ROOST ECOLOGY OF EASTERN SMALL-FOOTED BATS (*MYOTIS LEIBII*) IN THE SOUTHERN APPALACHIAN MOUNTAINS

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ABSTRACT

The eastern small-footed bat (*Myotis leibii*) is a rarely encountered species that has experienced declines in its populations and is currently being petitioned for federal listing. Throughout most of its range, *M. leibii* roost in rock fields and talus slopes with low canopy cover and high solar exposure. *M. leibii* also use man-made structures, such as buildings and bridges, as roost sites. However, we know little about roost characteristics in the southern portion of its range. Therefore, in summers 2011 and 2012, we studied a male-dominated, bridge-roosting population of *M. leibii* in the Southern Appalachian Mountains to document characteristics of their natural and man-made roosts and movement capabilities. I tracked 20 individuals via radio telemetry and found 15 rock or rock-like roosts and 2 tree roosts. Male and female *M. leibii* roosted in similar structures that were mostly large, south-facing rock expanses. Individuals had long continuous residency times and made long distance movements between roosts.

I also observed individuals within the bridge crevices to examine whether individuals chose particular crevices within the bridges, whether this was associated with temperature, and whether individuals associated with one another within the crevices. I PIT-tagged 44 bats for individual identification to be able to test whether associations were related to sex, reproductive condition, or genetic relatedness. I recorded a total of 842 "bat observations" and 53 instances of associations between 17 May – 26 September 2012. Bats chose particular crevices within each bridge, which seemed to be associated with particular micro-temperatures; however, this trend

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was not verified statistically. Bats very rarely associated with one another, and the associations that were observed were not related to genetic relatedness. These data illustrate the importance of rocky habitat with at least some solar exposure and demonstrate the impact human development is having on this species by creating a variety of roost habitat. They may also help managers understand the thermal and spatial requirements of *M. leibii* when creating artificial roosts, such as bridges. These data, when combined with similar data, will be important for the creation of a range-wide management plan for *M. leibii*.

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CHAPTER 1

ROOST CHARACTERISTICS AND MOVEMENTS OF MYOTIS LEIBII

Introduction

Research on bat ecology, management, and behavior has been rare, but significant strides have been made in the past 2 decades. Recently we have shifted our focus to trying to understand how bats interact with forested environments and how to manage forests to conserve bats (Brigham 2007). Roosts are important to bats for shelter, protection from predators, as well as a place to mate, raise young, and interact with other individuals (Brigham 2007). Selection of roosts and the movements among them has received more attention than all other questions concerning bats in forests combined (Hayes 2003, Kunz and Lumsden 2003, Miller et al. 2003), but because roosts are generally inaccessible, little is known about the characteristics and why bats select, and move among, certain roosts (Kunz 1982, Nagorsen and Brigham 1993). Roost switching behavior is important to understand because managers need to conserve entire forested areas for bats, not just single roost sites (Brigham 2007). However, studies on roost selection and switching have been limited by technology, logistics, costs, and sample sizes (Barclay and Kurta 2007). Furthermore, there is no universal definition of a roost.

Most studies on roost selection and switching have been conducted on tree-roosting bats (e.g., Brigham 1991, Betts 1995, Kalcounis 1995, Vonhof 1995, Willis and Brigham 2004),

while fewer studies have focused on rock-roosting bat populations of any species (e.g., Tuttle and Heaney 1974, Trune and Slobodchikoff 1976, Vaughan and O'Shea 1976, Lewis 1996, Chruszcz and Barclay 2002). Bats choose rock roosts based on conductive properties, distance to the ground (Lausen and Barclay 2002), aspect, distance to water, and distance to road (Johnson et al. 2011), among many other features, but preferred roost characters vary by bat species and geographical location. Some roosts may be chosen for reduced predation risk or commuting costs, but roost microclimate and its impact on thermoregulation is thought to be the primary factor in roost selection (Barclay and Kurta 2007), especially to bats roosting in buildings, bridges, or rock crevices (Ormsbee et al. 2007).

Roost selection is thought to be more critical for reproductive females than for males and non-reproductive females, as reproductive individuals need to select roosts to minimize thermoregulatory and commuting costs (Barclay and Kurta 2007). The availability of suitable roosts for females is more restricted than for males (Crampton and Barclay 1998, Vonhof and Barclay 1996). Therefore, most studies on roost selection have focused on reproductive females or combined data for males and females, while there are few data on roost selection by males. If the roosting requirements for sexes and reproductive classes differ, information about roosting habitat for males may be significant for management as it might mean a broader range of habitats are required to sustain bat populations (Barclay and Kurta 2007, Weller et al. 2009).

Two of the most common characteristics of bat roosting ecology are that individuals change roosts frequently and that they require multiple roosts during the season (Barclay and Kurta 2007). In 21 studies involving radiotracking of 10 bat species, bats changed roosts on average every 2.5 ± 0.2 days (Barclay and Kurta 2007). However, there is no consensus among studies as to whether roost switching behavior varies with reproductive condition, sex, age, or size of

young (Barclay and Kurta 2007). Roost switching may disrupt arthropod life cycles and decrease ectoparasite loads (Lewis 1995) or be an antipredator strategy, but neither of these factors explains either the continual movement of bats into and out of an occupied roost or the return of bats to an abandoned roost after only a few days (Lewis 1995). Thermal constraints are another possible reason for roost switching (Barclay and Kurta 2007). Weather may influence roost switching in some species (e.g., *Myotis sodalis*, Humphrey et al. 1977 and Callahan et al. 1997), but it is not the only explanation for this behavior because many bats change roosts more frequently than the weather changes, and some individuals remain within the roosts while others move out as the weather changes (Barclay and Kurta 2007). Individuals that are aware of alternate roosts are less likely to suffer if a favored roost is destroyed (Gardner et al. 1991, Kurta 1994, Willis 2003).

The ephemeral nature of bark and cavity roosts may be the most comprehensive explanation for roost switching (Lewis 1995, Kurta et al. 1996, Weller and Zabel 2001, Kurta et al. 2002). If ephemerality is a factor, then cavity-dwelling bats should switch roosts less often than bats that use more ephemeral bark roosts (Lewis 1995). This trend is not apparent in the literature (Barclay and Kurta 2007); however, research on species in which its members use a variety of roosts (e.g., bark, tree cavity, rock crevice, or building) may provide some insights. As an example, Barclay and Kurta (2007) note that silver-haired bats (*Lasinoycteris noctivigans*) remain in cavity roosts for longer periods of time than in bark roosts (Vonhof and Barclay 1996), and Indiana bats (*M. sodalis*) have longer residency times in crevices of trees than under bark (Kurta et al. 2002). However, rock crevice-roosting big brown bats (*Eptesicus fuscus*) in Alberta switch roosts frequently (Lausen and Barclay 2002). Thus, ephemerality is not the only factor.

Availability of suitable roosts on the landscape may also influence roost switching, with more frequent changes occurring when a large number of roosts are available (Lewis 1995).

When bats change roost trees, the distance traveled is usually short and, presumably, energetically inexpensive (Barclay and Kurta 2007). The average distance traveled between roosts in 14 studies involving nine species was 497 ± 97 m (Barclay and Kurta 2007). However, distance traveled between roosts varies greatly within species, which may reflect the difference in availability of roosts on the landscape (Barclay and Kurta 2007).

The eastern small-footed bat (*Mvotis leibii*) roosts almost exclusively in rock crevices. It is found from eastern Oklahoma east to northern Georgia and north through the Appalachian Mountains to southern Ontario (inset in Fig.1; Erdle & Hobson 2001). Little is known about its roosting habits (Barclay and Kurta 2007), and it is thought to be one of the rarest bats in the United States (Best and Jennings 1997). There are many published records of, and anecdotal remarks about, M. leibii found during cave surveys (Mohr 1942, Mohr 1952, Davis 1955, Tuttle 1964, Krutzsch 1966, Gunier and Elder 1973, McDaniel et al. 1982, Kirkland and Hart 1999, and Veilleux 2007), fewer records of bats found in summer roosts (Hitchcock 1955, Roble 2004, and O'Keefe and LaVoie 2010), and only two published radio-telemetry studies that have actually tracked these bats to their roosts (Johnson and Gates 2008, Johnson et al. 2011). Populations of *M. leibii* have declined in recent years; *M. leibii* is presently listed as a species of concern across its range and is being petitioned for federal listing (Erdle and Hobson 2001, Center for Biological Diversity 2010, USFWS 2011a). Much of this bat's life history remains unknown because it is not commonly observed in either summer or winter surveys (Erdle and Hobson 2001, Johnson et al. 2011). Myotis leibii's summer roosts are often inaccessible because of their location in rocky, mountainous areas, and it is rarely encountered through mist net surveys (Best and Jennings

1997, Erdle and Hobson 2001). A better understanding of the roosting ecology of *M. leibii* may be critical for conservation of the species.

M. leibii roosts in a variety of roost types including, but not limited to, ground-level rock crevices (Johnson et al. 2011), cliff faces and rock bluffs (McDaniel et al. 1982, Johnson et al. 2011), buildings (Hitchcock 1955, Barbour 1963, Peterson 1966, Barbour and Davis 1969, Neuhauser 1971, O'Keefe and LaVoie 2010), and bridge expansion joints (O'Keefe unpublished data). There are only two published radio-telemetry studies on the summer roosting ecology of *M. leibii* (Johnson and Gates 2008, Johnson et al. 2011). In West Virginia, lactating female and nonreproductive male *M. leibii* do not choose roosts randomly, as most roosts are located close to patches of vegetation within rock fields and talus slopes (Johnson et al. 2011). Roosts in West Virginia are in areas with low canopy cover and high solar exposure, so rocky habitat associated with patches of vegetation or forest edges seem to be of particular value as they provide both high solar exposure and are within a short distance of protective cover (Johnson et al. 2011). Roosts of female *M. leibii* in Maryland are also located in areas of high solar exposure (Johnson and Gates 2008). One roost located in western Virginia was within a boulder field with partially open canopy (Roble 2004).

M. leibii switch roosts often, with both males and females having a continuous residency time of only 1.1 days (Johnson et al. 2011). In West Virginia, *M. leibii* move relatively short distances from capture site to first roost site (415 m and 368 m, for males and females, respectively) and between consecutive roosts (41.2 m and 66.5 m, for males and females, respectively; Johnson et al. 2011). Short distances moved between roosts and a decline in capture rates with increasing distance from available rock habitat suggest that *M. leibii* have small home ranges (Johnson et al. 2011).

The main objective of the current project was to monitor the movements of individual *M. leibii* among roosts in the southern Appalachian Mountains and to characterize these roosts. To accomplish this objective, I used radio-telemetry to track individual *M. leibii* to natural and human-made roosts. I hypothesized that this population of *M. leibii* would have limited dispersal tendencies, as demonstrated by *M. leibii* studied by Johnson et al. (2011). To measure dispersal tendency, I measured distance moved between capture site and first known roost and distance between subsequent roosts. I hypothesized that bats would switch roosts frequently, about once per day, thus showing low fidelity to roosts. I tested for effects of sex and capture site (bridge) on distances moved and roost switching rates. Because characteristics of suitable day-roosts for *M. leibii* are not well known (Johnson et al. 2011), I characterized roosts that I found via radio telemetry. Based on Johnson et al.'s (2011) work, I expected that bats would roost in large, south-facing rocky outcrops.

