Received: 18 December 2025 | Revised: 24 July 2026 | Accepted: 26 August 2026

DOI: 10.1002/jwmg.70282

THE JOURNAL OF WILDLIFE MANAGEMENT | THE WILDLIFE SOCIETY

RESEARCH ARTICLE

Living on the edge: Habitat characteristics of northern myotis at the periphery of its distribution

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Funding information

U.S. Bureau of Land Management, Grant/Award Number: L21AC10345; Montana Fish, Wildlife and Parks, Grant/Award Number: FWP 23-0192; Montana Chapter of The Wildlife Society; Western Bat Working Group, Grant/Award Number: Bob Berry Holohil Award

Abstract

Populations at the edge of their distribution may occur in places with atypical and more variable conditions than at the core of the range. We characterized habitat selection for the northern myotis (*Myotis septentrionalis*) at the western edge of its known distribution in the United States, comparing roost selection to other peripheral populations and core populations. We focused on summer daytime roosts, which provide refuge while bats give birth, raise young, and prepare for hibernation or migration. We captured bats from May–August in 2022 and 2023 and attached transmitters to 36 northern myotis. We located 76 roosts from 33 tagged individuals and characterized roost (used) trees and the surrounding patch, comparing these with random (available) locations. Our findings support the notion that northern myotis select roosts based on characteristics of the tree and the surrounding patch, choosing areas that provide multiple possible roosts. Northern myotis showed strong associations with tall trees in patches having a relatively high average basal area that contained multiple trees similar to the roost tree; results are consistent with previous research. Bats roosted primarily in eastern cottonwoods (*Populus deltoides*; 97% of roosts), which was the most available tree species on the landscape, yet this species has been used infrequently in other

studies. Bats selected cottonwoods in early stages of decay with somewhat less canopy cover, whereas other studies in the core of the distribution have documented extensive use of snags and decaying trees; this difference was likely due to limited availability of later decay stages in our study area. Most consecutive roosts were relatively close together (range = 2–881 m) and each roost was used for 1.7 days on average (range = 1–7). In this landscape, large trees were mainly found in narrow linear bands along riparian corridors within an agricultural matrix, which differs from the larger areas of dense contiguous forest documented in the core of the species' range. Despite apparent limitations, this forest-dependent species is still finding roost locations, choosing the tallest trees in the densest patches available. Maintaining these resources and conditions is important for conservation of this endangered bat, especially as even-aged stands of cottonwoods mature. Improving our understanding of habitat selection of northern myotis at the periphery and core of their range is essential to support this endangered species in the face of environmental changes.

KEYWORDS

habitat selection, maternity roost, *Myotis septentrionalis*, northern long-eared myotis, peripheral populations, roost

During the summer, bats in temperate regions must find day roosts that provide refuge while they give birth, raise young, and prepare for hibernation or migration (Kunz and Lumsden 2003). As small, flying mammals, bats have unusually high energy demands, and therefore face unique challenges in selecting habitat features that balance the energetic trade-offs to support their needs (Kunz 1982). Habitat selection in bats is likely influenced by morphological features (e.g., wing shape, call characteristics) and the degree of sociality (Saunders and Barclay 1992, Weinbeer and Kalko 2004, Marinello and Bernard 2014, Patriquin and Ratcliffe 2016, Russo et al. 2017). High-quality roosts play a crucial role in reducing the energetic demands on bats by minimizing the need to fly long distances to find food and water, as well as creating an appropriate microclimate that allows bats to stay within their thermoneutral zone (Sedgeley and O'Donnell 2004).

The costs of flight and thermoregulation apply to all bats, but other energetic expenses, namely those associated with reproduction, differ among individuals (O'Keefe 2009). Reproductively active females expend substantial energy as they gestate, feed, and raise pups, underscoring the importance of reducing energetic costs through roost selection (Speakman and Thomas 2003, Garroway and Broders 2008). Pregnant females often form maternity colonies in a single roost, where many individuals give birth and raise pups (Kunz and Lumsden 2003, O'Keefe 2009, Slough and Jung 2020). In maternity colonies, bats reduce the individual costs of warming by clustering together, decreasing the exposed surface area. Additionally, the heat generated by the clustered group raises the ambient temperature (Hayes et al. 1992). In contrast, males are less likely to occur in colonies during summer, potentially because of different energetic needs, competitive exclusion, or other reasons (reviewed in Weller et al. 2009).

Owing to their ability to fly, habitat selection is likely a tiered process for bats (Gorresen et al. 2005, Lipsey et al. 2017). As bats move, they gain an aerial view of possible sites and can assess at a broad level whether an area will provide the necessary food, water, and shelter to survive and reproduce. Bats can also search for specific patches and trees or other structures within those patches that can serve as roosts. Considering characteristics of the roost location, the surrounding environment, and the roost's ambient microclimate collectively can provide important insights into roost selection that may not be captured separately (Bellamy and Altringham 2015).

The northern myotis (northern long-eared myotis [*Myotis septentrionalis*]) is a small, insectivorous bat that was uplisted to endangered under the Endangered Species Act in 2023 because of significant population declines due to white-nose syndrome, a disease caused by the fungus *Pseudogymnoascus destructans* (U.S. Fish and Wildlife Service [USFWS] 2022, 2023). Northern myotis is a forest-dependent species (Foster and Kurta 1999, Broders et al. 2006), relying on forested areas to meet most of their needs during summer. Their short, broad wings and steep echolocation calls allow them to maneuver through dense forests, gleaning insects directly from trees or the ground (Norberg and Rayner 1987). Like several species within the *Myotis* genus, northern myotis exhibit a fission-fusion social structure, with individuals moving among different roosts to maintain bonds within a group (Kerth and König 1999, Vonhof et al. 2004, Garroway and Broders 2007), adjust to changing weather conditions (Patriquin et al. 2016), and reduce disturbance from humans or predators (Olson and Barclay 2013), ectoparasite loads (Reckardt and Kerth 2007), and distances to foraging locations (Sedgeley and O'Donnell 2004). Northern myotis switch roosts every few days and have large networks of roosts containing lower numbers of maternally related individuals (reviewed in Silvis et al. 2016).

