BAT HOMES IN THE BIG SKY: HABITAT CHARACTERISTICS OF NORTHERN MYOTIS

(*MYOTIS SEPTENTRIONALIS*) IN NORTHEASTERN MONTANA

by

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DEDICATION

To my brother, Zachary Melhuish, for the guidance and energy.

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ABSTRACT

The northern myotis (*Myotis septentrionalis*) is one of 9 endangered bat species in the United States but the only one to inhabit Montana and the only resident bat species newly discovered in the state in the last 10 years. The need for conservation efforts is hampered by the large gaps in our understanding about northern myotis in Montana. We started to build our knowledge base by characterising habitat, specifically summer daytime roosts. Summer roosts provide refuge for bats while they give birth, raise young, and prepare for hibernation or migration. We mist-netted for bats from May-August in 2022 and 2023 and attached transmitters to 36 individual northern myotis. We located a total of 76 roosts from 33 tagged individuals. We quantified characteristics of the roost trees, as well as the surrounding patch, and compared these values with the same features at random locations. Bats roosted primarily in eastern cottonwood trees (*Populus deltoides*) (97% of roosts), which was the most available tree species on the landscape. Bats showed a strong preference for tall trees in patches with a relatively high basal area, containing multiple trees similar to the roost tree. Bats also selected for cottonwoods that were in an early to mid-stage of decay with somewhat less canopy cover. Most consecutive roosts were within a few hundred metres of previous roosts (range = 2-881 m) and each roost was used for 1.7 days on average. Our work supports the notion that northern myotis display some flexibility in roost selection in different parts of their range, with the common theme of selecting areas that provide multiple possible roosts and facilitate their social interactions. This is especially important as studied population is one on the edge of the species known range, and edge populations are shown to be more plastic in behaviour and resilient in the face of change. Improving our understanding of habitat preferences of northern myotis in Montana will provide us with a more developed toolkit to aid in their habitat management and conservation. Managers can then design strategies that protect critical roosts as well as surrounding habitat.

INTRODUCTION

As small, flying mammals, bats face unique challenges in selecting habitat that balances the energetic trade-offs to support their needs (Kunz 1982). Additionally, bats inhabit a variety of landscapes across the globe, each presenting their own complications to cost reduction. In temperate environments, some bat species manage energetic expenses in distinctly different ways throughout the year. They hibernate over the winter, drastically reducing the need for food and water, until warmer weather heralds the arrival of spring (White et al. 2020). Some bats then disperse from these hibernacula to forests where food, water, and trees for daytime roosts are more abundant (Neubam et al. 2017). Spring dispersals, combined with volancy, and the ability to travel large distances results in temperate bats having a unique view of the landscape and opportunities for habitat selection to reduce the energetic costs of life.

The costs of flight and thermoregulation apply to all bats, but other energetic expenses, namely those associated with reproduction, differ between males and females, or reproductively active and non-reproductively active bats (O'Keefe 2009). In temperate environments, bats copulate in the fall or spring and give birth to pups in mid-summer (Kunz 1982). 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 contrast, males and non-reproductive females more often roost solitarily. Pregnant and lactating bats expend much more 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).

Due to their ability to fly, habitat selection is likely a tiered process for bats, where they first explore a large area that appears to meet core needs before homing in on smaller habitat patches that provide sufficient resources to support the energetic costs (Lipsey et al. 2017). As bats move from winter hibernacula to summer habitat, 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 then search for specific habitat patches and the trees, or other structures, within those patches that can serve as roosts.

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, providing shelter from the elements and space for maternity colonies, creating an appropriate microclimate, ensuring safety from terrestrial predators, and facilitating social interaction (Sedgeley and O'Donnell 2004). Previous studies often have focused on characteristics of roost locations, patch quality, and the roost's ambient microclimate as separate determinants of roost quality instead of considering them together (Kunz 1982, Kerth et al. 2001, Sedgeley and O'Donnell 2004, Ingersoll et al. 2010).

Although a roost's ambient microclimate is undoubtedly important (Hilty 2020), bats can improve suboptimal roost conditions through social thermoregulation. In maternity colonies, bats reduce the individual costs of thermoregulation by clustering together, which decreases the exposed surface area. Additionally, the heat generated by the clustered group raises the ambient temperature within the roost structure (Hayes et al. 1992, Seguy and Perret 2005). Some studies suggest that social thermoregulation can have a more significant impact on roost microclimate

than the inherent conditions of the roost structure itself (Willis and Brigham 2007, Russo et al. 2017). Social thermoregulation is facilitated by complex social structures in many bat species.

The social structures of many bat species have a strong influence on roost selection beyond just social thermoregulation, as social interactions can help reduce other costs associated with survival and reproduction. Several species within the *Myotis* genus, such as the northern long-eared myotis (*Myotis septentrionalis*, northern myotis, MYSE), exhibit a fission-fusion social structure, which is characterised by individuals moving among different tree roosts to maintain community bonds within a group (Kerth and Konig 1999, Vonhof, Willis and Brigham 2004, Whitehead and Fenton 2004). These community bonds are crucial for pregnant or pup-rearing females, facilitating the sharing of generational knowledge (Wilde, Knight and Racey 1999, Kerth and Reckardt 2003). Roost switching, or moving among roost sites, can help reduce being disturbed by humans or predators (Olson and Barkley 2013), ectoparasite loads (Reckardt and Kerth 2007), and distances to foraging locations (Sedgeley and O'Donnell 2004). Thus, the need for social bonds and the benefits of roost switching suggest that for species such as the northern myotis, habitat quality isn't solely determined based on features of an individual roost, but also on a habitat patch that includes many available roosts.

