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Article

Microhabitat of *Myotis leibii* summer roosts at the southwestern periphery of their range

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Abstract

Understanding microhabitat use is needed to make sound conservation decisions for at-risk, patchy-habitat specialists, such as rock-habitat specialists. Rock habitats offer unique microclimatic refugia for reptiles and mammals. Eastern small-footed bats (*Myotis leibii* (Audubon and Bachman, 1842)) use rock roosts during the summer, but data on these summer roosts are lacking for this species classified as (critically) imperiled in several US states and Canadian provinces and globally endangered. Our goal was to characterize the structure and microclimate of *Myotis leibii* roosts at the southwestern periphery of their range. We predicted that *Myotis leibii* roost temperatures would be warmer and less variable than ambient temperatures and that solitary bats would use horizontal roosts cooler at night, whereas maternity group roosts would be vertical and warmer at night. During summers of 2019 and 2020, we recorded physical (e.g., width) and temperature attributes of 58 *Myotis leibii* roosts at 16 sites in the Ouachita Mountains. Crevice roosts of *Myotis leibii* had narrow dimensions like elsewhere in their range and roost temperatures (measured with iButtons) were warmer and more variable than ambient temperatures. Group roosts were larger and had more stable temperatures than solitary roosts. These findings may be useful for assessing population threats, monitoring roost suitability, identifying roost-rich areas that need protection, and even planning artificial roost structures where natural roosts are limited.

Key words: Eastern small-footed bat, microhabitat, *Myotis leibii*, rock roosts, summer roost, temperature

Introduction

Species that specialize in habitats with patchy distributions (i.e., habitats that are spatially disjunct on the landscape, such as high elevations, ephemeral pools, rock outcrops) are particularly at risk to habitat loss because habitat loss (quarrying, drainage, etc.) reduces the already limited availability of these patchy habitats across landscapes (Baguette 2004; Yanahan and Moore 2019). Populations of patchy-habitat specialists found along the margins of their geographic ranges are further jeopardized by climate change (Baguette 2004; Benedict et al. 2020; Sherpa et al. 2022) because the limits of thermal tolerance for a species may be reached around the margins of their distribution. In addition, abundance of species that rely on early succession forests, grasslands, or open rocky areas, including invertebrates (Korpela et al. 2015), reptiles (Pike et al. 2011), and mammals (Hunter and Cresswell 2014) has decreased as a result of growing forest cover due to altered natural ecological processes such as reductions in fire. Evaluating habitat suitability based solely on the landscape-scale can lead to incorrect estimates of a species' abundance, occupancy, and overall potential to persist (Ebert et al. 2013; Varner and Dearing 2014). Therefore, in conjunction with a landscape-scale evaluation, understanding microhabitat use and requirements is needed to make sound conservation decisions for patchy-habitat specialists at risk in our fast-changing Anthropocene (Smith and Ballinger 2001; Benedict et al. 2020).

Rock habitats are typically arranged in a patchy distribution across landscapes and offer unique microclimatic conditions such as moisture retention in crevices and reduce soil depth suppressing canopy formation (Mares 1997). Open canopies facilitate species-rich communities (Mares 1997; Korpela et al. 2015) and create basking opportunities for many ectotherm species (Smith and Ballinger 2001; Pike et al. 2011). Agglomerations of coarse rock debris, such as talus slopes, with layers of alternating solid material and air-filled spaces create a temperature gradient between the atmospheric surface and ground (Herz et al. 2003) allowing climatic refugia (Benedict et al. 2020). These rocky areas retain heat due to the high specific heat of rocks, which can benefit animals during cooler ambient temperatures. These types of rock habitats with ample crevices also provide predator refugia for many species, such as small mammals (Mares 1997) and reptiles (Smith and Ballinger 2001).

One such rock-habitat specialist is the Eastern small-footed bat (*Myotis leibii* (Audubon and Bachman, 1842)) as its summer roosting habitat consists of rock structures in forested hills and mountains (Saugey et al. 1993; Johnson et al. 2009; Moosman et al. 2015). Within these rock formations, diurnal roosts are often under rocks or in the cracks and crevices between rocks (Roble 2004; Whitby et al. 2013; Moosman et al. 2015). This species is threatened by White-nose syndrome in the winter (Turner et al. 2011; Alves et al. 2014). Furthermore, habitat of *Myotis leibii* may be threatened by mining and quarrying activities (Wickham et al. 2013), gas shale extraction (Moran et al. 2015), and possibly vegetation overgrowth of rock formations (Kearny et al. 2022). The species cannot be listed under the Endangered Species Act because data deficiencies in distribution, abundance, and roost requirements hinder the appropriate assessment of its conservation status. However, *Myotis leibii* is a rarely encountered species, considered globally endangered (Solari 2018) and classified as imperiled or critically imperiled in several Canadian provinces and US states, including Arkansas (Fowler and Anderson 2015; NatureServe 2022). Additional information is essential for the conservation of this species because natural roosting habitat is not well understood, particularly at the southwestern margin of their range (USFWS 2013; Fowler and Anderson 2015).