Habitat of northern myotis has been well studied throughout much of the species' broad geographic distribution (Figure 1); some researchers have completed meta-analyses and reviews of the existing literature to synthesize our understanding (e.g., Lacki et al. 2009, Silvis et al. 2016, Garcia et al. 2023). Although this bat shows some degree of generality in habitat selection, using a variety of conifer and deciduous tree species for roosting, these trees tend to be in later stages of decay and bats roost under bark or in cavities and crevices (reviewed in Lacki et al. 2009, Silvis et al. 2016, Garcia et al. 2023). Northern myotis also tend to roost in larger trees within forests with more continuous canopy cover (reviewed in Silvis et al. 2016). However, some researchers have documented variation in habitat selection, phenology, and disease effects for populations at the periphery of this species' range (e.g., Nebraska: Andersen and Geluso 2022, Louisiana: Garcia et al. 2023, Georgia: Grider et al. 2024, coastal New York and Massachusetts: Gorman et al. 2022, Hoff et al. 2024, 2025; Prince Edward Island: Henderson and Broders 2008; coastal South Carolina: Loeb et al. 2026). Peripheral populations may occur in places with atypical conditions, often resulting in lower abundance than at the core of a species' distribution (Brussard 1984, Lesica and Allendorf 1995, Munwes et al. 2010, Chevin and Lande 2011). Isolated peripheral populations also can be genetically distinct (Lesica and Allendorf 1995), resulting in potential refugia in the face of environmental changes (Gorman et al. 2022, Hoff et al. 2025).

We sought to characterize habitat selection for the northern myotis at the farthest western edge of its distribution currently documented in the United States, comparing roost selection to other peripheral populations and to core populations. We hypothesized that roost selection by northern myotis during summer was driven by their morphology, sociality, and minimizing the energetic costs of flight and thermoregulation, but we also thought that some features of the available roosting habitat for this peripheral population differed from the core of the species' range, potentially altering selection patterns. We measured covariates at 2 levels—the roost tree itself and the surrounding patch—and considered these features collectively to align with the hierarchical nature of habitat selection (reviewed in Silvis et al. 2016). We predicted that characteristics at both levels would be important for roost selection.

STUDY AREA

We focused our work in northeastern Montana, the location of the westernmost population of northern myotis found to date in the United States (Figure 1). Our study area extended from the banks of the Missouri River near Frazer, Montana, west to the confluence of the Missouri and Milk Rivers, below Fort Peck Dam and Reservoir. This

FIGURE 1 Range map for the northern myotis within the United States (USFWS 2025), including our study area (in northeastern Montana, in lavender), which is the westernmost extent of the distribution currently (2026) documented in the United States.

was a 28-km stretch of river, where captures and surveys occurred 1–2 km from the river on both the north and south sides, resulting in a study area of approximately 80 km^2. Land ownership was a mix of Bureau of Land Management, Fort Peck Reservation, United States Army Corps of Engineers, and private agricultural and ranching properties.

Forested areas were patchy, occurring as narrow, linear corridors along the rivers (Figure 2), and were largely dominated by eastern cottonwoods (*Populus deltoides*), interspersed with green ash (*Fraxinus pennsylvanica*) and some small patches of willow (*Salix* spp.). Eastern cottonwoods tend to seed into new floodplains and develop as pure, even-aged stands (Braatne et al. 1996). Cottonwood trees in our study area were of similar sizes and decay stages, whereas ash trees occurred in more variable sizes and decay stages. Sections of these forests, particularly on the southern side of the river, have experienced long periods of extensive cattle grazing resulting in little to no understory cover. The elevation along the Missouri and Milk rivers was relatively consistent, approximately 600 m above sea level; the maximum elevation observed in the Milk River Hills was 680 m. These river corridors hosted 5 myotis species: little brown myotis (*Myotis lucifugus*), long-eared myotis (*Myotis evotis*), long-legged myotis (*Myotis volans*), northern myotis, and western small-footed myotis (*Myotis ciliolabrum*), along with 4 other bat species: big brown bat (*Eptesicus fuscus*), eastern red bat (*Lasiurus borealis*), silver haired bat (*Lasionycteris noctivagans*) and hoary bat (*Lasiurus cinereus*; Montana Natural Heritage Program and Montana Fish, Wildlife, and Parks 2024).

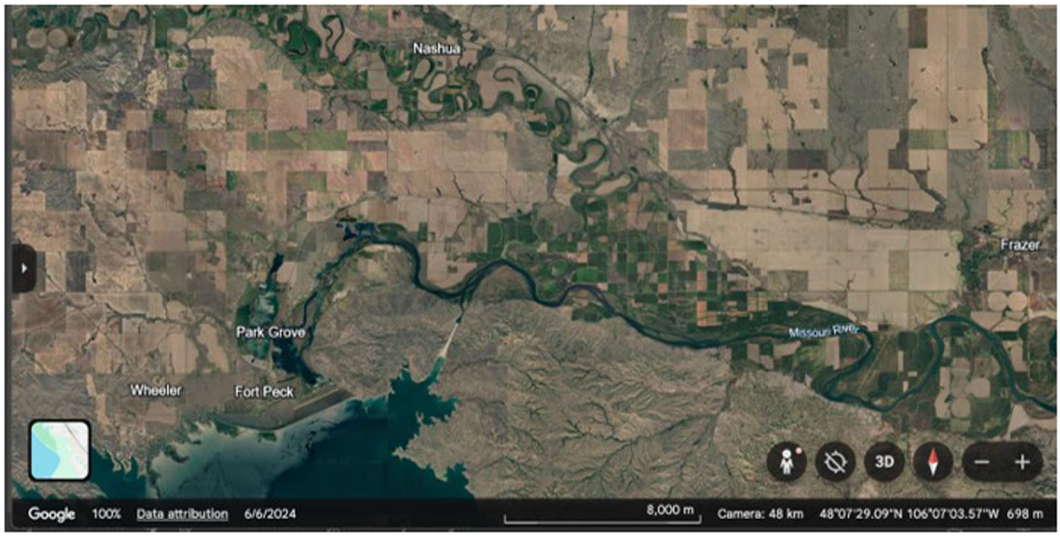

FIGURE 2 Satellite imagery of our general study area in northeastern Montana, USA (Google Earth; Google, Mountain View, CA, USA). This map includes data from Google and Airbus and imagery from 6 June 2024–18 October 2025.

