CHARACTERIZING SUMMER ROOSTS OF MALE LITTLE BROWN MYOTIS (MYOTIS LUCIFUGUS) IN LODGEPOLE PINE-DOMINATED FORESTS

by

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ABSTRACT

Although bat roosts have been well-studied in the eastern United States, we know less about roosts in the west. Western bats may make use of trees and snags, as in the eastern US, but the Rocky Mountains provide more exposed rock, which could contribute to western bat species using different roosting features. Additionally, roost studies often focus on maternity colonies, and information on roosts used by male bats is limited. Given that roosting sites may be limiting, we aimed to quantify structural features of roosts used by male little brown myotis (*Myotis lucifugus*) in forests dominated by lodgepole pine (*Pinus contorta*) during the summer and determine whether bats are selecting roosts with particular features disproportionately to what is available on the landscape. We mist-netted for bats during the summers of 2017 and 2018 and attached transmitters to 34 male little brown myotis. We located at least 1 roost for 20 individuals (average = 2.85 roosts/bat, range = 1-6). Although snags were available, most bats roosted in rock features (86% in rocks, 14% in snags); rock roosts were mainly in crevices with vertical orientations (85%) instead of rock cavities (15%). Male bats were more likely to select roosts with less canopy closure (mean for used locations = 14.1%, SE = 2.3) that were closer to water (1063.1 m, SE = 136.2). They also selected roosts with more overall rock cover (77%, SE = 3), wider entrances (3.1 cm, SE = 0.3), and access to a skyward-facing crevice, creating warmer microclimates. Our work indicates that rock features provide essential summer habitat for male little brown myotis and that lodgepole pine in this landscape may not provide appropriate roosting features. Understanding how other bat species may be using rock features, during summer and other seasons, remains a sizeable information gap. Learning more about hibernacula is of great importance due to the spread of white-nose syndrome and rock features may be essential autumn transitional roosts and winter hibernacula at higher elevations. Roosts that provide variation in microclimate, including the potential for passive warming, could be very beneficial for bats recovering from white-nose syndrome.

CHAPTER ONE

CHARACTERIZING SUMMER ROOSTS OF MALE LITTLE BROWN MYOTIS (MYOTIS LUCIFUGUS)

Introduction

The conditions (e.g., aspect, slope) and resources (e.g., shelter, food, water) that allow an animal to occupy an area, survive, and reproduce, comprise an animal's habitat (Krebs 2009, Krausman and Morrison 2016, Kirk et al. 2018). Habitat is therefore a fundamental component of an animal's life history, and successful conservation efforts consequently require an understanding of how animals use and select habitat (Pulliam and Danielson 1991, National Research Council 1995, Krebs 2009).

Shelter, a critical component of habitat for many mammals, provides refuge from predators and weather, protection for offspring, proximity to food and water, and aids in physiological homeostasis (Alcock 2001, Vaughan et al. 2015). Bats seek shelter in roosts, where they spend a large percentage of their lives (Kunz 1982, Chruszcz and Barclay 2002). Bats require different types of roost sites to support their distinctly temporal habitat needs and complete their life history (Neubaum et al. 2017). For example, bats spend much of their time at diurnal roosting sites (e.g., maternity and bachelor roosts) during the active season (Vaughan and O'Shea 1976, Randall et al. 2014). Reproductively active females often congregate in maternity roosts to raise their pups, roosting separately from groups with different energetic needs such as males and non-reproductive females (Kunz and Lumsden 2003, Randall et al. 2014). Roosts are essential for survival, reproduction, and social interaction, and their quality and availability may influence reproductive success and the distribution and abundance of bat populations (e.g., Kunz 1982, Sedgeley 2001, Kunz and Lumsden 2003, Ruczynski 2006, Barclay and Kurta 2007, Brigham 2007).

Roost quality depends on a number of factors (e.g., distance from the ground, proximity to food and water, capacity for social interactions) (Sedgeley and O'Donnell 2004). However, temperature and humidity, or microclimate, likely have the largest influence (Sedgeley 2001, Sedgeley and O'Donnell 2004). All bats in North America have high energetic demands and are vulnerable to evaporative water loss, due to their small size and mode of locomotion (Chruszcz and Barclay 2002, Cryan and Wolf 2003). Although bats are able to save energy by roosting communally or adjusting their body temperature and entering torpor or hibernation during periods of inactivity, temperature and humidity within the roost still play a major role in thermoregulation (Kunz 1982, Hamilton and Barclay 1994, Vonhof and Barclay 1997, Sedgeley 2001, Chruszcz and Barclay 2002, Wilcox and Willis 2016, Weber and Willis 2018). High-quality roosts provide bats with microclimates that assist in offsetting energetic demands (Kunz 1982, Kerth et al. 2001, Sedgeley and O'Donnell 2004, Ingersoll et al. 2010).

The microclimate of a roost likely is dictated by structural features occurring at different spatial scales. Although bats are small, their ability to fly long distances allows them to perceive resources and conditions at multiple spatial scales within a short amount of time, which presents a unique situation among mammals. For example, a western small-footed myotis (*Myotis ciliolabrum*) may fly up to 24 km within a single evening

(Rodhouse and Hyde 2014), allowing the bat to perceive available resources at a landscape scale. The same individual also might fly into a meadow surrounded by trees to forage, perceiving different resources, such as a pond where it can drink and insects that it can forage on within a smaller area. Finally, this individual may choose a microhabitat roost location on available rocks and trees. By identifying and quantifying structural features related to roost selection at different scales, we can better understand how bats are selecting roosts with particular microclimates.

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). Bats in the western U.S. may make use of abundant trees and snags, as in the east. However, the topography of the Rocky Mountains provides more exposed rock, which could mean that western bat species use different roosting features (Theobald et al. 2015, Neubaum 2018). Rocks may provide warm microclimates, as well as stable temperatures, that could create roosts of higher quality for certain species of bats in the west (Schwab 2006, Snider at al. 2013). Several species in the western U.S. have been documented roosting in low-elevation rock features during the summer (e.g., Chruszcz and Barclay 2002, Lacki and Baker 2007, Slough 2009, Rodhouse and Hyde 2014). Though some western species also use rock features in higher-elevation talus and rock outcrops as autumn transitional roosts (Neubaum et al. 2006, Johnson et al. 2017, Neubaum 2018), we know little about use of these features as summer roosts or winter hibernacula. Additionally, roost studies often focus on maternity colonies, and information on male roost use is limited (Barclay and Kurta 2007, Weller et al. 2009).

The little brown myotis (*Myotis lucifugus*) roosts in both trees and rocks during the summer in the eastern U.S. (Bell and Thomas 1964), where it is one of the species most severely impacted by white-nose syndrome (Frick et al. 2010, Langwig et al. 2015, Hayman et al. 2016, Rocke et al. 2019). Understanding which specific habitat features are important for selection and use by bats is essential to develop useful conservation and management strategies, especially as threats, such as white-nose syndrome, wind energy development, and habitat loss, continue to increase in the west (Crampton and Barclay 1998, Jung et al. 2014). Given that roosting sites may limit the distribution and abundance of bat populations (Kunz 1982, Barclay and Kurta 2007), we aimed to quantify structural features of day roosts used by male little brown myotis during the summer in lodgepole pine-dominated forests and determine whether bats are selecting roosts with certain characteristics disproportionally to what is available to them on the landscape.

Study Areas

We captured bats and conducted roost surveys in two drainages within the Helena-Lewis and Clark National Forest of southwestern and central Montana: 1) Moose Creek in the Little Belt Mountains, approximately 110 km east of the Continental Divide, and 2) Little Blackfoot River in the Boulder Mountains, 129 km southwest of Moose Creek and approximately 8 km west of the Continental Divide (Fig. 1). The Little Belt and Boulder Mountains are similar in elevation (i.e., Little Belts range from 1158 m to 2787 m, Boulders range from 1213 to 2652 m) and topography, consisting of foothills and riparian corridors at lower elevations that rise to small hills and rounded peaks

(USGS 2019). General weather patterns are similar between the two 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/-1.7/10.2ºC in the Boulder Mountains and 2.6/-2.8/7.9ºC in the Little Belt Mountains).

Foothills in both drainages are composed of lower montane grassland and sagebrush steppe (MTNHP 2017), dominated primarily by fescue (*Festuca* spp.) and sagebrush (*Artemisia* spp., MTNHP 2019a). Riparian corridors typically consist of willows (*Salix* spp.), cottonwood (*Populus* spp.), alder (*Alnus* spp.), Rocky Mountain juniper (*Juniperus scopulorum*), Rocky Mountain maple (*Acer glabrum*), lodgepole pine (*Pinus contorta*), and Douglas-fir (*Pseudotsuga menziesii*; MTNHP 2019b). As elevation increases, vegetation transitions into lodgepole pine and Douglas-fir dominated forests with scattered patches of montane grassland (MTNHP 2017). Talus slopes, rock outcrops, and old mines occur in both mountain ranges. Few human-made structures exist other than scattered cabins, trails, gravel roads, and ATV trails. Public vehicular road access is limited, with a single gravel road traversing the bottom of each drainage.