Methods

Study Area

This study took place in Monroe County, Tennessee and Graham County, North Carolina (Fig. 1). The study area was approximately 40,000 ha; however, the core area in which we found most of the roosts was only about 4,000 ha. The section of road on which most roosts were located ranges in elevation from 900 m to 1450 m. This study was located in the Blue Ridge Physiographic Province where the geology is mainly metamorphosed sandstone, siltstone, and shale (Clark 2008). The forest was composed mainly of hardwoods (*Quercus* spp., *Liriodendron tulipifera, Acer saccharum, Fagus grandifolia,* and *Betula allegheniensis*) with a conifer component (*Pinus strobus* and *Tsuga canadensis*), and a mean forest age of about 70-80 years. Two high-elevation bridges along this road were used as capture sites. Bridge 1(1340 m

elevation) was located in Graham County, North Carolina and Bridge 2 (1200 m elevation) was in Monroe County, Tennessee and ~ 4 km away from Bridge 1.

The average daily temperature from May through September 2011 for this region was 21.1 ± 1.3 °C (mean \pm SE), the mean maximum daily temperature was 27.7 ± 1.5 °C, the mean minimum daily temperature was 14.5 ± 1.3 °C, and the mean monthly precipitation was 13.9 ± 4.2 cm (State Climate Office of North Carolina 2013). The average daily temperature from May through September 2012 for this region was 20.3 ± 0.9 °C, the mean maximum daily temperature was 26.3 ± 0.8 °C, the mean minimum daily temperature was 14.3 ± 1.1 °C, and the mean monthly precipitation was 10.8 ± 1 cm. These temperatures were taken at a lower elevation weather station approximately 32 km away. The data on mean daily temperature and mean minimum daily temperature from 2012 coincide fairly well with data taken at a weather station I positioned between the two bridges in 2012. However, the mean maximum daily temperature at the weather station between the bridges (see Chapter 2 for data) was much lower than the temperature obtained via that State Climate Office of North Carolina. The weather station was located approximately 900 m higher than the station the State Climate Office weather station. *Field Methods*

From 5 July to 7 October 2011 and 1 July to 26 September 2012, I conducted a radio telemetry study using *M. leibii* captured from two high elevation bridges. Bats were captured approximately 30-90 min before dusk so that the bats could be released about the same time they would naturally emerge. To capture bats, I used a yardstick to gently coax the bats to the top opening of a crevice and then pulled out by hand. I recorded sex, age, reproductive condition, mass (g), forearm length (mm), and wing damage due to white-nose syndrome (Reichard and Kunz 2009) for each bat captured; adults were banded with a unique 2.9 mm forearm band

(Porzana Ltd, East Sussex, UK). Degree of ossification of the finger joints was used to assess age (juvenile or adult; Anthony 1988). Females were classified as non-reproductive, pregnant, or lactating based on the presence of a fetus or teat condition, and males as non-reproductive or scrotal based on the swelling of the epididymides (Racey 1988). For adults \geq 4.5 g, I trimmed the fur between the scapulae and used surgical glue to attach a LB-2X or LB-2N 0.30–0.36 g transmitter (5.8 – 7.7% of body weight; battery life 8 – 22 days; Holohil, Ltd, Ontario, Canada). The ratio of body weight to transmitter weight was comparable to other bat field studies (Kurta and Murray 2002, Arnett and Hayes 2009), including recent studies of *M. leibii* (Johnson and Gates 2008, and Johnson et al. 2011) and *M. ciliolabrum* (western small-footed myotis; Lausen 2007). All bats were released at the point of capture. While handling bats, I followed the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2011; ISU IACUC protocol, 226895-1 and 311101-1), and all white-nose syndrome decontamination protocols as specified by the U.S. Fish and Wildlife Service (USFWS 2012).

I used a 5-element yagi mounted in a car setup system and a receiver (Telonics TR-5, Mesa, AZ) to locate bats at day roosts. The 5-element yagi had a long range, which was beneficial for tracking bats in the mountains where signals were often blocked. I recorded Universal Transverse Mercators (UTMs) and photographed each roost. Bats were tracked until the transmitter fell off or the signal was lost (transmitter lifespan: 8 – 22 days).

Roosts were defined as an entire, contiguous surface of rock, including any rock that was covered by vegetation as long as it was connected to the rest of the rocky surface. This differs from how other *M. leibii* radio-telemetry studies have defined a roost as these researchers were able to more precisely pinpoint the exact crevice that the bats were roosting in (J. Veilleux unpubl. data, Johnson and Gates 2008, Johnson et al. 2011). Measurements were taken on roost

dimensions, aspect, slope, percent loose rock, percent solar exposure, and percent vegetation (definitions in Table 1). I measured height and width of each rock outcrop using a laser range finder and/or a meter tape. While facing downhill of the roost, I measured the aspect with a compass, and later verified this metric using ArcMap 10 (ESRI, Redlands, CA). I measured slope using a clinometer. All visual estimates, including percent loose rock, percent solar exposure, and percent vegetation, were estimated by my technician and me independently, then averaged to the nearest 10%. Distance to road was taken with a meter tape if \leq 100 m, but with ArcMap 10 if > 100 m. Because roosts had near vertical slopes, I was not able to measure microhabitat characteristics such as length and width of the crevice entrance, width and depth of the crevice, or orientation of the crevice as in Johnson et al. (2011). For tree roosts, I recorded tree species, height, diameter at breast height, whether the tree was dead or alive, roost entrance height and aspect, percent bark remaining, canopy closure above roost, distance to nearest live tree, distance to nearest tree of the same height or greater, and distance to road.

Analysis

Distances moved between roosts were measured in ArcMap 10 and averaged across all individuals. Mean distance from capture site to first known roost was equal to 0 when an individual returned to the bridge capture site on the first tracking day. Continuous residency was defined as days available for switching divided by the number of switches (Johnson et al. 2011). Differences in movement patterns and continuous residency was statistically compared for males and females, and for bats captured at Bridge 1 and bats captured at Bridge 2. I tested these data for normality using Shapiro-Wilk tests. The data were not normally distributed, so I used nonparametric Wilcoxon rank-sum tests in all cases.

I tested roost characteristic data (see Table 1) for normality using Shapiro-Wilk tests. None of the data were normally distributed, so I used non-parametric Wilcoxon rank-sum tests to compare characteristics of roosts used by bats captured at Bridge 1 to those used by bats captured at Bridge 2. Because aspect is a circular measurement, these data were transformed (Fisher 1993), and I compared values for roosts used by bats from Bridge 1 to Bridge 2 using two-sample Watson-Williams tests (Kolliker and Richner 2004). A sequential Bonferonni correction was performed to counteract the problem of multiple comparisons (Peres-Neto 1999). Bonferonni corrections are used to avoid committing excessive Type 1 errors when conducting multiple comparison tests; these tests control the number of inflated significance values. I also reported the number of bat days (days in which I successfully tracked the bat to a roost) for each roost. Data are presented as mean ± standard error (range) unless otherwise noted. All tests were conducted in Program R (R Development Core Team 2005) and assessed at a significance level of 0.05.

Results

Capture

From 5 July to 7 October 2011 and 2 July to 16 September 2012, I captured 43 adult *M. leibii* (32 males and 11 females). Twenty-eight of the males were non-reproductive and 2 were scrotal. One of the females was non-reproductive, 9 were post-lactating, and 1 was lactating. The lactating female was caught on 27 July 2011. Incidental captures included two northern myotis (*M. septentrionalis*). For one, age and sex were not noted; the other was a non-reproductive adult female.

I radio-tagged 30 *M. leibii* (19 males and 11 females). Of these, there were 17 nonreproductive and 2 scrotal males; for females, there was 1 was non-reproductive, 9 post-lactating, and 1 lactating. Mean weight for radio-tagged individuals was 4.7 ± 0.1 g (range 4.3 - 5.2 g). Four radio-tagged males and six females were never relocated after capture, despite extensive hiking and driving surveys. I tracked the remaining 20 bats for 12.9 ± 1.1 (range 2 - 23 days) to 15 rock roosts and 2 dead white pines.

Movements

The mean distance between capture site and first known roost was 1402 ± 508 m (range 0 – 8801 m; n = 20 bats). The mean distance between consecutive roost sites was 721 ± 461 m (19 – 8522 m; n = 8 bats). The mean continuous residency was 2.6 ± 0.5 days (0 – 6 days; n = 16). Both males (n = 11 bats) and females (n = 2 bats) had long continuous residency bouts (2.2 ± 0.4 days and 3 ± 1.7 days, respectively; Table 2); however differences were not tested statistically due to small sample size. I often observed use of roosts for > 1 day; 15 males and 3 females used ≥ 1 roost for > 1 day.

The longest amount of time I successfully tracked a single individual was 23 days until the transmitter died. This was a non-reproductive male that roosted in the bridge in which he was captured the day after capture, then moved 8.5 km to his next roost. He roosted in 3 roosts, including the bridge. Once at the roost 8.5 km from the bridge, he switched back and forth between 2 roosts that were approximately 50 m from each other for 20 days. Although his mean overall continuous residency was only 1.2 days, he showed high fidelity to these 2 roosts in close proximity to each other.

Distance to first known roost was greater for males $(1809 \pm 683 \text{ m}; n = 15 \text{ bats})$ than for females $(181 \pm 46 \text{ m}; n = 5 \text{ bats}; W = 61, p = 0.044)$. However, differences in distance between consecutive roosts for males $(820 \pm 519 \text{ m}; n = 6 \text{ bats})$ and females $(381 \pm 169 \text{ m}; n = 2 \text{ bats})$ were not tested statistically. While males moved as much as 8801 m between capture and first

known roost, females moved ≤ 251 m to their first roost. Distances between consecutive roosts up to 8522 m were observed for males, whereas the greatest distance for females was 550 m. Only 6 males and 2 females moved to new roosts after the first roost, so this apparent difference was not verified through the use of statistics due to small sample sizes.

Bats captured at Bridge 2 (n = 9) tended to stay closer to Bridge 2 when choosing natural roosts (mean distance between capture and first roost = 341 ± 53 m; Table 3), whereas bats from Bridge 1 (n = 11) tended to move farther from the bridge (mean distance between capture and first roost = 2269 ± 901 m); however this difference was not statistically significant (W = 61, p = 0.402). Bats captured at Bridge 2 also moved a shorter distance between roosts (mean = 13 ± 92 m; n = 12) than bats captured at Bridge 1 (mean = 487 ± 1407 m; n = 6). This difference was statistically significant (W = 12, p = 0.026). Bats from Bridge 1 and Bridge 2 also differed in their length of continuous residency, staying 1.3 ± 0.5 days (n = 8) and 3.5 ± 0.5 days (n = 8), respectively (W = 8.5, p = 0.015).

Roost Characteristics

I found 15 rock roosts in summers 2011 and 2012 (Table 1, Appendix A). Nine of the roosts were road cuts. Two were large rock walls/outcrops that were "natural," meaning that they existed before the road was built. One roost was the site of an old quarry, so it was composed mostly of loose rocks, and another was a single boulder within the forest. Another roost was a series of metal guardrails leading up to Bridge 2, while another roost was a cement retaining wall below the road. Two of the roosts were used in both 2011 and 2012, while the remaining 13 roosts were only used in 1 year or the other.

Overall, *M. leibii* roosts were in large, south-facing steep rock structures. Male and female bats roosted in very similar structures, often sharing the same road cut (Table 4). Bats captured at

separate bridges never shared the same natural roosts. Elevation (W = 25, p = 0.8639), distance to road (W = 14, p = 0.1404), width (W = 30, p = 0.4908), height (W = 19, p = 0.5604), aspect (F = 0.0013, p = 0.9722), percent vegetation (W = 24.5, p = 0.8036), percent solar exposure (W = 13.5, p = 0.3008), and percent loose rock (W = 17.5, p = 0.2682) did not differ between roosts used by bats from Bridge 1 and roosts used by bats from Bridge 2 (Table 5). Slope did differ significantly between roosts used by bats from Bridge 1 and bats from Bridge 2 (W = 47.5, p = 0.0179), but this difference was not significant after application of a sequential Bonferonni correction.