Bats generally select roosting microhabitats that facilitate thermoregulation, reproduction, and predator avoidance (Kunz 1982; Kerth et al. 2001; Lausen 2007). Many species of temperate insectivorous bats balance their high energetic demands through physiological adaptations (e.g., torpor) and behavioral adjustments such as roost selection and clustering (Wang and Wolowyk 1988; Kerth et al. 2001; Willis and Brigham 2007). Energy budgets of bats may be particularly challenging for females during the summer reproductive season, which increases the importance of selecting roosts that aid in energy conservation, optimize juvenile development, and protect from predators (Kunz 1982; Kerth et al. 2001; Olson and Barclay 2013). Females of many bat species form maternity groups from a handful (small group; Moosman et al. 2020) to thousands (colonies; Betke et al. 2008) of individuals to aid in offspring development; however, the degree to which group formation influences roost selection or whether selected roosts influence group formation is often difficult to determine (Olson and Barclay 2013).

Roost characteristics (e.g., microclimate, orientation, size) influence the selection of summer roosts by many bat species (Vaughan and O'Shea 1976; Kunz 1982; Chruszcz and Barclay 2002) and can vary with reproductive status and sex as thermal needs differ (Vaughan and O'Shea 1976; Olson and Barclay 2013). For example, western long-eared bats (*Myotis evotis* (H.Allen, 1864)) often roost among rocks in grasslands and change their roost preferences with reproductive condition. Pregnant *Myotis evotis* choose horizontal roosts (i.e., crevices whose longest dimension is horizontal) that warm quickly during the day (to reduce extended use of torpor and facilitate passive rewarming) and are cool at night. By contrast, lactating *Myotis evotis* choose vertical roosts (i.e., crevice oriented vertically) that stay warmer at night, which may keep nonvolant young warm (Chruszcz and Barclay 2002). Similarly, the western small-footed bat (*Myotis ciliolabrum* (Merriam, 1886)) selects rock roosts that aid in passive rewarming from torpor, i.e., with daytime roost temperatures that warm more quickly during lactation than pregnancy (Holloway and Barclay 2001; Lausen 2007).

Reproductive bats may also change their social behavior throughout the season (Kerth et al. 2001; Lausen and Barclay 2002; Olson and Barclay 2013). For example, female big brown bats (*Eptesicus fuscus* (Palisot de Beauvois, 1796)) often roost in groups during pregnancy and lactation and cluster less frequently during nonreproductive periods (Lausen and Barclay 2002). Similarly, female *Myotis leibii* tend to roost solitarily until parturition when they begin to cluster into small mother–pup groups of typically 3–4 bats although 7–10 individuals are not uncommon (Best and Jennings 1997; Moosman et al. 2020), and Moosman et al. (2015) even found one roost with ∼20 bats. Colonial or communal roosting by bats may inhibit heat loss, foster social relationships, and support rearing of young (Speakman et al. 1995; Garroway and Broders 2007; Popa-Lisseanu et al. 2008). However, communal roost sites (sun-exposed, ground roosts in rocks) increases predation risk from a wide range of generalist predators (Johnson et al. 2011; Lima and O'Keefe 2013), including snakes (USFWS 2013; Welch and Leppanen 2017). Small roost openings may help exclude predators and more than one opening may allow bats to escape from predators (Goldingay and Stevens 2009; Johnson et al. 2011; Hoeh et al. 2018).

Overall, roost selection is essential to fitness and population persistence of numerous bat species and understanding the roosting microhabitat requirements of a species may aid in conservation efforts (Kunz 1982; Chruszcz and Barclay 2002; Olson and Barclay 2013). Our first objective was to characterize roosts of *Myotis leibii* at the southwestern periphery of its range in the Ouachita Mountains of Arkansas, where roosting habits of *Myotis leibii* are not documented (Sasse et al. 2013) and may differ from other, nonperipheral study areas (Johnson et al. 2011; Whitby et al. 2013; Moosman et al. 2015). The second and third objectives were to determine how roost temperatures differed from ambient, and if solitary and group roosts differed in physical attributes or temperature. We predicted that *Myotis leibii* roost temperatures would be warmer and less variable than ambient temperatures (Sedgeley 2001; Webber and Willis 2018). We also predicted that roost characteristics would differ between solitary and group roosts. Specifically, we expected horizontal roosts cooler at night for solitary bats and vertical and warmer at night for maternity group roosts, similarly to roosts of *Myotis evotis* (Chruszcz and Barclay 2002) and *Eptesicus fuscus* (Lausen and Barclay 2002).