Both mountain ranges have been heavily impacted by mountain pine beetle (MPB) activity, and the timing of the onset of the MPB outbreak is similar, beginning between 1999 and 2000 and steadily increasing until 2009 (Johnson and Wittwer 2006, Egan 2014, USDA Forest Service 2018). However, lodgepole forests in the Boulder Mountains have suffered higher tree mortality overall (Egan 2014). MPB-caused tree mortality in lodgepole forests ranges from low (i.e., 2471 trees/km2; <10 trees/ac) to severe (i.e., 7413 trees/km2; >30 trees/ac) in both ranges (Joel Egan, USFS, *personal communication*, Egan 2014). However, these forests also contain areas of lodgepole regeneration, such that live trees and saplings, snags, and stumps were abundant in each mountain range.

Methods

Study Species

Of Montana's 15 bat species, 12 potentially occur within the Little Belt and Boulder Mountains of Montana (Bachen et al. 2018, MTNHP 2019c). Townsend's big-eared bat (*Corynorhinus townsendii*) are known to roost in caves and mines in Montana, which was not the focus of this study (Bachen et al. 2018). Spotted bat (*Euderma maculatum*) have not been documented roosting in Montana (Bachen et al. 2018) and although they have been documented on acoustic detectors within the state, they are infrequently captured in mist nets (MTNHP 2019c). Silver-haired bat *(Lasionycteris noctivagans*), hoary bat (*Lasiurus cinereus*), and big brown bat (*Eptesicus fuscus*) have been documented moving substantial distances (e.g., hoary bats have been recorded flying up to 20 km from a day roost to a foraging location, one-way; Barclay 1989, Loeb et al. 2015), such that ground tracking of transmittered bats would likely be ineffective. The 7 Myotis species (California myotis [*Myotis californicus*], western small-footed myotis, long-eared myotis [*Myotis evotis*], long-legged myotis [*Myotis volans*], fringed myotis [*Myotis thysanodes*], little brown myotis, and Yuma myotis (*Myotis yumanensis*) can be difficult to distinguish morphologically, acoustically, and/or genetically (Maxell 2015, Bachen et al. 2018). However, the little brown myotis can be identified in-hand with confidence in Montana based on the presence of a keel on the calcar, forearm length (> 36 mm), and characteristic frequency of echolocation calls (< 44 kHz; Weller et al. 2007, Bachen et al. 2018). For these reasons, and because information on summer roost use for this species in the west is limited, we focused our telemetry efforts on little brown myotis.

Bat Capture

Little brown myotis often forage over or near water (Fenton and Bell 1979, Mackey and Barclay 1989). We focused mist net efforts at sites where we were most likely to capture this species foraging and drinking, which generally were sections of slow-moving water created by beaver activity or backwater channels. Beaver activity is extensive along the riparian corridors of both Moose Creek and the Little Blackfoot River, and this activity creates the majority of slow-moving or stagnant water within both drainages. However, we also netted sections of river corridor with fast-flowing water with the hopes that bats would be using these features as flight paths. We captured bats in the Moose Creek area between June and August of 2017 and in the Little Blackfoot River area between June and August of 2017 and 2018. We deployed two to four mist nets (38 mm mesh, 4-18 m wide, Avinet, Portland, Maine) per survey. The dimensions and number of mist nets per survey were 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 (we did not detect bats with handheld acoustic detectors while netting below this temperature in either mountain range), or if we encountered persistent thunderstorms or heavy rains (although these situations were infrequent). We assumed that captures from our net efforts represented a reasonably representative sample of the bat populations in the Little Blackfoot and Moose Creek areas (Manly et al. 2002).

We checked nets every 10 minutes (Kunz and Parsons 2009) and removed bats in the order that they were captured. Each bat was identified to species (Bachen et al. 2018) and we assessed sex (Kunz and Parsons 2009) and reproductive status (i.e., pregnant, lactating, nulliparous, scrotal, or non-reproductive; Racey 1988, Kunz and Parsons 2009) and aged each bat as either adult or juvenile based on the degree of joint ossification in the phalanges (Anthony 1988). We measured forearm, foot, and ear length in millimeters with dial calipers and weighed each bat to the nearest 0.5 gram (10 and 50 g spring scales, Pesola, Schindellegi, Switzerland). We visually checked each individual for wing damage, fungus, or parasites. To distinguish little brown myotis with smaller forearm measurements (> 36 mm) from Yuma myotis, we used a handheld acoustic detector (Echo Meter Touch, Wildlife Acoustics, Maynard, Massachusetts) to determine the characteristic frequency of echolocation calls upon release (< 44kHz, Bachen et al. 2018). Non-target species were released immediately after processing.

Radiotelemetry

To locate day roosts, we attached radio transmitters (0.22-0.27 g; model LB-2X, Holohil Systems Ltd, Carp, Ontario, Canada) between the upper scapulae of the bat using skin glue (Osto-Bond, Montreal Ostomy, Montreal, Canada); radiotelemetry occurred between 20 July and 17 August 2017 and 4 June and 21 August 2018. Transmitter weight did not exceed 5% of the bat's body weight to minimize any influence of transmitter application on bat behavior (Aldridge and Brigham 1988). All bats were handled according to approved methods (Montana State University Institutional Animal Care and Use Committee, protocol 2017-26).

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). We first attempted to detect tagged bats from the road, but roads were extremely limited and located only at the bottom of drainages, so we often had to hike to high points to get signals. When we detected a signal, we tracked the bat on foot. 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 individual. Although we tracked a handful of individuals to tree roosts, the sample size was low (see details in Appendix) and we focused our analysis on rock roosts. Bats that roosted in rocks were easily observable, and we were confident in the bat's 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.

When we were unable to detect a bat's transmitter during the day, we checked for the signal during evening hours (i.e., between 21:00 and 01:00), when we assumed they 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 the capture locations one to two times a week during the day and evening in an attempt to detect bats that had seemingly disappeared.

Selecting Available Roosts

We used a paired use-availability design to investigate whether bats were selecting certain rock roost characteristics disproportionately to what was available on the landscape (Erickson et al. 2001, Keating and Cherry 2004, Thomas and Taylor 2006). We selected a single available roost location within a designated area around each used roost location, based on what we thought an individual bat could access in an evening (Thomas and Taylor 2006). By pairing each used day roost with an available roost in close proximity, we were able to examine selection at a fine scale (Thomas and Taylor 2006).

To determine what was available to a little brown myotis within an evening, we considered movement patterns as well as logistics within the landscape. 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 from Montana 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 direction (1-360 degrees) and distance (1-200 m) from the used roost. Once we reached this location, we selected the closest rock feature with a crevice or cavity large enough for a little brown myotis to roost in (i.e., minimum crevice or cavity 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 we encountered that met these requirements. We searched each available roost for bats and guano and if neither were present we assumed that the available roosts were unused at the time of survey (Chruszcz and Barclay 2002).

Characterizing Used and Available Roosts

We collected data on structural characteristics of each used and available roost at three spatial scales: landscape, plot, and roost (Table 1). We also characterized roost microclimates, so we could make associations with the structural features. We carefully selected these characteristics based on previous research and hypothesized habitat relationships.

Landscape-based Features:

At the landscape scale, we focused on quantifying distance to water and amount of forest edge, both of which are known to influence roost selection in several bat species (Anthony and Sanchez 2018, Snider et al. 2013, Broders et al. 2006, Schwab 2006). For each used and available roost, we used geospatial data to measure distances to the nearest water source, regardless of size (MTNHP 2018) and forest edge (MTNHP 2017) using the "Extract Multi Values to Points" tool in ArcMap (Version 10.4.1).

Bats need water to drink, support biological processes, such as lactation, and minimize evaporative water loss (Procter and Studier 1970, Adams and Hayes 2008, Amorim et al. 2018). Some species, such as the little brown myotis, preferentially forage over water bodies or along riparian corridors (Fenton and Bell 1979, Clare et al. 2011, Amorim et al. 2018). We therefore predicted that bats would select roosts closer to water.

Forest edges can provide foraging and commuting habitat and may influence bat activity (Limpens and Kapteyn 1991, Grindal and Brigham 1999, Morris et al. 2010, Pettit and Wilkins 2012, Jantzen and Fenton 2013, Amelon et al. 2014). However, if roosts are too close to a forest edge, they would likely be partially or completely shaded, influencing roost microclimate. For these reasons, we wanted to account for the distance to forest edge.

<u>Plot-based Features:</u> At the plot scale, we characterized the structure 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 (Vonhof and Barclay 1996, Weller and Zabel 2001, Broders and Forbes 2004, Rancourt et al. 2005, Neubaum et al. 2006, Anthony and Sanchez 2018). Using a compass (Ranger model, Silva, Switzerland) and iPhone clinometer (Models 8 and 8 Plus, Apple Incorporated, Cupertino, California), we recorded slope at the roost in degrees and aspect in four categorical levels (i.e., north, east, south, west). We recorded elevation in meters (World Geodetic System 1984) using a GPS, and elevation values recorded in the field were compared to geospatial data (USGS 2017). These topographic factors may affect roost selection in some species by influencing the amount of solar exposure a roost receives (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.

Clutter, or the degree and configuration of physical obstructions in an environment, may influence habitat selection by bats (Carter and Feldhamer 2005, Loeb and O'Keefe 2011, O'Keefe et al. 2014). 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, Buchalski et al. 2013, O'Keefe et al. 2014, Isbell and Horiuchi 2018). To quantify clutter and spatial complexity, we counted all trees and snags (i.e., any stem with DBH > 12.7 cm and height > 1.3 m) within each plot (Neubaum et al. 2006). We predicted that bats would select roosts in less cluttered environments (i.e., fewer trees and snags per plot).