The roost that was used by the greatest number of tracked individuals and had the most bat days was a roost that was within 200 m of Bridge 2 (Table 1, Appendix A). All individuals that were tracked to this roost were originally captured at Bridge 2 and never observed at Bridge 1. Both males and females from 2011 and 2012 were found at this roost. This roost had an elevation (1140 m) similar to the mean for all roosts, but was much closer to the main road (4 m) than average. It was smaller than average in width (59 m) and height (12 m), had a lower slope (65°) than average, and was more directly south-facing than average (179°). It had less vegetative cover (40%) than average and, thus, higher solar exposure (70%). It had a similar amount of loose rock (20%) as the mean.

I tracked one male bat to two different white pine (*Pinus strobus*) snags during the 2011 season. The bat used the first snag for 1 day, and then I lost his signal for a day. I found him again the next day in a different white pine snag about 10 m away that he used for 4 consecutive days. Characteristic data was not taken on the first white pine snag. The second snag was 20.5 m in height with a diameter of 40.3 cm. The roost entrance height was at 13.8 m with an aspect of 352°. The tree had 15% of its bark remaining. Canopy closure above the roost was 25%. It was

5.4 m to the nearest tree of the same height or greater. It was 40 m to the nearest road.

Discussion

In the Unicoi Mountains, *M. leibii* made long distance movements between summer roost sites and showed high fidelity, or long continuous residency, to particular roosts. Roosts were highly variable in their type and characteristics; most were road cuts, but bats also used rock fields, boulders, snags, guardrails, and retaining walls, plus the bridges where bats were captured. Our sample sizes were often too small for any statistical analyses, but these data represent one of only a few datasets describing *M. leibii* summer roost ecology.

Compared to other datasets on *M. leibii* movements, the individuals I tracked moved much further between roosts than has been previously documented (J. Veilleux, Franklin-Pierce University, Rindge, NH, unpubl. data from 2005 - 2008, Johnson and Gates 2008, and Johnson et al. 2011). Female *M. leibii* in Maryland move < 50 m between successive diurnal roosts (Johnson and Gates 2008). In West Virginia, male and female *M. leibii* have similar movement patterns; for both sexes, distance from capture site to 1st roost is < 882 m and distance between successive roosts is < 204 m (Johnson et al. 2011). At Surry Lake in New Hampshire, female *M. leibii* move no more than a few hundred meters between roosts, but a single male moved 2.4 km from a rock roost to a barn (J. Veilleux, unpubl. data).

Bats may have moved further in this study due to sex differences or differences in roost availability. The study sample in the Unicoi Mountains was composed mostly of male bats, whereas populations that have been studied in other parts of the range have been mostly reproductive females. Reproductive females may move less than males due to constraints of parental care and the burden of non-volant young. However, there is no difference in movement patterns of reproductive females and males in West Virginia (Johnson et al. 2011). Another explanation for the differences I observed is a difference in roost availability on the landscape. In West Virginia and New Hampshire, roosts are abundant on the landscape (e.g., numerous crevices in rock piles and talus slopes; Johnson et al. 2011 and J. Veilleux, unpubl. data). In contrast, there were relatively few suitable roosts in the Unicoi Mountains, as there were no talus slopes and the road cuts only had a limited number of crevices.

There may have been more suitable roosts near Bridge 2 than Bridge 1, which is a possible explanation for why movements were smaller for bats captured from Bridge 2 than Bridge 1. Bats from Bridge 2 used only roosts < 700 m from the bridge, whereas bats from Bridge 1 traveled up to 8800 m to find suitable roosts. On multiple occasions, I observed bats from Bridge 1 using roosts west of Bridge 2; to access these roosts, bats likely flew past Bridge 2 and the roosts used by bats captured in Bridge 2. This observation suggests that bats may travel longer distances for more optimal roosting habitat or that there are a limited number of suitable roosts in the area that bats can use.

M. leibii in the Unicoi Mountains exhibited high fidelity, and continuous residency, to roosts and, thus, had low switching rates. High fidelity in bats is directly related to roost permanency (Lewis 1995). Bats tend to exhibit high site fidelity to manmade structures and rock crevices, but low fidelity to tree cavities and foliage (Brigham 1991). For example, Indiana bats display low roost-site fidelity to roosts under the bark of green ash trees in Michigan (Kurta et al. 1993), but spotted bats (*Euderma maculatum*) are highly site faithful to rock crevices in British Columbia (Wai-Ping and Fenton 1989). Rock roosts in the Unicoi Mountains are relatively permanent structures, which may explain the high fidelity by bats that I observed.

High fidelity is inversely related to roost availability (Lewis 1995). It is possible that treeroosting species have multiple sites that they regularly move among, while bats that roost in rock

crevices and buildings have a more limited choice of quality sites and therefore are more faithful (Brigham 1991). This situation is true of Rafinesque's big-eared bats in Mississippi where bats show high fidelity to man-made structures, which are rare on the landscape, but low fidelity to hollow trees, which are common (Trousdale et al. 2008). This is also true of big brown bats (*E. fuscus*), which show high site fidelity to buildings that are rare on the landscape, but low site fidelity to tree cavities that are abundant on the landscape (Brigham 1991). Along the main road in my study area, there are road cuts every few hundred meters; however, there are very few rock fields or talus slopes such as those used by *M. leibii* in other parts of its range (J. Veilleux unpubl. data, Johnson and Gates 2008, Johnson et al. 2011). Further, although there are many road cuts, most appear to not have enough solar exposure and few crevices of the size that is optimal for *M. leibii* (P. Moosman, pers commun).

M. leibii in the Unicoi Mountains switched roosts less frequently than has been observed for the species in other parts of its range. Compared to *M. leibii* in Maryland, which roost in rock outcrops within shale barrens (Johnson and Gates 2008), *M. leibii* in the Unicoi Mountains switched roosts less frequently. This pattern holds when comparing the Unicoi Mountains *M. leibii* populations to those in West Virginia where bats that roost in talus slopes and rock fields in transmission line clearings switch roosts every 1.1 days (Johnson et al. 2011). In both of these cases, there were numerous crevices for the bats to roost in, but there are fewer such crevices in the road cuts in the Unicoi Mountains. At Surry Lake in New Hampshire, *M. leibii* tend to switch roosts more frequently when roosting in the rip-rap near a dam, where suitable crevices were numerous, than when roosting in the rock outcrops and large rock wall, where suitable crevices were sparse (J. Veilleux, unpubl. data).

Associations between bats and roosts range from obligatory to opportunistic, with selection of a particular type of roost dependent upon its availability (Kunz 1996). M. leibii seems to be more opportunistic with regards to roost selection, choosing a variety of roost sites across its range. I observed bats using rock, bridges, guardrails, trees, and cement retaining walls, and this species has also been observed using buildings throughout its range (J. Veilleux, unpubl. data, Hitchcock 1955, Barbour 1963, Neuhauser 1971, O'Keefe and LaVoie 2010). The roosts in the Unicoi Mountains were similar to the rock wall used by *M. leibii* at Surry Lake in New Hampshire (J. Veilleux, unpubl data). Both were large, fairly solid rock structures. However, roosts in the Unicoi Mountains were dissimilar to the roosts used in Maryland (Johnson and Gates 2008) and West Virginia (Johnson et al. 2011), where bats roost in rock outcrops, talus slopes, and rock fields. Roosts in the Unicoi Mountains were also dissimilar to other roosts found in rip-rap and rock outcrops at Surry Lake, New Hampshire (J. Veilleux, unpubl data). The use of trees as roosts by *M. leibii* is undocumented in the published literature. There are, however, anecdotal remarks that this species will use trees (Jones 1964, Thompson 2006). The use of trees in this species is probably rare, and data from this study represent some of the only observations of this phenomenon.

Roosts in the Unicoi Mountains were high elevation, close to roads, large, and southfacing; however, these roosts had lower solar exposure and more vegetation than expected based on other observations of roosting habitat for the species (Johnson and Gates 2008, Johnson et al. 2011). Reproductive females may use lower elevation roosts because they require warmer roosting conditions to minimize thermoregulatory costs, whereas males may select cooler, high elevation sites that allow for greater use of torpor as an energy-saving mechanism (Barclay 1991, Hamilton and Barclay 1994, Cryan et al. 2000, Kerth et al. 2000). Reproductive females do not

use torpor as often as non-reproductive females and males because torpor slows gestation (Racey 1973, Racey and Swift 1981), milk production (Wilde et al. 1999), and juvenile growth, which is costly to the females and their young (Hoying and Kunz 1998). However, male bats are also sometimes found roosting in the same habitats and roosts as reproductive females during the summer (Kurta and Kunz 1988, Hamilton and Barclay 1994), demonstrating that males are highly variable in their roosting strategies (Weller et al. 2009).

Roosts may be in close proximity to roads due to sampling and observer bias, as bats were caught on a road, and roads are more accessible for radio telemetry. Another explanation for roosts being near a road is that rock roosts are limited on the larger landscape. The large size of the roosts is comparable to the studies in Maryland and West Virginia (Johnson and Gates 2008 and Johnson et al. 2011, respectively). The bigger the rock face or pile, the more opportunities there are to find a suitable crevice. The south-facing aspect of the roosts coincides with observations of roosts across the temperate zone (e.g., Vonhof and Barclay 1997, Kalcounis and Brigham 1998), as bats tend to choose warmer roosts for energy conservation. Opposite of what I expected and what is observed in West Virginia, roosts in the Unicoi Mountains had a lot of vegetation and low solar exposure. This result is probably an artifact of the differences in definitions of a roost. I defined a roost as the entire rock face, whereas Johnson et al. (2011) defined a roost as the particular crevice within the rock outcrop. My measurements of vegetation and solar exposure take into account the entire rock outcrop, not just the crevice in which the bat was roosting. Therefore, while roosts in the Unicoi Mountains may have low solar exposure overall, the particular crevices in which bats were roosting may have had higher solar exposure.

These data represent some of the only known information on roost ecology of *M. leibii*. I was not able to obtain exact locations for where individuals were roosting within a rock face

because of the nature of the roosts, which were very steep, close to a major road, and often with a lot of loose debris that made them difficult to climb. When I pinpointed a radio tagged individual in a rock face, I avoided climbing on roosts to avoid personal injury and to avoid flushing or crushing other bats that were roosting on the same rock face. In future studies of roost ecology of *M. leibii*, microhabitat and microclimate measurements should be stressed, when possible, as they may be the key to identifying specific characteristics preferred by this species. Because this population of *M. leibii* was mostly male, it is also important to note that roost characteristics may not apply to habitats used by reproductive females. It is essential to characterize both male and female roosts to get a broad picture of roosting preferences for the species as a whole. For example, western long-eared myotis (M. evotis) differ in their microclimate preferences according to sex and reproductive condition, which is then reflected in differences in microhabitat roost preferences (Solick and Barclay 2006, 2007). Reproductive females roost closer to the surface of the ground in rock fields where roosts warm quickly, while nonreproductive females roost deeper within crevices where microclimate is cooler and allows them to use torpor more often (Solick and Barclay 2006, 2007).

Because *M. leibii* showed high fidelity to particular roosts in the Unicoi Mountains, management plans should take into account the characteristics of roosts that were used most often. Since roosts used were so variable in structure and type, there is the potential that managers could create artificial roosts if natural roosts are destroyed. Artificial roosts for this species have already been designed and installed in Pennsylvania (G. Turner, PA Game Commission, personal communication). Local rock was used to create rock piles with small crevices that could mimic natural roosts used in rock piles, talus slopes, and riprap. With regular

monitoring (e.g., exit counts at newly created roosts), managers should be able to determine if providing these structures is a successful mitigation technique for loss of *M. leibii* roost habitat.