The northern myotis is one of 15 bat species currently known to spend at least part of their annual lifecycle in Montana, but the only species in Montana whose known range is limited to the most eastern parts of the state (Fig. 1). Additionally, apart from one historic observation of the northern myotis in 1978, the species was not recognised to be in Montana until 2016, based on genetic testing of a museum specimen. After this species confirmation, concerted efforts were made to confirm presence in the state. The northern myotis possesses a larger, broader wing area

than most other *Myotis* bats of size, meaning they fly more slowly but are more agile (Norberg and Rayner 1987). This unique wing shape allows them to use more dense forest for travelling, foraging, and roosting. As a result, netting strategies changed to include sampling within forests, instead of focusing on water bodies. Although some northern myotis were captured based on these efforts, we knew very little about their roosting behaviours in Montana, at the western edge of their distribution in the US (Fig. 1). We focused our work on northern myotis due to this large gap in knowledge, its relatively limited known range in the state, and its federally endangered status (USFWS 2023).

To best inform conservation and management, we characterised roosts used by the northern myotis at three scales – roost, habitat patch, and landscape – to align with the hierarchical nature of habitat selection. By examining these scales, we can better understand the trade-offs involved in roost selection, including the influence of social interactions on roost choice. With a greater understanding of habitat preferences and the factors driving roost selection, we can develop more effective strategies to protect habitat and manage populations, ultimately contributing to northern myotis conservation.

<u>Study Area</u>

Our study area extended from the banks of the Missouri River in Frazer, Montana, wast to the confluence of the Missouri and Milk Rivers, below Fort Peck Dam and Reservoir (Fig. 2). This is a 28-km stretch of river, where captures and surveys occurred on both the north and south sides, resulting in a study area of approximately 80 km^2. We netted as far west as Hinsdale, Montana, 68 km from the confluence but did not catch any northern myotis. Land ownership along the Missouri and Milk Rivers is a mix of Bureau of Land Management, Fort Peck

Reservation, U.S. Army Corps of Engineers, and private agricultural and ranching properties so there was a great amount of collaboration required for netting efforts to take place.

Riparian forests occur along the rivers, largely dominated by eastern cottonwoods (*Populus deltoides*) and interspersed with green ash (*Fraxinus pennsylvanica*) and some small patches of willow species (*Salix* spp.). Eastern cottonwoods tend to seed into new floodplains and develop as pure, even-aged stands, eventually being replaced by more drought-tolerant ash (S.D. Department of Agriculture 2024). 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. Still, the forests largely are comprised of cottonwood trees of similar sizes and decay stages, whereas the ash occur in more variable sizes and decay stages. The elevation along the Missouri and Milk rivers is relatively consistent, approximately 600 m above sea-level; the maximum elevation observed in the Milk River Hills is 680 m.

These river corridors host 5 myotis species: the 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: the big brown bat (*Eptesicus fuscus*), eastern red bat (*Lasiurus borealis*), silver haired bat (*Lasionycteris noctivagans*) and hoary bat (*Lasiurus cinereus*) (MTNHP and MTFWP 2024).

METHODS

Bat Capture

We captured bats between May 29 and August 10, 2022, and between June 1 and August 4, 2023. All bat captures, and handling were performed in accordance with approved protocols and permits (Montana State University Institutional Animal Care and Use Committee Protocol #2022-197; Montana Fish, Wildlife and Parks permits 2022-69-W, 2023-045-W).

Because we were focused on northern myotis, we selected areas for sampling based on the species' ecology. Traditionally, northern myotis are captured as they drink or forage over water, or as they traverse the landscape using forest corridors (Garroway and Broders 2008, Hyzy et al. 2020). However, in our study area, the main water sources are too large to mist-net and the cottonwood gallery forests lack clearly defined flight corridors. Other researchers in the area captured our focal species using triple-high mist nets placed in the cottonwood gallery forests; we adopted this approach. To increase the odds of successful capture in this open environment, we deployed 2 to 6 triple-high mist nets (38 mm mesh polyester nets, Avinet Research Supplies, Portland, Maine) per night. Nets were opened shortly after sunset to decrease the chance of accidental bird capture and were closed sometime between midnight and 2 a.m. the following morning. Nets were checked every 10-12 minutes and closed immediately if there was some level of persistent rain or wind. We netted the same site for 1-6 nights in total (maximum 4 in a row) depending on previous capture success or observed bat presence in the area.