We hypothesized that locations with increased rock cover would provide more roosting opportunities for bats and therefore, predicted that bats may select roosts surrounded by areas with a higher density of rocks. To characterize this, we recorded two factors at the plot level: overall rock cover and the structure type of the rocks housing the roost.

We estimated the percentage of rock cover to the nearest percent within the circular plot; we predicted that bats would select roosts in areas with greater rock cover. To ensure consistency, we compared estimates among observers during a training period. We also classified the main structure within the plot as a rock outcrop, scree, or talus; 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 the rock was embedded in the ground, such that interstitial space under the structure was not available for roosting (although crevices and cavities may have existed within the outcrop itself). We defined scree as loose, gravel-sized rocks less than 20 cm in diameter (similar to the smallest rock size class defined in Tyser 1980). Slopes with loose rocks larger than 20 cm were considered talus; these structures may provide different roosting options for bats (Bachen et al. 2019). For example, in scree slopes, we only observed cavity roosts because the rocks were generally too small to offer crevices. In contrast, talus and rock outcrops provided cavities (often formed by boulders stacked on top of one another), as well as crevices of varying sizes and orientations. Scree slopes were relatively homogenous with regards to rock size (i.e., rocks < 20 cm). Conversely, the size of the rocks in talus and outcrops varied substantially. For these reasons, we hypothesized that bats would select roosts in talus and rock outcrops preferentially over scree.

At talus slopes, we estimated the percent of rock in five size classes: 1) scree, 2) small boulders (defined as < 4-m2 surface area, 3) medium boulders (5-15-m2 surface area), 4) large boulders (>16-m2 surface area), and 5) slab rocks based on shape (Tyser 1980, Turnock et al. 2017).

Roost-based Features: We collected data on several structural characteristics at the roost scale, for both used and available roosts. This included identifying the structure housing the roost, classifying the roost type, as well as measuring the aspect of the roost entrance, canopy closure over the roost, the distance to the nearest horizontal obstruction, and the dimensions 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, scree, or talus. We classified each used or available roost as either a crevice or cavity. These two roost types differed in shape and size, and these differences may affect the microclimate of a roost. We defined a crevice as a narrow fissure or crack in a rock. A rock cavity (hereafter, cavity) was defined as any hollow space in a rock feature created by something other than a crack (e.g., hollow formed by multiple rocks stacked on top of one another) (Bogen et al. 2003, Solick and Barclay 2006). Bats occasionally roosted in rock crevices that extended onto more than one rock face. In this situation, the additional roost was often on a skyward-facing crevice. We defined the main roost as the crevice to which the bat was physically closest and noted whether there was access to a skyward-facing 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-facing crevice.

When possible, we classified the aspect of the roost and plot as a categorical variable with four levels (i.e., north, east, south, west), using a compass corrected for true north (Vonhof and Barclay 1996, Vonhof and Barclay 1997, Russell et al. 2006, Chambers et al. 2011). Bats may be more likely to select south-facing roosts (e.g., Vonhof and Barclay 1997, Rabe et al. 1998, Slough 2009, Chambers et al. 2011), as these roosts likely receive more solar exposure leading to warmer thermal conditions (Vonhof and Barclay 1997). Canopy closure also may influence the amount of solar exposure a roost receives, as well as the physical obstructions immediately surrounding a roost that may inhibit flight and echolocation (Armitage and Ober 2012, Fabianek et al. 2015, Jachowski et al. 2016). We predicted that bats would select roosts with lower canopy closure compared to what was available on the landscape (Vonhof and Barclay 1996, Brigham et al. 1997, Vonhof and Gwilliam 2007, Perry and Thill 2008). Using a spherical crown densiometer (Forestry Supplies, Jackson, Mississippi) held at elbow height, we estimated the percent canopy closure (Schwab 2006, Armitage and Ober 2012). We took one reading in each cardinal direction and used the average of the four as our estimate of canopy closure surrounding the roost/random location (Lemmon 1956). 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, Cox et al. 2016). We recorded the 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 the dimensions and orientation of each used and available roost. Some roosts had multiple openings (e.g., crevices or cavities 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 the width of the roost entrance and the maximum depth of the roost. The width of the roost often varied at different parts of the roost opening. To address this, we averaged the maximum and minimum width of the roost entrance. We measured the depth of the roost by probing throughout the roost with a meter tape and taking the maximum measurement. If the roost was a crevice, we used a compass to classify the orientation of the roost as either horizontal (i.e., 70-110 degrees), vertical (i.e., 160-200 degrees), diagonal (other), or skyward-facing with respect to the ground

(Lausen and Barclay 2002, Rancourt et al. 2005, Lacki and Baker 2007, Johnson et al. 2011). Orientation may affect roost microclimate, and other bat species may preferentially select vertical crevices (Lausen and Barclay 2002, Lacki and Baker 2007). Roosts in rock cavities were classified as having a cavity orientation.

Characterizing Microclimates: We hypothesized that the structural characteristics of each roost at different spatial scales (roost, plot, and landscape, as collected and described above) dictate the microclimate of each roost (i.e., temperature and humidity). However, we also were interested in specifically exploring how temperature and humidity may affect roost selection in male little brown myotis. We predicted that bats would select for roosts with warmer average temperatures.

To characterize roost microclimates, we deployed an iButton (Hygrochron Temperature-Humidity Logger iButton, model DS1923, Maxim Integrated, San Jose, California) in each detected roost (and paired random location) in 2018. These units measure temperature (°C) and relative humidity (%; Neubaum et al. 2006, Neubaum 2018). At used roosts, we deployed the iButton at approximate depth of the bat. Given that bats were absent from available roosts, we deployed iButtons at the same depth as the bat in the used roost. iButtons were deployed for three to five days, beginning when we first located the roost, and programmed to take a reading every half hour. To measure ambient temperature and humidity, we deployed two 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 (1842-2075 m).

Each iButton was housed in a small plastic fob and attached to a galvanized steel hanger wire (2 cm × 34 cm); this casing helped facilitate deployment and retrieval in rock features (Fig. 2, Dan Neubaum, *personal communication*). We compared temperature and humidity readings from iButtons with and without casings and found that the casings had little effect on either metric.

We assumed that bats spent time in day roosts between sunrise and sunset of each day. Therefore, we defined an iButton survey day as the time period between sunrise and sunset. On the first iButton survey day (i.e., the day we located the roost), data were potentially skewed by the body temperature of the bat. In an attempt to standardize surveys, we calculated the average temperature and relative percent humidity collected on the second survey day for analysis. We assumed this day was representative of what the bat had experienced within the roost because iButtons were deployed for a short amount of time (3-5 days) and most days during the tracking period were clear and sunny, with few weather events.

General Features of Used Roosts Only

We characterized some features that were only relevant at used roost locations (Table 2). In addition to visually confirming the bat, we noted whether the bat's antenna was visible. We tried to observe both bat and antenna because bats often roost in groups and we wanted to confirm the location of tagged individuals. We recorded whether the roost structure (i.e., talus, scree, or rock outcrop) was a new or reused location. When possible, we also recorded whether the individual roost (i.e., crevice or rock cavity) was a new or reused location. For example, several bats re-roosted in the same talus slope, but used different rocks or crevices (i.e., reused roost structure). Conversely, some bats re-roosted in the exact same talus, rock, and crevice (i.e., reused roost). Lastly, if the bat was visible, we measured the approximate depth of the bat, taking great care to not disturb it.

Data Analysis

Exploratory Data Analysis: Before developing resource selection models, we examined correlations among the variables of interest at each scale (landscape, plot, roost, microclimate). Because our data were paired, we examined correlations between continuous variables using the difference between used and available roost pairs. Distance to water and distance to major rivers were strongly correlated (Pearson's r = 0.91), as were average temperature and average humidity (0.68). To examine potential correlations between continuous and categorical variables, we examined box and whisker plots. Canopy closure and rock structure type were related, with talus having the least canopy closure, followed by rock outcrops and scree; talus slopes in both mountain ranges were large and, for the most part, unvegetated. Rock structure type also was somewhat related to the number of trees and the rock cover within a plot. Rock roost type was moderately associated with both roost length and width. Lastly, we examined contingency tables to look for potential collinearity between categorical variables. Rock roost type and rock structure type were related; rock outcrops were almost exclusively crevices. When covariates were correlated, we did not include both in the same model. Instead, we selected the covariate in the pair that we thought would best characterize the roost at a particular spatial scale with the most biological relevance and included it in the relevant global model.

<u>Modeling:</u> To assess selection, we built 4 global models based on the suite of covariates collected at the roost, plot, landscape, or microclimate levels, with conditional logistic regression (coxme package in RStudio (Therneau 2019, RStudio Team 2016). 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 in all models.

We began with a global model for each of the four levels, 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. We then used backward variable selection, removing individual covariates that did not explain sufficient variation in roost selection (P > 0.1).

<u>Landscape Global Model:</u> The global model included distance to forest and distance to water. Bats need water for drinking and little brown myotis preferentially forage over water (Anthony and Kunz 1977, Fenton and Barclay 1980, Barclay 1991, Nelson and Gilliam 2017).

<u>Plot Global Model:</u> We included 5 covariates in the global model at the plot scale: elevation, plot aspect, plot slope, trees per plot, and percent rock cover.

Roost Global Model: We included 7 covariates at the roost scale: roost orientation, roost aspect, roost length and width, distance to the nearest horizontal obstruction, canopy closure immediately surrounding the roost, and access to a skyward-facing crevice.