Materials and methods

Study area, sites, and roosts

Our study took place in summers of 2019 and 2020 in three mountainous regions of the greater Ouachita Mountains in west-central Arkansas: Rich and Black Fork Mountains, Mount Magazine, and Mount Nebo (Kearny et al. 2022). These mountains consist of folded and rugged formations of sandstone, shale, and chert and are east–west-oriented. Forests are predominantly pine–oak–hickory and there are extensive areas of planted loblolly pine (*Pinus taeda* L.; Fowler and Anderson 2015). Annual precipitation is 150.57 cm, with average spring precipitation of 48.97 cm and average summer precipitation of 33.78 cm. Based on data collected from 15 weather stations across the study area from 2006 through 2020, average spring temperature was 15.93 °C and average summer temperature was 26.42 °C (National Centers for Environmental Information and National Oceanic and Atmospheric Administration 2020).

We reviewed orthoimagery of the three mountainous regions to identify study sites. We considered each talus slope, delimited by the surrounded forest, as a site. These sites (i.e., talus slopes) averaged 0.6 ± 0.1 ha (range 0.3–15.7 ha). We considered sites accessible if the slope was <35% and a road or trail was present within 1.5 km (Kearny et al. 2022). Johnson et al. (2011) reported consecutive roosts up to 204 m apart; thus, the selected sites were ≥250 m apart and placed five to ten random points in these sites. We navigated to each point with Garmin 64s handheld global positioning system units and marked a 6 m radius circle with chalk to conduct searches (Moosman et al. 2015). A team of two looked for roosting bats in all the cracks and crevices within each plot with flashlights. Upon discovering a bat, we determined the species using Morgan et al.'s (2019) key. We recorded the number of bats within the roost and any noticeable characteristics of individuals (e.g., behaviors or unique marks). Because adult male bats typically roost alone (Moosman et al. 2020), any roost containing two or more bats was considered a maternity group, i.e., a group of only adult females, possibly with pups (Moosman et al. 2020).

Roost variables

For each roost, we recorded the following variables using a measuring tape (in cm): maximum length, width, and depth of the roost opening. We categorized crevice orientation as vertical or horizontal when orientation was within ±20° of horizontal or vertical plane in relation to the ground and as diagonal if it did not fall into one of these categories (Johnson et al. 2011). We also noted if the roost had multiple openings and the presence or absence of bat feces.

We deployed 74 iButton temperature data loggers (DS1921G-F5 and DS1923; Maxim Integrated, San Jose, CA) during the 2020 field season to record roost and site-level ambient temperatures ($n = 58$ roosts across 16 sites). These iButtons (17.35 mm in diameter, 5.89 mm in height) record temperature up to 85 °C with a 0.5 °C resolution. We conducted trials to ensure precise calibration among iButtons before field deployment. After collecting roost measurements, we attached pipe cleaners to uniquely marked iButtons that were inserted into the roost, away from direct solar exposure and at a similar depth to the bats without disturbing bats or blocking their exits. We taped the trailing end of the pipe cleaner to rocks with flagging tape that was visible for later retrieval. For each site where we deployed iButtons in roosts, we stationed another iButton on rocks about 5 m from the site edge to collect the ambient temperatures. We placed ambient iButtons under the forest canopy to ensure no direct solar exposure. All iButtons recorded temperatures at 30 min intervals for more than or equal to five consecutive nights. We retrieved all iButtons to download these temperature data.

Data analysis

To determine how roost and ambient temperatures differed, we used package lme4 (Bates et al. 2015) in statistical program R (R Core Team 2019) and built mixed-effect logistic regressions (generalized linear-mixed models (GLMMs) with a binomial error distribution), in which iButton location (roost = 1 versus ambient = 0) was the response variable. We used the following predictor variables: maximum daytime temperature, coefficient of variation (CV) of daytime temperatures, minimum nighttime temperature, CV of nighttime temperatures, and the number of 30 min intervals it took for nighttime temperature to drop from maximum to minimum (cool length). We defined daytime and nighttime as 0600–1930 hours and 2000–0530 CDT, respectively. We only considered single-predictor models because of significant correlations among temperature variables (Spearman correlation tests; $\alpha = 0.05$; Supplementary Table S1). To account for potential pseudoreplication among iButtons placed at the same site, we used site ID as a random effect. Maximum daytime and minimum nighttime temperatures likely occurred at different times of day for roosts and ambient locations. Therefore, we determined means of each temperature variable for roost and ambient locations in steps: (1) over 0600–1930 (daytime) or 2000–0530 (nighttime), (2) across days of sampling, (3) across roosts at the same site to avoid a bias among sites with a different number of roosts/iButtons.