Once bats were captured, they were carefully removed from the net and placed in holding bags (Avinet Research Supplies, Portland, Maine) until they could be processed. Bats were held for no longer than 20 minutes. We then weighed the bat in the bag using spring scales (50-g

Pesola Light-Line Spring Scale, Forestry Suppliers, Reedsburg, Wisconsin) and determined the individual's sex, age, and reproductive status. Sex was determined 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). Reproductive status for males was classed as either testicular when testes were enlarged and clearly visible or non-reproductive if otherwise. We considered females to be pregnant if weight was higher than normal, belly was visibly swollen, and in-uterine pup could be felt by gently palpating the abdomen; lactating if nipples were conspicuously visible and sometimes red/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).

Many myotis species look similar, even in hand, making them difficult to distinguish. For each captured individual, we identified species based on morphology and 3 main diagnostic measurements: weight, 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, specifically testing two regions of mitochondrial DNA (*cytochrome oxidase I* and *cytochrome b*). Samples were stored 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, Montana).

We also checked each bat for signs of white-nose syndrome (WNS) and the associated fungus (*Pseudogymnoascus destructans*) and assigned a wing score (Reichard and Kunz 2009, Reichard 2018). Non-target species were released immediately after our assessments. All

equipment used to process bats was decontaminated between individuals and latex gloves were changed for handling every bat. All equipment and clothing were decontaminated when we finished netting a site, in accordance with the National White-Nose Syndrome Decontamination Protocol (USFWS 2018). Additionally, N-95 masks and other protective gear were worn to protect against the transmission of COVID-19.

Radiotelemetry

We attached radio transmitters (0.27 g, model LB2X, Holohil Systems Ltd., Carp, Ontario, Canada) to individual 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 scapula 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. We aimed to track 5 to 7 bats at the same time to combat moderate to high rates of transmitter loss through shedding or bats leaving the study area. We attempted to locate daily roosts for all bats with active transmitters. We used R1000 receivers (Communications Specialists Inc., Orange, California) and 3-element Yagi antennae (Telonics, Mesa, Arizona). We began tracking efforts at or near the capture site and worked outwards, utilising high points when necessary.

Selecting Available Roost Trees

We used a paired use-availability design to determine if northern myotis were preferentially selecting day roosts based on specific features of the trees, patches, or areas in the surrounding landscape (Thomas and Taylor 2006). We selected at least one random paired location for every roost found. We selected more than one random location when time allowed, to increase our understanding of what was available.

Successive roost locations for northern myotis have been shown in previous studies to be on average, 152 and 230 m (Johnson et al. 2009) and 227 m apart (Henderson and Broders 2008). Based on these previous studies and the small size of the riparian cottonwood forests, we decided that random roost trees should fall within 0-300 m of the used roost, in any direction (0-360°). When we arrived at the random bearing and random distance, we selected the closest tree to be our available roost, regardless of tree species. If our random bearing led us in a direction without trees, we selected a new random bearing until we could travel the requisite random distance. We were unable to visually determine if the random tree had been or was being used by bats as a roost.

Characterising Used and Available Roosts

Bats can select habitat on a landscape level because of their flight capabilities but they also can make fine-scale decisions at the levels of the patch and roost. We measured characteristics of used and available roosts at three scales: landscape, patch and roost tree. We chose characteristics to measure based on northern myotis literature and our own thoughts about which features would potentially influence selection.

Landscape-Level Features and Roost Proximity

Previous studies focused on bat habitat selection examined the proximity of the roosts to 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 (O'Keefe 2009, Hilty 2020). In our study area, forest patches are narrow, lie along rivers, and are bordered by agricultural fields or roads. Meaning, if bats are roosting in trees, the variation in distance to these features was negligible, making them less biologically relevant in our study area. Instead of characterising these landscape-scale features to include in our habitat models, we focused on quantifying 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.

Patch-Level Features

We created a 1-ha circular plot (17.8-m radius) centred on the used and available roosts to characterise features of this surrounding patch. This plot size has been used in previous studies focused on bat roosts (Vonhoff and Barclay 1996, Schwab 2006) and we believe characteristics of a patch this size likely influence roost selection, given the social nature of this species and its propensity for dense forests. We measured several quantities to characterise the degree of clutter (e.g., density of trees, branches, etc.) and potential number of roosts in the patch.

We temporarily flagged the structure (roost and random trees) and marked the location on our GPS units (Universal Transverse Mercator, NAD83 coordinate system). We measured the diameter at breast height (DBH) of every tree in the plot (Forestry Suppliers Inc., Jackson, MS).

We also recorded species and decay stage of each of those trees and checked for the presence of cavities. Trees were assigned a decay stage (1-7) based on Jung (2000). Diameter at breast height (DBH), tree species, decay stage, and presence of cavities in trees have been shown to be strong indicators for roost selection of northern myotis in other studies (Thalken and Lacki 2018, Hyzy et al. 2020). We used these measurements to compute two variables to characterise each patch around the roost or random tree.

We used the DBH measurements of all trees in the patch to calculate basal area (Department of Environment, Climate Change and Water, 2010), to represent the density of trees and degree of clutter in the patch. We also 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 variable the similar tree proportion. To be considered similar, the tree had to be classified in the same decay class and be ±20 cm DBH of the roost tree. Patches with a higher similar tree proportion contain more trees that are like the roost, providing multiple roosting options in close proximity.