Microclimate Global Model: We also wanted to explore how specific microclimates influence roost selection and hypothesized that the characteristics modeled at the other 3 spatial scales create the unique microclimate observed at each used and available roost . We collected microclimate data during 2018 only, therefore this model was based only on data from used and random locations collected in 2018.

Results

We mist netted a total of 35 net nights during summer 2017 and 34 net nights during summer 2018. We captured 222 bats of 7 species during both sampling seasons, with little brown myotis (32%) and silver-haired bats (29%) comprising the majority of captures (Table 3). In 2018, we netted two new locations within the Little Blackfoot River drainage that were in dense lodgepole forest; we captured 15 of the 16 long-eared myotis at these sites. The sex ratio of captured bats was male skewed (80% male), however, this male bias was higher for Myotis species (86% male), and considerably higher for little brown myotis (94% male) (Table 3).

We attached radio transmitters to 34 male little brown myotis and located at least one day roost for 20 individuals (we also tagged several individual long-legged and long-eared myotis [see Appendix] and one female little brown myotis). Overall, we identified 57 day roosts for these 20 bats (average = 2.85 roosts/bat, range = 1-6). The majority of located roosts were in rock features (*n* = 49 from 18 individuals), but a small number were observed in trees (*n* = 8 from 4 individuals; see Appendix for details about tree-roosting individuals). Most individuals roosted only in rock features (80%, 16 of 20 total individuals). Ten percent of individuals roosted only in trees (*n* = 2) and 10% used both rock and tree roosts (*n* = 2). Although we searched the study area once a week during the day and listened for tagged bats during evening hours, we were unable to locate 14 individuals after release. We did detect a distant signal from 1 of these individuals, but we were unable to locate him before the sun went down, and we never detected this individual again.

Given that so few roosts were in trees, we focused on analyzing data from the rock roosts. We visually confirmed either the bat or the transmitter antenna at 86% (*n* = 42) of the 49 rock roosts. For the majority of these observations, bats were close enough to the roost's surface to be in direct sunlight. We were able to measure the exact depth of the bat for 29 of the 49 observations and we estimated the depth for 12 additional observations. Bats were located an average of 11 cm deep (SE = 1.6, range = 2-30) within roosts. Thirteen of the 20 located individuals (72%) reused a roost structure at least once, and some individuals reused the exact same roost (33%, 6 of 20).

The majority of rock roosts were in talus slopes (65%), but some individuals roosted in rock outcrops, and one individual roosted in a scree slope (Table 4). Crevices (90%) were used much more often than rock cavities; bats used vertical crevices most often (35%), followed by diagonal, skyward-facing, and horizontal crevices (Table 4). The majority of roosts had access to a skyward-facing crevice (59%). Roosts ranged from 1791 to 2117 m in elevation (mean = 1964, SE = 15). Almost half of the roosts (49%, *n* = 24) were located on south-facing slopes, followed by east-facing (29%, *n* = 14), west-facing (18%, *n* = 9), and north-facing slopes (4%, *n* = 2). Most (60%) roost entrances were south- or east-facing (Table 4). For roosts in talus slopes, the majority of rocks in the plot surrounding the roost were small boulders (mean = 46%, SE = 3), followed by scree (mean = 28%, SE = 4), medium boulders (mean = 13%, SE = 2), large boulders (mean = 8%, SE = 2) and slabs (mean = 4%, SE = 2).

Ambient temperature differed slightly between north-facing (mean = 18.8°C, range = 5.1-38.6°C between 13 July and 14 August, 24 hours/day) and south-facing slopes (mean = 20.6°C, range = 7.0-39.0°C). The average temperature in available roosts was slightly warmer than ambient temperatures over the same time period, and the average temperature of used roosts was even warmer (Table 5).

Modeling Habitat Selection

We analyzed data from 47 pairs of rock roosts (used/available) in our landscape, plot, roost, and microclimate models, as we were unable to access two of the rock roosts due to safety constraints.

At the landscape scale, bats were 0.38 times (95% CI = 0.37 to 0.38) less likely to select a roost with every 100 m increase in distance from water (Tables 5 and 6, Fig. 3). We did not detect evidence that these bats were selecting roosts based on proximity to forest edge.

At the plot scale, bats 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 5 and 6, Fig.

4). However, we did not find evidence to suggest that plot elevation, aspect, or slope influenced roost selection. Similarly, we found little evidence that tree density influenced which roosts bats selected.

At the roost-scale, bats were more likely to select roosts that were wider, in areas with less canopy closure, and that provided access to a skyward-facing crevice (Tables 5 and 6). Bats 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 additional 10% of canopy closure. Bats were 13.9 times (95% CI = 2.1 to 93.6) more likely to use a roost with access to a skyward-facing 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 for roost selection.

When we focused on microclimate, we found that bats 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 5 and 6, Fig. 5).

Discussion

Little brown myotis roost in trees, under sloughing bark, and in tree crevices and cavities, but have been documented roosting in lodgepole pine only infrequently (Psyllakis and Brigham 2006, Schwab 2006). Although lodgepole pine trees and snags were abundant within our study area, male little brown myotis selected roosts in rock features more often than trees or snags. Roosts in lodgepole pine occasionally have been documented for other bat species (Vonhof and Barclay 1996, Psyllakis and Brigham

2006, Schwab 2006, Vonhof and Gwilliam 2007), and we tracked a long-eared myotis and long-legged myotis to roosts in lodgepole pine in 2018 (see Appendix).

Given that the male bats in this study preferentially chose to roost in rocks, lodgepole pine in this landscape may not provide appropriate roosting features for male little brown myotis. Although we observed crevices and woodpecker cavities in lodgepole pine snags, these openings were often very shallow or too small (< 1.6 × 2.2 cm) to be accessible to a little brown myotis (Greenhall 1982). The bark of lodgepole pine is generally thin and adheres tightly to the tree bole (Vonhof and Barclay 1996, Chan-McLeod 2006). In larger lodgepole pine snags (i.e., old growth, large DBH), the bark is rough and may peel away from the bole, leaving space for potential roosts (Chan-McLeod 2006). Stands of old-growth lodgepole were lacking in our study area and trees were generally smaller in diameter, although we did observe the occasional large lodgepole pine. Exfoliating bark on lodgepole pine in our study area tended to be flaky and may not provide the same microclimate features or level of protection as other coniferous trees with thicker bark, such as ponderosa pine and Douglas fir.

Roost Microclimate

The microclimate within the roost, namely temperature and humidity, 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). Rock roosts may provide a more stable microclimate than tree roosts (Rancourt et al. 2005, Schwab 2006, Snider et al. 2013, Anthony and Sanchez 2018), which may, in part, explain why bats in our study selected rock roosts instead of trees. We found that male bats selected roosts with features that created higher temperatures relative to other locations available on the landscape. Temperature and humidity were correlated, such that roosts with higher temperatures also tended to have higher humidity.

We identified several structural features of rock roosts that were important for roost selection and may dictate the microclimate of a roost. Bats preferred roosts with less canopy closure, which is consistent with numerous previous studies (e.g., Vonhof and Barclay 1996, Vonhof and Gwilliam 2007, Perry and Thill 2008, Fabianek et al. 2015). Canopy closure affects roost microclimate, such that less canopy closure generally means more exposure to solar radiation (Fabianek et al. 2015). More than half of roosts were on south-facing slopes, which often provide more solar exposure. Bats preferred to roost in rock structures when the immediate surroundings included more overall rock cover. These larger areas of rock (e.g., large talus slopes or outcrops) likely receive more solar radiation and hold heat more effectively than smaller structures surrounded by vegetation. We regularly observed bats sunning themselves; during this behavior, bats roosted in skyward-facing crevices that were wide enough to receive direct sunlight. Sunning behavior has been documented in other studies focused on rock-roosting bats (Slough 2009, Mooseman et al. 2015), and access to a skyward-facing crevice also may be an important selection characteristic in other forest types.

Orientation of rock roosts affects thermal conditions and selection may differ by elevation, environment (e.g., plains versus mountains), and the energetic requirements of the individual. Male little brown myotis preferentially selected crevices with a vertical orientation, which may be better buffered against ambient temperatures than roosts of other orientations (Chruszcz and Barclay 2002). These vertical roosts also provided options to change locations within a roost, which could facilitate thermoregulation. Skyward-facing roosts also provided options for the bat to retreat into deeper or other connected crevices during inclement weather. Conversely, horizontal roosts may heat up more quickly during the day and likely receive a similar amount of solar radiation throughout the entire crevice, offering little variability in microclimate throughout the roost (Chruszcz and Barclay 2002).

Roosts Microclimate and White-nose Syndrome

White-nose syndrome mainly affects bats during winter, yet some recent research suggests that habitat characteristics used during spring and summer could have important effects on bats' response to this disease (Reichard et al. 2014, Wilcox and Willis 2016, Fuller et al. 2020). Roosts that provide variation in microclimate, including the potential for passive warming, could be very beneficial for bats that are recovering from white-nose syndrome (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. By reducing energy needed for thermoregulation, bats may be able to devote more energy to healing and better maintain energy balance (Fuller et al. 2020).

