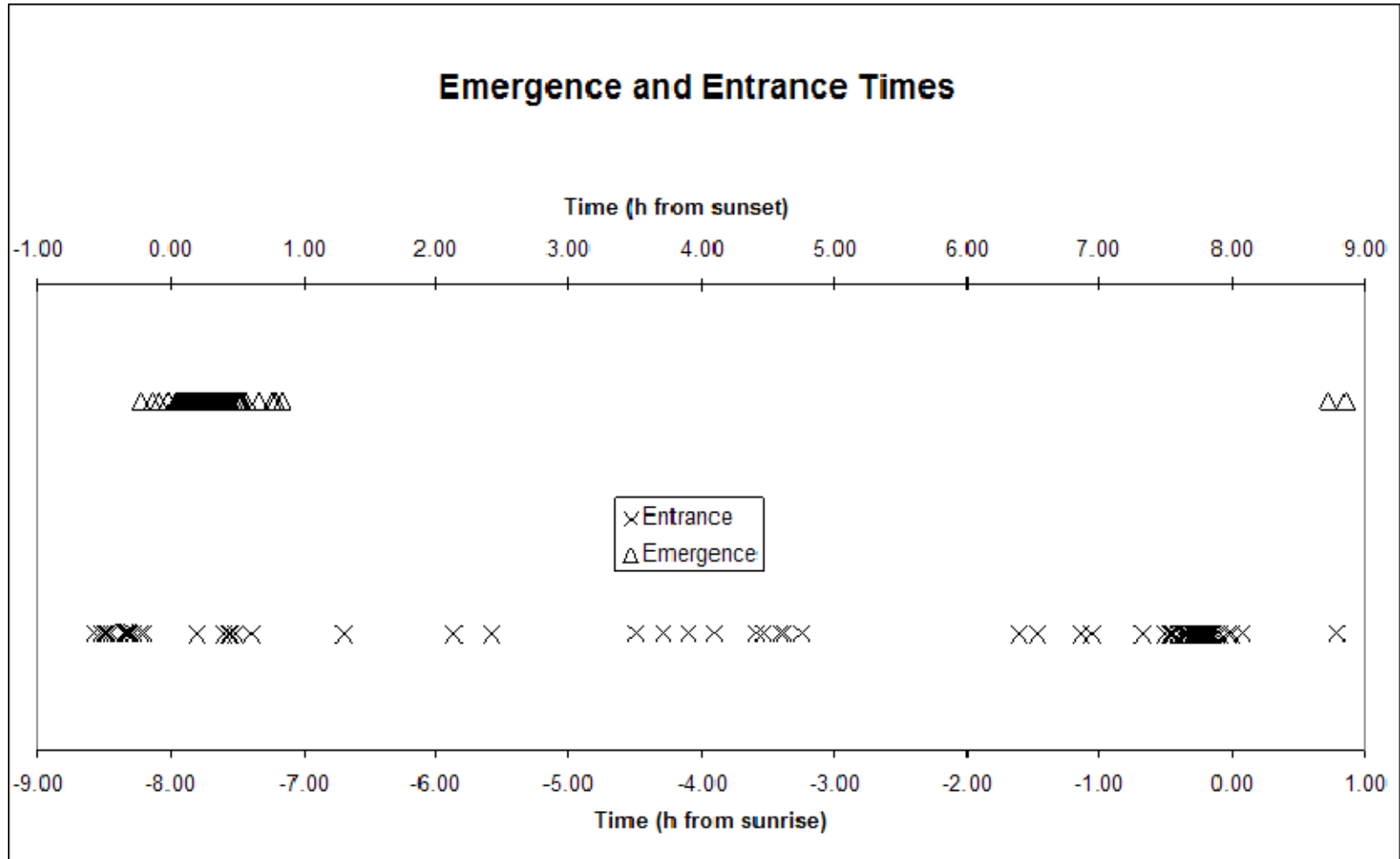


Figure 2.2.— Final entrance times for individuals and groups. Groups are pregnant (PG), lactating (LA), post-lactating (PL) females, and juveniles (J).

