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Research Article

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Characterizing diurnal roosts of male Little Brown Myotis (*Myotis lucifugus*) during summer

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Abstract

Shelter is one critical aspect of an animal's habitat, providing refuge from predators and weather, protection for offspring, and aiding in physiological homeostasis. During the day, bats find shelter in roosts—spaces created under tree bark, in tree cavities, or between rocks—after spending the night searching for food. Finding a roost with a microclimate that enables bats to remain in their thermoneutral zone could reduce energetic demands or allow bats to allocate energy to other activities such as reproduction and fighting disease. We aimed to characterize the structural features and microclimate (i.e., temperature) of roosts used by male Little Brown Myotis (*Myotis lucifugus*) during the summer and determine whether bats select certain characteristics disproportionally to what is available at different spatial scales. During the summers of 2017 and 2018, we radio-tracked 34 male *M. lucifugus* in Lodgepole Pine-dominated forests. We located at least 1 roost for 20 individuals (average = 2.85 roosts/bat, range = 1 to 6). Although snags were available, most of the roosts were in rock features (86% in rocks, 14% in trees or snags). Male *M. lucifugus* were more likely to select rock roosts with less canopy closure that were closer to water compared to available roosts on the landscape. They also selected roosts in rock features occurring within larger areas of rock cover that had wider entrances and access to crevices that faced the sky; these roosts also had warmer microclimates relative to other locations available on the landscape. Crevices that allow the bat to bask in the sun and change locations within a roost, minimizing energy needed for active thermoregulation, could be very beneficial for individuals recovering from diseases such as white-nose syndrome. Our work indicates that rock features provide habitat for male *M. lucifugus* during summer; other studies have shown that bats roost in these features during autumn and winter, further supporting their importance. By protecting these important rock structures, managers can help bats meet their habitat needs throughout the year.

Key words: bat, Chiroptera, habitat selection, microclimate, *Myotis lucifugus*, roost, scree, thermoregulation.

Caracterizando dormideros diurnos de machos de *Myotis lucifugus* durante el verano

Resumen

Los refugios son un aspecto crítico del hábitat de un animal, proporcionando protección contra los depredadores y el clima, resguardo a la descendencia, y ayudan en la homeostasis fisiológica. Durante el día, los murciélagos encuentran refugio en dormideros—espacios creados debajo de la corteza de árboles, en las cavidades de los árboles, o entre rocas—después de pasar la noche buscando comida. Encontrar un refugio con un microclima que permita a los murciélagos permanecer en su zona termoneutral podría reducir las demandas energéticas o permitir que los murciélagos asignen energía a otras actividades, como la reproducción y la lucha contra enfermedades. Nuestro objetivo fue caracterizar los atributos estructurales y el microclima (i.e., temperatura) de los dormideros utilizados por los machos de *Myotis lucifugus* durante el verano y determinar si los murciélagos seleccionan ciertas características desproporcionadamente a lo que está disponible en diferentes escalas espaciales. Durante los veranos de 2017 y 2018, a través de radio-telemetría, seguimos a 34 machos de *M. lucifugus* en bosques dominados por pinos contorta. Ubicamos al menos un dormidero para 20 individuos (promedio = 2.85 dormideros/murciélago, rango = 1 a 6). Aunque había tocones arbóreos disponibles, la mayoría de los dormideros estaban en rocas (86% en rocas, 14% en árboles o tocones). Los machos de *M. lucifugus* tenían más probabilidad de seleccionar dormideros en rocas con menos cobertura del dosel que estaban más cerca al agua, en comparación con los dormideros disponibles en el paisaje. También seleccionaron dormideros en rocas que ocurren dentro de áreas más grandes de cubierta rocosa, con entradas más amplias y acceso a grietas expuestas al cielo; estos dormideros también tenían microclimas más cálidos en relación con otras ubicaciones disponibles en el paisaje. Grietas que permitan al murciélago asolearse y cambiar ubicaciones dentro de un dormidero, minimizando la energía necesaria para la termorregulación activa, podrían ser muy beneficiosas para los individuos que están recuperándose de enfermedades como el síndrome de la nariz blanca. Nuestro trabajo indica que las rocas proporcionan

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hábitat para los machos de *M. lucifugus* durante el verano; otros estudios han demostrado que los murciélagos se posan en estas rocas durante el otoño y el invierno, lo que respalda aún más su importancia. Al proteger estas importantes estructuras rocosas, los manejadores de recursos naturales pueden ayudar a los murciélagos a satisfacer sus necesidades de hábitat durante todo el año.

Palabras Claves: Chiroptera, dormidero, microclima, murciélago, *Myotis lucifugus*, rocas, selección de hábitat, termorregulación.

Habitat is a fundamental component of animal natural history, and successful conservation efforts consequently require an understanding of how animals use and select habitat (Pulliam and Danielson 1991; Krebs 2009). Shelter is one critical aspect of habitat, providing refuge from predators and weather, as well as protection for offspring (Alcock 2001). For example, bats seek shelter in roosts during the day after spending the night searching for food (Vaughan and O'Shea 1976; Randall et al. 2014). The availability and quality of roosts influence the distribution and abundance of bat populations (Kunz 1982; Ruczynski 2006; Barclay and Kurta 2007). High-quality roosts provide access to food and water and the capacity for social interactions (Sedgeley and O'Donnell 2004).

Bats are endotherms with a large surface area to volume ratio and thus quickly lose heat and water to the environment (Ruczynski 2006; Wilcox and Willis 2016; Webber and Willis 2018). The microclimate (e.g., temperature, humidity) within the roost therefore plays an important role in thermoregulation (Sedgeley and O'Donnell 2004). Energetic demands of a bat differ based on sex and reproductive status; reproductively active females and their young often roost separately from males and nonreproductive females (Randall et al. 2014). Bats can save energy by roosting communally or entering torpor or hibernation (Hamilton and Barclay 1994; Vonhof and Barclay 1997; Chruszcz and Barclay 2002; Alston et al. 2022). Alternatively, finding a roost with a microclimate that minimizes the need to thermoregulate could reduce energetic demands or allow bats to allocate energy to other activities such as reproduction and fighting disease (Kunz 1982; Sedgeley and O'Donnell 2004; Ingersoll et al. 2010).

When searching for a roost, bats can make use of their ability to fly long distances, perceiving resources at multiple spatial scales within a short amount of time. By identifying and quantifying habitat features at different scales, we can better understand this selection process. Further, understanding which specific habitat features are important for selection and use by bats at different spatial scales is essential to develop useful conservation and management strategies, especially as threats including white-nose syndrome, wind energy development, climate change, and habitat loss continue to increase (Crampton and Barclay 1998; Jung et al. 2014). Although characteristics of bat roosts have been well-studied in the eastern United States, we know much less about how bats select roosts in the West (Neubaum 2018).

Western bat species may use different roosting features than bats in the east, given that the topography of the Rocky Mountains provides extensive rocky areas (Theobald et al. 2015; Neubaum 2018). Rocks may provide warm microclimates as well as stable temperatures (Alston et al. 2022) that could create high-quality summer roosts for certain species of bats (Schwab 2006; Snider et al. 2013). Some western bat species have been documented using rock features as roosts during summer (e.g., Lausen and Barclay 2002; Solick and Barclay 2006; Lacki and Baker 2007; Schorr and Siemers 2013) and autumn (Neubaum et al. 2006; Johnson et al. 2017; Neubaum 2018), and some species use these features as hibernacula (Neubaum et al. 2006; Neubaum 2018; Blejwas et al. 2021). However, we do not have a complete understanding of how all bat species use these features in the West.