Tree-Level Features

We chose each tree variable because we thought they influenced the availability and quality of roost space within that tree. As small endotherms, myotis bats are susceptible to temperature changes in their environment and selecting for roosts with higher thermal stability is likely more optimal because it reduces energy cost.

For each used and available tree, we recorded the species and DBH; both features influence thermal stability of the tree with changing weather conditions. Tree species is a useful metric because it helps managers quickly identify potential roosts while surveying but also

because it's interchangeable with the class of wood (e.g., hardwood, softwood, etc.) and related features. Hardwoods, such as the eastern cottonwood, have a complex cellular structure leading them to be denser and more thermally stable than softwoods (Burns and Honkala 1990). Additionally, as trees increase in diameter, they become slower to warm but also more thermally stable and retain heat over longer periods of time.

Level of solar exposure is also considered to be an important factor influencing roost microclimate; we characterised this by measuring canopy cover and tree height. Canopy cover is a direct measurement of how much of the tree trunk is shaded by leaves and branches, whereas tree height is less direct. Taller trees should on average, receive more solar exposure because can they grow above the shade created by surrounding trees. In addition, taller trees generally have more space for roosting because of their increased trunk length but also because they're often older and in later stages of decay than younger, healthier trees. We measured canopy cover at the used or random tree in the four cardinal directions using a spherical crown densiometer (Forestry Suppliers Inc., Jackson, Mississippi). Using a clinometer (Suunto, Vantaa, Finland) at a distance of 50 feet from the tree, we measured the slope (in degrees) to the top and bottom of the tree. We were then able to calculate tree height using the distance and degree measurements.

As trees age and decay, bark begins to slough off and branches begin to break. There's also a higher likelihood that cavities have been created by bird species in the area. This natural decay creates space for bat maternity colonies. So, we recorded decay stage (1-7, Jung 2000) and the percentage of bark remaining (0, 25, 50, 75, 100) for each roost and random tree to characterise tree age.

Roost Locations and Exit Counts

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, in a crevice, or under the bark. When possible, we returned to the roost the same night to perform an exit count and confirm roost location within the tree. Exit counts were performed at new roosts of female and juvenile male northern myotis, to confirm whether the location was a maternity roost. One to two observers arrived at the roost 20-30 minutes prior to sunset. We recorded time of arrival, time of sunset, time of first bat emergence, time of tagged bat emergence, the total number of bats seen emerging as well as some general weather conditions (temperature C°, moon phase, % cloud cover). Observation of the roost continued until at least 30 minutes past sunset, or 10 minutes after we no longer observed bats emerging.

Data Analysis

Roost Proximity

We used roost locations to calculate the average, minimum, and maximum distances between consecutive different roosts for each bat. We also calculated these values for all roost pairs by year. We then calculated the same statistics for each sex and reproductive status group: non-reproductive females, reproductive females (pregnant, lactating, post-lactating), and males; all our 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.

<u>Modelling Patch and Roost Selection</u>

Researchers often assess roost selection at different scales by modelling each scale separately (e.g., Johnson et al. 2009, Thalken and Lacki 2018, Hilty et al. 2024). We believe bats in our study area likely are selecting roosts based on the quality of roost trees as well as the quality of the surrounding patch. We therefore created a global model that included patch and tree-level features, comparing this with models that included all possible combinations of these variables. Prior to model building, we explored correlations among explanatory variables (tree height, DBH, average canopy cover, basal area of the plot, and the similar tree proportion). The highest level of correlation was $r = 0.54$ (between tree height and DBH), so we retained all variables for use in our models. We completed all analyses using R version 2024.04.2 (R Core Team 2021).

We used a conditional logistic regression model to pair data collected from each roost with the relevant random location(s) (coxme package, Therneau 2024); we also included a random intercept for each bat to account for repeated observations for some individuals. Our global model consisted of 5 covariates – 3 tree-level features: DBH, tree height, and average canopy cover, and 2 patch-level features: basal area and the proportion of similar trees. Average canopy cover is the average of the canopy cover in each four cardinal directions at each roost or random tree. We also calculated total canopy cover and ran the same models but found no difference in results. We initially considered both tree species and decay class as independent categorical variables but did not include them in our final global model because of very low variation in both metrics.

We used an information-theoretic approach (Burnham and Anderson 2002) to compare 32 candidate models, representing all possible combinations of our 5 covariates. 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 (AICc). All continuous variables were centred 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

<u>Bat Capture</u>

We mist-netted 24 nights in 2022 and 35 nights in 2023, using 1 to 6 triple-high nets per night, resulting in a total of 69 and 111 net nights (1 net night = 1 single-high net/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 the majority of captures, followed by little-brown myotis (14%) and northern myotis (12%). We divided our netting efforts between two primary areas – south of Vandalia, MT and near the confluence of the Milk and Missouri Rivers, but all northern myotis were caught near the confluence.

<u>Radiotelemetry</u>

We attached radio transmitters to 36 individual northern myotis, including 3 juvenile and 25 adult females, as well as 2 juvenile and 6 adult males (Table 2). We also attached transmitters to 20 little brown myotis but were unable to locate enough roosts for additional analysis (13 roosts in 2022, 1 in 2023).