METHODS

Bat capture

Traditionally, northern myotis are captured as they drink or forage over water, or when using forest corridors (Garroway and Broders 2008, Hyzy et al. 2020). However, in our study area, the main water sources were too large to net, and the cottonwood gallery forests lacked clearly defined flight corridors. To increase the odds of successful capture in this open environment, we deployed 1–6 triple-high mist net sets (38-mm mesh polyester nets, Avinet Research Supplies, Portland, ME, USA) per night. We captured bats between 29 May and 10 August 2022, and between 1 June and 4 August 2023. We opened nets shortly after sunset to decrease the chance of accidental bird capture and closed them between 2400 and 0200 hours. We checked nets every 10–12 minutes and immediately closed nets when there was persistent rain or wind. We netted each site for 1–6 nights (maximum 4 in a row) depending on previous capture success or observed bat presence in the area.

We carefully removed captured bats from the net and placed them in holding bags (Avinet Research Supplies) until they could be processed, no longer than 20 minutes. We weighed the bat in the bag (50-g Pesola Light-Line Spring Scale, Forestry Suppliers, Reedsburg, WI, USA) and determined the individual's sex, age, and reproductive status. We determined sex via the presence of the penis for males, or vaginal orifice for females. We determined age based on the degree of epiphyseal-diaphyseal ossification observed; juveniles display a gap in the finger joint because it has not yet ossified (Krochmal and Sparks 2007). We classified reproductive status for males as either testicular when testes were enlarged and clearly visible or non-reproductive otherwise. We considered females to be pregnant if weight was higher than normal, belly was visibly swollen, and an intrauterine pup could be felt by gently palpating the abdomen; lactating if nipples were conspicuously visible and sometimes red or raw; post-lactating if the fur around the nipples was growing back; and non-reproductive if we observed none of these characteristics (Owen et al. 2002).

For each captured individual, we identified species based on morphology and 3 main diagnostic measurements: weight (g), forearm length (mm), and ear length (mm; Bachen et al. 2018). For any individuals identified as northern myotis, we also collected guano and a 3-mm wing punch to validate species identification based on genetics. We

stored samples in silica gel beads in 1.5-ml microcentrifuge tubes. We sent these samples for genetic analysis to the National Genomics Center for Wildlife and Fish Conservation (Missoula, MT, USA).

We checked each bat for signs of white-nose syndrome and the associated fungus and assigned a wing damage score (Reichard and Kunz 2009, Reichard 2018). We released non-target species immediately after our assessments. We decontaminated all equipment used to process bats between individuals and changed latex gloves for handling every bat. We decontaminated all equipment and clothing when we finished netting a site, in accordance with current accepted protocols (White-nose Syndrome Disease Management Working Group 2020). Additionally, we wore N-95 masks and other protective gear to protect against the transmission of COVID-19.

Radiotelemetry and roost tree characteristics

We attached radio-transmitters (0.27 g, model LB2X, Holohil Systems Ltd., Carp, Ontario, Canada) to northern myotis when the transmitter weight was less than 5% of the bat's body weight (Aldridge and Brigham 1988). We glued the transmitter between the upper scapulae of the bat (Osto-Bond Skin Bonding Cement, Montreal Ostomy and Home Care Center, Montreal, Quebec, Canada). We aimed to tag reproductively active females, but we attached transmitters to all northern myotis captured unless they weighed too little or had previous wing damage that would seem to hamper flight.

Daytime telemetry began as soon as we had bats with active transmitters, beginning near the capture site and working outwards. We used R1000 receivers (Communications Specialists, Orange, CA, USA) and 3-element Yagi antennae (Telonics, Mesa, AZ, USA). We attempted to locate roosts for all bats with active transmitters each day, typically tracking 5–7 bats simultaneously. We tracked bats daily until transmitters fell off or failed (i.e., battery died) or the bat left the landscape and could no longer be detected.

When possible, we returned to the roost the same night to confirm roost location within the tree and perform an exit count. We performed exit counts at new roosts of all female (adults and juveniles) and juvenile male northern myotis to determine whether the location was a maternity roost. One to 2 observers arrived at the roost 20–30 minutes prior to sunset. Observation continued until at least 30 minutes past sunset, or 10 minutes after we no longer observed bats emerging, whichever was later.

After tracking the bat to the day roost, we attempted to determine where in the tree the bats were roosting. We recorded the aspect and height of the bat's estimated location within the tree. We also recorded which type of feature the bat was using: a cavity, a crevice, or under the bark.

We used roost locations to quantify the distances between consecutive roosts used by the same bat, proximity of all roosts of northern myotis within a year, and proximity of these same roosts separated by sex and reproductive status: non-reproductive females, reproductive females (pregnant, lactating, post-lactating), and males; all tracked males were non-reproductive. We assessed roost fidelity by calculating the number of days each bat spent in each roost, for all bats and for the 3 sex and reproductive status groups.

Characterizing habitat selection

We used a paired use-availability design (Thomas and Taylor 2006) to characterize habitat selection, sampling at least 1 random (available) location for each roost (used) location. By comparing characteristics of used locations to what was likely available to bats, we could assess whether northern myotis were selecting day roosts based on specific environmental features. We used movement information to determine availability. Successive roost locations for northern myotis typically are 152–230 m apart (Henderson and Broders 2008, Johnson et al. 2009, Gorman et al. 2023). Based on previous studies and the small size of the riparian cottonwood forests, we selected random (available) locations within 0–300 m of each roost (used), in any direction (0–360°). When we arrived at the random bearing and random distance, we selected the closest tree, regardless of tree species. If the random bearing and distance led us to an area without trees, we selected a

new random bearing until we could travel the requisite random distance and encounter a tree. We were unable to visually determine if the random (available) tree had been or was being used by bats as a roost. For each roost (used) and random (available) location, we quantified environmental features at 2 spatial levels (tree and patch) for potential inclusion in habitat selection models. Previous studies focused on modeling habitat selection by bats measured the distance between roosts and important landscape features facilitating flight, foraging, and drinking, such as distances to forest edges and flight corridors (roads, trails), agricultural fields, and bodies of water (e.g., O'Keefe 2009, Gorman et al. 2022, Hilty et al. 2025). However, in our study area, forest patches are narrow, lie along rivers, and are bordered by agricultural fields or roads (Figure 2), such that the variation in distance to these features was negligible, making them less biologically relevant. As a result, we did not include landscape-level features in our models of habitat selection.