Myotis lucifugus (Little Brown Myotis) is now threatened by regional and global extinction; this species is listed as Endangered under the Species at Risk Act by the Committee on the Status of Endangered Wildlife in Canada (Environment Canada 2015; Slough et al. 2023) and under review in the United States for listing under the Endangered Species Act (Kunz and Reichard 2010; USFWS 2024), despite having once been one of the most common species of bats in eastern North America (Frick et al. 2010). Little Brown Myotis have been observed roosting in rock features during the summer (Randall et al. 2014; Johnson et al. 2017, 2019), autumn (Johnson et al. 2017; Neubaum 2018), and winter as actual or presumed hibernacula (Neubaum 2018; Blejwas et al. 2021). Johnson et al. (2019) documented male Little Brown Myotis roosting in rocks during summer and explored temperatures of the roosts and bats in these places. However, to our knowledge, no studies explicitly focus on selection of summer rock roosts by male Little Brown Myotis, comparing characteristics of used roosts to what is available on the landscape. Given that roosting sites may limit abundance of bat populations (Kunz 1982; Barclay and Kurta 2007), we aimed to characterize roosts used by male *M. lucifugus* during the summer and determine whether bats select certain characteristics at different spatial scales (landscape, plot, roost) disproportionally to what is available. We also focused specifically on connecting characteristics of used roosts to microclimate—namely temperature—and predicted that male *M. lucifugus* would select roosts with characteristics that created warmer conditions.

Materials and methods

Study areas

We captured bats and conducted roost surveys in 2 drainages within the southwestern and central portion of the Rocky Mountains in Montana—Moose Creek in the Little Belt Mountains and Little Blackfoot River in the Boulder Mountains (Fig. 1). Both drainages are within the Helena-Lewis and Clark National Forest. The Little Belt and Boulder Mountains are similar in elevation, topography, vegetation, and general weather patterns (NOAA 2019; USGS 2019); we used covariates in models to characterize variation. Elevation ranges from 1,158 to 2,787 m in the Little Belt Mountains and 1,213 to 2,652 m in the Boulder Mountains. The western portion of the Little Belt Mountains is dominated by Paleozoic Mississippian rocks and Middle Proterzoic Ravalli and Lower Belt Groups (Hyndman and Thomas 2020). The study area in the Boulder Mountains is dominated by the Cretaceous Boulder batholith and Elkhorn Mountains Volcanics, as well as volcanic rocks from the Tertiary (Hyndman and Thomas 2020). Although geology differs between the 2 ranges, rock structures (i.e., cliffs, rock outcrops, and scree) are similar, providing a large quantity of exposed rock with both cavities and crevices. Foothills in both drainages are composed of lower montane grassland and sagebrush steppe, transitioning into Lodgepole Pine (*Pinus contorta*)- and Douglas-fir (*Pseudotsuga menziesii*)-dominated forests

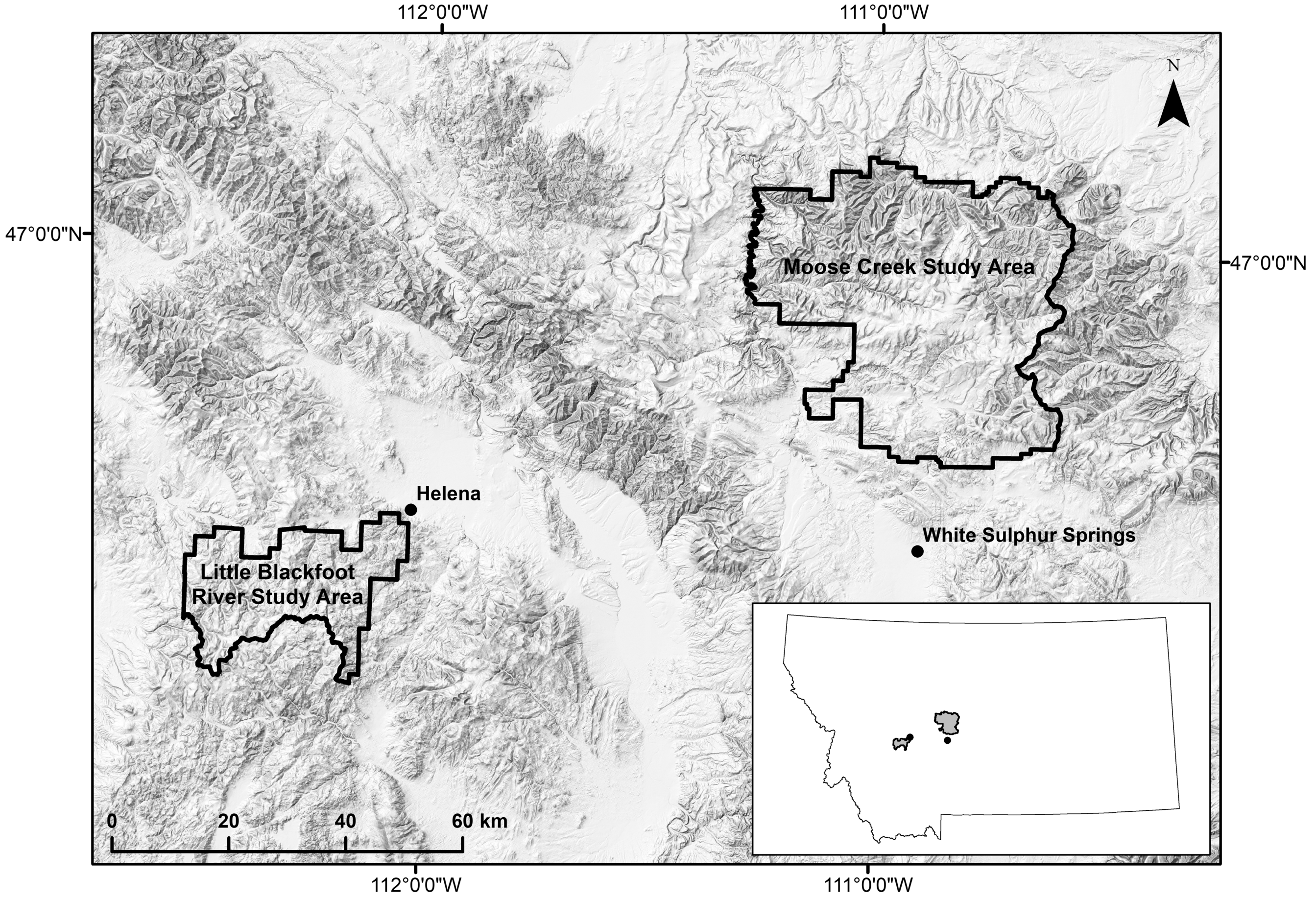

Fig. 1. Locations of radiotelemetry work on male *Myotis lucifugus* in the Little Blackfoot River study area in the Boulder Mountains (left, outlined in black) and the Moose Creek study area in the Little Belt Mountains (right, outlined in black). 2017 to 2018, west-central Montana (inset map).

with scattered patches of montane grassland at higher elevations (MTNHP 2017). General weather patterns are similar between the 2 ranges (NOAA 2019). Average annual precipitation between 2008 and 2018 was 894.2 mm in the Little Belt Mountains (NOAA Global Summary of the Year, Onion Park, Station No. USS0010C22S) and 656.5 mm in the Boulder Mountains (NOAA Global Summary of the Year, Frohner Meadows, Station No. USS0012C13S). Average annual, average annual minimum, and average annual maximum temperatures for the past 11 years were low in both ranges (i.e., 4.3/−1.7/10.2 °C in the Boulder Mountains and 2.6/−2.8/7.9 °C in the Little Belt Mountains).

Both areas have been heavily impacted by Mountain Pine Beetle (*Dendroctonus ponderosae*; Johnson and Wittwer 2006; USDA Forest Service 2018). Few human-made structures exist, and public vehicular road access is limited. Of the 15 bat species in Montana, 12 potentially occur within these areas (Bachen et al. 2018).