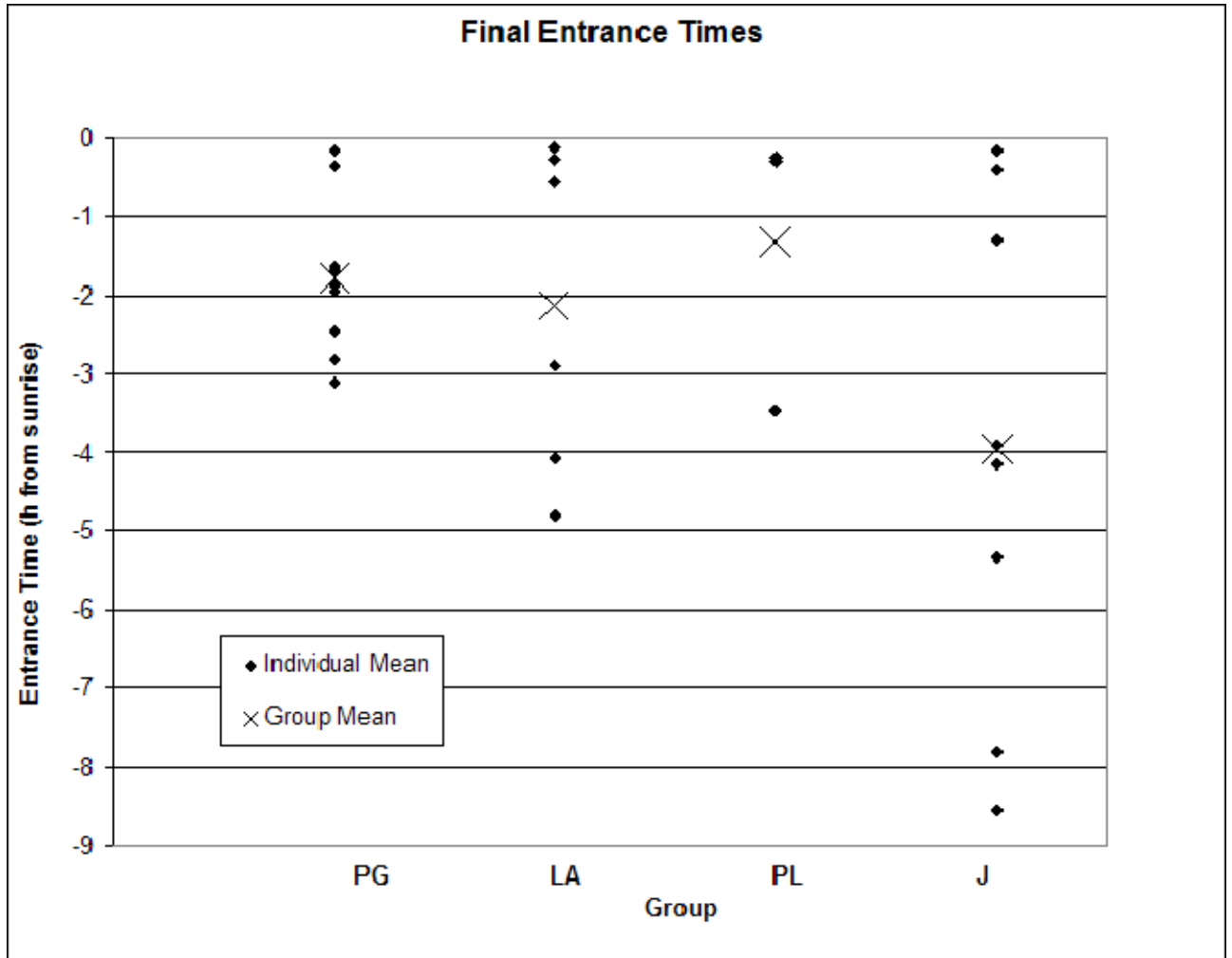


Figure 2.3.—Number of visits to the roost between first emergence and final entrance presented for both individuals and groups.