Bridges could also be designed to provide roost habitat for this species. In a study conducted by Bat Conservation International, 4,250,000 bats of 24 species were found to be living in 211 highway structures (Keeley and Tuttle 1999). It is estimated that within the southern U.S., approximately 33 million bats are using 3,600 highway structures. Day roosts are often in the crevices of the bridge, while night roosts are located in more open areas between bridge support beams. Western small-footed bats (Myotis ciliolabrum), big brown bats (Eptesicus fuscus), and fringed myotis (M. thysanodes) are just a few of the bat species that use bridge crevices as day roosts (Keeley and Tuttle 1999). Providing bat habitat in bridges, either during initial construction or through subsequent retrofitting, could be a feasible and popular means of mitigation that is cost-effective. Further, unlike a lot of mitigation projects, these enhancement projects for bridges can be conducted onsite. Artificial structures have been used as a mitigation tool for bats across the world. For example, 9 types of bat houses were placed on woodlots near the Indianapolis International Airport as a mitigation tool for the endangered Indiana bat (Whitaker et al. 2006). After 10 years in place, Indiana bats acclimated to the boxes and showed inter- and intra-annual fidelity to 6 boxes (O'Keefe et al. 2012).

Although mitigation projects are already underway for *M. leibii*, more research is needed to understand the roost ecology of this species across its range. This is particularly important at this time because *M. leibii* is being considered for federal listing (USFWS 2011). Mounting evidence suggests that this species is highly plastic in its roost selection capabilities but in general prefers some kind of rock substrate or similar man-made structure with small crevices (J. Veilleux, unpubl data, Johnson and Gates 2008, Johnson et al. 2011, and this study). While

males and females of this species may choose similar roosts at the macro scale, their use of

different microhabitats needs further investigation (Johnson et al. 2011). In the future,

researchers may be able to modify crevice temperatures to understand if crevice temperature

preference differs between the sexes. Understanding the microhabitat needs of the sexes of this

species can lead us to more effective ways of preserving and creating roost habitat across the

species' range.

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Table 1. Definitions of characteristics for roost habitat measured for *M. leibii* rock roosts found

in Graham County, North Carolina and Monroe County, Tennessee, July - October, 2011 -

2012.

** * 1 1	
Variable	Description
Elevation	Elevation taken by GPS at center point of roost (m)
Distance to Road	Straight line distance from roost to road (m)
Roost Height	Vertical measurement of entire roost at its tallest point
Roost Width	Horizontal measurement of entire roost at its widest point
Aspect	Direction roost faces (°)
Slope	Steepness of roost taken from directly below roost at its steepest point (%)
Percent Vegetation	Percent of roost covered in vegetation, including any vegetation growing in
	front of roost that casts shadow on roost in 10% increments (%)
Percent Solar	Percent of roost exposed to sun between 10:00 and 15:00 EST in 10%
	increments (%)
Percent Loose	Percent of roost composed of loose/gravel in 10% increments (%)

Table 2. Comparison of roost-switching behavior and movements for male and female *M. leibii* in Graham County, North Carolina and Monroe County, Tennessee, July – October, 2011 –

2012. Data are presented as mean \pm SE (range).

	Males	Females
Length of continuous residency (days)	$2.2 \pm 0.4 \ (0 - 3.3)^a$	$3.0 \pm 1.7 (0-6)^{a}$
Distance between capture and first roost (m)	$1809 \pm 683 (0 - 8801)^*$	$181 \pm 46 (0 - 251)^*$
Distance between consecutive roosts (m)	$820 \pm 519 (19 - 8522)^{a}$	$381 \pm 169 (212 - 550)^{a}$

^a indicates a relationship that was not tested statistically

* indicates a statistically significant result

Table 3. Comparison of roost-switching behavior and movements in *M. leibii* captured at Bridge1 and Bridge 2 in Graham County, North Carolina and Monroe County, Tennessee, July –

October, 2011 - 2012. Data are presented as mean \pm SE (range).

	Bridge 1	Bridge 2
Length of continuous residency (days)	$1.3 \pm 0.5 (0-4)^*$	$3.5 \pm 0.5 (2-5)^*$
Distance between capture and 1^{st} roost (m)	$2269 \pm 901 \ (0 - 8801)$	341 ± 53 (212 – 703)
Distance between consecutive roosts (m)	$1487 \pm 1407 (19 - 8522)^*$	$413 \pm 92 (129 - 1076)^*$

* indicates a statistically significant difference

Table 4. Characteristics of roosts used by *M. leibii* in Graham County, North Carolina and Monroe County, Tennessee, 2011 - 2012. Data are presented for all bats combined, males, and females. Two roosts were used by both male and female individuals, so data for these roosts are presented in both the male and female column. Data are presented as mean \pm SE (range).

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All bats $(n = 15)$	Male $(n = 13)$	Female $(n = 4)$
$1145 \pm 36 (913 - 1441)$	$1132 \pm 39 (913 - 1441)$	$1187 \pm 48 (1130 - 1332)$
99 ± 78 (1 – 1187)	$112 \pm 90 (3 - 1187)$	$8 \pm 6 (1 - 25)$
74 ± 12 (2 – 146)	73 ± 10 (20 – 144)	63 ± 30 (2 – 146)
$14 \pm 2 \ (0.6 - 30)$	$15 \pm 2 (7 - 30)$	11 ± 4 (0.6 – 16)
199 ± 26 (110 – 340)	187 ± 27 (110 – 324)	$202 \pm 29 (179 - 340)$
$70 \pm 4 (47 - 90)$	$69 \pm 4 (47 - 90)$	$76 \pm 6 (65 - 90)$
$61 \pm 7 (0 - 90)$	64 ± 6 (20 – 90)	$50 \pm 19 \; (0 - 80)$
$31 \pm 9 (0 - 70)$	33 ± 10 (0 – 70)	$30 \pm 16 (0 - 70)$
$17 \pm 5 \ (0 - 60)$	$19 \pm 5 \ (0 - 60)$	$8 \pm 5 (0 - 20)$
$8 \pm 2(1-28)$	$7 \pm 2 (1 - 28)$	$13 \pm 6 (1 - 28)$
	All bats (n = 15) $1145 \pm 36 (913 - 1441)$ $99 \pm 78 (1 - 1187)$ $74 \pm 12 (2 - 146)$ $14 \pm 2 (0.6 - 30)$ $199 \pm 26 (110 - 340)$ $70 \pm 4 (47 - 90)$ $61 \pm 7 (0 - 90)$ $31 \pm 9 (0 - 70)$ $17 \pm 5 (0 - 60)$ $8 \pm 2 (1 - 28)$	All bats (n = 15)Male (n = 13) $1145 \pm 36 (913 - 1441)$ $1132 \pm 39 (913 - 1441)$ $99 \pm 78 (1 - 1187)$ $112 \pm 90 (3 - 1187)$ $74 \pm 12 (2 - 146)$ $73 \pm 10 (20 - 144)$ $14 \pm 2 (0.6 - 30)$ $15 \pm 2 (7 - 30)$ $199 \pm 26 (110 - 340)$ $187 \pm 27 (110 - 324)$ $70 \pm 4 (47 - 90)$ $69 \pm 4 (47 - 90)$ $61 \pm 7 (0 - 90)$ $64 \pm 6 (20 - 90)$ $31 \pm 9 (0 - 70)$ $19 \pm 5 (0 - 60)$ $8 \pm 2 (1 - 28)$ $7 \pm 2 (1 - 28)$

Table 5. Characteristics of roosts used by *M. leibii* in Graham County, North Carolina and Monroe County, Tennessee, 2011 - 2012. Data are presented for roosts used by all bats, bats that used Bridge 1, and bats that used Bridge 2. Data are presented as mean \pm SE (range).

	All bats $(n = 15)$	Bridge 1 $(n = 9)$	Bridge 2 $(n = 6)$
Elevation (m)	$1145 \pm 36 (913 - 1441)$	$1149 \pm 61 \ (913 - 1441)$	$1139 \pm 9 (1120 - 1177)$
Distance to Road (m)	99 ± 78 (1 – 1187)	160 ± 129 (3 – 1187)	$8 \pm 4 (1 - 29)$
Width (m)	74 ± 12 (2 – 146)	66 ± 17 (2 – 144)	84 ± 16 (45 – 146)
Height (m)	$14 \pm 2 (0.6 - 30)$	$15 \pm 2(7 - 26)$	$13 \pm 4 \ (0.6 - 30)$
Aspect (°)	199 ± 26 (110 – 340)	207 ± 36 (110 – 340)	208 ± 30 (179 – 254)
Slope (°)	$70 \pm 4 (47 - 90)$	63 ± 5 (47 – 85)	82 ± 4 (65 – 90)
Percent Vegetated	$61 \pm 7 (0 - 90)$	66 ± 7 (20 – 80)	53 ± 15 (0 – 90)
Percent Solar	$31 \pm 9 (0 - 70)$	43 ± 12 (0 – 70)	17 ± 11 (0 – 70)
Percent Loose Rock	$17 \pm 5 (0 - 60)$	$22 \pm 7 (0 - 60)$	$8 \pm 3 (0 - 20)$
Total Bat Days	$8 \pm 2 (1 - 28)$	$6 \pm 2(1-13)$	$11 \pm 4 (1 - 28)$

Figure 1. Roost locations of radio tracked *M. leibii* in Graham County, North Carolina and Monroe County, Tennessee, 2011 – 2012. Black circles represent roosts used by bats captured at Bridge 1 (black star to the east), and white circles represent roosts used by bats captured at Bridge 2 (white star to the west). Roosts were only used by bats captured at a single bridge. The inset map shows the approximate range of *Myotis leibii* (blue hatching), with the black box indicating the study area (range map adapted from Erdle and Hobson 2001).



CHAPTER 2

BRIDGE USE AND ASSOCIATIONS IN MYOTIS LEIBII

Introduction

Selection of particular roosts by bats has been explained in many ways; however, most of the evidence is observational rather than experimental (Hayes 2003). Bats select roosts based on a multitude of factors including, but not limited to, microclimate, predation risk, and presence of other bats (Fenton 1983, Morrison 1980, Barclay and Kurta 2007, Kerth 2008, Ormsbee et al. 2007). Roost microclimate influences roost selection in many bat species; however, most studies on roost preference only report structural characteristics of the roost and surrounding habitat (Boyles 2007). When microclimate has been measured, we have learned that bats roosting in structures other than tree cavities or bark, such as buildings, bridges, or rock crevices, generally select roosts with particular thermal characteristics (Ormsbee et al. 2007). These man-made structures usually maintain warm temperatures during the day and have highly variable temperatures that allow bats to be flexible in their thermoregulatory strategy (see Barclay and Kurta 2007 for review). Temperatures within natural roosts are also generally cooler during the day, warmer at night, and more stable than ambient temperatures (e.g., Campbell et al. 2010). Roosts used by reproductive females should provide conditions that minimize the costs of maintaining high embryonic and juvenile growth rates, while roosts of non-reproductive

individuals should provide conditions conducive to the use of torpor. Roosts with differing microclimates are required to fulfill all of these demands. Many species of bats have been shown to choose roosts based on roost temperature (e.g., Lourenco and Palmeirim 2004, Smith and Racey 2005). This is true of Natterer's bat (*Myotis nattereri*) in Europe, which requires a large number of roosts with a range of temperatures that they can use depending on reproductive state and energy requirements (Smith and Racey 2005).