Bat capture

We captured bats in the Moose Creek area of the Little Belt Mountains between June and August of 2017 and in the Little Blackfoot River area of the Boulder Mountains between June and August of 2017 and 2018. We focused mist net efforts over sections of slow-moving water created by beaver activity or backwater channels where we were most likely to capture *M. lucifugus* while foraging and drinking (Fenton and Bell 1979; Mackey and Barclay 1989). However, we also netted sections of river corridor with fast-flowing water with the hope that bats would be using these features as flight paths. We deployed 2 to 4 mist nets (38 mm mesh, 4 to 18 m wide, Avinet, Portland, Maine) per survey, with the dimensions and number determined by the size of the site and the number of bat handlers present. To minimize accidental bird captures, we opened nets at sunset, or later if birds were still active. Nets were left open until 01:00 unless air temperature dropped below 5 °C or if we encountered persistent thunderstorms or heavy rains (which occurred infrequently).

We checked nets every 10 min (Kunz and Parsons 2009) and removed bats in the order captured. Each bat was identified to species (Bachen et al. 2018) and sex (Kunz and Parsons 2009), reproductive status (pregnant, lactating, nulliparous, scrotal, or nonreproductive; Racey 1988; Kunz and Parsons 2009), and age (adult or juvenile based on the degree of joint ossification in the phalanges; Anthony 1988) were recorded. We measured forearm, foot, and ear length in millimeters with dial calipers and weighed each bat to the nearest 0.5 g (10 and 50 g spring scales, Pesola, Schindellegi, Switzerland). We visually checked each individual for wing damage, fungus, or parasites. To distinguish *M. lucifugus* with smaller forearm measurements (<36.5 mm) from *M. yumanensis*, we used a handheld acoustic detector (Echo Meter Touch, Wildlife Acoustics, Maynard, Massachusetts) to determine the characteristic frequency of echolocation calls upon release (<44 kHz; Bachen et al. 2018). Nontarget species were released immediately after processing. All research activities followed guidelines and approved methods (Sikes et al. 2016; Montana

State University Institutional Animal Care and Use Committee, protocol 2017-26).

Radiotelemetry and used roosts

We attached radio transmitters (0.22 to 0.27 g; model LB-2X, Holohil Systems Ltd, Carp, Ontario, Canada) between the upper scapulae of the bat using skin glue (Osto-Bond, Montreal Ostomy, Vaudreuil-Dorion, Quebec, Canada) between 20 July and 17 August 2017 and 4 June and 21 August 2018. Transmitter weight did not exceed 5% of body weight to minimize any influence of transmitter application on bat behavior (Aldridge and Brigham 1988).

We tried to locate individual day roosts for all bats with active transmitters daily using a digital receiver (Model R-1000, Communication Specialists, Orange, California) and 3-element Yagi antennae (Advanced Telemetry Systems, Isanti, Minnesota). Once we identified the general location of an individual bat, we tried to locate the roost and, ideally, confirm the roost location with a visual observation of the bat. Although we tracked a handful of individuals to tree roosts, the sample size was low and we focused our analysis on rock roosts. Bats that roosted in rocks were easily observable, and we were confident in their location within these roosts. After identifying the roost, we used a handheld GPS unit (Garmin GPSMAP 64s, Garmin International Incorporated, Olathe, Kansas) to record latitude and longitude of the roost in decimal degrees to within 6 m of precision.

When we were unable to detect a transmitter during the day, we checked for the signal at night (i.e., between 21:00 and 01:00) when we assumed bats would be foraging. The objective of this was to confirm that the individual was still active in the area. We also drove all accessible roads within 16 km of capture locations 1 to 2 times a week during the day and night to detect bats that were otherwise not detected.

Selecting available roosts

We used a paired use–availability design to investigate whether *M. lucifugus* were selecting certain rock roost characteristics disproportionately to what was available (Thomas and Taylor 2006). Given that we were focused on understanding selection of rock roosts, the paired available roost also was in a rock feature. We selected a single available roost within a designated area around the location of each used roost, based on what we thought an individual bat could access in an evening and field logistics. In Montana, male Little Brown Myotis have been documented moving an average of 970 m between successive roosts (Schwab 2006); this distance is much greater than observed in other states (e.g., 275 m in Broders et al. 2006). We originally intended to use this movement information to select a random distance and account for all possible available roosts, but this was logistically infeasible. To select available roosts, we randomly generated a compass bearing and distance (1 to 200 m) from the used roost. Once we reached this location, we selected the nearest rock feature with a crevice or opening large enough for *M. lucifugus* (i.e., minimum crevice or opening size of 1.6 by 2.2 cm; Greenhall 1982). If no features met these requirements at the randomly selected point, we kept walking along the random bearing and selected the first feature that met these requirements. We searched each available roost for bats and guano. If neither were present, we assumed that the available roosts were unused at the time of survey (Chruszcz and Barclay 2002). By pairing each used rock roost with an available rock roost in close proximity, we were able to examine selection at a fine scale.

Characterizing used and available roosts

We collected data on physical characteristics and microclimates of each used and available roost at 3 spatial scales: landscape; plot; and roost. We also characterized roost microclimates for used and available roosts sampled in 2018 so that we could make associations with the measured covariates.

Landscape-based features

At the landscape scale, we focused on quantifying distance to water and forest edge for each used and available roost. We predicted that bats would select roosts closer to water so that they could drink or because these areas provide foraging locations (Fenton and Bell 1979; Amorim et al. 2018). Forest edges can provide foraging and commuting habitat (Morris et al. 2010; Pettit and Wilkins 2012; Jantzen and Fenton 2013); therefore, we predicted that bats would select a roost location closer to these resources. We used geospatial data to measure distances to the nearest water source and forest edge (MTNHP 2017, 2018) using the "Extract Multi Values to Points" tool in ArcMap (Version 10.4.1).

Plot-based features

At the plot scale, we characterized structural features of the immediate area surrounding roosts. We established a 17.8-m-radius plot (i.e., 0.1-ha circular plot) centered on the used or available roost location, similar to previous studies (e.g., Vonhof and Barclay 1996; Rancourt et al. 2005; Anthony and Sanchez 2018).

Topographic features may affect roost selection by influencing the amount of solar exposure (Perry et al. 2008; Jachowski et al. 2016). We predicted that bats would select roosts on south-facing slopes, where they would receive the most solar exposure. Using a compass (Ranger model, Silva, Switzerland) and iPhone clinometer (Models 8 and 8 Plus, Apple Incorporated, Cupertino, California), we recorded aspect (north, east, south, west) and slope (in degrees) at the used/available roost. We recorded elevation (in meters) using a GPS, which we compared to a digital elevation model (USGS 2017).

Clutter, or the degree and configuration of physical obstructions in an environment, may influence habitat selection by bats. In highly cluttered environments such as forests, bats have to contend with obstructions to flight (i.e., when entering and exiting a roost, foraging, or commuting) and echolocation (Mackey and Barclay 1989; Loeb and O'Keefe 2011; O'Keefe et al. 2014). We predicted that bats would select roosts in less cluttered environments (i.e., fewer trees and snags per plot). To quantify clutter and spatial complexity, we counted all trees and snags (i.e., any stem with diameter at breast height > 12.7 cm and height > 1.3 m) within each plot (Neubaum et al. 2006).