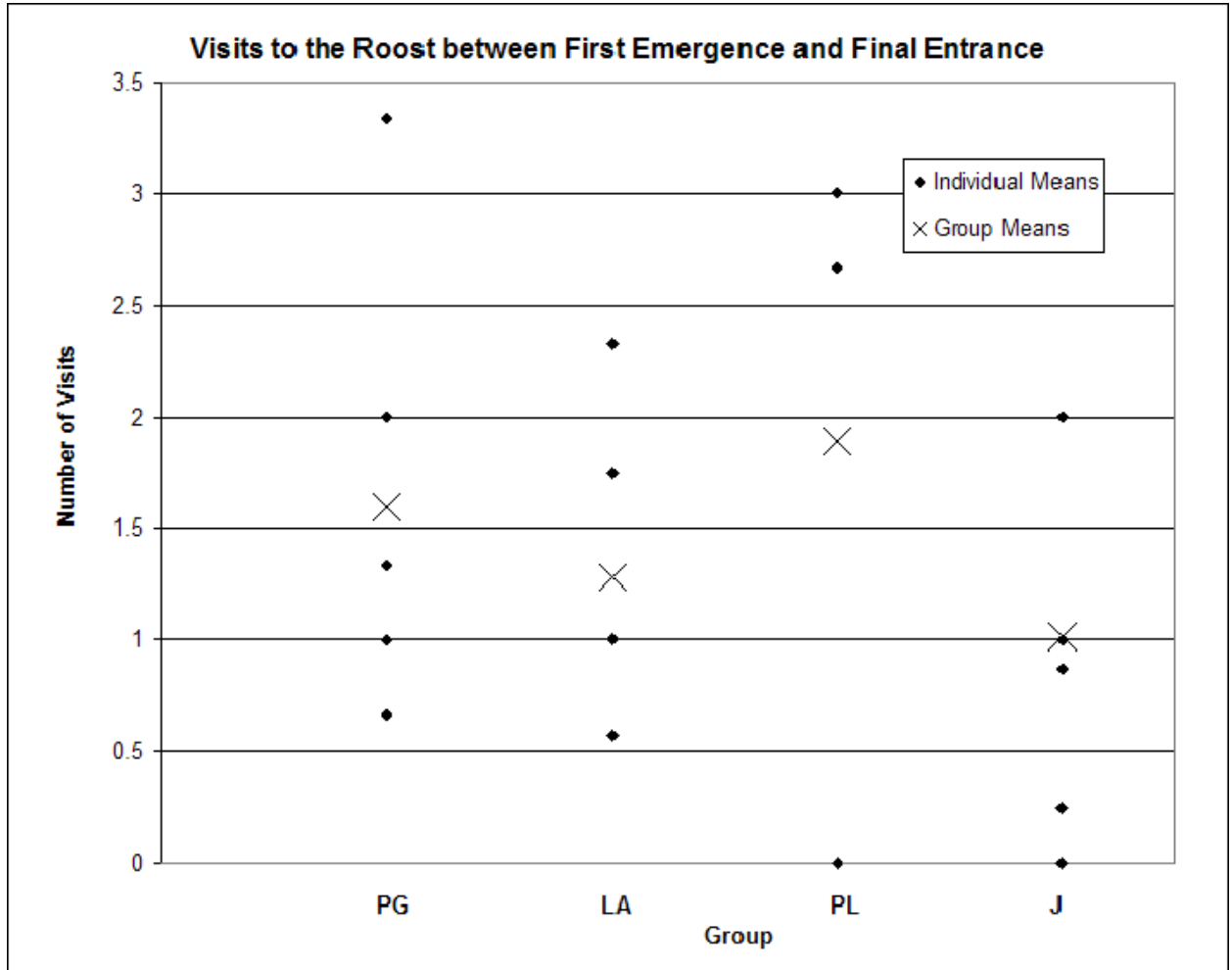


Figure 2.4.—Duration of visits to the roost for individuals and groups.