Tree-level features

As small endotherms, myotis bats are especially susceptible to temperature changes in their environment, and selecting roosts that create temperatures within the bats' thermoneutral zone reduces energy costs (Speakman and Thomas 2003, Bergeson et al. 2021). We chose each tree variable because we thought they would influence the thermal conditions and roost space within that tree.

For each roost (used) and random (available) tree, we recorded the tree species and diameter at breast height (DBH), as differences in these features could affect the thermal conditions bats experience in roosts (Zakrzewska et al. 2022). Northern myotis roost in diverse species of trees (reviewed in Garcia et al. 2023), but tree species can capture a collection of characteristics that may be informative. For example, different species of trees vary in the thickness, color, and texture of the bark (Nicolai 1986), the likelihood of cavities developing (Foster and Kurta 1999), and the cellular structure, canopy architecture, and other features (Zakrzewska et al. 2022). Additionally, as trees increase in diameter, they become slower to warm or cool (Coombs et al. 2010). We predicted that northern myotis would select trees with larger DBH values because of the increased stability in temperature.

Level of solar exposure is also an important factor influencing roost microclimate; we characterized this by measuring canopy cover and tree height. Canopy cover provided a direct measurement of how much of the tree trunk was shaded by leaves and branches. We predicted that northern myotis would prefer the warmer conditions created by less canopy cover. We measured canopy cover at the roost (used) or random (available) tree in the 4 cardinal directions using a spherical crown densiometer (Forestry Suppliers). Tree height provided a different and more nuanced perspective. Taller trees should receive more solar exposure because they can grow above the shade created by surrounding trees (Owen et al. 2002). Taller trees also likely have more space for roosting because of their increased trunk length and because these trees often are older and in later stages of decay than shorter trees. Based on these ideas, we predicted that northern myotis would select taller trees. Using a clinometer (Suunto, Vantaa, Finland) 15 m from the tree, we measured the slope (in degrees) to the top and bottom of the tree, which we then used to calculate tree height.

Finally, we recorded decay stage based on Jung (2000, modified from Thomas et al. 1979, 1 = live tree, 2 = declining, 3 = recently dead with branches and most bark, 4 = dead with loose bark and few branches, 5 = clean, 6 = broken, or 7 = decomposed) and the percentage of bark remaining (0, 25%, 50%, 75%, 100%) for each used and random (available) tree. As trees age and decay, bark begins to slough off, branches begin to break, and birds may have created cavities, creating space for bat maternity colonies.

Patch-level features

To characterize patch-level features, we created a 1-ha circular plot (17.8-m radius) centered on each used and random (available) tree. This plot size has been used in previous studies focused on bat roosts (e.g., Vonhof and Barclay 1996, Schwab 2006). We measured the species, decay stage, presence of cavities, and DBH of every tree in the plot (patch).

Based on these data, we computed 2 variables to characterize the patch around each used or random (available) tree. First, we calculated basal area by summing the DBH of all trees in the patch; basal area quantified the patch density and degree of clutter. We predicted this forest-dependent species would select patches with higher basal area.

Second, we used the DBH measurements and decay classifications of all trees in the patch to calculate the proportion of trees that were similar to the roost tree; we called this patch-level variable the similar tree proportion. For this computation, we simplified the original decay classification into 3 categories (low = decay stages 1 and 2, medium = decay stage 3, and high = decay stages ≥4), given that few trees were in late decay stages. To be considered similar, the tree had to be classified in the same simplified decay class (low, medium, or high) and be within 20 cm DBH of the roost tree. Patches with a higher similar tree proportion contained more trees that are like the roost tree, providing multiple, nearby roosting options with the same properties; we predicted northern myotis would select these conditions.

Modeling habitat selection

Prior to model building, we explored the ranges of values for our explanatory variables, and correlations among pairs of variables. We found little variation in tree species, decay stage, and the percentage of the bark remaining, so we did not include these in candidate models. For the 5 remaining variables (DBH, average canopy cover, tree height, basal area, and similar tree proportion), we found correlations (r) between variables were ≤ 0.54, so we retained all 5 variables for use in our models. We completed all analyses using R version 4.3.3 (R Core Team 2024).

We used a conditional logistic regression model to pair data collected from each roost (used) with the associated random (available) location(s) (coxme package; Therneau 2024). We included a random intercept for each bat to account for repeated observations for some individuals. We used an information-theoretic approach (Burnham and Anderson 2002) to compare 32 candidate models, representing all possible combinations of the 5 covariates: the 3 tree-level features, DBH, average canopy cover, and tree height, and the 2 patch-level features, basal area and the proportion of similar trees. We considered only linear relationships and additive effects of variables, in part because of relatively small sample sizes. We compared models based on Akaike's Information Criterion corrected for small sample size (AIC_c) and considered competing models as those with $\Delta AIC_c \leq 4$ (Anderson 2008). All continuous variables were centered and scaled to compare relative contributions of each variable. In results, we compare these contributions but also present odds ratios based on back-transformed coefficients and confidence intervals. We evaluated effect sizes using 85% confidence intervals to maintain consistency between the model selection and parameter evaluation criteria (Arnold 2010).

RESULTS

Bat capture

We mist-netted for 24 nights in 2022 and 35 nights in 2023, resulting in 57 and 115 net nights (1 net night = 1 net set open for 1 night) each year, respectively. We captured 113 bats of 6 species in 2022 and 212 bats of 7 species in 2023 (Table 1). Silver-haired bats (51%) and big brown bats (21%) comprised most of the captures, followed by little brown myotis (14%) and northern myotis (12%).