To characterize rock features, we recorded 2 variables at the plot level: overall rock cover and the type of rock structure that housed the used/available roost. We estimated percentage of rock cover to the nearest percent within each plot. To ensure consistency, we compared estimates among observers during a training period. We also classified the main structure within a plot as a rock outcrop, small scree, or large scree; these structures vary in the amount and type of interstitial space available to a roosting bat (Bachen et al. 2019). We classified the structure as a rock outcrop if the majority of rock was embedded in the ground such that interstitial space under the structure was not available for roosting (although crevices may have existed within the outcrop itself). We defined small scree as loose, gravel-sized rocks less than 20 cm in diameter (similar to the smallest rock size class in Tyser 1980). Slopes with loose rocks larger than 20 cm were considered large scree, and these structures may provide different roosting options for bats (Bachen et al. 2019). At large and small scree, we estimated the percent of rock in 5 size classes: (1) small scree; (2) small boulders (defined as <4-m^2 surface area; (3) medium boulders (5- to 15-m^2 surface area); (4) large boulders (>16-m^2 surface area); and (5) slab rocks based on shape (Tyser 1980; Turnock et al. 2017). We predicted that bats would prefer locations with larger areas of rock cover, as these areas would provide more roosting opportunities, and that they would select roosts in large scree and rock outcrops preferentially over small scree.

Roost-based features

We collected data on several structural characteristics at the roost scale for both used and available roosts including classifying the type of rock structure that housed the roost and the roost type, and measuring the aspect of the roost entrance, canopy closure over the roost, distance to the nearest horizontal obstruction, and dimensions (length and width) and orientation of the roost.

Similar to features characterized at the plot level, we classified the structure housing the used or available roost as rock outcrop, small scree, or large scree. We classified each used or available roost as either (1) Milieu Souterrain Superficiel (MSS; Mammola et al. 2016) or (2) a crevice; these 2 roost types differed in shape and size, which may affect the microclimate of a roost. MSS generally is “the underground network of empty air-filled voids and cracks developing within multiple layers of rock fragments” (sensu Mammola et al. 2016:1). We defined a crevice as a narrow fissure or crack in a rock forming an opening (Bogan et al. 2003; Blejwas et al. 2021). Bats in our study occasionally roosted in rock crevices that extended onto more than 1 rock face. We defined the main roost as the crevice to which the bat was physically closest; for available roosts, we selected the closest rock feature with a space large enough for *M. lucifugus* (i.e., at least 1.6 by 2.2 cm; Greenhall 1982).

When possible, we classified aspect of the roost and predicted that bats would be more likely to select south-facing roosts, which generally receive more solar exposure leading to warmer conditions (Vonhof and Barclay 1997). Using a spherical crown densiometer (Forestry Supplies, Jackson, Mississippi) held at elbow height, we estimated percent canopy closure (Schwab 2006; Armitage and Ober 2012). We took 1 reading in each cardinal direction and used the average as our estimate of canopy closure surrounding the roost/available location (Lemmon 1956). We predicted that bats would select roosts with lower canopy closure compared to what was available on the landscape (Vonhof and Barclay 1996; Perry and Thill 2008) in order to increase solar exposure and reduce obstacles for flight and echolocation (Armitage and Ober 2012; Fabianek et al. 2015; Jachowski et al. 2016). Lastly, physical obstructions such as trees and other vegetation may hinder flight or foraging for some bat species by influencing echolocation (O’Keefe et al. 2014). We recorded distance from the roost to the nearest horizontal obstruction and predicted that bats would select roosts farther from these obstructions.

To further characterize structural features of rock roosts, we collected data on dimensions and orientation of each used and available roost, as these characteristics may affect roost microclimate. Some roosts had multiple openings (e.g., crevices or MSS where the bat could enter or exit the roost). However, we identified the entrance to each roost as the opening to which the bat was closest. Using a meter tape, we measured width of the roost entrance and maximum depth of the roost. The width of the roost often varied at different parts of the roost opening. To address this, we averaged maximum and minimum width of the roost entrance. We measured depth of the roost by visually examining the crevice or MSS with a flashlight, probing throughout the roost, and taking the maximum measurement. If the roost was a crevice, we used a compass to classify orientation of the roost as either horizontal (i.e., 70 to 110°), vertical (i.e., 160 to 200°), or diagonal (other) with respect to the ground (Lacki and Baker 2007; Johnson et al. 2011). If the crevice was on the top portion of the rock, facing the sky, we classified the roost as a skyward-oriented crevice. Roosts in MSS were classified as having an MSS orientation.

Finally, we noted whether used and available roosts provided access to a skyward-oriented crevice. Based on our previous observations and other studies (Rancourt et al. 2005), we predicted that bats would select roosts with access to a skyward-oriented crevice, as this generally meant access to direct sunlight.

Characterizing microclimates

We hypothesized that structural characteristics of each roost at different spatial scales (landscape, plot, and roost) dictate the microclimate of each roost. However, we also were interested in specifically exploring how changes in temperature would affect roost selection in male *M. lucifugus*.

We deployed an iButton (model DS1923, Maxim Integrated, San Jose, California) in each used roost and paired available location sampled in 2018 to collect data on temperature. Each iButton was housed in a small plastic fob and attached to a galvanized steel hanger wire (2 cm × 34 cm) helping to facilitate deployment and retrieval in rock features. We compared data from iButtons with casings (average temperature = 11.3 °C, $n = 22$) and without (average temperature = 11.5 °C, $n = 22$) and found that casings had little effect on collected data.

At used roosts, we deployed the iButton at the approximate depth of the bat. For available roosts, we deployed iButtons at the same depth to best match the paired used roost. iButtons were deployed for 3 to 5 days, beginning when we first located the roost, and programmed to take a reading every half hour. We defined an iButton survey day as the time period between sunrise and sunset based on when bats were likely in day roosts. Data collected on the first iButton survey day (i.e., the day we located the roost) were potentially skewed by body temperature of the bat, whereas data from the last survey day were potentially incomplete depending on the timing of retrieval. Based on these assumptions and given variation in deployment duration, we averaged data collected between sunrise and sunset on the second survey day to standardize microclimate data in models.

We also measured ambient temperature by deploying 2 iButtons in the Little Blackfoot River drainage between 13 July and 14 August 2018. We deployed these at ground level, in unshaded areas (no canopy closure) on north- and south-facing slopes at similar elevations (1,842 to 2,075 m). We again averaged daily temperatures between sunrise and sunset.

General features of used roosts

We characterized some features that were only relevant at used roost locations, recording whether the roost structure (i.e., small scree, large scree, or rock outcrop) and the individual roost (i.e., crevice or MSS) represented a new or reused location. For example, several bats re-roosted in the same scree, but used different rocks or crevices (i.e., reused roost structure). Conversely, some bats re-roosted in the exact same scree, rock, and crevice (i.e., reused roost). Lastly, if the bat was visible, we measured approximate depth of the bat, taking great care to not disturb it.

Data analysis

To assess roost selection, we built 4 separate models, 1 for each scale (landscape, plot, roost) and for microclimate (for 2018 data), with conditional logistic regression (*coxme* package; Therneau 2019). Although sampling methods we used to collect these 4 data sets were centered at the same pairs of used and available locations, explanatory variables did not overlap, allowing us to model each data set separately. Given their ability to fly, bats could be exploring and perceiving the environment at different scales as they select a roost location. As such, we also thought it appropriate to explore these scales separately. For each analysis, we began with a global model including only additive effects because we had no a priori knowledge of any multiplicative relationships between covariates. Although we recognize that threshold values may exist for some covariates (e.g., temperature and roost width), we considered only linear relationships in our models, based on the range of observed values for covariates. We then used backward variable selection, removing individual covariates that did not explain sufficient variation in roost selection ($P > 0.1$). We located some individual bats more than once; to account for this and potential differences in roost selection between individual bats, we included a random intercept for each individual bat in all models.

Before developing global models, we examined correlations among variables of interest at each scale (landscape, plot, roost) and microclimate, accounting for our paired data. When covariates were correlated, we did not include both in the same model. Instead, we included the covariate in the pair that we thought would best characterize the roost at a particular spatial scale with the most biological relevance.