To assess if temperature differed between group and solitary bat roosts, we used GLMMs with a binomial error distribution, in which roost type (solitary roost = 1 and group roost = 0) was the response variable with site ID included as a random effect. Fixed effects were the same daytime and nighttime temperature variables described above, except that we only included data from the 10 sites that had at least one of each roost type.

Finally, to assess if group and solitary roosts differed in physical characteristics, we used generalized linear models without a random effect (site ID was associated with no variance for this analysis). We included all roosts in this analysis. Roost type was the response variable and predictors were roost width, depth, length, and orientation. However, models included only one quantitative predictor because of significant correlations among physical roost characteristics (Spearman correlation tests; $\alpha = 0.05$; Supplementary Table S1). For models with combinations involving roost orientation (a categorical variable), we used a variance inflation factor < 2, to check for collinearity issues.

For all analyses, we identified which variables best characterized *Myotis leibii* roosts using model selection and an information-theoretic approach based on an Akaike Information Criterion corrected for small samples (AIC_c; Burnham and Anderson 2002) using the AICcmodavg package (Mazerolle 2019) in statistical program R (R Core Team 2019). The best model had the lowest AIC_c; however, if two models, including those with an additive effect of roost orientation and a quantitative physical characteristic, had a $\Delta\text{AIC}_c \leq 2$, we considered them equivalent and retained the most parsimonious, single-predictor model (Burhnam and Anderson 2002). We report all means and slope estimates *SE*.

Ethics approval

The US Forest Service and Arkansas State University Institutional Animal Care and Use Committees approved all protocols (USFS IACUC 2019-006; A-State IACUC FY18-19-213). We followed mammal safety guidelines (Sikes and the Animal Care and Use Committee of the American Society of Mammalogists 2016) and conducted this study under appropriate permits (Arkansas Game and Fish Commission Scientific Collection Permit 010820191/011420205; Arkansas Department of Parks, Heritage and Tourism Collection Permit 068-2020).

Results

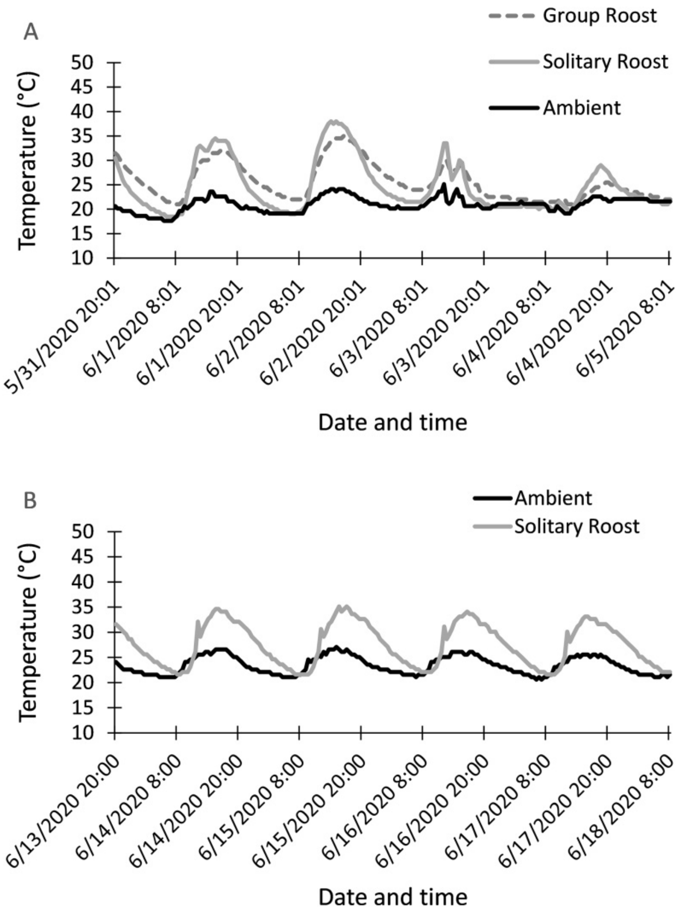
We found 91 rock crevice roosts containing a total of 150 *Myotis leibii*. Of the 91 *Myotis leibii* roosts, 58 consisted of a solitary bat and 33 were groups of two to seven individuals. Among all roosts, average crevice length was 34.23 ± 1.61 cm, average depth was 32.61 ± 2.01 cm, and width was 1.54 ± 0.08 cm. Roosts were predominantly vertically oriented (45.05% vertical, 27.47% horizontal, 27.47% diagonal). We noted bat feces inside 14 roosts and in 5–10 unoccupied crevices (not considered roosts in this study) at sites with *Myotis leibii* present. One roost had a single opening and appeared as a nook-like recess in the rock. Most roosts were crevices between boulders that had multiple openings.