Regardless of the sex or reproductive condition of inhabitants, optimal roosts should provide protection from predators (see Lima and O'Keefe 2013 for review, Barclay and Kurta 2007). Bats may actively trade-off between optimal thermoregulatory conditions and reduced predation risk by switching to different types of roosts, as is seen in large-footed myotis (*Myotis macropus*) that switch between tree cavities that provide an optimal thermal environment and man-made tunnels that provide protection from predators (Campbell et al. 2010). Overall, the effect of predators on bat behavior and roost selection is ambiguous (Lima and O'Keefe 2013, Barclay and Harder 2003). Bats' ability to fly and their nocturnal habits may reduce their risk of predation, as predation on bats is rarely observed (Barclay and Harder 2003); however, there are many contradictory results on the effects of predators and perception of risk by bats (Lima and O'Keefe 2013).

Bats are susceptible to predation while entering and leaving their roosts (Barclay et al. 1982, Fenton et al. 1994) and while within their roosts (Martin 1961, Mumford 1969). Thus, the risk of predation should have a strong influence on the selection of roost sites by bats. Tree-roosting bats may choose the height of their roosts based on predation pressure (Vonhof and Barclay 1996, Menzel et al. 2002). Northern long-eared bats (*Myotis septentrionalis*) in West Virginia select roosts located below the forest canopy, which creates a more maneuverable path for them

to enter and exit the roost to avoid predation with relative ease (Menzel et al. 2002). Treeroosting bats, such as *Eptesicus fuscus, Lasionycteris noctivigans, Myotis evotis, and M. volans,* in British Columbia choose roosts above the forest canopy in openings, which may also be related to predation pressure, as the height may protect the bats from terrestrial predators and the open canopy provides an easy flight path, thus minimizing the time spent exposed to predators (Vonhof and Barclay 1996, Vonhof and Gwillam 2007). Less is known about selection of rock crevices by bats and the link to predation. Rock roosts selected by silver-haired bats (*Lasionycteris noctivigans*) in Manitoba, Canada are thought to function as shelters against predators, but there are no data to support this claim (Barclay et al. 1988).

Bats may select roosts based on the presence of other bats as well (Morrison 1980). Bats are unique among mammals because of the high numbers and proportions of species that are social (Kerth 2008). Social interactions with conspecifics may yield many fitness benefits for animals (Alexander 1974). Some of these benefits may include larger groups for defense, intimidation of predators and increased vigilance against attacks, information transfer and communication, social learning (MacDonald 1983), more effective foraging (Crespi 2001), cooperation in building shelter, cooperative reproduction, and more effective dispersal behavior (see Komdeur 2006 for review).

Most bats have small body sizes, but relatively long life expectancies (Barclay and Harder 2003). Bats are volant and able to disperse over great distances, but many have strong fidelity to particular sites (Kerth 2008). Group sizes range from solitary to highly gregarious (Kerth 2008). All of these factors make bats an interesting group for research on the causes and consequences of sociality. However, bats can be difficult to study because of these factors and others, such as their ability to make extensive seasonal movements (Vonhof et al. 2008) and to roost in

inaccessible places. Therefore, bats are often underrepresented in behavioral ecology and, in particular, studies of social behavior (Kerth 2008). However, with advances in field technology, such as smaller radio transmitters, passive integrated transponders, and molecular methods, bats sociality is becoming easier to study (Kerth 2008).

Bats may be predisposed to a social lifestyle by three factors: (1) roost limitation, (2) thermoregulation, and (3) longevity (Kerth 2008). If suitable roosts are limited, bats may need to gather together in a few suitable places. Because of their small body size, bats may need to aggregate to conserve energy and promote thermoregulation. Bats' natural tendency toward philopatry and their long life spans lead to overlapping of generations that may need to share roosts. These three factors may work synergistically to explain why most bat species are social (Kerth 2008). The benefits of a social life for bats may include information sharing about foraging sites (McCracken and Bradbury 1981, Wilkinson 1992a), mutual warming of pups (Trune and Slobodchikoff 1978), guarding of juveniles (O'Farrell and Studier 1973), communal nursing (Wilkinson 1992b), cooperative breeding (Kerth 2008), reduced costs of thermoregulation (Racey and Swift 1981, Wilde et al. 1995), and reduced predation risk (Kalcounis and Brigham 1994, Speakman et al. 1999).

Many bat species form fission-fusion societies, in which casual groups of variable size and composition form, break-up and reform at frequent intervals (Conradt and Roper 2005), which allows individuals to choose new roostmates each time they re-enter a roost (Metheny et al. 2008). Fission-fusion behavior is common among cetaceans (Conner 2000) and primates (McGrew et al. 1996), as well as in other mammals, such as spotted hyenas (*Crocuta crocuta*, Holekamp et al. 1997) and kinkajous (*Potos flavus*, Kays and Gittleman 2001). The fusion of groups is thought to be an antipredator response, whereas the fission occurs because of

fluctuating availability of patchy resources (Barclay and Kurta 2007). Group members may interact with each other randomly or nonrandomly; in the latter case, they associate with specific individuals more often than expected by chance (Metheny et al. 2008). Nonrandom associations seem to be common in bats (common vampire bat, *Desmodus rotundus*, Wilkinson 1985; Bechstein's bat, *Myotis bechsteinii*, Kerth and Konig 1999) and especially in fission-fusion societies (big brown bat, *Eptesicus fuscus*, Willis and Brigham 2004; northern long-eared bat, *Myotis septentrionalis*, Patriquin et al. 2010). According to Wilkinson (1985), nonrandom associations may arise for two reasons: (1) passive aggregation - roosts differ in their suitability so individuals who share common preferences will be found together more often than by random chance; (2) active aggregation - bats may selectively associate with certain individuals, such as those of the same reproductive condition or of high relatedness.

Knowledge about relatedness among individuals within a group may help us to better understand the potential for indirect fitness benefits and kin selection, as well as bat sociality as a whole (Kerth et al. 2000a, Kerth et al. 2002). While some species of bats associate with close relatives more often than expected by random chance, others do not. Groups of greater spearnosed bats (*Phyllostomus hastatus*; McCracken and Bradbury 1977, 1981), big brown bats (*Eptesicus fuscus*; Metheny et al. 2008), and Bechstein's bats (*Myotis bechsteinii*; Kerth and Konig 199) are all composed of unrelated individuals with random genetic structure. Sex and reproductive condition seem to have more of an impact than genetic relatedness on roosting associations in bats (Kerth and Konig 1999). Reproductive females, especially those in the lactation stage, often roost together more than expected by chance, perhaps to reduce the need to use torpor, as this negatively impacts milk production and survival of young (Kerth and Konig 1999, Patriquin et al. 2010). However, non-reproductive females and reproductive females

sometimes roost together (Kerth and Konig 1999), so reproductive condition does not completely explain roost associations.

Male-biased groups of bats present a unique opportunity to study roost associations, as most studies have focused on female-biased groups of highly gregarious bat species (e.g., *D. rotundus*, Wilkinson 1985; *M. bechsteinii*, Kerth and Konig 1999; *E. fuscus*, Willis and Brigham 2004, Metheny et al. 2008). During summer, males and non-reproductive females of many bat species roost solitarily or in small groups in more exposed or cooler roosts than those used by reproductive females, and these non-reproductive individuals use torpor more often (Kunz and Lumsden 2003). Males are less likely to form colonies during summer (Weller et al. 2009) because they do not need to roost with others to facilitate maternal care as do reproductive females (Willis and Brigham 2004).

I studied two very accessible *Myotis leibii* populations that demonstrate strong fidelity to the expansion joints of two high-elevation bridges in Tennessee and North Carolina. Bridges offer a stable, protected site for bats to roost, provide a range of potential roosting temperatures, and are generally located over waterways that bats use for drinking, commuting, and foraging (Ormsbee et al. 2007). These bridge-roosting populations presented a unique chance to more easily study the social structure of a normally cryptic animal.

Individuals from these populations return to these bridges within and between seasons even after being handled and banded (O'Keefe unpublished data), or radio transmittered (this study). The study sample sex ratio is male-biased, which gave us insights into sociality among males. Because males from this population were coming back to the same roosts during the breeding season and between years, this created a unique opportunity to study why males demonstrate philopatry and if sociality is a factor. *M. leibii* are generally observed hibernating

singly or in small groups (Best and Jennings 1997), but no observations of roosting associations exist.

My objectives were to examine whether individuals chose particular roost locations (crevices) within the bridges and then to determine why they made these choices. Next, I investigated whether individuals associated with one another and, if they did, whether these associations were based on sex, reproductive condition, individual, or relatedness. Passive Integrated Transponder (PIT) tags allowed us to track roost associations and movements without handling bats. PIT tags have been used to study many species of animals (e.g., Gibbons and Andrews 2004), including bats (Garroway and Borders 2007), with no reported cases of mortality, morbidity, or impact on behavior. I expected bats to choose particular locations in the bridges and that microclimate, rather than predation risk and sociality, would be the largest factor in this decision, with these male bats choosing cooler temperatures within the bridges. I did not expect individuals to associate very often, but when they did, predicted that these associations would be based on sex, reproductive condition, individual, and to a lesser degree, relatedness. I hypothesized that relatedness would be less of a factor because the population is predominantly male.

Methods

Study Area

I conducted this study on two high-elevation bridges in Graham County, North Carolina (Bridge 1) and Monroe County, Tennessee (Bridge 2; Fig 1). Bridge 1 runs northwest-southeast, whereas Bridge 2, ~ 4 km away, runs east-west. Therefore, Bridge 1 (1340 m elevation) has one side of crevices that face northeast (n = 41) and one side that face southwest (n = 39). Bridge 2 (1200 m elevation) has one side of crevices that face north (n = 42) and one side that face south

(n = 42). Bridge 1 has slightly larger crevices on average, measuring 38.0 x 1.1 x 20.7 cm (height x width x depth), than Bridge 2, measuring 38.0 x 1.0 x 20.2 cm.

In the vicinity of these bridges, the average daily air temperature from 27 May to 25 September 2012 was 19.1 ± 0.3 °C, the mean maximum daily temperature was 21.3 ± 0.3 °C, and the mean minimum daily temperature was 16.2 ± 0.3 °C. Temperature data were collected with a Hobo U23 Pro v2 Temp/RH data logger (Onset Hobo Data Loggers, Bourne, MA) located approximately 1.8 km northwest of Bridge 1 and 2 km east of Bridge 2. The mean monthly precipitation was 10.8 ± 1.0 cm for the same period (State Climate Office of North Carolina 2013).

Since 2004, researchers and U.S. Forest Service personnel have monitored the populations of *M. leibii* in these two bridges. In 2004, bats were banded with red and blue forearm bands, whereas in years following this, they were banded with silver bands. Prior to 2011, banding data from multiple visits indicates that Bridge 1 was used by \geq 36 male and \geq 7 female *M. leibii*, while Bridge 2 was used by \geq 8 bats (M. Frazer and J. O'Keefe unpublished data). Prior to 2011, there were generally 10–15 bats present at Bridge 1 and 3–8 bats present at Bridge 2. Some banded individuals had used the bridges for at least 7 years, as indicated by the presence of bats with blue or red bands in 2011. Most of the bats captured from the bridges are male; however, females and juveniles were found in 2004, 2010, and 2011.