The global model at the landscape scale included distance to forest and distance to water. At the plot scale, we included 5 covariates in the global model: elevation; aspect; slope; number of trees; and percent rock cover. At the roost scale, the global model included 7 covariates: orientation; aspect; length; width; distance to the nearest horizontal obstruction; canopy closure immediately surrounding the roost; and access to a skyward-oriented crevice. Finally, the microclimate model included temperature and was based only on data from used and available roost locations collected in 2018. We report odds ratios and 95% confidence intervals to measure the effect sizes of covariates based on these roost selection models.

Results

We captured 222 bats during summer 2017 (35 net-nights) and 2018 (34 net-nights). These captures were comprised of 7 species, dominated by *M. lucifugus* (32%) and *Lasionycteris noctivagans* (29%, silver-haired bat; Supplementary Data SD1). The sex ratio of captured bats was male-skewed (80% male, on average), especially for *Myotis* species in general (86% male) and *M. lucifugus* specifically (94% male; Supplementary Data SD1).

We attached radio transmitters to 34 male *M. lucifugus*. We were unable to locate 14 individuals after release, despite our daily tracking efforts and the additional strategies we used specifically to locate unlocated bats. We found no obvious morphological differences between bats we did and did not locate. These individuals could have been missing because: (1) transmitters failed or fell off; (2) bats roosted too deep in rock features for detection; or (3) bats moved out of our study area. We suspect that 2 transmitters failed due to faulty batteries, but other explanations are more likely for the other 12 individuals. We detected only 2 of the missing bats when listening for signals at night. Researchers in Colorado struggled to detect signals from test transmitters in scree at depths greater than 2.4 m (Neubaum D, Colorado Parks and Wildlife, Grand Junction, CO, USA, personal communication, February 2023) and rock features in our study area provided roosting options at greater depths. In our study, signal from 1 bat disappeared while we were filling out a datasheet. This bat was roosted in a large rock outcrop perched above scree. We did not see this bat exit the roost and assumed that it had moved deeper into the crevice. We first detected most transmitter signals at distances between 400 and 800 m; the maximum distance at which we were able to detect a tagged bat was approximately 1.5 km.

We located at least 1 day roost for 20 male *M. lucifugus* (total = 57 day roosts, average = 2.85 roosts/bat, range = 1 to 6). We captured most (17/20) of these bats in the Boulder Mountains, where individual and clusters of roosts were located throughout the study area (Fig. 2). Most (86%) of the 57 roosts were in rock features (*n* = 49 from 18 individuals), but a small number were in trees (*n* = 8 from 4 individuals). Tracked bats used a total of 49 rock roosts. Although we were unable to locate roosts for every bat every day, several individuals did switch roosts. Fourteen individuals switched roosts at least once; 8 individuals reused a roost (3 of these roosts are shown in Fig. 2). Two male *M. lucifugus* roosted only in trees or snags and 2 individuals used both rock and tree roosts. Most male *M. lucifugus* (80%, 16 of 20 total individuals) we tracked roosted only in rock features; hereafter, results focus on these rock roosts.

Roost use.

We visually confirmed the bat or transmitter antenna at 86% (*n* = 42) of the 49 rock roosts. For most of these observations, bats were close enough to the roost surface to be in direct sunlight. We were able to measure exact depth of the bat for 29 of the 49 observations and we estimated depth for 12 additional observations. We were unable to estimate depth of the bat at 8 roosts. Bats were located an average of 11 cm deep (*SE* = 1.6, range = 2 to 30) within roosts.

Most rock roosts were in large scree (65%), but 6 individuals roosted in rock outcrops, and 1 individual roosted in small scree (Table 1). For roosts in large scree, most rocks in the plot surrounding the roost were small boulders (mean = 46%, *SE* = 4), followed by small scree (32%, *SE* = 6), medium boulders (10%, *SE* = 2), large boulders (mean = 7%, *SE* = 2), and slabs (5%, *SE* = 3). All roosts in rock outcrops were crevices. At the single roost in small scree, the plot was comprised of small boulders (70%) and small scree (30%), which were insulated with dirt and vegetation, including moss. Crevices (90%) were used much more often than the MSS. Bats used vertical crevices most often (35%), followed by diagonal, skyward-oriented, and horizontal crevices (Table 1). Nearly all (4 of 5) of the roosts in MSS lacked a substantial soil layer, such that these areas could be better described as occurring in bare colluvial MSS, an early stage of the colluvial MSS (Mammola et al. 2016); the other MSS roost occurred in small scree covered in soil (colluvial MSS; Mammola et al. 2016). Most (60%) roost entrances were south- or east-facing and many roosts (59%) provided access to a skyward-oriented crevice (Table 1). Roosts ranged from 1,791 to 2,117 m in elevation (mean = 1964, *SE* = 15).