Both roost and ambient temperatures decreased throughout the evening, reaching minima during the early morning and maxima between 1500 and 1700 CDT (Fig. 1; Supplementary Fig. S1). Roosts that had higher daytime maximum temperatures stayed warmer later into the night. All single-covariate models comparing roost and ambient temperatures performed better than the null model, suggesting that roosts differed from ambient locations in all considered temperature variables (Table 1). Generally, roosts had higher temperatures and were more variable than ambient (Table 2). However, the best model differentiating roosts' temperatures from ambient temperatures was the maximum daytime temperature model (Table 1). The probability of a location to be a roost (versus an ambient location) increased as maximum daytime temperature increased (Fig. 2A) or, in other words, maximum daytime temperature was greater in roosts than at ambient locations.

Using temperature data from 10 sites where both roost types (solitary and group) were present, both models based on daytime temperatures in roosts performed better than the null model (Tables 1 and 2). Overall, solitary roosts had a higher maximum daytime temperature and a higher CV of daytime temperatures (Tables 1 and 2). In other words, a roost had a higher probability of containing a solitary bat over a group of *Myotis leibii* as the maximum daytime temperature in roosts increased and as the CV of daytime temperature increased (Figs. 2B and 2C).

Group and solitary bat roosts also differed in physical characteristics (Tables 3 and 4). The best model included only length. The probability that a roost contained a solitary bat versus a group of *Myotis leibii* decreased as crevice length increased (−0.04 ± 0.02; Fig. 2D). Overall, smaller roosts were more likely to contain solitary roosting *Myotis leibii* versus two or more bats. Although orientation was included in a model equivalent in AIC to the best model, the model with orientation as a single predictor did not perform better than the null model, indicating that this variable did not differ between solitary and group roosts.

Fig. 1. Example temperatures of Eastern small-footed bat (*Myotis leibii*) solitary and group roosts (grey lines) and corresponding ambient temperatures (black line) over time at Mount Nebo site 503 (top; panel (A)) and Rich Mountain site 3 (bottom; panel (B)), Arkansas, during summer 2020.



Discussion

Rock roosts of *Myotis leibii* in the Ouachita Mountains were most often in narrow crevices with multiple openings. Average width of *Myotis leibii* roosts were within the expected range for the species (0.75–4 cm; Moosman et al. 2015) and similar to the width of roosts used by *Myotis ciliolabrum* in the western United States (<3.5–9 cm; Holloway and Barclay 2001). To our knowledge, no studies have explicitly mentioned presence of multiple openings of *Myotis leibii* roost. However, based on descriptions (e.g., flat rocks laying on a solid rock surface are likely open on more than one side), the

Table 1. Generalized linear-mixed models (with individual site as a random effect) comparing temperature variables used (A) between roosts and ambient and (B) between solitary and group roosts of Eastern small-footed bat (*Myotis leibii*) during summer 2020 in west-central Arkansas.

	(A) Roost versus Ambient				(B) Solitary versus Group			
Predictor	AIC_c[a]	ΔAIC_c[b]	ω_i[c]	Slope[d]	AIC_c[a]	ΔAIC_c[b]	ω_i[c]	Slope[d]
Day maximum[e]	273.63	0.00	1.00	0.51 ± 0.07	371.58	0.00	0.57	0.06 ± 0.03
Day CV[e]	297.62	23.99	<0.01	0.30 ± 0.04	372.62	1.05	0.34	0.05 ± 0.02
Night CV	345.53	71.89	<0.01	0.43 ± 0.05	434.37	62.79	<0.01	0.04 ± 0.03
Cool length	451.30	177.66	<0.01	0.25 ± 0.04	435.37	63.80	<0.01	−0.07 ± 0.05
Night minimum	489.84	216.21	<0.01	0.22 ± 0.06	436.36	64.78	<0.01	−0.03 ± 0.04
Null	505.24	231.61	<0.01	NA	435.04	63.47	<0.01	NA

[a] Akaike Information Criterion corrected for small samples (AIC_c).
[b] Difference between AIC_c and lowest overall AIC_c.
[c] AIC_c weight.
[d] Slope is the untransformed (logit) parameter estimate ± *SE*.
[e] Best overall model for the roost versus ambient analysis is maximum daytime temperature, whereas the best models for the solitary versus group roost analysis are maximum daytime temperature and coefficient of variation of daytime temperatures (equivalent models; $\Delta AIC_c < 2$).

Table 2. Mean (±*SE*) temperature variables for all Eastern small-footed bat (*Myotis leibii*) roosts, nearby ambient locations, solitary roosts, and group roosts per site, in summer 2020 in west-central Arkansas.