Roosts for Predator Evasion

Although microclimate is an important criterion, 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). In our study area, various species of owls

(*Strigiformes*), weasels (*Mustelidae*), hawks (*Accipitridae*), as well as terrestrial gartersnake (*Thamnophis elegans*), gophersnake (*Pituophis catenifer*), striped skunk (*Mephitis mephitis*), red fox (*Vulpes vulpes*), and coyote (*Canis latrans*) may prey on bats. Rock roosts in talus slopes may be more accessible to terrestrial predators, and wider crevices could expose bats to a higher risk of aerial predation. However, bats within these talus slopes may select roosts with structural features that balance the risk of predation with an appropriate microclimate. Bats are likely able to evade most predators by moving deeper into roost crevices and by switching roosts (Kunz 1982). Rock structures with higher densities of rocks provide more roosting options, allowing bats to switch roosts, while saving energy by remaining in the same general area (Lewis 1995, Kunz 1982, Anthony and Sanchez 2018). Roosts with skyward-facing crevices provide a panoramic view of a bat’s surroundings upon exit of the roost and may aide in predator evasion (Rancourt et al. 2005).

Roosts within the Broader Landscape

The landscape surrounding the roost provides bats access to other basic resources, such as water sources for drinking and foraging for insects (Entwistle et al. 1997, Jenkins et al. 1998). Similar to numerous other studies, we found that bats selected roosts that were closer to water (e.g., Gellman and Zielinski 1996, Rabe et al. 1998, Evelyn et al. 2004, Kalcounis-Ruppell et al. 2005). Although little brown myotis are generalists and can forage in different environments, they preferentially forage over water on aquatic insects (Anthony and Kunz 1977, Fenton and Barclay 1980, Barclay 1991, Nelson and Gilliam 2017). Water bodies in our study areas were concentrated along a few drainage bottoms. During mist netting, we noticed these riparian areas had higher concentrations of insects compared to our netting locations in lodgepole pine stands. Bats that did not roost in proximity to these drainages may need to commute farther to reach foraging and drinking sites, increasing energy expenditure.

Thresholds and Temporal Variation

Given the observed range of values for covariates, we had no reason to suspect curvilinear relationships and instead considered only linear relationships. However, many animals may prefer intermediate values for habitat features, such that future studies should consider the potential for thresholds in preferences. For example, there is likely an upper limit for bats selecting warmer roosts, above which individuals instead must expend energy to stay cool (Rueegger 2019). Bats are endotherms with a large surface area to volume ratio and thus lose heat to the environment quickly (Ruczynski 2006, Wilcox and Willis 2016, Webber and Willis 2018). When roost temperatures are within a bat's thermoneutral zone, individuals passively maintain a low metabolic rate to minimize energy expenditure (Ruczynski 2006, Vaughn et al. 2015, Rueegger 2019). However, once temperatures increase beyond some threshold, bats must instead work to dissipate heat and reduce evaporative water loss, which is energetically costly (Ruczynski 2006, Humphries et al. 2005). Although our study areas are at higher elevations, many bats were in direct sunlight for some portion of the day, based on the temperature readings from the iButtons. Upper thermal limits for little brown myotis are estimated to be 39 to 42°C in the summer (Stones and Wiebers 1967), but these temperature ranges have not been well studied. The maximum average roost temperature we recorded

(33.7°C) may not exceed the thermal preferences of male little brown myotis in this landscape. Similarly, very wide roosts may no longer provide protection from predators or create areas with different microclimates. The widest roost we measured was 11 cm, which may still balance the risk of predation and the energetic benefits received from the extra solar exposure. However, the width of this particular roost narrowed to a width typical of other observations after the entrance and this change in structure may provide additional protection.

Environmental conditions change over time, even within a season, and bats may select different roosts throughout the summer to account for these fluctuations. We did not model potential changes in temperature preferences over the sampling season. We tracked male bats and did not suspect that there would be temporal differences in selection when ambient temperatures remained consistent during our tracking period (the second week of July and mid-August). However, 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).

Variation in Roost Selection Between Sexes

The majority of roost research is focused on female bats (e.g., Weller et al. 2009, Fabianek et al. 2015) and numerous studies demonstrate the importance of microclimate for this group (e.g., Grindal et al. 1992, Solick and Barclay 2007, Randall et al. 2014, Johnson et al. 2019). Reproductively active females require warm roosts to recoup energy spent gestating and lactating (Racey 1973, Racey and Swift 1981, Hamilton and

Barclay 1994), and some species can offset this cost by roosting colonially or entering a torpor state (Burnett and August 1981, Barclay 1991, Kurta 1986). In contrast, male bats often roost alone during the active season (Weller et al. 2009) and may need to thermoregulate or use torpor during the day (Rambaldini and Brigham 2008, Johnson and Lacki 2014). As such, microclimate conditions may be equally as important to males (Chruszcz and Barclay 2002), especially at higher elevations where males likely also face large energetic requirements due to cooler temperatures (Johnson et al. 2019). These relationships require additional research (Weller at al. 2009).

We observed a male-skewed sex ratio for all bat species except long-eared myotis (Table 3). Other studies have found this bias in sex ratios along an elevational gradient, with proportionately more males at higher elevations (Barclay 1991, Cryan et al. 2000, Neubaum et al. 2006, Johnson et al. 2019). Lodgepole forests occur at mid- to high elevations in mountainous regions (MTNHP 2020a, b), where mean annual temperatures are cooler. Pregnant and lactating bats in cooler environments would need to increase their metabolic rate to remain warm or use torpor to minimize energy expenditure, if roosts cannot provide the microclimate needed to remain in the thermoneutral zone (Ruczynski 2006). The ability to go in and out of torpor provides large advantages to males and non-reproductive females (Barclay 1991, Willis et al. 2006), but torpor can slow fetal development and hinder the ability to produce milk, and thus may not always be advantageous to reproductively active females (Geiser 2006, Ruczynski 2006). For these reasons, reproductively active female bats of most species generally are found at lower elevations in mountainous regions (Barclay 1991, Cryan et al. 2000, Senior et al.

2005, Weller et al. 2009). Female bats may not use lodgepole forests in the same manner as males. However, many of the long-eared myotis we captured were females (Table 3), which may be due to the ability of this species to persist in less hospitable environments, even when gestating or lactating (Chruszcz and Barclay 2003).

Variation in Roost Selection Among Species

Lodgepole pine-dominated forests and exposed surface rock are abundant throughout the Rocky Mountains (Coops and Waring 2011, Theobald et al. 2015), especially at higher elevations, potentially providing important habitat for numerous species of bats in western North America. We captured 7 species during our study (Table 3). Of these, 4 species have been observed roosting in rock features at high elevations in the Rocky Mountains during the summer (little brown myotis [Schwab 2006, Johnson et al. 2019], long-legged myotis [Storz and Williams 1996], western small-footed myotis [McEwan and Bachen 2017], and long-eared myotis [Barclay 1991, Solick and Barclay 2006, 2007, Schwab 2006, McEwan and Bachen 2017]). Relatively few studies have examined rock roost selection in detail and the existing research has focused almost exclusively on long-eared myotis in these landscapes (Barclay 1991, Solick and Barclay 2006, 2007, Schwab 2006). We also documented several long-eared myotis within crevices in talus slopes, and at one location, we observed a long-eared myotis sharing a roost crevice with a tagged little brown myotis during a rainstorm. However, we are aware of only one other study (besides our own) that describes the use of higher-elevation rock roosts by little brown myotis during the summer (Johnson et al. 2019).

Understanding how other bat species may be using rock features at higher elevations remains a sizeable information gap.

Lodgepole forests can be incredibly dense (MTNHP 2020a, b), such that only highly maneuverable species, such as long-eared myotis, would be successful in navigating through them in situations where most of the trees are standing and have needles. We captured reproductively active female long-eared myotis soon after sunset when we netted in dense lodgepole pine forest, suggesting that they had day roosts nearby. Long-eared myotis use a foraging strategy that includes gleaning prey off of surfaces and aerial hawking prey in the air (Barclay 1991, Faure and Barclay 1994, Chruszcz and Barclay 2003). This may allow them to capitalize on other sources of prey and persist in harsher environments such as higher elevations or areas with lower prey abundance than some other bat species (Barclay 1991, Chruszcz and Barclay 2003). Little brown myotis and other bat species that do not glean may forage less where prey are limited (Barclay 1991, Chruszcz and Barclay 2003) and may therefore need to select warmer roosts to conserve energy. We did not quantify nightly insect abundance, but while capturing bats within lodgepole pine stands, we noticed that densities of aerial insects declined immediately after sunset (similar to Barclay 1991). When aerial insects declined in abundance, we suspected that long-eared myotis were capitalizing on their ability to glean insects from the trees. For these reasons, we suspect that lodgepole forests are especially important to long-eared myotis.

Challenges Associated with Studying Roosts

Understanding roost selection of insectivorous bats in temperate environments is challenging because individuals are difficult to capture and track due to their relatively small size and ability to fly. Radio transmitter technology often is limited by the size of the animal and telemetry projects need substantial personnel for tracking. We were unable to locate roosts for approximately 40% of the little brown myotis we tagged, but found no obvious morphological differences between bats we did and didn't locate. Bats that we did find were rarely located the day after release and were not always located on consecutive days. These missing observations could be because: 1) transmitters failed or fell off, 2) bats roosted too deep for detection, or 3) bats moved out of our study area. We suspect the latter two explanations are most likely for 12 of the missing bats, but in two cases during 2018, we suspect the transmitters failed due to faulty batteries. Telemetry on bats is extremely difficult in rocky terrain, especially without vehicular or aerial access, due to topography and because transmitter signals attenuate quickly in rock features. In most cases, we first detected 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. Researchers in Colorado deployed test transmitters in talus slopes and struggled to detect signals from transmitters at depths greater than 2.4 m (Dan Neubaum, *personal communication*). Different types of rock features (i.e., scree, talus, rock outcrop) were available in our study area, but the majority of bats used scree and talus. Both of these features provided roosting options deeper than 2.4 m, such that we may have been unable to detect individuals that roosted deep in rocks. We detected two of the “lost” individuals at night, indicating they were actively foraging in the area. We suspect they were roosting deep in rock features and were undetectable during the day. We did not detect the other 10 individuals at night, which suggests that they had left the general area.