Field Methods

From mid-May through late June 2012, I captured *M. leibii* from crevices of the two bridges. Captures at the two bridges were conducted on different nights to minimize the risk of spreading *Geomyces destructans* (Hayes 2012) between the two bridges. To capture the bats, I used a yardstick to gently coax the bats to the top opening of the crevice where I pulled them out by hand. I recorded time of capture, sex, age, reproductive condition, right forearm length, and mass. I then took two 3-mm biopsy punch samples, one from each wing, for molecular analysis. I cut a small patch of fur on the back and cleaned the injection site, then injected a PIT tag (Biomark HPT8, Boise, ID) just under the skin using a needle (Biomark N165) loaded in a Biomark MK165 Implanter. The hole was closed with a small drop of surgical glue, the tag was moved to the side near the wing joint, and the bat was released at its point of capture. I followed federal and state white-nose syndrome protocols (USFWS 2012), and the guidelines for the use of wild mammals in research (Sikes et al. 2011, IACUC protocol 226895-1 and 311101-1).

I used a handheld Biomark FS 2001 Reader to survey each bridge most days between 07:00 and 19:00 from 17 May to 26 September 2012. I walked the length of each bridge scanning each crevice for PIT tagged bats. I recorded bridge name, crevice number, time, PIT tag ID of any other bat in the crevice or band color if an individual did not have a PIT tag.

DS1921G iButtons (Maxim Integrated, San Jose, CA) were placed in approximately every 7th crevice on both bridges to monitor temperature within the crevices (micro-climate). Specific placement varied slightly if an iButton could not fit in particular crevice. iButtons were wrapped in plastic packaging of the type used to wrap electronic components per recommendations by Willis et al. (2009) for dampening high frequency sound. iButtons were tested with Anabat SD2 bat detectors (Titley-Scientific, Columbia, MO) after wrapping to ensure that no high frequency sounds could be detected. I also tested wrapped iButtons to assess accuracy of temperature recordings.

Biopsy punch samples were stored in a mixture of dimethyl sulfoxide and salt (25% DMSO/saturated NaCl solution) and sent to Western Michigan University to be processed and analyzed. Total genomic DNA from membrane punches was extracted using a DNeasy Tissue

Extraction Kit. Ten microsatellite loci were amplified in multiplex PCR reactions and subsequently pooled before genotyping on an ABI 3100 DNA sequencer. Cycling conditions followed those in Vonhof et al. (2002), with a longer extension step (10s), and variable annealing temperatures depending on the multiplex reaction. Fragments were visualized and analyzed using GeneMarker software (SoftGenetics). Departures from Hardy-Weinberg and linkage equilibrium were examined using FSTAT 2.9.3.

Analysis

I used generalized linear models (glm) with a Poisson distribution to assess the effect of site-specific factors, temporal factors, and temperature on number of bats observed in each crevice each day. The dependent variable was the number of bats in each crevice each day, and the independent variables were bridge, crevice, aspect, distance to edge, daily air temperature mean, air temperature minimum, air temperature maximum, and Julian date (defined in Table 1). Aspect was treated as a categorical variable with 4 values: north, south, east, and west. Program R was used for all statistical analyses (R Development Core Team 2005). Daily air temperatures were calculated by averaging the temperature recordings from the first reading after sunrise through the last reading before sunset. Sunrise and sunset was determined using the U.S. Naval Observatory Astronomical Applications Department's (2012) sunrise/sunset table for Tellico Plains, TN ((http://aa.usno.navy.mil/data/docs/RS_OneYear.php).

I fit a global regression model using number of bats in each crevice each day as the dependent variable and the 8 site, temperature, and temporal variables listed above as independent variables. I tested the global model for goodness of fit (GOF) using the Hosmer-Lemeshow statistic (Hosmer and Lemeshow 2000). In addition to the global model, I selected 28 of a possible 255 candidate models based on hypotheses relating roost use to site, temperature,

and temporal variables. All variables appeared in an equal number of models, creating a balanced model set (Burnham and Anderson 2002).

I calculated Akaike model weights to evaluate and select the most parsimonious model and predict variable importance (Burnham and Anderson 2002). I created a confidence set of models by including models with Akaike weights within 10% of the highest value, which is comparable with the minimum cutoff point suggested by Royall (1997). I used model averaging of Akaike weights to incorporate model selection uncertainty directly into parameter estimates and standard errors (Burnham and Anderson 2002).

Micro-temperature data obtained from the iButtons was not used in the regression analysis due to incomplete data for the entire survey period. However, I compared mean daily crevice temperature to the number of bats in each bridge to see if there was a trend in temperature observed when the most bats were in the bridges. Once again, daily crevice temperatures were calculated by averaging the temperature recordings from the first reading after sunrise through the last reading before sunset. I compared micro-temperatures and number of bats from 22 June – 22 July 2012 because this was the period in which all iButtons were working.

Associations

I observed associations among individual bats, defined as a pair of individuals in a situation in which interactions usually take place (Whitehead 2008). An interaction is defined as the behavior of an individual being affected by the presence or behavior of another, and requires a prolonged observation. I used associations because they can be determined from instantaneous observations, as I was not able to observe the bats for a prolonged amount of time each day.

I used the half-weight association index to estimate the proportion of time a dyad, two paired individuals, spent in association (Whitehead 2008). This index was chosen because assumptions for other association indices were violated as a result of my methods for marking and resighting individuals. The half-weight association index is less biased when individuals are more likely to be identified when not associated or not all associates are identified. The halfweight association index was calculated with the following equation: $\frac{x}{x+yAB+\frac{1}{2}(yA+yB)}$ where x is the number of sampling periods with A and B observed associated, vA is the number of sampling periods with just A identified, yB is the number of sampling periods with just B identified, and vAB is the number of sampling periods with A and B identified but not associated. To assess whether the mean half-weight association index was significant, I compared my sample to a sample of random associations by using permutations in SocProg 2.4 (Halifax, Nova Scotia, Canada). If observed values were greater than values that are expected if individuals randomly associated, then individuals were exhibiting preferential associations. I continued to increase the number of permutations until the p-values stabilized, which was at 10,000 permutations.

I used a sociogram to visually display the social structure of the population, which is the recommended display by Whitehead (2008). In a sociogram, individuals are arranged as points in a plane and lines showing links are drawn between them indicating the strength of the relationship. The thickness of the linking lines indicates the size of the association index. Sociograms display almost all of the data, can indicate the form of social structure (unlike histograms), and unlike cluster analyses and ordinations using principal component analysis, can preserve and depict information on symmetric relationships.

To assess relatedness of individuals, genotypes of the individuals and allele frequencies for the population were input into the program MLRelate, which calculates maximum likelihood estimates of relatedness and relationship categories (e.g., full sibling, half sibling, parent offspring; Kalinowski et al. 2006). Genotypes of individuals from these two populations (n =74) and from Jackson County, North Carolina (n = 10), located approximately 100 km to the east, were included in this analysis. Allele frequencies were calculated from this population, the Jackson County population, and all other *M. leibii* sampled in the Appalachian Mountains (n = 81). Relatedness values range between 0 and 1, with higher values indicating greater allele sharing. An alternate parentage analysis was also run using program CERVUS 3.0 which uses a maximum-likelihood approach to assign parentage combined with simulations to determine confidence of parentage assignments (Kalinowski et al. 2007).

Results

Capture

I captured 46 *M. leibii* (42 male and 4 female) from 17 May – 8 August 2012 and I PITtagged 44 M. leibii (41 male and 3 female). I PIT tagged 33 non-reproductive (5 of which were juvenile) and 8 scrotal males, and 3 non-reproductive females (1 was a juvenile). The one male that was captured but not PIT tagged was a non-reproductive adult . The female that was not PIT tagged was post-lactating and had a shoulder injury, but was in the same crevice as a juvenile female. I also incidentally captured 4 northern long-eared bats (*M. septentrionalis*) during this time.

Bridge Use

I performed daily counts of both bridges and identified any bats in the crevices, if possible, from 17 May to 26 September 2012. I counted a total of 842 "bat-observations" in both

bridges over the entire study period, but bats observed were not independent of the bats observed the next day. Six hundred and sixty three of these observations came from Bridge 1 (Fig. 1) and the remaining 179 observations from Bridge 2 (Fig. 2). There was a mean of 0.075 bats/crevice/day in Bridge 1 and 0.020 bats/crevice/day in Bridge 2. Thirty of the PIT-tagged bats returned to the bridges during the study period. I counted 332 "observations" of the PIT tagged bats; 269 observations were at Bridge 1 and 63 observations were at Bridge 2. PIT tagged bats were always observed at the bridge at which they were originally captured, and therefore, I never observed movements by identifiable bats between the two bridges.

There was a gradual increase in the number of bats in Bridge 1, with a peak in mid-July, then a gradual decrease until the end of September when the study ended (Fig. 3). The increase in bats throughout the study period was not as gradual at Bridge 2, where I observed a sudden peak in number of bats in the crevices occurring in late July, with a continual increase through mid-August and then a gradual decrease through the end of September (Fig. 4).

Bats chose to roost in particular crevices more often than others in both bridges. In Bridge 1, bats tended to roost in the northeast-facing side of the bridge rather than in the southwest-facing side of the bridge. Over the entire study period, 57% of the bat observations (n = 380) came from the east side of Bridge 1 and the remaining 43% from the west side (n = 283; Fig. 1). Bats used low and high numbered crevices of Bridge 1, which correspond with the ends of the bridge, more than they used the center crevices (81% of observations from crevices 1 - 21northeast, 36 - 41 northeast, and 1 - 18 southwest combined). A similar situation was seen at Bridge 2, but at a lesser magnitude (Fig. 2). Sixty nine percent of the bat observations came from the north side of Bridge 2 (n = 123), while 31% came from the south side (n = 56). Bats also

used low and high numbered crevices more often than center crevices at Bridge 2 (80% of observations from 1 - 7 south, 1 - 11 north, and 32 - 42 north combined).

In Bridge 1, more bats were observed in parts of the bridge with an intermediate microclimate (Fig. 5). The extreme ends of the bridge (very high and low numbered crevices) tended to be the coldest parts of the bridge from 22 June – 22 July. The center of the bridge tended to be the hottest. There were not as many bats in the center of the bridge when the mean daily crevice temperature exceeded 26.5°C. This same trend could not be verified at Bridge 2 because of the low number of bats that roosted in this bridge from 22 June – 22 July (Fig. 6). However, the mean daily crevice temperature seemed to be less variable in Bridge 2 than Bridge 1. The ends of Bridge 2 did not have a sudden drop in crevice temperature as observed in Bridge 1.

The best approximating model for the number of bats in crevices each day ("roost use") contained all of the variables except distance to edge; there was a 49.0% probability that this model was the best approximating model (Table 2). This model was 2 times more likely than the next best approximating model, which contained all of the possible variables. The confidence set of models included the top 3 models (Table 2). The sum of Akaike weights for the confidence set was 0.953, indicating a 95.3% chance that one of those models was the best approximating model based on the data and set of candidate models. Bridge, aspect north and west, mean daily air temperature, and Julian date were all positively related to roost use, while crevice, aspect south, minimum daily air temperature, and maximum daily air temperature were negatively related to roost use (Table 3). All 3 aspect variables included within the confidence set had model-averaged 90% confidence intervals that included zero (Table 3), indicating they provided little information regarding roost use.

Relatedness

Most pairs of individuals from this population had low relatedness, as indicated by the pairwise relatedness estimates calculated in MLRelate. The mean relatedness estimate for this population and the Jackson County population was 0.06, meaning that there was very little allele sharing in these populations. Most individuals in these populations were also unrelated, as indicated by the parentage analysis calculated in CERVUS. There were 3388 unrelated pairs, 424 half sibling pairs, 6 full sibling pairs, and 10 parent-offspring pairs. The confidence of the parentage assignments often included more than one relationship because only 10 markers were used. This means that I could not reliably distinguish between the relationships based on the power of this marker set. However, I chose to assume the lowest level of relationship if two relationships were included in the confidence set (i.e., if unrelated and half siblings were in the confidence set, I assumed the pair was unrelated).