Temperature variables	Roost	Ambient	Solitary	Group
Day maximum (°C)	33.3 ± 1.0	25.2 ± 0.7	33.5 ± 1.3	31.9 ± 1.3
Day maximum (°C)	33.3 ± 1.0	25.2 ± 0.7	33.5 ± 1.3	31.9 ± 1.3
Cool length[b]	17.2 ± 0.3	14.1 ± 0.7	17.0 ± 0.4	17.5 ± 0.2
Night CV[a]	10.4 ± 0.7	4.0 ± 0.3	10.5 ± 0.7	9.6 ± 0.9
Night minimum (°C)	20.9 ± 0.6	19.4 ± 0.5	20.3 ± 0.9	20.9 ± 1.0

Note: The solitary and group columns were based on 10 sites that contained at least one of each roost type (solitary and group), whereas the roost and ambient columns were based on all sites.
[a] Coefficient of variation is the standard deviation divided by the mean.
[b] Number of 30 min intervals between nighttime maxima and minima.

Fig. 2. Eastern small-footed bat (*Myotis leibii*) roost probabilities based on generalized linear-mixed models during summer 2020 in west-central Arkansas. Dashed lines represent the 95% confidence interval. Probability of *Myotis leibii* roost versus an ambient location based on maximum daytime temperature (A), probability of *Myotis leibii* roosting solitarily versus in a group based on maximum daytime temperature (B), probability of *Myotis leibii* roosting solitarily versus in a group based on the coefficient of variation of daytime temperature (C), and probability of *Myotis leibii* roosting solitarily versus in a group based on crevice length (D).

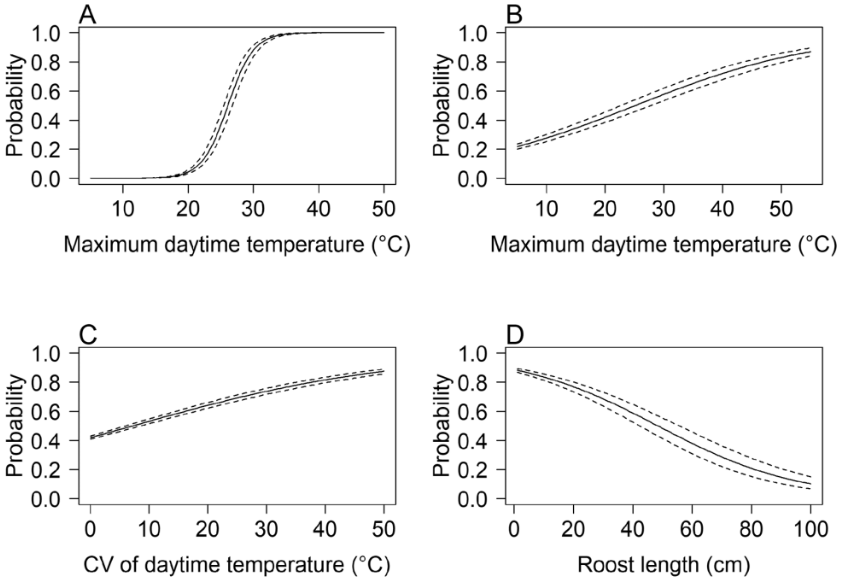


Table 3. Generalized linear model summary results of physical and temporal roost characteristics to distinguish Eastern small-footed bat (*Myotis leibii*) solitary roosts from group roosts during summer 2020 in west-central Arkansas.

Model	AIC_c[a]	ΔAIC_c[b]	ω_i[c]
Length[d]	115.15	0.00	0.51
Length + orientation	117.13	1.98	0.19
Width	117.48	2.33	0.16
Width + orientation	118.89	3.74	0.08
Depth	121.20	6.04	0.02
Null	121.24	6.09	0.02
Orientation	122.73	7.57	0.01
Depth + orientation	123.29	8.13	0.01

[a] Akaike Information Criterion corrected for small samples (AIC_c).
[b] Difference between AIC_c and lowest overall AIC_c.
[c] AIC_c weight.
[d] Best model (lowest ΔAIC_c and most parsimonious).

Table 4. Mean (±*SE*) roost characteristics and most frequent orientation for Eastern small-footed bat (*Myotis leibii*) roosts containing a solitary bat and those containing multiple bats (≥2 individuals).