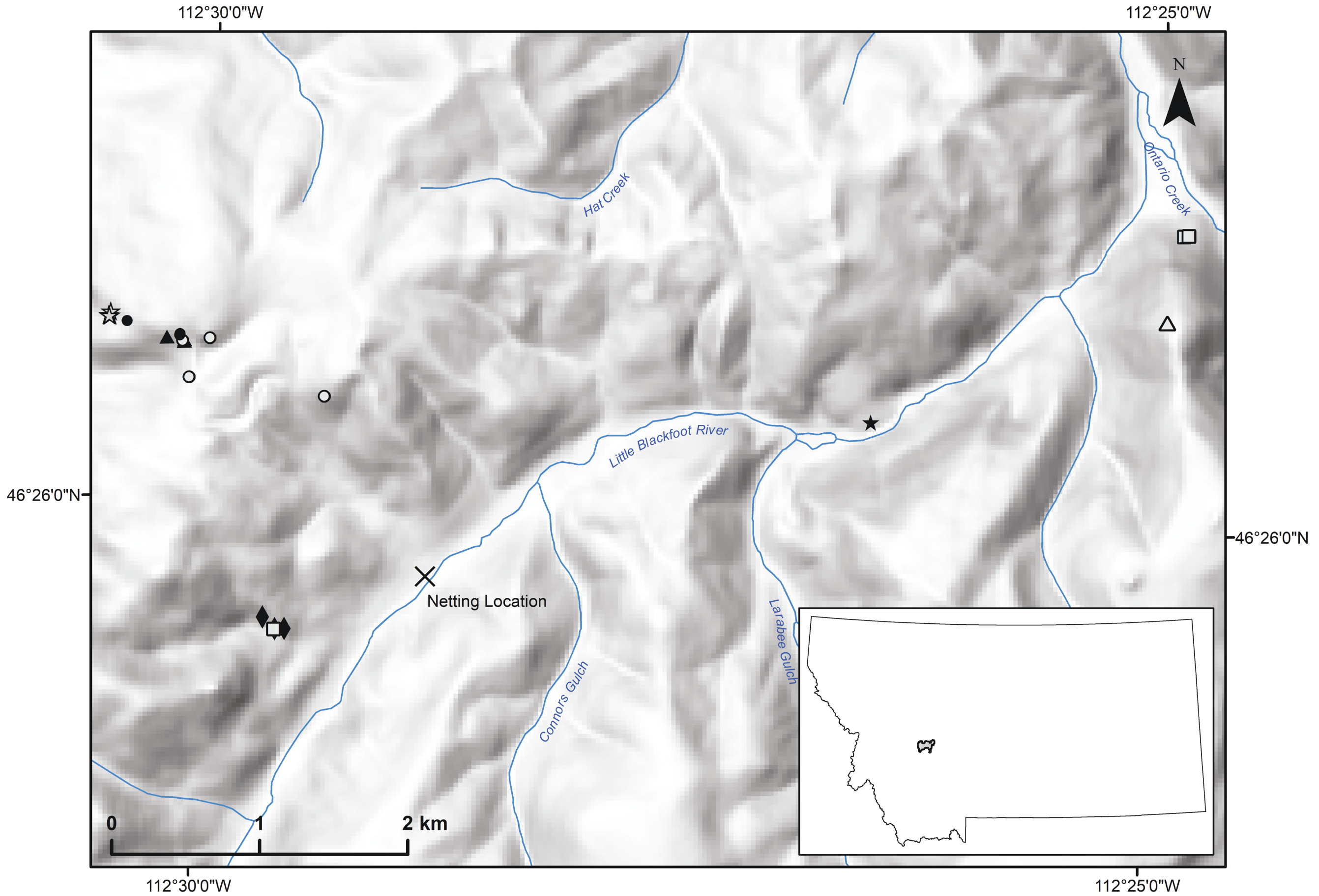

Fig. 2. Locations of 25 roosts for 8 male *Myotis lucifugus* (1 to 4 roosts/individual) captured at 1 netting location (labeled and denoted with an X) in the Little Blackfoot River study area in the Boulder Mountains, 2018, Montana (inset map). Twenty-two of these roosts were used only once, whereas 3 roosts were reused (3 different bats each reused a roost). Each shape/color combination denotes a unique individual; repeated shapes denote different roosts used by that individual. We captured and radio-tagged bats at 4 netting locations in this study area; all 4 sites were within 2.5 km along the Little Blackfoot River. Bat 35 moved the farthest between roost locations (denoted by the gray squares). We captured this bat on 7 August 2018 and found the first roost on 11 August, 5.65 km from the netting location. The second roost (on 12 August) was 6.7 km from the first roost and the third roost (13 August) was 6.8 km from the second roost.

Canopy closure at the roost was lower for roosts in large scree (mean = 10%, *SE* = 2) compared to roosts in rock outcrops (mean = 21%, *SE* = 5). Canopy closure was 45% at the single roost in small scree. Average canopy closure for roosts in rock crevices (mean = 13%, *SE* = 2) was lower than roosts in MSS (mean = 25%, *SE* = 10).

Ambient temperature differed slightly between north-facing (mean = 21.7 °C, range = 5.1 to 38.6 °C) and south-facing slopes (mean = 22.6 °C, range = 4.0 to 39.0 °C). Average temperatures of used roosts were warmer than available roosts and both were warmer than ambient temperatures for the study area (averaged between sunrise and sunset; Table 2). Temperatures in used roosts ranged from a minimum of 9 °C to a maximum of 42.6 °C over a 24-h period.

Roost selection

We analyzed data from 47 pairs of rock roosts (used/available) in our landscape, plot, roost, and microclimate models of roost selection (Table 2); we were unable to access 2 of the rock roosts due to safety constraints. At the landscape scale male *M. lucifugus* selected roosts located closer to water; odds of selection decreased by a factor of 0.38 (95% CI = 0.37 to 0.38) with every 100-m increase in distance from water (Tables 2 and 3; Fig. 3a). We did not detect evidence that these bats were selecting roosts based on proximity to the forest edge. At the plot scale male *M. lucifugus* were 2.13 times (95% CI = 2.03 to 2.23) more likely to select a roost with every 10% increase in rock cover within a plot (Tables 2 and 3; Fig. 3b). However, we did not find evidence to suggest that elevation, aspect, slope of the plot, or tree density influenced roost selection. At the roost scale male *M. lucifugus* were more likely to select roosts that were wider, in areas with less canopy closure, and that provided access to a skyward-oriented crevice (Tables 2 and 3). Male *M. lucifugus* were 78% (95% CI = 9.8% to 188%) more likely to select a roost with every 1-cm increase in roost width and 53.5% (95% CI = 50.8% to 56.1%) less likely to select a roost for each 10% increase in canopy closure. Male *M. lucifugus* also were 13.9 times (95% CI = 2.1 to 93.6) more likely to use a roost with access to a skyward-oriented crevice compared to those without. Although we included other covariates in the global model at the roost level (i.e., roost length, crevice orientation, and distance to the nearest horizontal obstruction), we did not find evidence that these were important characteristics for roost selection. When we focused on microclimate, we found that male *M. lucifugus* were 1.24 times (95% CI = 0.99 to 1.55) more likely to select a roost with every 1 °C increase in temperature (Tables 2 and 3; Fig. 3c).

Discussion

Myotis lucifugus often roost in trees (Psyllakis and Brigham 2006; Schwab 2006), yet male *M. lucifugus* in our study area most often used roosts in rock features despite the abundance of trees and snags. Most of the trees in our study areas were Lodgepole Pine, with bark that was generally thin and adhered tightly to the tree bole (Vonhof and Barclay 1996; Chan-McLeod 2006). Larger Lodgepole Pine snags may have rough bark that peels away from the bole, leaving space for potential roosts (Chan-McLeod 2006). We did observe the occasional large Lodgepole Pine, but the bark tended to be flaky and the snags had hollows that were shallow or too small (<1.6 × 2.2 cm) to be accessible to *M. lucifugus*. Johnson et al. (2019) found that temperatures measured within tree roosts increased with the ambient temperature (positive relationship), whereas rock roosts were better able to retain warmth on cooler days (negative relationship). Roosting in rock features may provide more protection or enable bats to remain in their thermoneutral zone and reduce energy expenditure (Rancourt et al. 2005; Snider et al. 2013; Anthony and Sanchez 2018; Alston et al. 2022).

The microclimate within the roost is thought to be a major driver of roost selection for many bat species (Chruszcz and Barclay 2002; Barclay and Kurta 2007; Fabianek et al. 2015; but see Alston et al. 2022). We found that male *M. lucifugus* selected rock roosts with features that created higher temperatures relative to the ambient environment or other roost locations available on the landscape. We identified several structural features of rock roosts that were important for roost selection and likely create a warmer microclimate. Male *M. lucifugus* preferred roosts on south-facing slopes with less canopy closure, which generally means more exposure to solar radiation (Fabianek et al. 2015). The larger areas of rock that male bats preferred also likely receive more solar radiation and hold heat more effectively than smaller structures surrounded by vegetation.

Male *M. lucifugus* roosted in or had access to skyward-oriented crevices that were wide enough to receive direct sunlight, and we regularly observed bats basking in the sun in both scree and rock outcrops. Basking behavior has been documented, although infrequently, in other studies focused on rock-roosting bats (Slough 2009; Moosman et al. 2015). This behavior could provide bats with a passive strategy for thermoregulation, minimizing energy expenditure (Vaughan 1987; Geiser et al. 2004). Male *M. lucifugus* also preferentially selected crevices with a vertical orientation, which may be better buffered against fluctuations in ambient temperature than other orientations (Chruszcz and Barclay 2002). Vertical roosts also provide options to change locations within the same roost, allowing the bat to retreat during inclement weather and minimize energy needed for active thermoregulation. Conversely, horizontal roosts receive a similar amount of solar radiation throughout the entire crevice, offering little spatial variation in microclimate (Chruszcz and Barclay 2002).

Roosts that provide variation in microclimate, including the potential for passive warming, may be particularly beneficial for bats recovering from white-nose syndrome (Wilcox and Willis 2016; Fuller et al. 2020). Although white-nose syndrome mainly affects bats during winter, some recent research suggests that

Table 1. Summary of covariates describing roosts ($n = 49$) used by male *Myotis lucifugus*, 2017 to 2018, west-central Montana.