We located northern myotis in 76 different roosts across both years (Table 3, Fig. 2); all roosts were in trees. We found 26 roosts for non-reproductive females: 15 for adults, and 11 for juveniles. We found 32 roosts of reproductive females (Table 3); we classed these as maternity roosts if we were able to perform an exit count and observe more than one bat exiting the tree. We successfully observed and confirmed 11 roosts as maternity roosts. We also found 14 roosts of non-reproductive adult males, and 4 roosts of juvenile males (Table 3). 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).

Roost Trees, Proximity, and Fidelity

Of the 76 roost trees we found, 74 roosts were in cottonwoods and 2 were in unidentified willow species. Almost all the roosts we found appeared to be under bark or in crevices created by broken branches or tops of trees. However, we could not 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 one day (Fig. 3). Most of our roosts were in trees in an early to intermediate stage of decay, with an average decay across all roosts of 2 (range of decay classes = 1-4, Table 4).

We located more than one roost for 23 individuals. The distances between consecutive roosts used by each bat averaged 147 m but ranged from 2 to 881 m (Table 5). On average, non-reproductive females moved longer distances between consecutive roosts than males, who moved farther than reproductive females (Table 5). 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 on a total of 133 roost days (roost day = a single day of roost use by a bat). 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 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 one roost in 2023 that had been used by a bat in 2022, and two roosts in 2023 that were used by more than one 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 two 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.

<u>Modelling Patch and Roost Selection</u>

We examined data from 130 pairs of roost and random locations, one pair for each roost day, from 32 individual bats. We found evidence that northern myotis selected roosts based on characteristics of both the tree and surrounding patch. All 6 of the competing models (ΔAICc $\leq$ 4) contained a combination of patch and tree variables, while models that included only patch or roost characteristics were less supported (Table 6).

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

Bats were selecting taller trees that occurred in patches with a higher basal area and higher proportion of similar trees, but slightly less canopy cover (Fig. 4). Based on our top

model, northern myotis were 1.5 times (85% CI = 1.35-1.77) as likely to select a roost with every

0.5 m increase in basal area, 1.2 times (1.11-1.29) as likely to select a roost with every 5-foot

increase in tree height, and 1.2 times (1.06-1.35) as likely to select a roost with every 10%

increase in similar tree proportion (Fig. 4). Northern myotis were 0.99 times (0.9963-0.9998) as

likely to select a roost with every 10% increase in average canopy cover (Fig. 4).

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 the characteristics of the roost tree itself as well as the attributes of the surrounding patch. Our findings are consistent with observations of roost selection in other northern myotis populations where this species selected large trees in patches with multiple trees of a similar size and decay stage, in more cluttered forests (Jung et al. 2004, Henderson and Broders 2008, Ford et al. 2016, Thalken and Lacki 2018). However, previous studies typically treated tree and patch characteristics as independent influences (Owen et al. 2001, Thalken and Lacki 2018). In our study, we opted to compare models for roost selection that considered features at the tree and patch levels separately and collectively. This approach allowed us to evaluate the notion that patch characteristics are at least as significant as the conditions of the tree.

We found strong evidence that northern myotis prefer tall trees situated in dense forest patches (higher basal area) with other similar trees nearby (similar tree proportion). Tall trees provide more roosting space and receive greater solar exposure in shaded forest patches, reducing the energy costs a bat needs to stay warm, or reducing the need to enter daytime torpor. Although less pronounced, bats also showed a preference for trees with lower canopy cover, again likely increasing the tree's solar exposure and limiting the necessity of torpor. Although torpor greatly reduces energetic costs associated with maintaining body temperature, it also delays reproductive timing for pregnant females, increases predation risk, can alter social

behaviours, and requires that bats rewarm to resume activity (Mayberry et al. 2018). Selecting a roost that reduces the need to enter torpor can provide bats with increased opportunities for active behaviours, including drinking, foraging, and social interactions.

Although warm roost temperatures generally lower energy costs for heterothermic mammals such as bats, excessively high temperatures also can 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 with higher canopy cover, that can provide shade and reduce the risk of overheating. Although we did not observe bats selecting for roosts with higher canopy cover, the relatively high 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, and for cavity-roosting species, this also may involve switching trees during the day (Roby et al. 2019).

Previous studies have shown that northern myotis typically roost in cavities or cavity-like structures (Owen et al. 2002, Whittle 2022). However, our observations revealed only one instance of cavity use (Fig. 3). Although we observed cavities in the cottonwoods within our study area, 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. This suggests that, instead of switching roosts midday, northern myotis in our study may have been able to move to different parts of the tree throughout the day to regulate their exposure to heat or cold or switched roosts at night. In addition to the high energy cost,

switching roost trees during the heat of the day increases the risk of predation or interaction with humans.