Management Implications

The little brown myotis was once one of the most common species of bats in eastern North America (Frick et al. 2010). However, the little brown myotis was proposed for federal listing in 2010 under the Endangered Species Act (ESA 16 U.S.C. §§ 1531- 1544; Kunz and Reichard 2010). Mortalities due to white-nose syndrome have led to population collapses in the eastern U.S., such that this species is now threatened by regional and global extinction and proposed for emergency federal listing under the Endangered Species Act (Kunz and Reichard 2010, Langwig et al. 2015). As white-nose syndrome and the causative agent, *Pseudogymnoascus destructans*, become more prevalent in the west, future research identifying important roosts is vital, especially winter hibernacula where bats are most likely to be impacted.

We found that rock features in our study area provided essential roosting habitat for male little brown myotis during the summer. These features are also are likely important all year, for numerous bat species throughout mountainous regions in the western United States (Johnson et al. 2017, Johnson et al. 2019, Neubaum 2018). Although we did not track bats during the autumn, we did locate two roosts in scree slopes in heavily shaded locations that could serve as potential hibernacula. Each roost had a cavity opening, formed by several rocks stacked together. As we searched for bats, cold air billowed out of the cavities. We were able to extend a measuring tape 8 meters into one of these cavities, suggesting these roosts were quite deep. Bats, including little brown myotis (Johnson et al. 2017, Neubaum 2018), big brown bat (Neubaum et al. 2006, Lausen and Barclay 2006), western small-footed myotis (Johnson et al. 2017), and western long-eared myotis (Johnson et al. 2017), are known to use talus slopes and rock outcrops as autumn transitional roosts and some species use these features as hibernacula (Johnson 2017, 2019, Neubaum 2018). Given the importance of these rock structures, management efforts that protect rock structures with particular characteristics (e.g., larger talus slopes that are close to water with low canopy cover) should be considered in areas where they exist. For example, managers can avoid prescribing timber harvest in forested areas with talus slopes that meet some of these criteria.

Our current understanding about roosts is based on relatively few studies and biologists in western states have been working collaboratively to identify roosts. Ongoing work includes tracking bats to autumn transitional roosts and winter hibernacula (e.g., Neubaum 2018, Laura Beard, *personal communication*, Montana Fish, Wildlife, and Parks, *personal communication*), identifying fall swarming locations using acoustic bat detectors (e.g., Montana Natural Heritage Program, *personal communication*, Karen Blejwas, *personal communication*), and investigating alternative methods to assist in identifying these features, such as conservation dogs (Amie Shovlain and Karen Blejwas, *personal communication*) and eDNA (e.g., Julie Weckworth, *personal communication*). These collaborative efforts, in combination with our work, add to the growing body of literature regarding bat roost use in the western North America.

Tables

Table 1. Characteristics measured at used and available roosts at 4 different scales (landscape, plot, roost, and microclimate) to characterize roost selection of *Myotis lucifugus*, 2017-2018, west central Montana.

Characteristic	Description	Categories or Units
Landscape		
Distance to forest	Distance to the forest edge	m
Distance to water	Distance to water (i.e., streams or rivers)	m
Distance to major river		m
Plot		
Roost Structure Type	Classification of structure housing the roost	talus, scree, rock outcrop
Plot aspect	Aspect of the ground at the roost	North, East, South, West
Slope	Slope of the ground at the roost	Degrees
Elevation	Elevation at the plot	M
Tree per plot	Number of trees and snags per plot	Integer
Percent rock per plot	Estimated percentage of ground within plot that was rock	%
Roost		
Roost Type	Roost classification	crevice, cavity
Aspect of roost entrance	Aspect of roost entrance	North, East, South, West
Canopy closure	Estimated % canopy closure at roost	%
Horizontal obstruction	Distance to the nearest horizontal obstruction	m
Skyward-facing crevice present	If the main roost was not defined as a skyward-facing crevice, was it attached to a skyward-facing crevice?	Yes/No
Roost length	Maximum length of the main roost crevice or cavity	to nearest 0.1 cm
Roost width	Average of maximum and minimum roost crevice or cavity	to nearest 0.1 cm
Crevice orientation	Orientation of crevice based on the slope of the crevice	horizontal, vertical, diagonal, skyward-facing, cavity

Microclimate		
Mean temperature	Mean temperature during the second day of survey	ºC
Mean humidity	Mean relative humidity during the second day of survey	%

Table 2. Characteristics measured only at roosts used by *Myotis lucifugus*, 2017-2018, west central Montana.

Characteristic	**Description**	**Categories or Units**
Bat visible	Was bat visible to observer?	Yes/No
Entrance visible	Was entrance to roost visible to observer?	Yes/No
Antenna visible	Was antennae visible to observer?	Yes/No
New structure	Roost located in a new roosting structure (i.e., talus, rock outcrop, tree) for this individual?	Yes/No
New roost	New roost for this individual or had it previously been used?	Yes/No
Bat depth	Depth of bat within roost	cm

Table 3. Number of bats captured by species and sex (% male versus female or unknown), west central Montana, 2017-2018. Unidentified Myotis species were individuals that escaped or were released before definitive identification was made. Individuals with a questionable fringe on their uropatagium were classified as *Myotis evotis/thysanodes*. Individuals with forearm measurements > 36 mm or those that produced indistinguishable characteristic frequencies were classified as *Myotis lucifugus/yumanensis.*

Species	**Number Captured**	**% male**
Myotis lucifugus	71	94.4
Lasionycteris noctivagans	64	70.3
Eptesicus fuscus	19	84.2
Myotis Volans	18	88.9
Lasiurus cinereus	17	88.2
Myotis evotis	16	56.3
Myotis thysanodes	2	100.0
Unidentified *Myotis* spp.	6	50.0
Myotis evotis/thysanodes	6	50.0
Myotis lucifugus/*yumanensis*	3	66.7
Total	**222**	**80.2**

Table 4. Summary of covariates describing roosts (*n* = 49) used by male *Myotis lucifugus*, 2017-2018, west-central Montana.

Covariate	No. Observations	% of total
Rock Structure Type		
Talus	32	65.3
Rock Outcrop	16	32.7
Scree	1	2.0
Roost Type		
Crevice	44	89.8
Cavity	5	10.2
Aspect of Roost Entrance*		
Skyward-facing	8	17.0
North	2	4.3
East	10	21.3
South	18	38.3
West	9	19.1
Crevice Orientation		
Skyward-facing	8	16.3
Horizontal	5	10.2
Vertical	17	34.7
Diagonal	12	24.5
Cavity	7	14.3
Skyward-facing 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

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

Table 5. Means (and ranges) for values observed at used and available (random) roost sites of male little brown myotis (*n* = 47 pairs of used/available roosts), 2017-2018, west-central Montana.

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

Table 6. Estimates (on the log-odds scale), standard errors, test statistics, and p-values for covariates included in the four final models (one at each of four spatial scales) for roost site selection by male little brown myotis (*n* = 47 pairs of used/random roosts), 2017-2018, west-central Montana.

Model	**Covariate**	**Estimate**	**Standard Error**	***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-facing crevice present	2.6300	0.9485	2.77	0.0056
Microclimate	Temperature (°C)	0.2116	0. 1098	1.93	0.0540