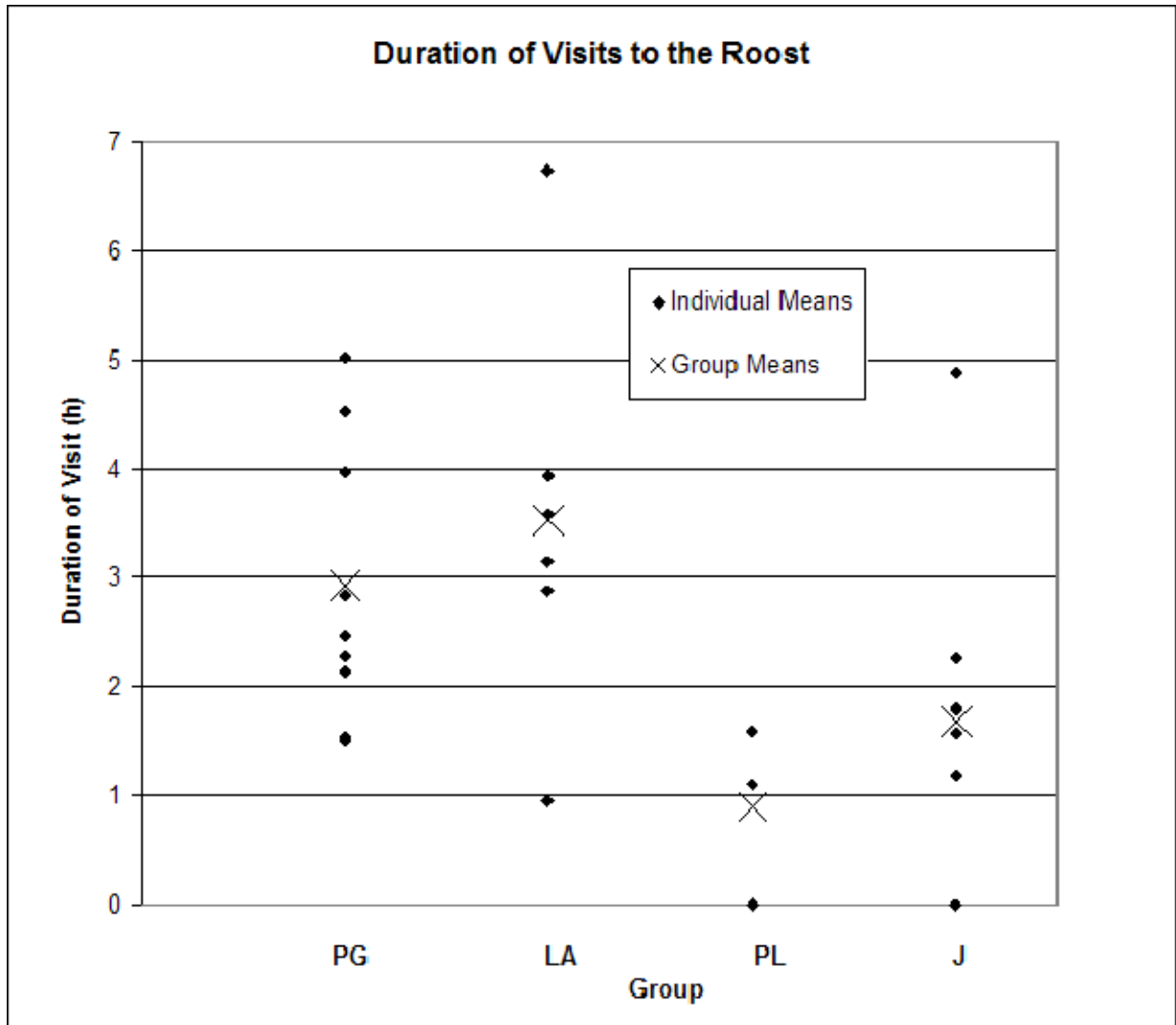


Figure 2.5.—Proportion of the night spent in the roost for individuals and groups.