Roost characteristic	Solitary roost	Group roost
Length (cm)[a]	30.78 ± 1.68	40.28 ± 3.06
Width (cm)[a]	1.47 ± 0.10	1.65 ± 0.15
Depth (cm)[a]	30.92 ± 2.67	35.55 ± 2.92
Orientation[b]	Vertical	Vertical

Note: Data were collected during the summer of 2019 and 2020 in west-central Arkansas.
[a] Models with length, width, and depth variables performed better than the null (Table 3).
[b] Orientation categories were vertical, horizontal, and other.

presence of multiple openings can be assumed in many cases (Johnson et al. 2011; Whitby et al. 2013; Moosman et al. 2015). Size of roost opening may be strongly related to body size and exclusion of heterospecifics (Goldingay and Stevens 2009), although multiple small roost openings may also facilitate predator avoidance (Goldingay and Stevens 2009; Johnson et al. 2011; Hoeh et al. 2018).

In addition to width, structure (e.g., rock crevices) of *Myotis leibii* roosts at the periphery of their range (i.e., in the Ouachita Mountains) was similar to *Myotis leibii* roosts described in other areas of their range (Johnson et al. 2011; Whitby et al. 2013; Moosman et al. 2015). In West Virginia, *Myotis leibii* were found in cracks on cliff faces and crevices between rocks on the ground (Johnson et al. 2011) and *Myotis leibii* were found between large, stable boulders in Virginia (Moosman et al. 2015). However, Whitby et al. (2013) reported *Myotis leibii* roosting under flat rocks that needed to be flipped during searches. We found roosts in crevices between rocks that were small enough to be moved by observers. Roosts among these smaller, loose rocks that are easily moved by humans or large wildlife may pose a risk of disturbance and injury to bats, including during searches (Moosman et al. 2015). Furthermore, we found *Myotis leibii* primarily roosting in vertically oriented crevices, regardless of group size. By contrast, Johnson et al. (2011) reported evenly distributed numbers of *Myotis leibii* roosts among vertical, horizontal, and diagonal orientations. In studies of both *Myotis evotis* and fringed bats (*Myotis thysanodes* Miller, 1897), roost orientation changed with changes in reproductive status: pregnant females choose horizontal roosts, whereas lactating and post-lactating females more likely roost in vertical crevices (Chruszcz and Barclay 2002; Lacki and Baker 2007). Therefore, selection of crevice orientation and roost structure (e.g., size and number of openings), which influence roost microclimate (Kerth et al. 2001; Boyles 2007; Lausen 2007), may change as thermal needs change with reproductive status (Chruszcz and Barclay 2002; Lausen and Barclay 2002; Lacki and Baker 2007) and additional research is warranted.

Roost temperature is an important factor influencing selection of diurnal summer roosts by many bat species (Vaughan and O'Shea 1976; Kunz 1982; Chruszcz and Barclay 2002). As predicted, maximum daytime temperatures were greater in *Myotis leibii* roosts than in ambient locations. The high specific heat of rocks could also explain greater maximum daytime temperatures as solar radiation heated rocks (Schärli and Rybach 2001; Lausen and Barclay 2002; Radmanovic et al. 2014). Similarly, although both roost and ambient iButtons were in the shade (iButtons were usually shaded by rocks in roosts), differences in canopy cover may partially explain higher daytime maxima and relatively similar (but still higher) minima compared with ambient locations (Kerth et al. 2001; Moosman et al. 2015). Cloud cover may have also modulated the difference between roost and ambient temperature. Although roost temperatures were warmer than ambient temperatures as predicted, roost temperatures were more variable, which was not expected. *Myotis leibii* often roost in hibernacula with greater temperature variability than many other *Myotis* (Best and Jennings 1997; Johnson et al. 2016). This tolerance or preference for greater temperature variability might also apply to summer roosts, as seen in *Eptesicus fuscus*, another rock-roosting species. *Eptesicus fuscus* tend to hibernate in roosts with high temperature variability (Johnson et al. 2016) and seem tolerant of the higher daily temperature fluctuations in buildings relative to rock crevices (Lausen and Barclay 2006).

Although some species of bats use roosts with more stable temperatures than ambient during the reproductive season (Sedgeley 2001), *Myotis leibii* may be adapted for more extreme heterothermy (i.e., with high variability in body temperature regulation) than larger bodied or more gregarious bat species. This may be possible through their frequent use of shallow daily torpor (facilitated by cooler temperatures) and passive warming (enabled through warm temperatures; Solick and Barclay 2006; Lausen 2007). Solick and Barclay (2006) suggest that the initial drop in body temperature seen in shallow torpor used by reproductive *Myotis evotis* (a small, solitary, rock-roosting bat) may produce energy savings that outweigh reproductive costs.