The relatively dense patches where we found northern myotis roosts contained a greater proportion of trees similar in size and decay stage to the roost itself. Roosting in areas that contain multiple potential roosts allows for roost switching and other social interactions. We observed northern myotis switching roosts every 1.7 nights on average and occupying 2 different roosts on average, over a 5 to 7-day tracking period. The high number of potential roosts and frequent roost switching behaviour we observed align with the relatively low numbers of bats we saw exiting roosts during exit counts. Although some species, like the little-brown bat, roost in large numbers in a single structure, northern myotis have been shown to have large networks of roosts containing lower numbers of maternally related individuals and exhibit more roost-switching (Neilson and Fenton 1994, Silvis et al. 2015). Patches of dense forest also provide conditions that support the northern myotis' slow and agile flight. Our findings highlight the significance of habitat selection in facilitating social interaction for northern myotis during the summer reproductive season, a period when costs are highest due to pregnancy in females and pups learning to navigate their surroundings.

Our sample sizes were not large enough to discern differences in the characteristics of roosts used by bats based on sex and reproductive status. However, we observed that reproductively active females moved the shortest distances between consecutive roosts compared to non-reproductive females and males. This finding suggests two things: first, that these females were likely minimizing travel costs as much as possible while expending a great amount of

energy to reproduce, and second, that staying in a smaller area facilitated maintaining social bonds and switching among shared maternity roosts.

Although we observed northern myotis selecting for more cluttered patches that occurred close together, the forests in northeastern Montana are smaller in area and more open compared to most, if not all, forests in the rest of this species' range in the country (Owen et al. 2002, Johnson et al. 2009). This limited potential habitat in the region also likely reduced some associated costs. Bats often roost in one area during the day and travel to different foraging and drinking sites at night (Barclay 1982). With roosting areas confined to the riverine floodplains in our study area, the distance to drinking and foraging sites is significantly reduced. The relative lushness of these floodplains likely provides ample insect prey for bats to consume in the same areas where they drink and roost. All the northern myotis roosts we found were within a 20 km stretch (Fig. 2) and distances between consecutive roosts were generally within a few hundred metres (Table 5). Similar to other studies (Henderson and Broders 2008, Johnson et al. 2009), northern myotis in northeastern Montana selected habitat in an area where they can maintain a relatively small summer home range. We were not able to discern actual distances from roosting locations to foraging locations, but we did observe abundant foraging activity near roost locations.

Our study represents, to our knowledge, the first observation of northern myotis roosting in eastern cottonwood trees, which accounted for 97% of the roosts we identified. Previous studies (Owen et al. 2002, Whittle 2022, Garcia et al. 2023) have shown northern myotis roosting in various tree species, so their strong preference for cottonwoods in our study area may seem surprising at first. However, cottonwoods were the most abundant trees that could provide

the right conditions for roosting. Although there were many green ash trees present, they often lacked the decay or size necessary to be appropriate roosts. In contrast to other studies, which have found northern myotis roosting in trees in later stages of decay (Thomas 1988, Sasse and Pekins 1996, Lacki and Schwierjohann 2001, Jung et al. 2004, Kalcounis-Ruppell et al. 2005, Hyzy et al. 2020), we observed roosts in relatively healthy, live trees in early stages of decay. However, cottonwoods in our study area maintain foliage and canopy, but slough bark and have numerous crevices, which may differ from other species of living trees. As forest succession progresses and cottonwood stands in late stages of decay become more abundant, northern myotis may shift their roost selection to green ash trees.

These differences in roosting behavior could be attributed to studying the westernmost population found to date in the United States, a species at the edge of their distribution (Fig. 1). Edge populations have been shown to be more persistent and to have a wider range of flexibility in behaviors compared to non-edge populations (Corina et al. 2023). We have seen flexibility in behaviours in our study area as we documented northern myotis roosting in a new tree species at earlier stages of decay, in a novel, more open environment. The importance of this edge population must not be overlooked given its potential contribution to northern myotis persistence in the face of a 99% population decline, largely due to WNS (BATCON 2023).

The fungus that causes WNS, *Pseudogymnoascus destructans* (*Pd*), was first found in Montana in 2020 and WNS was first detected in little-brown myotis a year later, in several counties across the state, including Valley County, where most of our work was conducted (MTFWP 2024). To date, there have been no confirmed cases of *Pd* or WNS in northern myotis in Montana. However, *Pd* and WNS are most often detected in hibernacula during winter, and we

do not know where the northern myotis we studied spend their winters. Although we sampled during the summer, we did not see any clear signs of northern myotis having had the fungus or disease. It appears we currently have a healthy population in northeastern Montana, however abundance still may be affected by WNS during winter. There are often time lags in the effect of WNS on abundance, and these can range from 1 to 5 years depending on the species and location (Frick et al. 2016, Bernard and McCracken 2017, Nocera et al. 2020, Barr et al. 2021, Perea et al. 2022).

Although vaccines and treatments for *Pd* and WNS are still in development, we can influence conservation of bat species by focusing on habitat. Forests in northeastern Montana have been reduced over decades due to agriculture and development. During the construction of the Fort Peck Dam (1933-1940), the cities of Glasgow and Fort Peck, MT had an estimated population of 50,000, while the current population of Glasgow is just over 3000 and Fort Peck is 237 (U.S. Census Bureau 2022, Montana Historical Society 2024). Even though northeastern Montana once supported a large human population, stretches of forest remain along the Missouri and Milk rivers, thanks in part to ranchers, the Assiniboine and Sioux people, and managers. Northern myotis rely on cluttered areas for foraging and roosting (Perry and Thill 2007), so it's important that cottonwood stands in these forests are left alone to decay naturally, along with allowing green ash to reach later successional stages. These forests contain even-aged stands of cottonwoods, so eventually, there will be a natural, mass loss of cottonwoods as potential roosts, which could be replaced by mature, green ash. Conservation efforts also should focus on retaining entire stands and not just single trees, as both were essential to roost selection by

northern myotis in the area. These forests, although limited, provide very important summer

habitat for northern myotis, and likely many other bat species.