Associations

From 17 May to 26 September 2012, I counted 842 bat observations, with only 51 of these instances involving > 1 bat in a crevice; hence, associations were very rare. Nine of these instances involved 3 bats together in one crevice. Forty-one of the overall instances occurred at Bridge 1, while 10 occurred at Bridge 2. At Bridge 1, 18 of these instances occurred on the northeast-facing side of the bridge, while 23 occurred on the southwest-facing side. Instances of > 1 bat in a crevice spanned the entire length of the bridge; i.e., groups were not clustered at one end or another. All but 2 instances occurred after 1 July, and 23 instances occurred between 14 July and 31 July. At Bridge 2, 6 of the instances in which I observed > 1 bat in a crevice occurred on the bridge, all at low numbered crevices (see Fig. 6 for reference to location of low numbered crevices), and 4 occurred on the north side, all at high numbered

crevices. All 10 instances occurred on or after 21 July, with 9 of the instances occurring from August through September.

Since an association was defined as an instantaneous observation of a pair of individuals, if there were 3 bats in a crevice together, there were 3 separate associations within that crevice. I counted 13 associations in which I could identify all bats involved in the association. These 13 associations were among 14 individuals. The kinship analysis suggests that in 10 of these associations, the individuals were unrelated, while in 1 of the associations the individuals were half-siblings (Table 4). I did not take a genetic sample from 2 of the individuals, so I was unable to obtain relationship results for the last 2 associations. For 7 of the associations, the individuals had a pairwise relatedness estimate of 0. The highest pairwise relatedness estimate was 0.16.

The mean association index of all identifiable bats was 0.03 (sd = 0.16). Thus, identifiable bats were found together approximately 3% of the time. In a test of significance for associations, the mean random association index was 0.04, and the stabilized p-value was 0.0006. A low p-value suggests that there were low real values compared to random values. However, there were no significant associations and, therefore, individuals did not preferentially prefer or avoid each other. The association indices were no different than would be expected from random associations. The sociogram shows that there are a few identifiable individuals, plotted as points, who had relatively high association indices, indicated by the thickness of the lines, meaning that they associated with each other more frequently (Fig. 7). However, most of the individuals are not even linked by a line, meaning they never associated.

Discussion

M. leibii within this population roosted within bridge crevices that had a cooler microtemperature than expected. The most probable reason for this phenomenon is that nonreproductive male bats dominate this population and tend to roost in exposed or cool roosts (Hamilton and Barclay 1994, Kerth et al. 2000b, Kunz and Lumsden 2003). Cooler roosts allow non-reproductive individuals to use torpor as a mechanism for energy conservation (Kunz and Lumsden 2003). On the other hand, reproductive individuals do not use torpor as often because torpor slows gestation (Racey 1973, Racey and Swift 1981), milk production (Wilde et al. 1999), and juvenile growth, which is costly to the females and their young (Hoying and Kunz 1998). The high number of males in this study sample most likely also explains the lack of associations, as males should not have a need cluster during the active season to maintain body heat or to facilitate maternal care (Willis and Brigham 2004).

There are many possible reasons why bats used Bridge 1 more often than Bridge 2. The three variables that I was able to measure include crevice temperature, crevice size, and number of natural roosts nearby. Bridge 1 offered a greater variability in micro-temperatures than Bridge 2, which created a situation in which males could easily choose crevices based on which ones allowed for the greatest use of torpor for energy conservation. Other bat species, such as Natterer's bat (*M. nattereri*), require a large number of roosts with a range of temperatures that they can use depending on reproductive state and energy requirements (Smith and Racey 2005).

Bridge 1 also had slightly larger crevices, particularly in width, which could accommodate larger individuals, whereas Bridge 2 probably could not house individuals over 5 g in its smaller crevices. Tree-hole bats (e.g., *Eptesicus vulturnus*, *Chalinolobus morio*, *Nyctophilus geoffroyi*, and *Mormopterus planiceps*) of southeastern Australia choose roosts in trees and man-made

structures partially based upon the entrance dimensions (Tidemann and Flavel 1987). Bats tend to select holes with entrances that are just a little larger than themselves. It has been hypothesized that bats choose the size of the particular crevice or hole to exclude other species, but whether that of predators or competitors, or both, is still unknown (Tidemann and Flavel 1987). In the Unicoi Mountains study area, the size of the bridge crevices does not exclude eastern garter snakes (*Thamnophis sirtalis*) or ringneck snakes (*Diadophis punctatus*), two potential predators that were commonly observed in the crevices. Adult garter snakes are capable of eating full-grown frogs, toads, mice, and nestling birds (Ernst and Ernst 2003). Ninety percent of the eastern garter snakes' diet is composed of amphibians; however, there has been no documentation of an eastern garter snake eating bats (Ernst and Ernst 2003). Thus, while it is possible that the garter snakes could eat the bats, it is not likely. Ringneck snakes prey on a variety of small animals, including salamanders, frogs, snakes, lizards, slugs, and earthworms; however, their diet does not include any mammals (Ernst and Ernst 2003). The ringneck snakes in the bridges were also very small in body size, so it is very unlikely that they could consume a bat. However, the size of the crevices likely does exclude many other bat species, such as northern myotis (*M. septentrionalis*) and big brown bats (*Eptesicus fuscus*), which are both known to use bridge crevices (Keeley and Tuttle 1999).

From the radio telemetry study I conducted on this same population of individuals (Chapter 1), I found that there are fewer natural roosts close to Bridge 1 than Bridge 2. Bats captured at Bridge 2 moved a maximum of 700 m to any natural roost on the landscape, whereas bats captured at Bridge 1 moved up to 8800 m to natural roosts on the landscape (Fig. 1 from Chapter 1). Bats captured at Bridge 1 tended to disperse much farther from the bridge, even traveling past Bridge 2 to get to a natural roost. This result indicates that there are fewer suitable natural roosts

available near Bridge 1 and is a possible reason for why Bridge 1 is used as a roost more often than Bridge 2. If there are fewer natural roosts on the landscape surrounding Bridge 1, then bats may prefer the bridge because of its suitable conditions. Artificial roosts are known to supplement natural habitat where natural roosting structures are lacking (Chambers et al. 2002), and occupancy of artificial roosts is negatively correlated with the abundance of natural roosts (Ciechaneowski 2005). Nathusius' pipistrelles (*Pipistrellus nathusii*) and brown long-eared bats (*Plecotus auritus*) in Poland occupy bat boxes at a much higher concentration when there is a lack of natural roosts on the landscape (Ciechanowski 2005).

The site-specific factors, bridge and crevice, were important in predicting the number of bats that used a crevice on each day. These two factors are important for reasons previously mentioned. However, the site-specific factors aspect and distance to edge were not good predictors of number of bats in each crevice each day. I expected aspect to be a good predictor of roost use because aspect, particularly a south-facing aspect, has proven to be an important predictor of roost selection across the temperate region (e.g., Vonhof and Barclay 1997, Kalcounis and Brigham 1998), as bats tend to choose warmer roosts to facilitate more rapid gestation (Racey 1973) and growth of young (Hoying and Kunz 1998). The fact that these populations consist mostly of male bats provides a good explanation for why aspect may not be important in this case, as males do not participate in raising young. Also, the crevices have multiple aspects due to the fact that they open on both sides and the top. For example, a crevice labeled as north-facing actually faces both north and south. Bats may optimize solar exposure via positioning within the crevice, but this would be difficult to measure as the bats probably move throughout the day and as a result of disturbance.

I also expected distance to edge to be an important predictor variable because I thought it would mirror micro-temperature differences across the bridge. The distance to edge measurement was also not a good predictor of number of bats in each crevice each day. Contrary to expectation, solar exposure and micro-temperatures were not always lowest on the ends of the bridges near the tree line. Although I saw this trend for the northeast facing side of Bridge 1, it is not as clear on the southwest facing side or either side of Bridge 2.

The air temperature variables were good predictor variables of number of bats in each crevice each day. Air temperature has been demonstrated as a good predictor of roost selection in rock-roosting bats previously. Roost microclimate, which is an important factor in roost selection by western long-eared bats (Myotis evotis) in Alberta, Canada, is strongly influenced by external air temperatures (Chruszcz and Barclay 2002). However, the roosts are buffered against ambient temperature, as they are warmer than ambient temperature at night and the daily highs and lows are less extreme than ambient highs and lows (Chruszcz and Barclay 2002). In general, a higher mean air temperature corresponded with more bats in the crevices in the bridges in the Unicoi Mountains. This same pattern was observed in 2011 at these 2 bridges (unpubl data). This indicates that the bats most likely need the air temperature to reach a certain point before the crevices of the bridges warm up enough that they are habitable. Until the point in mid-July when most bats begin to roost in the bridges, they may either be in natural roosts in the surrounding area or in roosts at lower elevations. It is unlikely that the bats are still in their wintering locations until this point because *M. leibii* generally leave their wintering locations by March (Mohr 1936, Thompson 2006). We saw a great increase (i.e., approximately 300%) in the number of bats in the bridge crevice in mid-to-late July, which corresponds with warming air

temperatures. These observations correspond with Julian date being a good predictor variable for number of bats in each crevice each day.

Seasonal changes in roost type have been observed in another rock-roosting bat species, the pallid bat (*Antrozous pallidus*; Vaughan and O'Shea 1976, and Lewis 1996). Pallid bats in Oregon and Arizona were more likely to roost in slabs of rock when ambient temperatures were cooler and in crevices of rocks when ambient temperatures were higher (Vaughan and O'Shea 1976, and Lewis 1996). The sun warmed slab roosts quickly, whereas crevice roosts were buffered against temperature changes due to thick walls and had a wider range of temperatures within each roost. The bridges used by *M. leibii* in the Unicoi Mountains are most likely comparable to the thick-walled crevice roosts used by pallid bats in Oregon and Arizona (Vaughan and O'Shea 1976, and Lewis 1996). Thus, bats may be using the bridges, or crevice roosts, when ambient temperatures are higher because they can buffer against temperature changes that occur later in the summer. Earlier in the season, *M. leibii* may use roosts more like the slab roosts used by pallid bats that are more easily warmed by the sun.

Associations may be rare in this population if the costs of associating outweigh the benefits. Associating to maintain body warmth may benefit some bats; however, torpor use may be a better strategy for energy savings depending on reproductive state (see Speakman and Thomas 2003 for a review). Males and other non-reproductive individuals use torpor for energy conservation more often than reproductive females because they do not have to pay the costs of torpor, such as slowed gestation (Racey 1973, Racey and Swift 1981), milk production (Wilde et al. 1999), and juvenile growth, which is costly to females and their young (Hoying and Kunz 1998). Therefore, for males, clustering to maintain body heat may be more costly than using torpor; however, this hypothesis has yet to be confirmed.

Another benefit to associating is to minimize the risk of predation. Individual animals in groups can reduce their vigilance against predators because the presence of more eves and ears allows for an increase in overall predator detection (Pulliam 1973). Further, the more bodies a predator has to target, the less likely the predator is to choose a particular individual (the "dilution effect;" Foster and Treherne 1981). However, predation at the bridge sites does not seem to be an important source of mortality as it might be difficult or dangerous for a predator to get onto the bridges in the first place. I observed eastern garter snakes (Thamnophis sirtalis) and ringneck snakes (Diadophis punctatus) in the crevices of Bridge 1 on a daily basis from mid-May through the end of July, and on 2 occasions observed timber rattlesnakes (Crotalus *horridus*) either on or in the riprap of Bridge 2. As mentioned previously, garter and ringneck snakes are likely not preying upon these bats either because of preference for other animals or size restrictions. I have even observed a ringneck snake sharing a crevice with a bat on 1 occasion. Unlike garter snakes and ringneck snakes, timber rattlesnakes prefer mammalian prev and are known to eat bats (Clark 2002, Ernst and Ernst 2003); thus, these snakes could be a threat to the bats. This may provide another reason why I generally saw fewer bats at Bridge 2 than Bridge 1. Risk of predation could also explain why I saw occasional associations. Bats clustering together in one crevice, or even bats congregating in crevices nearby other bats, may be benefit each other by increasing the vigilance of the group against predators (Pulliam 1973).