Covariate	Number of observations	% of total
Rock structure type		
Large scree	32	65.3
Rock outcrop	16	32.7
Small scree	1	2.0
Roost type		
Crevice	44	89.8
MSS	5	10.2
Aspect of roost entrance[a]		
Skyward-oriented	8	17.0
North	2	4.3
East	10	21.3
South	18	38.3
West	9	19.1
Crevice orientation		
Skyward	8	16.3
Horizontal	5	10.2
Vertical	17	34.7
Diagonal	12	24.5
MSS	7	14.3
Skyward-oriented crevice present		
Yes	29	59.2
No	20	40.8
Plot aspect		
North	2	4.1
East	9	18.4
South	24	49.0
West	14	28.6

[a] We were only able to safely record this covariate at 47 of the 49 roosts.

Table 2. Means (and ranges) for values observed at used and paired available roost sites of male *Myotis lucifugus* ($n = 47$ pairs of used/available roosts), 2017 to 2018, west-central Montana. Temperatures listed below represent an average between sunrise and sunset for a single day at a used or available roost. Temperatures in used roosts ranged from a minimum of 9 °C to a maximum of 42.6 °C, over an entire 24-h period.

Model	Covariate	Used	Available
Landscape	Distance to water (m)	1063.0 (38.2 to 2741.2)	1107.3 (125.0 to 2768.3)
Plot	Rock cover (%)	77 (20 to 100)	52 (10 to 98)
Roost	Roost width (cm)	3.1 (0.7 to 11.2)	2.8 (0.9 to 7.1)
	Canopy closure (%)	14.1 (0.2 to 63.9)	35.7 (0.2 to 99.0)
	Skyward-oriented crevice present (% yes)	59	32
Microclimate	Temperature (°C)	24.9 (15.8 to 33.7)	23.1 (16.3 to 30.1)

Table 3. Estimates (on the log-odds scale), standard errors, test statistics, and *P*-values for covariates included in the 4 final models (landscape, plot, roost, microclimate) for roost site selection by male *Myotis lucifugus* (*n* = 47 pairs of used/available roosts), 2017 to 2018, west-central Montana. The microclimate model included only used/available roosts sampled in 2018 (*n* = 29 pairs of used/available roosts).

Model	Covariate	Estimate	*SE*	z	*P*
Landscape	Distance to water (m)	–0.0097	0.0047	–2.07	0.0380
Plot	Rock cover (%)	0.0754	0.0233	3.23	0.0012
Roost	Roost width (cm)	0.5767	0.2399	2.40	0.0160
	Canopy closure (%)	–0.0766	0.0280	–2.74	0.0062
	Skyward-oriented crevice present	2.6300	0.9485	2.77	0.0056
Microclimate	Temperature (°C)	0.2116	0. 1098	1.93	0.0540

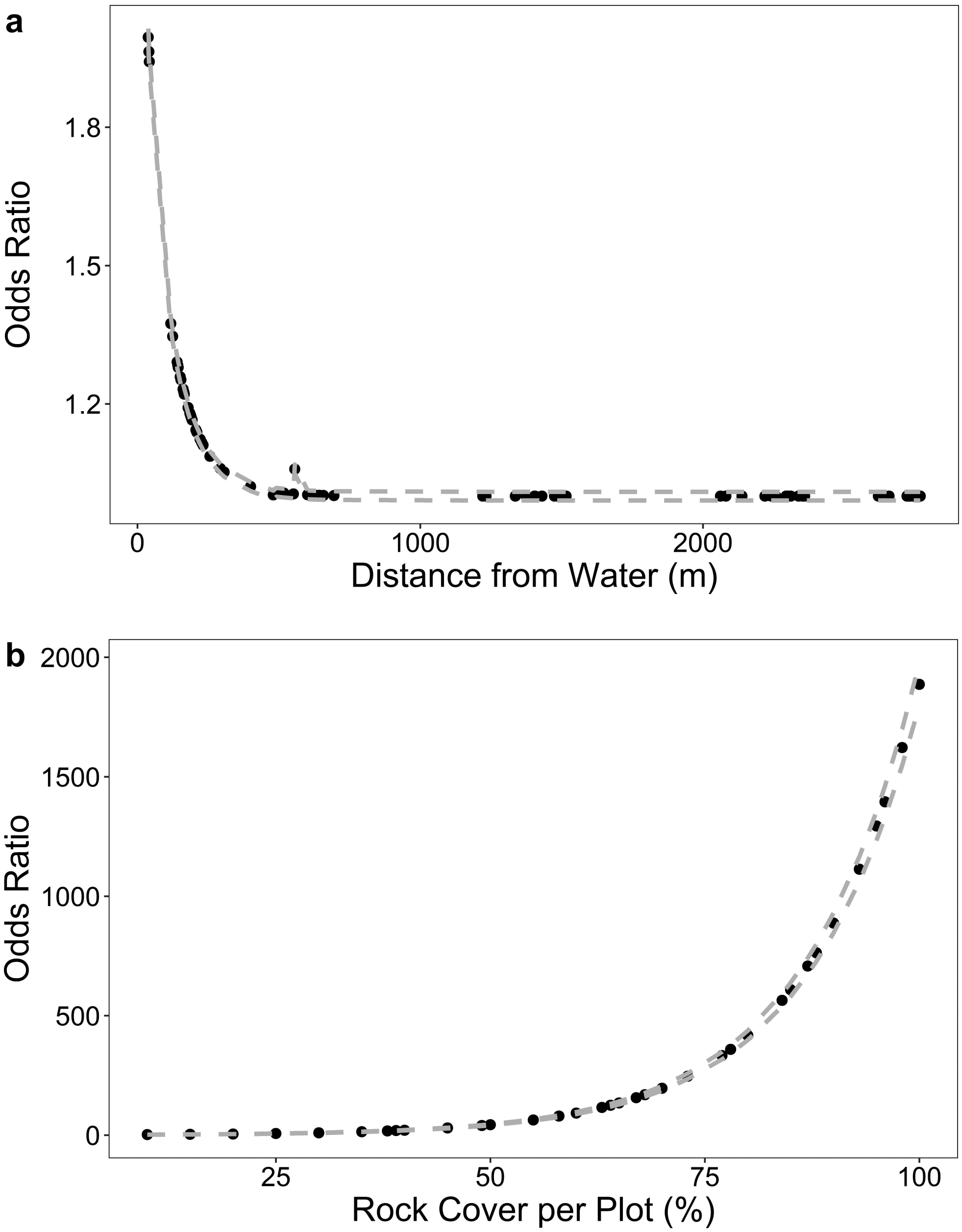

Fig. 3. Odds (black dots) and 95% confidence intervals (dashed lines) of a male *Myotis lucifugus* selecting a roost as a function of: (a) distance from water; (b) rock cover (%) within a 17.8-m-radius plot; and (c) average temperature.