Radiotelemetry and roost tree characteristics

We attached radio-transmitters to 36 individual northern myotis, including 28 females (3 juveniles and 25 adults) and 8 males (2 juveniles and 6 adults). Of the 25 adult females, 4 were pregnant, 6 were lactating, 7 were

TABLE 1 Number of bats captured by species and year, and the percentage of total captures, summer 2022 and 2023, northeastern Montana, USA.

Species name		2022	2023	% total captures
Big brown bat	*Eptesicus fuscus*	33	35	21
Hoary bat	*Lasionycteris noctivagans*	23	142	51
Eastern red bat	*Lasiurus borealis*	1	0	<1
Silver-haired bat	*Lasiurus cinereus*	2	3	1
Long-eared myotis	*Myotis evotis*	0	2	<1
Little brown bat	*Myotis lucifugus*	38	6	14
Northern myotis	*Myotis septentrionalis*	16	23	12
Long-legged myotis	*Myotis volans*	0	1	<1
Total		113	212	

post-lactating, and 8 were non-reproductive. We tracked these individuals to 76 different roosts across both years; all roosts were in trees. We found 32 roosts of reproductive adult females: 7 roosts of pregnant females, 10 roosts of lactating females, and 15 roosts of post-lactating females. We confirmed 11 of these as maternity roosts, where we performed an exit count and observed more than 1 bat exiting the tree. We also found 26 roosts for non-reproductive females (15 for adults and 11 for juveniles) and 18 roosts of non-reproductive males (14 for adults and 4 for juveniles). Juvenile females and males may have been in maternity roosts. We were unable to locate roosts for 3 tagged females (1 pregnant, 1 lactating, and 1 post-lactating).

Of the 76 roosts we found, 74 were in cottonwoods and 2 were in unidentified willow species. Most roosts were in trees in early stages of decay (used: mean = 1.7, range = 1–4). Almost all roosts appeared to be under bark or in crevices created by broken branches or tops of trees. However, we could not always confirm or precisely identify the roost structure because roost locations were usually in the tops of trees and not safely accessible. We found only 1 of the 76 roosts in a confirmed cavity and it was in an atypical tree; a pregnant female bat roosted in a cavity of a small, young willow (8.9 cm DBH) for 1 day.

We located more than 1 roost for 23 individuals. The distances between consecutive roosts used by each bat averaged 147 m (range = 2–881 m); on average, reproductively active females moved the shortest distances between consecutive roosts (Table 2). Distances between consecutive roosts were consistent between years. Roosts were an average of 169 m apart (range = 2–881) in 2022 and 131 m (20–565) in 2023.

Roosts often were reused by individuals over multiple consecutive days. The 76 roosts we found were used for a total of 130 roost days (roost day = a single day of roost use by a bat); we used data from these 130 roosts, paired with random trees to model habitat selection. The average number of days each bat spent in a single roost before switching was very consistent among the sex and reproductive status groups. Non-reproductive females spent an average of 1.6 days in each roost (range = 1–7), reproductive females spent 1.7 days (1–7), and males (all non-reproductive) spent 1.7 days (1–5). We observed bats using different numbers of roosts, with an average of 2.4 unique roosts per bat (1–5).

We also observed a few instances of different tagged bats using the same roosts. We located 1 roost in 2023 that had been used by a bat in 2022, and 2 roosts in 2023 that were used by more than 1 tagged bat at the same time. One roost was shared by 3 different pregnant females, and another was shared by 2 of those 3 same pregnant females. These 2 roosts were shared for a total of 12 roost days and led to 2 successful exit counts where 7 and 13 bats were seen emerging, including the tagged individuals.

TABLE 2 Distances (in m) between consecutive roosts (mean, minimum, and maximum) used by the same individual northern myotis, by sex and reproductive status, summer 2022 and 2023, northeastern Montana, USA. The values presented in the final row represent the overall average distance between consecutive roosts, the overall average of the minimum distances, and the overall average of the maximum distances.

		Mean	Minimum	Maximum
Females	Reproductive	91	2	439
	Non-reproductive	216	14	881
Males	Non-reproductive	136	11	347
	Overall mean	147	90	213

Roost tree selection

We examined data from 130 pairs of roost (used) and random (available) locations from 23 individual bats. We found that northern myotis selected roosts based on characteristics of both the tree and surrounding patch. All 6 of the competing models ($\Delta AIC_c \leq 4$) contained a combination of tree and patch variables, whereas models that included only tree or patch characteristics were less supported (Table 3).

Basal area was the strongest predictor for roost selection (included in 6 of 6 competing models), based on the sizes of the coefficients in competing models (Table 3; Figure 3). Tree height (6 of 6 models) and the proportion of similar trees in the patch (similar tree proportion, 4 of 6 models) were the next strongest predictors. Average canopy cover and DBH were also included in some competing models (Table 3) but were weaker predictors of roost selection, as confidence intervals typically approached or included 1 (even odds, Figure 3). Estimates for coefficients were consistent among competing models (Figure 3).

Northern myotis selected roosts in patches with a greater basal area and greater proportion of similar trees; bats also selected trees that were taller with slightly less canopy cover compared to what was available on the landscape (Figure 3). Based on the top model (Table 3), northern myotis were 1.5 times (85% CI = 1.35–1.77) as likely to select a roost in a patch for every 0.5-m increase in average basal area, and 1.2 times (1.06–1.35) as likely to select a roost in a patch with every 10% increase in similar tree proportion (Figure 3). Northern myotis were 1.2 times (1.11–1.29) as likely to select a roost in a tree with every 1.5-m increase in tree height and 0.99 times (0.9963–0.9998) as likely to select a roost in a tree with every 10% increase in average canopy cover (Figure 3).