Figures

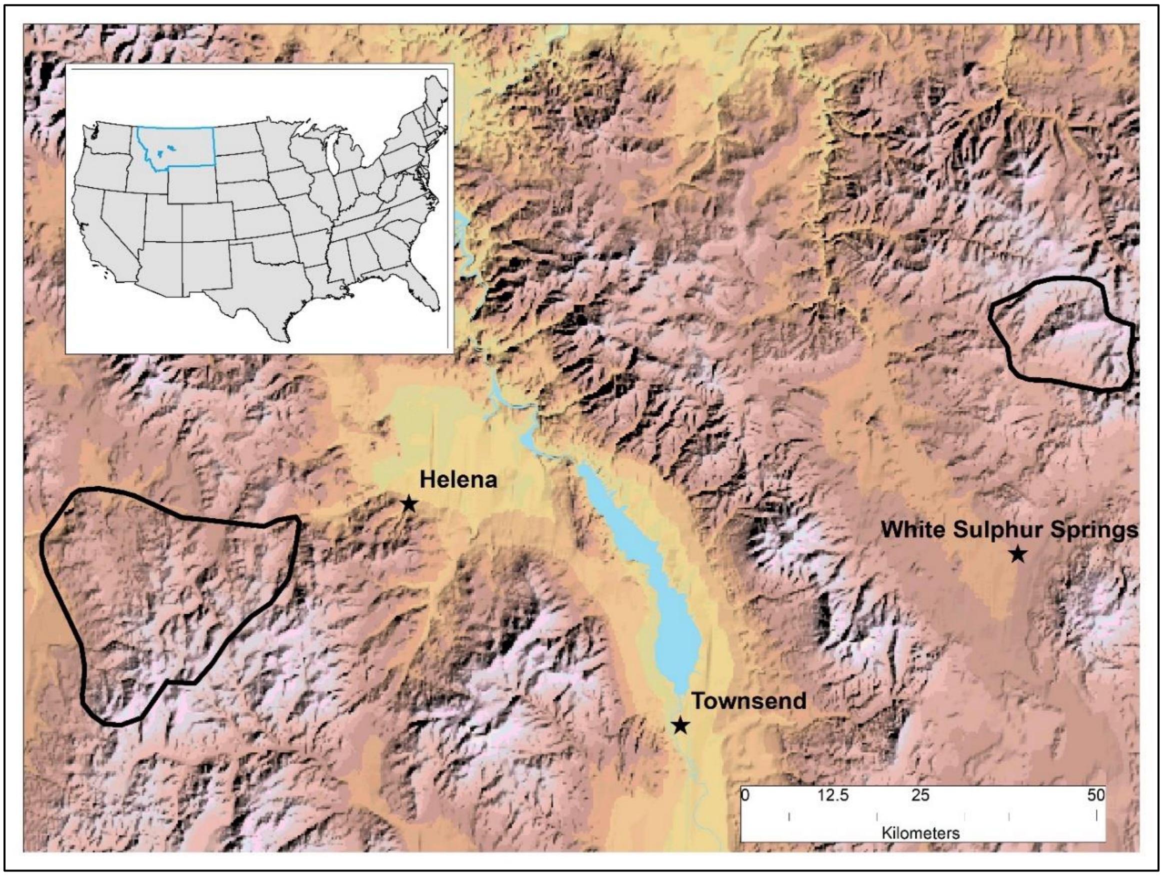

Figure 1. Locations of radio telemetry work, 2017-2018, west central Montana (see inset). We collected data in the Little Blackfoot River study area in the Boulder Mountains (delineated in black on the left) and the Moose Creek study area in the Little Belt Mountains (delineated in black on the right).

Figure 2. iButton in plastic fob (left) and iButton and fob with galvanized steel strapping (right). iButtons were deployed within used and available roosts to collect temperature and humidity data.

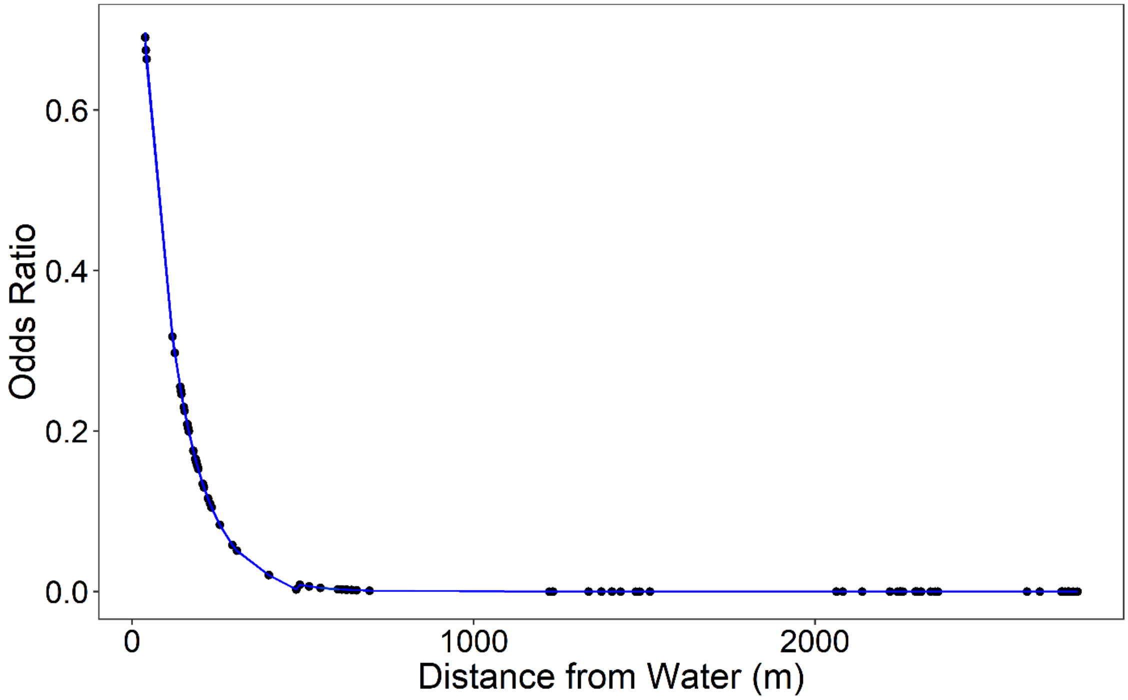

Figure 3. Odds of a bat selecting a roost with increasing distance from water. Blue lines indicate 95% confidence interval.

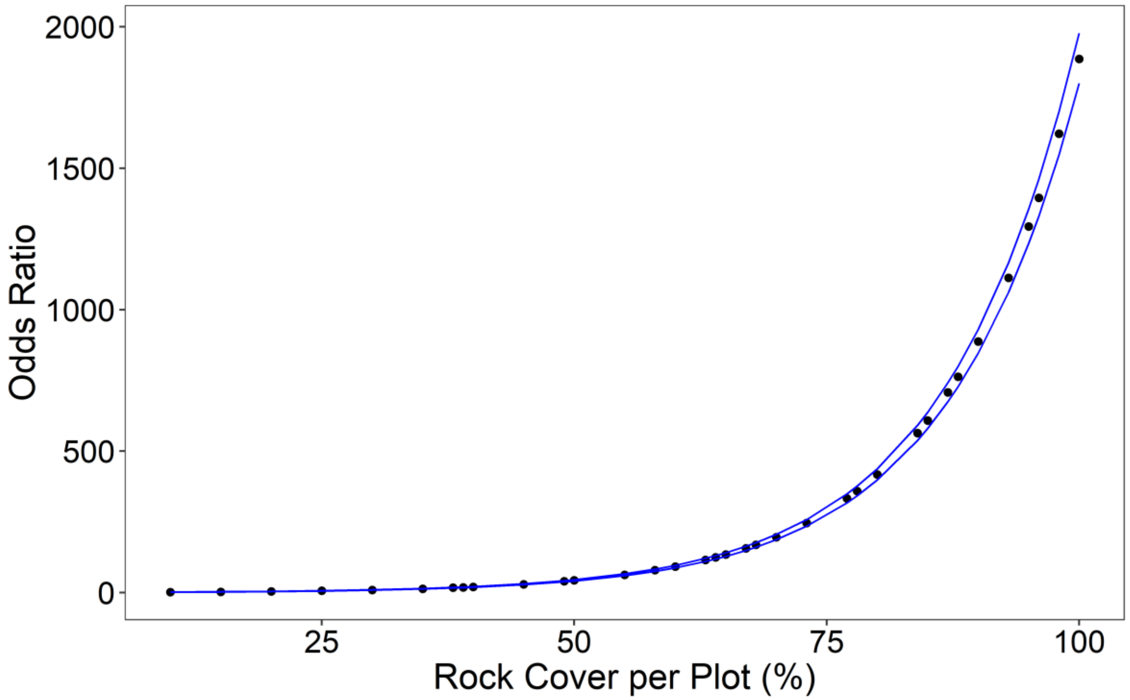

Figure 4. Odds of a bat selecting a roost with increasing rock cover (%) within a 17.8 m-radius plot. Blue lines indicate 95% confidence interval.

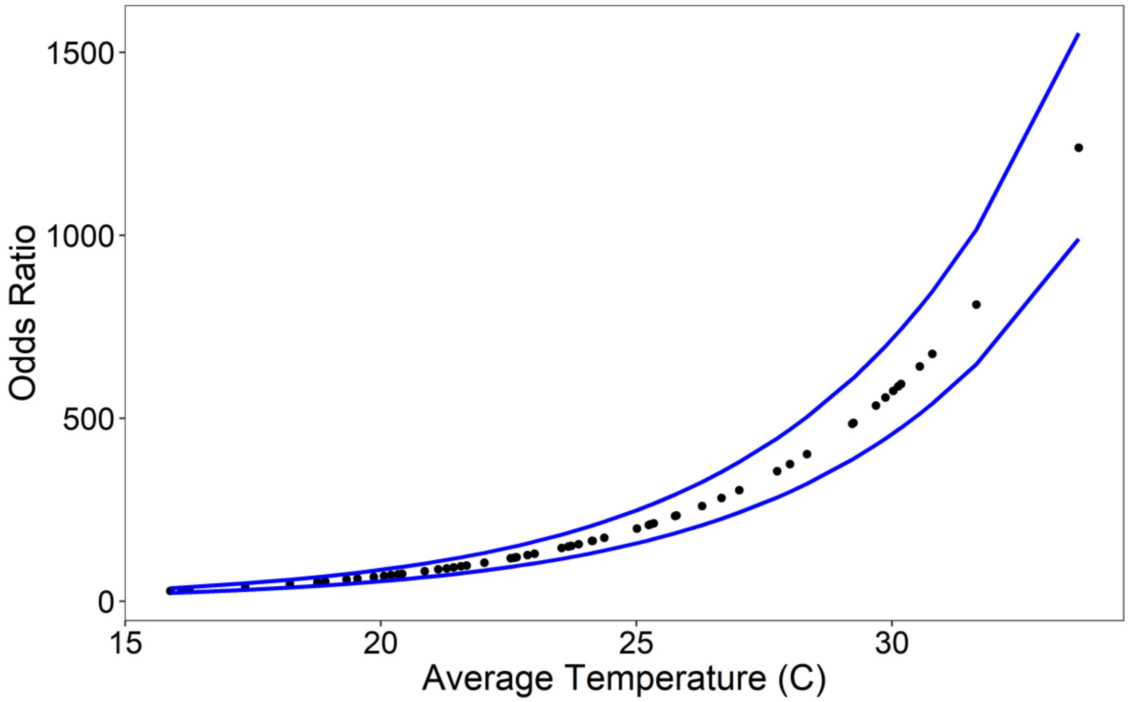

Figure 5. Odds of a bat selecting a roost with increasing average temperature. Blue lines indicate 95% confidence interval.