TABLES

Table 1. Number of bats captured by species and year, summer 2022 and 2023, northeastern Montana. All captured northern myotis were genetically tested and confirmed as northern myotis based on testing two regions of mitochondrial DNA (*cytochrome oxidase I* and *cytochrome b*). One northern myotis was mistakenly identified as a little brown myotis; numbers in this table reflect this change.

Species	2022	2023	% of Total Captures
Eptesicus fuscus	33	35	21
Lasionycteris noctivagans	23	142	51
Lasiurus borealis	1	0	<1
Lasiurus cinereus	2	3	1
Myotis evotis	0	2	<1
Myotis lucifugus	38	6	14
Myotis septentrionalis	16	23	12
Myotis volans	0	1	<1
Total	**113**	**212**	

Table 2. Number of northern myotis with transmitters by age, sex, and reproductive status, summer 2022 and 2023, northeastern Montana.

	Juvenile Female	Adult Female	Juvenile Male	Adult Male
Non-Reproductive	3 (9%)	8 (22%)	2 (5%)	6 (17%)
Pregnant		4 (11%)		
Lactating		6 (17%)		
Post-Lactating		7 (19%)		
Total	**3**	**25**	**2**	**6**

Table 3. Number of roosts used by transmittered northern myotis by age, sex, and reproductive status, summer 2022 and 2023, northeastern Montana.

	Juvenile Female	Adult Female	Juvenile Male	Adult Male
Non-Reproductive	11 (14%)	15 (15%)	4 (6%)	14 (18%)
Pregnant		7 (9%)		
Lactating		10 (13%)		
Post-Lactating		15 (20%)		
Total	**11**	**47**	**4**	**14**

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Table 4. Characteristics (mean values and ranges) of trees and surrounding patches for used roosts of Northern myotis, as well as random locations, *n* = 130 roosts and *n* = 130 random locations, summer 2022, and 2023, northeastern Montana.

	Roost	**Random**
Tree Height (ft)	51.0 (10-98.5)	33.2 (4-86.5)
DBH (cm)	64.6 (8.9-129.6)	45.41 (6.1-194)
Canopy Cover Average	13.00 (0-68.5)	17.49 (0-85)
Decay Stage	1.75 (1-4)	1.77 (1-6)
Bark Remaining (%)	92.9 (25-100)	93.9 (0-100)
Basal Area	3.35 (0.43-10.74)	1.60 (0.01-5.70)
Similar Tree Proportion	0.32 (0-1)	0.26 (0-1)

Table 5. Distances (m) between consecutive roosts (average and range) used by the same northern myotis, by group and overall, summer 2022 and 2023, northeastern Montana. 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.

	Average	Minimum	Maximum
Reproductive Female	91	2	439
Non-Reproductive Female	216	14	881
Non-Reproductive Male	136	11	347
Overall Average	**147**	**90**	**213**

Table 6. Candidate models and model selection results for roost selection by northern myotis, summer 2022 and 2023, northeastern Montana. We used conditional logistic regression models to compare characteristics of paired used and available (random) roosts; all models include a random intercept for each bat. We included covariates to describe the characteristics of the roost (or random) tree and the patch around the tree. Tree covariates included: AvgCan = Average Canopy Cover, TreeHt = Tree Height, and DBH = Diameter at Breast Height. Patch covariates included: BA = Basal Area and STP = Similar Tree Proportion (the proportion of trees in the patch with DBH ± 20 cm and same decay stage as the roost tree). We used Akaike's Information Criterion, corrected for small sample sizes (AIC$_c$) to compare models. K represents the number of parameters estimated in the model.

Model	AIC$_c$	ΔAIC$_c$	K
BA + AvgCan + TreeHt + STP	215.28	0.00	4
BA + TreeHt + STP	215.73	0.45	3
DBH + BA + AvgCan + TreeHt + STP	217.28	2.00	5
DBH + BA + TreeHt + STP	217.41	2.13	4
BA + AvgCan + TreeHt	218.92	3.64	3
BA + TreeHt	219.18	3.90	2
DBH + BA + AvgCan + TreeHt	220.98	5.70	4
DBH + BA + TreeHt	221.08	5.80	3
DBH + BA + STP	222.15	6.87	3
DBH + BA + AvgCan + STP	223.84	8.56	4
BA + STP	226.57	11.29	2
DBH + BA	227.42	12.14	2
BA + AvgCan + STP	227.64	12.36	3
DBH + BA + AvgCan	229.27	13.99	3
BA	231.08	15.80	1
BA + AvgCan	232.42	17.14	2
AvgCan + TreeHt + STP	247.53	32.25	3
DBH + AvgCan + TreeHt + STP	249.30	34.02	4
AvgCan + TreeHt	250.62	35.34	2
DBH + AvgCan + TreeHt	252.57	37.29	3
TreeHt + STP	254.81	39.53	2
DBH + TreeHt + STP	255.32	40.04	3
TreeHt	258.40	43.12	1
DBH + TreeHt	259.34	44.06	2
DBH + STP	277.07	61.79	2
DBH + AvgCan + STP	277.43	62.15	3
DBH	285.78	70.50	1
DBH + AvgCan	286.46	71.18	2
AvgCan + STP	311.02	95.74	2
STP	313.77	98.49	1
AvgCan	318.67	103.39	1
Null	**320.94**	**105.66**	**1**