DISCUSSION

Like many other temperate bat species, northern myotis depend on summer day roosts for population persistence and successful reproduction (Vaughan and O'Shea 1976, Randall et al. 2014). Our research strongly supports the notion that in northeastern Montana, northern myotis select these roosts based on characteristics of the roost tree and the attributes of the surrounding patch. Multiple factors—morphology, sociality, and energetic costs—likely drive habitat selection in this species. Our findings also support our predictions that northern myotis select roosts in trees that are taller and have less canopy cover in dense patches that have a larger proportion of similar roost trees. Although many of these patterns match habitat preferences documented in previous work, we found some differences in roost selection could be attributed to studying a species at the edge of its distribution, where conditions are less typical than is observed in the core of the species' range (Brussard 1984, Lesica and Allendorf 1995, Munwes et al. 2010, Chevin and Lande 2011). Our findings more closely match roost characteristics documented in northwestern Nebraska by Andersen and Geluso (2022), another edge population, than much of the existing literature on this species (reviewed in Silvis et al. 2016, Garcia et al. 2023),

TABLE 3 Model selection results for roost selection by northern myotis, summer 2022 and 2023, northeastern Montana, USA. We used conditional logistic regression models to compare characteristics of paired roost (used) and random (available) locations; all models included a random intercept for each individual bat. We included covariates to describe the characteristics of the tree and patch (1 ha) surrounding the tree for each roost (used) and random (available) location. Tree covariates included diameter at breast height (DBH), average (avg) canopy cover, and tree height. Patch covariates included basal area and similar tree proportion (STP), which was the proportion of trees in the patch with DBH ± 20 cm and the same decay stage as the roost tree. We compared models based on Akaike's Information Criterion corrected for small sample size (AIC_c); *K* represents the number of parameters estimated in the model.

Model	AIC_c	ΔAIC_c	*K*
Basal area + avg canopy cover + tree height + STP	215.28	0.00	4
Basal area + tree height + STP	215.73	0.45	3
DBH + basal area + avg canopy cover + tree height + STP	217.28	2.00	5
DBH + basal area + tree height + STP	217.41	2.13	4
Basal area + avg canopy cover + tree height	218.92	3.64	3
Basal area + tree height	219.18	3.90	2
DBH + basal area + avg canopy cover + tree height	220.98	5.70	4
DBH + basal area + tree height	221.08	5.80	3
DBH + basal area + STP	222.15	6.87	3
DBH + basal area + avg canopy cover + STP	223.84	8.56	4
Basal area + STP	226.57	11.29	2
DBH + basal area	227.42	12.14	2
Basal area + avg canopy cover + STP	227.64	12.36	3
DBH + basal area + avg canopy cover	229.27	13.99	3
Basal area	231.08	15.80	1
Basal area + avg canopy cover	232.42	17.14	2
Avg canopy cover + tree height + STP	247.53	32.25	3
DBH + avg canopy cover + tree height + STP	249.30	34.02	4
Avg canopy cover + tree height	250.62	35.34	2
DBH + avg canopy cover + tree height	252.57	37.29	3
Tree height + STP	254.81	39.53	2
DBH + tree height + STP	255.32	40.04	3
Tree height	258.40	43.12	1
DBH + tree height	259.34	44.06	2
DBH + STP	277.07	61.79	2
DBH + avg canopy cover + STP	277.43	62.15	3
DBH	285.78	70.50	1
DBH + avg canopy cover	286.46	71.18	2
Avg canopy cover + STP	311.02	95.74	2
STP	313.77	98.49	1

(Continues)

TABLE 3 (Continued)

Model	AIC_c	ΔAIC_c	*K*
Avg canopy cover	318.67	103.39	1
Null	**320.94**	**105.66**	**1**

including Cryan et al. (2001) and Alston et al. (2019), the existing studies that occurred closest to our study area. However, even in peripheral populations, northern myotis seem to be selecting to roost in the tallest trees within the densest patches of forest they can find on the landscape to meet their needs.

Previous studies have shown northern myotis roosting in various tree species, including pines (*Pinus* spp.), firs (*Picea* spp.), oaks (*Quercus* spp.), and other deciduous trees (e.g., maples [*Acer* spp.], black locust [*Robinia pseudo-acacia*], sassafras [*Sassafras albidum*]; reviewed in Garcia et al. 2023). We are aware of only 3 other studies that found this species roosting in eastern cottonwoods (Timpone et al. 2010: Missouri, $n = 3$ roosts; Andersen and Geluso 2022: Nebraska, $n = 2$ roosts; Burrell and Bergeson 2022: Indiana, $n = 1$ roost), so the strong selection for cottonwoods in our study area may seem surprising at first. However, cottonwoods were the most abundant (Garcia et al. 2023) and largest (height and DBH) trees available that could provide the right conditions for roosting. Although there were many green ash trees present in the areas we studied, these trees generally lacked the size (height, DBH) or structures (crevices, cavities) necessary to create appropriate roosts. As forest succession progresses and cottonwoods die, northern myotis in this area may shift their roost selection to different species (e.g., green ash), if the right conditions are provided (Garcia et al. 2023).

Many studies have documented northern myotis roosting in crevices and cavities of snags and trees in later stages of decay (reviewed in Lacki et al. 2009, Silvis et al. 2016, Garcia et al. 2023), including studies in the nearby Black Hills of South Dakota (Cryan et al. 2001, Alston et al. 2019). In contrast, we observed roosts under bark and in crevices in relatively healthy, live trees in early stages of decay, similar to peripheral populations studied by Andersen and Geluso (2022) in Nebraska, Garcia et al. (2023) in Louisiana, and Loeb et al. (2026) in coastal South Carolina. In these areas, bats may have limited access to dead and dying trees, but they still selected to roost in trees with some degree of decay (Andersen and Geluso 2022, Loeb et al. 2026, reviewed in Garcia et al. 2023). During our study, we observed relatively little variation in decay stage and few snags or trees in late decay (used: range = 1–4; available: range = 1–6), but as these even-aged stands of cottonwoods mature, the decay stages available to bats will also change. Cottonwoods in this study area maintained foliage and canopy but also had sloughing bark and numerous crevices. Other species of trees used in much of this bat's range may not provide these roosting features until later stages of decay.