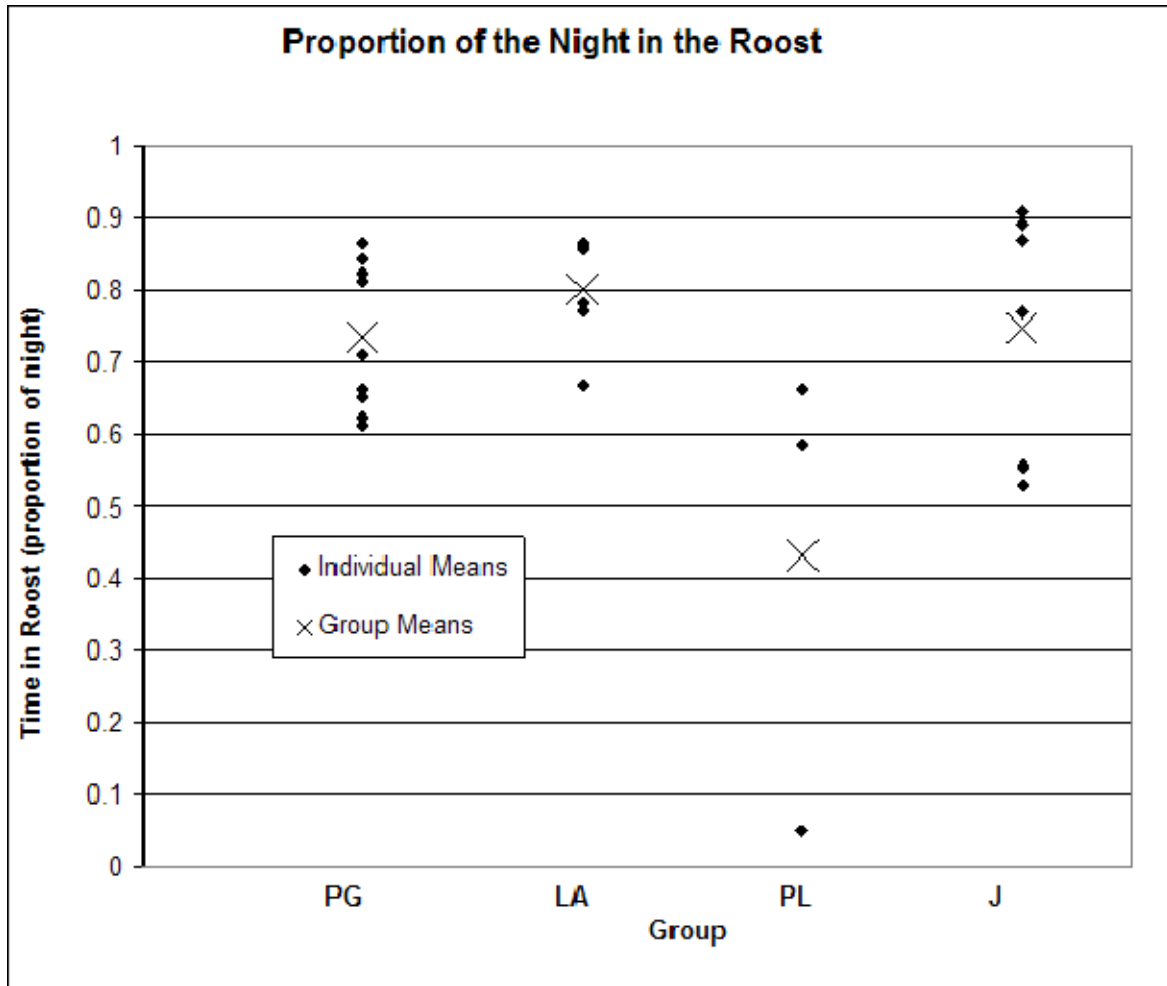


Figure 2.6.—All behaviors listed by time each behavior was observed. Number 1 is pass, 2 is take-off, 3 is dip, 4 is land, 5 is crawl, 6 is emerge, and 7 is enter. Behaviors are described in Table 2.1.