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APPENDIX

APPENDIX A

SUMMER TREE USE BY MALE LITTLE BROWN MYOTIS, LONG-EARED MYOTIS, AND LONG-LEGGED MYOTIS IN LODGEPOLE PINE-DOMINATED FORESTS

During the 2018 field season, we placed radio transmitters on 4 male long-legged myotis and 2 male long-eared myotis, in addition to the 34 little brown myotis we described in the main text. Between 12 July and 17 August 2018, we worked to locate individual roosts for these bats following methods outlined in the main text. Once located, we used a handheld GPS unit (Garmin GPSMAP 64s, Garmin International Incorporated, Olathe, Kansas) to record latitude and longitude of the roost structure in decimal degrees.

Bats that roosted in rock structures were easily observable, and we were confident in the bat's location within these roosts. Conversely, bats that roosted in trees roosted high in the structure, and trees were often decayed, essentially making them inaccessible. Due to our low sample size of tree roosts, and because we were unable to climb trees and snags to determine whether bats were using available tree roosts on the day of survey, we did not collect data on random, available tree roosts.

Once we located a roost, we collected data on structural characteristics that we thought would best characterize the area surrounding the roost (Table A). We recorded elevation, slope, and aspect at the roost and estimated percent rock cover, canopy closure, the number of trees and snags per plot using methods described in the main text.

At each tree roost, we collected data on several additional physical roost characteristics. We identified the tree species housing each roost. When the roost was located in a lodgepole snag, we recorded signs of mountain pine beetle (MPB), (i.e., vertical egg galleries, pitch tubes, and blue-stain fungus as per Gibson et al. 2009). We classified each tree or snag to 1 of 9 decay classes based on degree of decay and the percent of branches and canopy remaining (Vonhof and Barclay 1996); trees could be classified as decay classes 1 and 2, whereas snags could be categorized as decay classes 3-7. Several species of bat have been observed roosting under exfoliating bark (Hayes 2003, Lacki et al. 2013, Bachen et al. 2019) and we estimated the percent bark remaining on each roost structure as a measure of potential bark available for roosting. Several studies have demonstrated that bats roost in large trees in forest types other than lodgepole pine (Brigham 1991, Schwab 2006, Perry and Thill 2008, Arnett and Hayes 2009, Lacki et al. 2013). We measured the diameter at breast height (DBH) (i.e. 1.3-m high) with a DBH tape (Forestry Suppliers, Jackson, MS). We used a clinometer to calculate the tree height, and when possible, the height of the roost (Vonhof and Barclay 1996).

We tried to determine the aspect of the bat's location within the roost, even if the bat and antenna were not visible; we later converted aspect to a categorical variable with 4 levels (i.e., north, east, south, west). When we were able to see the bat's antenna or determine a location within the tree, we classified the roost as exfoliating bark, cavity, or crevice. We defined exfoliating bark as any bark that showed evidence of detachment from the phloem; loose bark like this can create crevices or cavities large enough to create a roost (Rabe et al. 1998, Lacki et al. 2013). Cavities were defined as any hollow space in trees and crevices were defined as any fissure in the tree stem. Roosts where we were unable to discern the bat's location were classified as unknown roost types. We recorded whether the roost structure was in a new or reused location to determine if bats were switching roosts. We did not deploy iButtons within tree roosts due to safety concerns.

We located at least one tree roost for 1 long-eared myotis, 3 long-legged myotis, and 4 little brown myotis. Overall, we located 21 roosts for these 8 individuals (2.65 roosts/bat, range 1-6). We were only able to visually confirm the location for one bat (long-legged myotis). However, we observed antennae at 4 roosts (2 long-legged myotis). Each of the tree roosting bats reused a roost at least once and 62% (*n* = 13) of roosts were reused overall. Some individuals used both rock and tree roosts (38%, 2 little brown myotis and 1 long-eared myotis), but the majority used only tree roosts (62%, 2 little brown myotis and 3 long-legged myotis).

Roosts ranged from 1781 m to 2111 m in elevation (mean = 1961, SE = 23.4), with long-legged myotis roosting in slightly higher elevations (Fig. A). The slope of the area immediately surrounding the roost ranged from 7 to 41 degrees (mean = 18.8, SE = 2). Most roosts were on slopes with east- (48%, *n* = 10) and south-facing aspects (24%, *n* = 5); west- and north-facing slopes were used equally (*n* = 3). However, most bats were on south-facing sections of the roost tree, when we were able to determine a roosting aspect (48%, *n* = 10). Roost trees were located in dense stands (mean = 69 trees/snags per plot, SE = 11.7) with high canopy closure (mean = 84.9%, SE = 2.2). Overall rock cover was low (mean = 8%, SE = 3.1).

Most tree roosts were in Douglas-fir (*n* = 8) and lodgepole pine (*n* = 11) snags, but two of the roost trees used by one long-legged myotis were classified as live Douglas-fir (i.e., decay class 2). We did not locate any roosts in stumps (i.e., decay classes 8 and

9). Trees retained most of their bark (mean = 85%, SE = 2.7). Roosts trees were 45.4 cm DBH (SE = 4.6) and 21 m tall (SE = 1.5), on average. We were able to determine the height of 13 roosts (mean = 11 m, SE = 1.5).

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<u>Tables</u>

Table A. Characteristics measured at tree roosts to characterize tree roosts, 2018, west central Montana.

Characteristic	Description	Categories or Units
Elevation	Elevation at the plot	m
Slope	Slope of the ground at the roost	degrees
Plot aspect	Aspect of the ground at the roost	North, East, South, West
Percent rock per plot	% of plot that was rock	%
Canopy closure	Estimated % canopy closure at roost	%
Trees and snags per plot	Number of trees and snags per plot	integer
Tree species	Species of tree housing roost	lodgepole pine, Douglas-fir
MPB signs	Whether tree had been impacted by MPB	Yes/No
Decay class	Degree of decay in the tree housing the roost	1-9
Tree or Snag	Whether the roost was located in a tree or snag, based on decay class	Tree/Snag
Bark	% bark remaining on tree	%
DBH	Diameter at breast height or roost tree	cm
Roost tree height	Height of roost tree	m
Roost height	Height of roost tree	m
Bat aspect	Aspect of tree where bat is located	North, East, South, West
Roost type	Roost classification	Exfoliating bark, crevice, cavity, unknown
New roost	New or reused roost	Yes/No

Figures

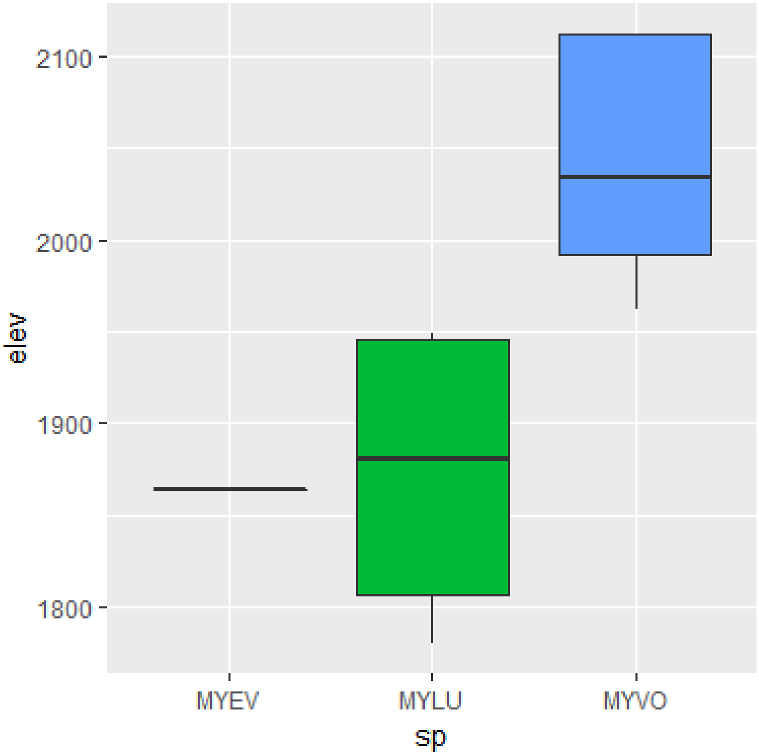

Figure A. Box and whisker plot of elevations recorded at tree roosts for three Myotis species: *Myotis evotis* (MYEV, *n* = 2), *Myotis lucifugus* (MYLU, *n* = 8), *Myotis volans* (MYVO, *n* = 11), 2017-2018, west central Montana.