Basal area was a consistently important characteristic for roost selection of northern myotis in this study (Table 3; Figure 3), as in many other populations throughout the species' distribution (Jung et al. 2004, Henderson and Broders 2008, Ford et al. 2016, Thalken and Lacki 2018, Gorman et al. 2022, Garcia et al. 2023). Although this species has been documented across a range of forest densities (reviewed in Silvis et al. 2016), northern myotis can easily fly and forage in dense forests given the morphology of their wings and echolocation calls (Norberg and Rayner 1987). Areas with greater basal area and more trees with similar characteristics as those selected for roosting (similar tree proportion) could also facilitate roost switching and social interactions. We observed northern myotis using multiple roosts and switching roosts fairly frequently during the tracking period; these patterns are consistent with other studies (range = 1.2–5.3 days on average; reviewed in Silvis et al. 2016), with some of the more frequent switching documented in peripheral populations (e.g., coastal South Carolina, average = 1.3 days, Loeb et al. 2026; western Nebraska, average = 1.8 days, Andersen and Geluso 2022; reviewed in Silvis et al. 2016, Garcia et al. 2023). Although we observed northern myotis selecting more cluttered patches (i.e., greater basal area was an important predictor), as expected, the forests in northeastern Montana are more open and smaller in area compared to most forests in the core of this species' range (Owen et al. 2002, Johnson et al. 2009, reviewed in Silvis et al. 2016). Our study area and another western peripheral population in Nebraska (Andersen and Geluso 2022)

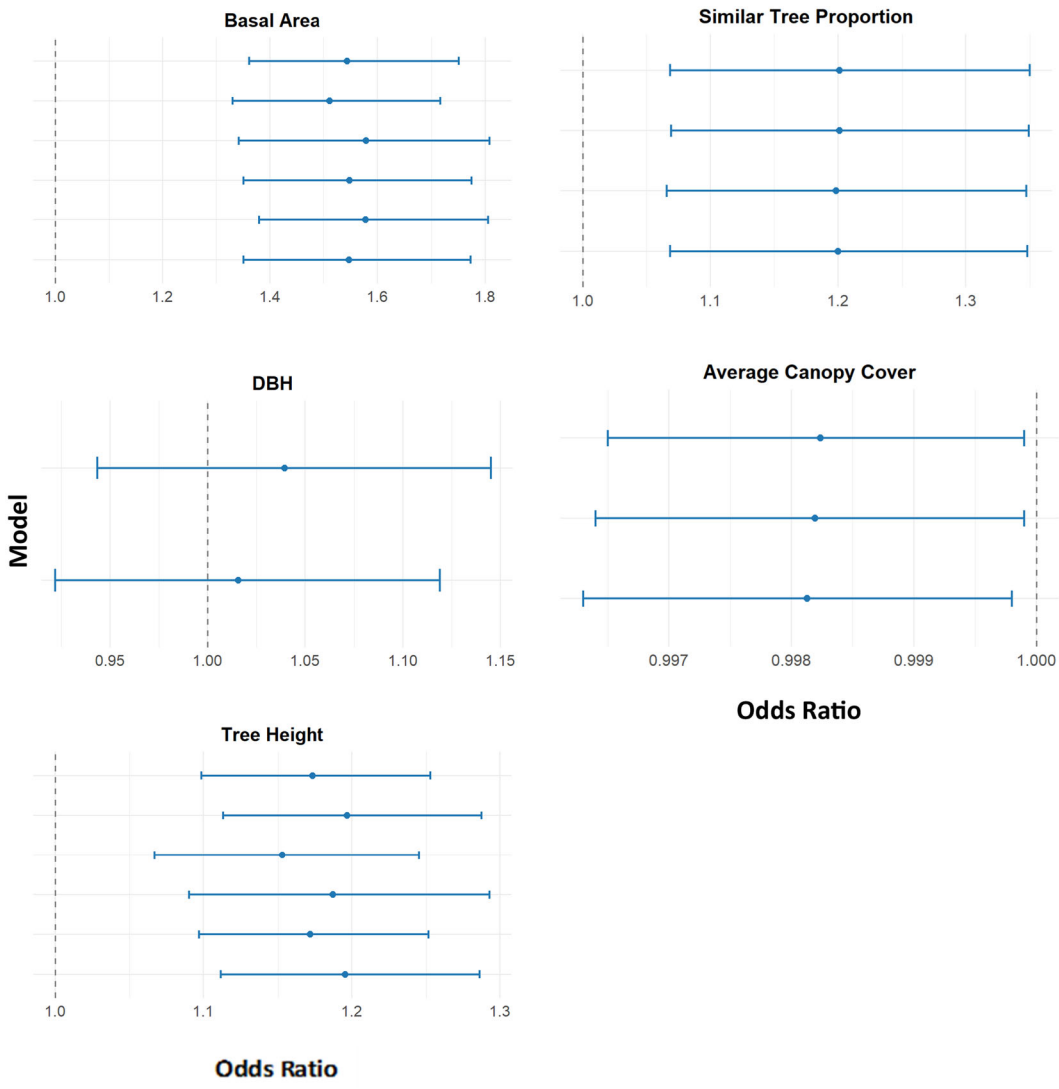

FIGURE 3 Estimates and 85% confidence intervals for odds ratios for the patch-level (basal area and similar tree proportion) and tree-level (DBH, average canopy cover, and tree height) features influencing roost selection by northern myotis, summer 2022 and 2023, northeastern Montana, USA. Different estimates for each covariate come from the 6 competing models. Vertical dotted lines at 1 indicate no selection (even odds); values > 1 indicate bats were more likely to choose a roost as the variable increased, whereas values < 1 indicate bats were less likely to choose a roost as the variable increased. We centered and scaled covariates to compare relative contributions of each variable.

lack large areas of contiguous forest used for roosting in other areas (reviewed in Silvis et al. 2016). Instead, stands of trees mainly occur in narrow linear bands along the riparian corridors within a matrix of agricultural lands (Figure 2). Some previous studies in the periphery and core of the species' range have documented northern myotis roosting in small forest fragments (Prince Edward Island, Henderson and Broders 2008; coastal New York, Gorman et al. 2022) or more open areas, including forested pastures (Michigan, Foster and Kurta 1999) and thinned forests (West Virginia, Menzel et al. 2002), suggesting some degree of flexibility in this aspect of their habitat preferences (reviewed in Silvis et al. 2016). However, the availability of habitat also could be limited at the edge of the species' distribution (Safriel et al. 1994, Grider et al. 2024), as forest transitions to prairie (Silvis et al. 2016).