Overall, warmer roost temperatures are often beneficial to reproductive female bats during the active season because low temperatures and associated deeper levels of torpor can delay juvenile development (Kerth et al. 2001; Lausen and Barclay 2006; Webber and Willis 2018). Although roost and ambient temperatures followed a similar pattern (i.e., warming during the day and cooling in the evening), roosts tended to remain warmer later into the afternoon and evening. This delayed cooling likely facilitates passive warming that saves bats energy before emerging at sunset to forage (Vaughan and O'Shea 1976; Moosman et al. 2015). Roosts also tended to have a slower nighttime cooling rate (greater cool length) and warmer nighttime temperatures than ambient temperatures, as expected based on the high specific heat of rocks. Generally, roosts reached minimal temperatures in the morning, possibly facilitating torpor by bats returning from nightly foraging (Hamilton and Barclay 1994). Moosman et al. (2015) reported a similar pattern while monitoring skin temperatures of *Myotis leibii* from June to October, with both skin and ambient temperatures reaching minima around dawn and maxima after noon.

Both physical and microclimate roost characteristics differed between solitary and group roosts, with group roosts being in longer crevices with a larger volume than solitary roosts. Furthermore, temperature was more variable for solitary roosts (higher daytime maxima and slightly cooler daytime minima) than for group roosts. These physical and microclimate differences correlate; roosts that are deeper and have larger volumes provide more stable microclimates (Lausen and Barclay 2002; Lausen 2007). However, large group roosts may be warmer than small, solitary roosts when bats are present because the body heat of clustering bats may warm the space (Willis and Brigham 2007; Webber and Willis 2018). Large roosts can physically host more bats, which may facilitate social relationships, and the more stable microclimates could benefit lactating bats by relying less on torpor that inhibits milk production (Lausen and Barclay 2002; Willis and Brigham 2007; Webber and Willis 2018). The differences between solitary and group roosts may have reflected a difference in reproductive status (i.e., solitary pregnant versus clustered lactating females) but also in sex (i.e., clustered lactating females versus solitary males). We were not able to determine sex because the COVID-19 pandemic prevented us from extracting bats from roosts as a precaution to minimize potential virus spread when interspecies transmission was unknown (Abdel-Moneim and Abdelwhab 2020). This comparison of solitary versus group roosts is novel and future research could help fine-tune the habitat requirements to reflect potential sex-specific needs.

We found most bats close to crevice openings, which may be a result of detectability bias (bats at the surface are more easily seen than those deep in crevices). Preference in roosting depth may also reflect microclimate preference. Behavioral shifts associated with microclimate preferences are seen in other talus dwellers, such as American pika (*Ochotona princeps* (Richardson, 1828)) that spend more time close to the surface during the middle of the day when temperatures are warmer than in deep crevices (Benedict et al. 2020). Alternatively, bats may have selected to roost closer to crevice openings to detect predators. Bats occasionally retreated deeper into crevices during roost assessments, suggesting a larger roost volume may be used to avoid predators. To better assess the conservation status and needs of *Myotis leibii*, future research is needed to quantify mortality from predators during the reproductive season and to identify this bat's responses to predators of various types (Scott 2022).

Although our study of *Myotis leibii* roosting was conducted in the southwestern periphery of their range, they appeared to roost similarly to *Myotis leibii* in other parts of their range, including the northeastern US (Moosman et al. 2015). As previously reported, solitary bats and maternity groups use narrow crevices between rocks, and larger roosts had more stable microclimates. However, our study also uncovered the importance of multiple openings to the roosts, the delayed cooling of rocks and its likely role in passive rewarming, and this species' tolerance for high temperature variability in the roost. Overall, warm roosts in tight spaces most likely facilitated energy conservation and may have provided protection from predators. Finally, we found that group roosts are the larger and more thermally stable crevices, possibly to facilitate social relationships and lactation.

Understanding microhabitat use and requirements is essential in determining habitat suitability and species distribution (e.g., occupancy), particularly for patchy-habitat specialists at the periphery of their range. Population viability metrics (e.g., abundance, fecundity) cannot be assessed without knowing species' needs. Thus, microhabitat information is crucial in determining overall species ability to persist and in mitigating potential viability impediments, such as habitat loss or fragmentation and climate change (Baguette 2004; Ebert et al. 2013; Varner and Dearing 2014). For example, if roosts for *Myotis leibii* become limited further, alternative roost sites may be needed. We recommend designing artificial roost sites, such as rock piles or concrete structures (e.g., Thomson 2013) with narrow crevices oriented both horizontally and vertically offering a thermal gradient. Providing such additional roost sites that may otherwise be limited may help boost reproductive success, and therefore, curb population declines of not only *Myotis leibii* but also other rock-habitat specialists with similar microhabitat preferences. Finally, these findings can also be used to monitor roost microhabitat suitability and identify suitable roost-rich areas that need protection.

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Data availability

Code and data generated or analyzed during this study are available from the corresponding author upon reasonable request.

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Competing interests

The authors declare there are no competing interests.

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Supplementary material

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