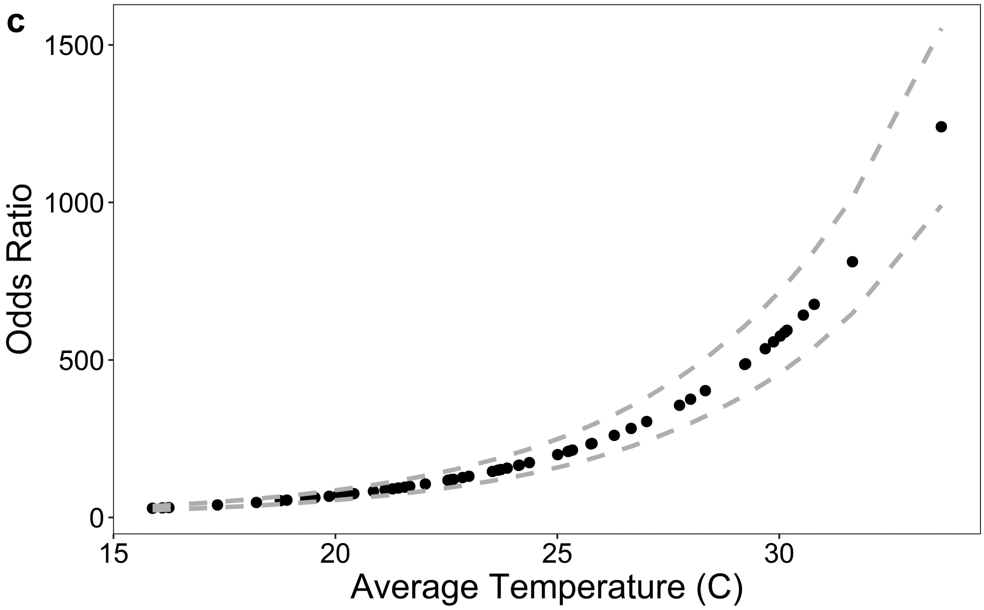

Fig. 3. Continued

habitat characteristics used during spring and summer could have important effects on their response to this disease (Reichard et al. 2014; Wilcox and Willis 2016; Fuller et al. 2020). Wilcox and Willis (2016) found that bats affected by and recovering from white-nose syndrome were especially likely to select warmer (heated) roosts, compared to healthy individuals. Recovering from white-nose syndrome is energetically expensive (Meierhofer et al. 2018; Fuller et al. 2020)—by reducing the use of torpor or the energy needed for active thermoregulation, bats may be able to devote more energy to healing or other activities (Fuller et al. 2020).

Reproductively active females require warm roosts to recoup energy spent gestating and lactating (Racey and Swift 1981; Hamilton and Barclay 1994) and often roost colonially (Kurta 1986; Barclay 1991). In contrast, male bats typically roost alone during the active season (Weller et al. 2009). We observed a male-skewed sex ratio for most bat species, suggesting that female bats have a lower capture probability with mist nets or may not use lodgepole forests at higher elevations in the same manner as males. Other studies also have found bias in sex ratios along an elevational gradient, with proportionately more males at higher elevations (Barclay 1991; Neubaum et al. 2006; Johnson et al. 2019; O’Shea et al. 2021). Male bats may be more likely than females to use daily torpor as a way to reduce energy needs (Grinevitch et al. 1995), allowing them to roost at higher elevations.

Male bats roosting in areas with cooler temperatures also could provide more opportunities for *Pseudogymnoascus destructans* to persist and cause increased spread of white-nose syndrome (Ballmann et al. 2017; Neubaum and Siemers 2021). Although *P. destructans* is a cold-loving fungus with optimal growth between 12.5 and 15.8 °C (Verant et al. 2012), spores of this fungus remained viable for 180 days when incubated on bat fur at 24 °C (Campbell et al. 2020); the average temperature within our used roosts was 24.9 °C (Table 2). Spores of *P. destructans* incubated on bat fur at 37 °C were viable for 5 days (Campbell et al. 2020). Based on Campbell et al. (2020), spores of *P. destructans* can remain viable on bat fur for at least several days and perhaps several weeks across much of the range of temperatures we documented in used roosts.

Although we found that male *M. lucifugus* selected warmer roosts, bats must expend energy to dissipate heat and minimize evaporative water loss once roost temperatures increase beyond a certain threshold (Humphries et al. 2005; Ruczynski 2006). Upper thermal limits for *M. lucifugus* are estimated to be 39 to 42 °C in the summer (Stones and Wiebers 1967; Noakes et al. 2021), but these temperature ranges have not been well-studied. Most temperatures that we recorded in used roosts did not exceed the thermal preferences of male *M. lucifugus* in this higher-elevation landscape, but future studies should consider the potential for thresholds in preferences, especially given predicted shifts in climate patterns. Higher temperatures and lower humidity predicted for this area during summer (Whitlock et al. 2017) could alter energetic demands for thermoregulation and osmoregulation for bats. We did not model potential changes in temperature preferences over the sampling season, but bats may select different roosts throughout the summer to account for changing conditions. Considering temporal differences in selection may be important when tracking bats over a longer time period or when tracking females that represent different reproductive conditions (Chruszcz and Barclay 2002).

Microclimate is an important criterion, yet roosts also must provide protection from predators, creating a safe space for bats to rest during the day (Vonhof and Barclay 1996; Jenkins et al. 1998). Rock roosts may be more accessible to terrestrial predators than trees. However, bats may select roosts with structural features that balance this risk with finding an appropriate microclimate. For example, the widest roost we measured was 11 cm, but narrowed to a width typical of other observations after the entrance, potentially balancing the risk of predation and the energetic benefits received from extra solar exposure. Bats also are likely able to evade most predators by moving deeper into crevices and by switching roosts (Kunz 1982). Similar to other studies, bats in our study did switch roosts. Rock structures with higher densities of rocks provide more roosting options, allowing bats to change roosts while saving energy by remaining in the same general area (Kunz 1982; Lewis 1995; Anthony and Sanchez 2018). Roosts with skyward-oriented crevices provide a panoramic view of the surroundings upon exit of a bat from the roost and may aid in predator evasion (Rancourt et al. 2005).

The landscape surrounding the roost provides bats with access to other basic resources such as water sources for drinking and foraging for insects (Entwistle et al. 1997; Jenkins et al. 1998). Although *M. lucifugus* are generalists and can forage in different environments, they preferentially forage over water in search of aquatic insects (Anthony and Kunz 1977; Fenton and Barclay 1980; Nelson and Gillam 2017). Similar to other studies, we found that male *M. lucifugus* selected roosts that were closer to water (e.g., Rabe et al. 1998; Kalcounis-Rüppell et al. 2005), which may have higher concentrations of insects compared to stands of Lodgepole Pine. Bats that do not roost in proximity to these drainages may need to commute farther to reach foraging and drinking sites, increasing energy expenditure.

We developed separate models of habitat selection for the spatial scales of interest, yet bats may be evaluating and considering trade-offs among habitat characteristics at multiple scales simultaneously. Future efforts focused on understanding habitat requirements and preferences could consider integrating covariates measured at multiple scales in the same model, which could generate potential insights about their relative importance.

Conservation and management implications

We found that rock features in our study area, namely crevices in rock outcrops and larger scree that are close to water with low canopy cover, provided essential roosting habitat for male *M. lucifugus* during the summer. A few bats made use of spaces within the MSS. We are aware of only 1 other study that describes use of higher-elevation rock roosts by *M. lucifugus* during the summer (Johnson et al. 2019). Although Johnson et al. (2019) focused on use of buildings by *M. lucifugus*, they also documented several male bats using rocks as summer roosts, supporting the idea that rock features may be an important habitat component for different groups of bats. Numerous bat species also use these features during other seasons throughout mountainous regions in the western United States as transitional roosts during autumn and hibernacula during winter (Johnson et al. 2017; Neubaum 2018; White et al. 2020; Blejwas et al. 2021; Lewis et al. 2022). Rock features and the MSS are abundant throughout much of the western United States and our work suggests that these areas should be studied further to understand their use and importance for bat species, especially as habitat decreases in abundance and quality. By protecting important rock structures, managers can help bats meet their thermal and other needs throughout the year. As white-nose syndrome becomes more prevalent in the West, identifying and protecting roosts is vital.

Supplementary data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Number and sex ratios of bats captured by species.

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Author contributions

SLH contributed in conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft, review, and editing; ARL contributed in conceptualization, formal analysis, funding acquisition, methodology, project administration, supervision, writing—original draft, review, and editing; BAM contributed in conceptualization, resources, writing—review and editing; CNG contributed in conceptualization, funding acquisition, resources, writing—review and editing; RAG contributed in conceptualization, writing—review and editing; LH-B contributed in conceptualization, funding acquisition, resources, writing—review and editing.

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Conflict of interest

None declared.

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