Traveling to select roosts and flying among roosting, foraging, and drinking areas incurs energetic costs for bats. Choosing roosts in dense patches with other roosting options (i.e., higher similar tree proportion) likely minimizes some of these costs. Individual bats also used consecutive roosts that were relatively close together (mean = 147 m, range = 2–881), especially females that were reproductively active (Table 2). As in other studies throughout the species' distribution (Henderson and Broders 2008, Johnson et al. 2009, Andersen and Geluso 2022, Gorman et al. 2022, Loeb et al. 2026), northern myotis selected habitat in an area where they can maintain a relatively small summer home range. However, in northeastern Montana, these bats may be necessarily restricted, as they are occupying the small patches of trees that occur along relatively narrow riparian corridors, embedded within a more open landscape (Figure 2), similar to some other peripheral populations (e.g., Henderson and Broders 2008, Andersen and Geluso 2022). With roosting areas confined to the riverine floodplains in this study area, travel distances necessary to reach drinking and foraging sites are likely significantly reduced.

In addition to traveling, bats expend energy to maintain their body temperature. Some aspects of roost selection we observed may help to minimize these costs. Bats' selection of taller trees may reflect that these structures provide more roosting space and receive greater solar exposure (Owen et al. 2002), reducing the energy needed to stay warm or the need to enter daytime torpor. Although less pronounced, bats also select trees with less canopy cover, which again likely increases the tree's solar exposure and limits the necessity of torpor. Torpor can greatly reduce energetic costs associated with maintaining body temperature, but there may be tradeoffs, especially for reproductive individuals (Rintoul and Brigham 2014). Selecting a roost that reduces the need to enter torpor can provide bats with increased opportunities for active behaviors, including drinking, foraging, and social interactions.

Although warm roost temperatures generally lower energy costs for bats, excessively high temperatures can also increase the energy expenditure required for thermoregulation (Welbergen et al. 2007, O'Shea et al. 2016). This issue can be mitigated by roosting in trees that can provide shade and reduce the risk of overheating. Variation in preferences for the degree of canopy cover documented in the literature likely relates to different conditions in each geographic location (reviewed in Lacki et al. 2009, Silvis et al. 2016, Garcia et al. 2023). We did not observe bats selecting roost trees with greater canopy cover, but the importance of basal area of the patches suggests that the surrounding vegetation may offer sufficient shading, even if the roost tree itself lacks dense canopy cover. Additionally, bats can avoid excessive heat by changing their locations within the roost tree or by switching trees (Roby et al. 2019), potentially leading to more frequent roost switching (Patriquin et al. 2016). The primary roost sites we identified were under sloughing bark, in broken branches, or in treetops. These types of roosting areas may have heterogeneous microclimates, providing multiple options for a roosting bat to avoid extreme temperatures as conditions change throughout the day and summer season. Northern myotis in this study may have been able to regulate their temperature by moving to different parts of the tree throughout the day or switching roosts at night.

Northern myotis were listed as endangered mainly because of population declines resulting from the effects of white-nose syndrome (USFWS 2022). Although white-nose syndrome and the related fungus have been detected in some bat species in Montana (Montana Fish, Wildlife, and Parks 2024), there have been no confirmed cases in northern myotis in the state (S. Hilty, Montana Fish, Wildlife and Parks, personal communication). Populations at the edges of their range, such as the one we studied, can serve as potential refugia in the face of disease and other environmental changes, in part because of novel conditions or genetic variation (Lesica and Allendorf 1995, Gorman et al. 2022, Hoff et al. 2025). Understanding and retaining the atypical habitat conditions available for this peripheral population seem important to support persistence.

CONSERVATION IMPLICATIONS

Researchers are exploring multiple treatments for white-nose syndrome (White-nose Syndrome Response Team 2025), yet we can also influence conservation of bats by focusing on habitat. Conserving habitat for tree-roosting bats often means an emphasis on trees, ensuring that individual trees with the right conditions are available

for use. But for this species, we found that roosting habitat also requires considering characteristics of the surrounding patches. In our study area, roosting habitat consists of large cottonwood trees that occur in denser patches with other similar trees. Conservation actions that maintain these areas and conditions are essential for this endangered species. These forest patches currently contain even-aged stands in early stages of decay, so eventually, there will be a natural, mass loss of cottonwoods as potential roost trees. Continuing to learn about this peripheral population will inform conservation, as what we have learned about this endangered species elsewhere may not apply to this part of the distribution.

ACKNOWLEDGMENTS

Funds and support for this research were provided by the Bureau of Land Management (L21AC10345), Montana Fish, Wildlife and Parks (FWP 23-0192), and the Montana Chapter of The Wildlife Society. JJM received additional support from a Bob Berry Holohil Award (Western Bat Working Group). We are grateful for field and logistical assistance from D. Bachen, M. Barker, S. Hilty, K. Cate, G. Hershberg, K. Karch, M. McGrath, B. Tarnowsky, and many others that made this project possible. The Nickels and Adkins families, as well as the Fort Peck Assiniboine and Sioux Tribes graciously allowed us access to their lands. We also are appreciative of comments from the Associate Editor and 2 reviewers that strengthened our manuscript. Findings and conclusions in this article are those of the authors and do not necessarily represent the views of the Bureau of Land Management.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

We performed capture and handling in accordance with approved protocols and permits (Montana State University Institutional Animal Care and Use Committee Protocol 2022-197; Montana State University Institutional Biosafety Committee Protocol 2022-385; Montana Fish, Wildlife and Parks permits 2022-69-W, 2023-045-W).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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Associate Editor: Amy Kuenzi.

How to cite this article: Melhuish, J. J. E., A. R. Litt, M. J. Borgreen, and H. F. Harris. 2026. Living on the edge: habitat characteristics of northern myotis at the periphery of its distribution. Journal of Wildlife Management e70282. https://doi.org/10.1002/jwmg.70282