The observation that most of the bats that did associate were unrelated non-reproductive males confirms my hypothesis that associations would be based more upon sex and reproductive condition than relatedness. In general, sex and reproductive condition seem to have more of an impact than relatedness on roosting associations in bats (Kerth and Konig 1999). This is true in *P. hastatus* (McCracken and Bradbury 1977, 1981), *E. fuscus* (Metheny et al. 2008) and *M*.

bechsteinii (Kerth and Konig 1999), in which roosting associations are not related to genetic relatedness. However, I have few data to support this claim and suggest additional monitoring of these populations to confirm this trend.

The fact that male bats generally roosted solitarily within crevices with cooler microtemperatures and the fact that one bridge was used more than another may have important management implications. These data indicate that male *M. leibii* in this population have a preference for certain microhabitats (crevices) and macrohabitats (bridges) over others. These preferences could relate to crevice temperature, crevice size, availability of natural roosts on the surrounding landscape, or other unmeasured factors. Bats from this population would benefit most from the retention of natural roosts or the construction of artificial roosts that have a large number of crevices with a wide variety of micro-temperatures. More research is needed to verify the factors that affect the number of bats using particular crevices each day. Knowing what these factors are would aid in creating more suitable artificial roosts for this species.

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Table 1. Variables measured at 2 high elevation bridges used as roosts by *M. leibii* in Monroe

County, Tennessee and Graham County, North Carolina.

Variable	Definition
Bridge (brg)	Bridge 1 or Bridge 2
Crevice (crev)	Crevice number (low and high numbers
	located near bridge edge)
Distance to edge (disedg)	The distance from a particular crevice to
	whichever end of the bridge is closer,
	measured in meters
Aspect: Aspect north (aspn), Aspect south	The cardinal direction that each side of the
(asps), and Aspect west (aspw)	bridge faces. This was divided into three
	subcategories: aspect north, aspect south,
	and aspect west.
Mean daily temperature (tmean)	The mean daily air temperature measured
	from the first reading after sunrise to the
	last reading before sunset
Minimum daily temperature (tmin)	The minimum daily air temperature
	measured from the first reading after
	sunrise to the last reading before sunset
Maximum daily temperature (tmax)	The maximum daily air temperature
	measured from the first reading after
	sunrise to the last reading before sunset
Julian Date (jdate)	The Julian date of year 2012

Table 2. Variables, number of parameters in the model (K), Akaike's Information Criterion (AIC), difference in AIC value between the model and the model with the lowest AIC (Δ AIC), and AIC weight (w_i) for 29 models used to predict roost use by *M. leibii* (number of bats per crevice per day) in 2 high elevation bridges in the Monroe County, Tennessee and Graham County, North Carolina, May – September, 2012. Variable definitions given in Table 1.

Model	K	AIC	ΔΑΙϹ	Wi
brg crev aspn asps aspw tmean tmin tmax jdate	9	7130.8	0	0.490
brg crev disedg aspn asps aspw tmean tmin tmax jdate	10	7132.3	1.5	0.231
crev disedg aspn asps aspw tmean tmin tmax jdate	9	7132.3	1.5	0.231
brg crev disedg aspn asps aspw tmean tmax jdate	9	7135.5	4.7	0.047
brg crev disedg aspn asps aspw tmean tmin jdate	9	7144.2	13.4	0.001
brg crev disedg tmean tmin tmax jdate	7	7151.7	20.9	0.000
brg crev disedg aspn asps aspw tmin tmax jdate	9	7157.2	26.4	0.000
brg disedg aspn asps aspw tmean tmin tmax jdate	9	7158.9	28.1	0.000
brg crev disedg aspn asps aspw tmean tmin tmax	9	7202.7	71.9	0.000
brg crev disedg aspn asps aspw tmean	7	7216.9	86.1	0.000
disedg aspn asps aspw tmean	5	7243.4	112.6	0.000
crev disedg aspn asps aspw jdate	6	7276.6	145.8	0.000
brg crev jdate	3	7294.4	163.6	0.000
brg crev disedg aspn asps aspw	6	7303.4	172.6	0.000
brg jdate	2	7320.9	190.1	0.000
brg crev	2	7321.2	190.4	0.000
aspn asps aspw	3	7328.0	197.2	0.000
disedg aspn asps aspw	4	7330.0	199.2	0.000
brg	1	7347.8	217	0.000
tmean tmin tmax jdate	4	7579.8	449	0.000
tmean jdate	2	7589.7	458.9	0.000
tmin tmax jdate	3	7604.7	473.9	0.000
crev tmin tmax	3	7631.9	501.1	0.000
tmean tmin tmax	3	7650.1	519.3	0.000
tmean	1	7664.3	533.5	0.000
tmin	1	7665.2	534.4	0.000
tmin tmax	2	7666.7	535.9	0.000
tmax	1	7681.8	551	0.000
disedg	1	7749.2	618.4	0.000

Table 3. Model-averaged parameter estimates for variables explaining roost use by *M. leibii* in Monroe County, Tennessee and Graham County, North Carolina, May – September, 2012. Variable definitions given in Table 1.

Parameter	Estimate	SE	Lower 90% CI	Upper 90% CI	Importance
intercept	-11.54	1.00	-13.19	-9.90	1.00
crev	-0.02	0.003	-0.02	-0.01	1.00
tmean	0.28	0.06	0.18	0.38	1.00
jdate	0.01	0.001	0.01	0.01	1.00
aspn	0.32	0.71	-0.85	1.49	1.00
asps	-0.45	0.35	-1.02	0.12	1.00
aspw	0.07	0.08	-0.05	0.19	1.00
tmax	-0.14	0.04	-0.21	-0.08	0.999
tmin	-0.05	0.02	-0.08	-0.01	0.95
brg	1.94	0.15	1.69	2.18	0.77
disedg	0.001	0.002	-0.002	0.004	0.51

Table 4. Associations among individual *M. leibii* at 2 high elevation bridges in Graham County, North Carolina and Monroe County, Tennessee, May – September 2012. Location refers to the bridge where the association occurred. The half weight association index was calculated for that particular association. Parentage refers to the most likely relationship between the two individuals in the association. Relatedness refers to the pairwise relatedness estimate for the two individuals within the association, ranging from 0 to 1, with higher numbers indicating more allele sharing.

Bat A ID	Bat B ID	Location	x^{1}	yA^1	yB^1	yAB^1	Half weight index	Parentage	Relatedness
3	4	1	2	5	0	0	0.44	unrelated	0.00
5	6	1	1	27	3	2	0.06	unrelated	0.00
8	9	1	2	4	16	3	0.13	unrelated	0.00
5	9	1	1	18	10	9	0.04	unrelated	0.00
11	1	1	1	11	30	5	0.04	unrelated	0.00
1	8	1	2	29	3	5	0.09	unrelated	0.00
1	9	1	1	24	10	9	0.04	unrelated	0.00
5	10	1	1	18	9	9	0.04	unrelated	0.03
7	5	1	1	2	26	2	0.06	unrelated	0.05
12	10	1	1	30	5	13	0.03	Half siblings	0.15
9	10	1	1	10	9	9	0.05	unrelated	0.16
1	2	1	3	26	2	5	0.14	_ 2	- ²
13	14	2	3	5	7	4	0.23	- 2	- 2

 ^{1}x is the number of sampling periods with *A* and *B* observed associated, *yA* is the number of sampling periods with just *A* identified, *yB* is the number of sampling periods with just *B* identified, and *yAB* is the number of sampling periods with *A* and *B* identified but not associated.

²There are no parentage or relatedness values for the last 2 associations because genetic samples were not taken from one of the bats in each association.



Figure 1. Total number of *M. leibii* in each crevice of Bridge 1 from 17 May – 26 September 2012 in Graham County, North Carolina. The top graph shows the north-east facing side of the bridge, and the bottom graph shows the south-west facing side.



Figure 2. Total number of *M. leibii* in each crevice of Bridge 2 from 17 May – 26 September 2012 in Monroe County, Tennessee. The top graph shows the north facing side of the bridge, and the bottom graph shows the south facing side.



Figure 3. Total number of *M. leibii* in Bridge 1, Graham County, North Carolina, with all crevices combined for each day from 17 May – 26 September 2012.



Figure 4. Total number of *M. leibii* in Bridge 2, Monroe County, Tennessee, with all crevices combined for each day from 17 May – 26 September 2012.



Figure 5. Total number of *M. leibii* in each crevice of Bridge 1, Graham County, North Carolina, and the corresponding mean daily crevice temperature (\pm SE), measured with iButtons, from 22 June – 22 July 2012. This is the time period in which all iButtons were functioning properly.



Figure 6. Total number of *M. leibii* in each crevice of Bridge 2, Monroe County, Tennessee, and the corresponding mean daily crevice temperature (\pm SE), measured with iButtons, from 22 June – 22 July 2012. This is the time period in which all iButtons were functioning properly.



Figure 7. Sociogram of half-weight association indices of observations of PIT-tagged *M. leibii* roosting in Bridge 1, Graham County, North Carolina, May – September, 2012. Dots represent identifiable individuals and lines represent the strength of the relationship. The thickness of the lines indicates the size of the association index.

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APPENDIX A: INDIVIDUAL ROOST CHARACTERISTICS

Table 1. Characteristics of all roosts found via radio telemetry in Graham County, North Carolina and Monroe County, Tennessee, 2011 - 2012. Definitions of characteristics are in Table 1, Chapter 1. Bat days are the number of days a bat was successfully tracked to that roost. Sex indicates the sex of any bats found at that roost. Bridge indicates the capture location (bridge 1 or bridge 2) of bats from that roost.

	Elevation	Distance to	Width	Height	Aspect		%		% Loose			
Roost	(m)	Road (m)	(m)	(m)	(°)	Slope (°)	Vegetation	% Solar	Rock	Bat Days	Sexes	Bridge
1	1140	4.1	58.8	12	179	65	40	70	20	28	F,M	2
2	1147	3.1	44.8	16	210	81	80	10	10	16	F,M	2
3	1006	3.7	39.9	17	140	47	20	70	10	13	М	1
4	986	1187	-	-	282	80	70	0	10	12	М	1
5	1441	163	45.1	7	135	49	80	70	60	12	М	1
6	1177	4.9	54.9	11	192	90	30	10	10	9	М	2
7	1121	29.3	109.4	30	204	75	80	10	10	7	М	2
8	913	13.7	110.6	12	110	55	80	-	30	6	М	1
9	1130	1.4	146.4	0.6	254	90	0	0	0	5	F	2
10	1150	6.1	96.0	18	155	85	40	70	10	2	М	1
11	1181	25.0	143.9	26	291	65	80	-	0	2	М	1
12	1323	14.1	20.1	8	324	63	80	0	30	2	М	1
13	1011	2.8	70.1	14	141	51	60	50	50	2	М	1
14	1332	25.0	2.4	16	340	68	80	40	0	1	F	1
15	1120	4.7	86.7	10	214	90	90	0	0	1	М	2