FIGURES
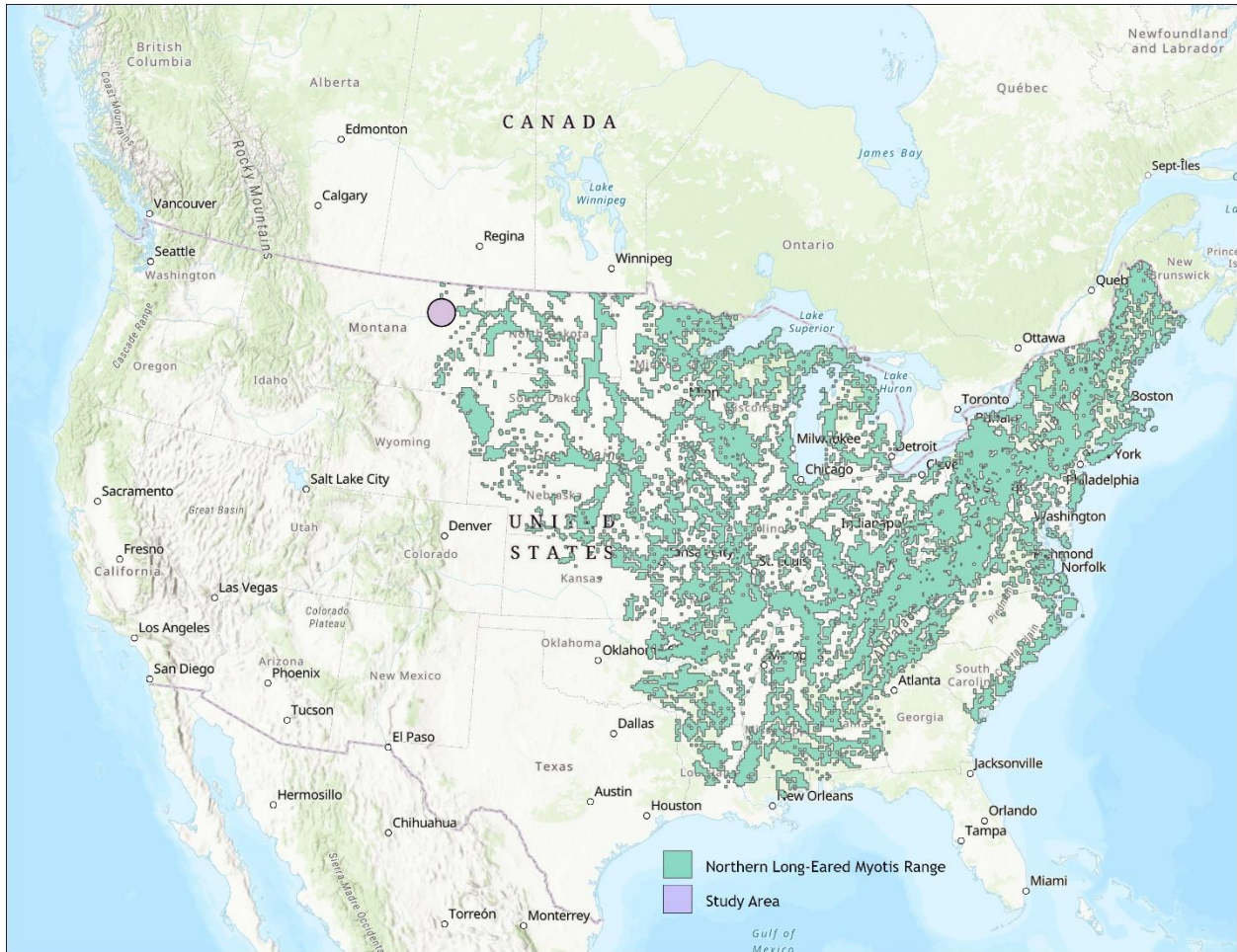
Figure 1. Range map for the northern long-eared myotis (USFWS 2024), including our study area (in lavender), which is the westernmost extent of the distribution in the US.

Figure 2. Northern myotis roost locations from 2022 and 2023 on the confluence of the Milk and Missouri rivers in northeastern Montana, depicted by the northern myotis in the inset map. Roosts are distinguished based on sex and reproductive status: reproductively active females = pink stars, non-reproductive females = blue/green squares, and males (all non-reproductive) = orange triangles.

Figure 3. The only confirmed cavity roost we found, in northeastern Montana, 2022. This represents an atypical roost for our study. The bat, a reproductively active female, inhabited it for only a day.
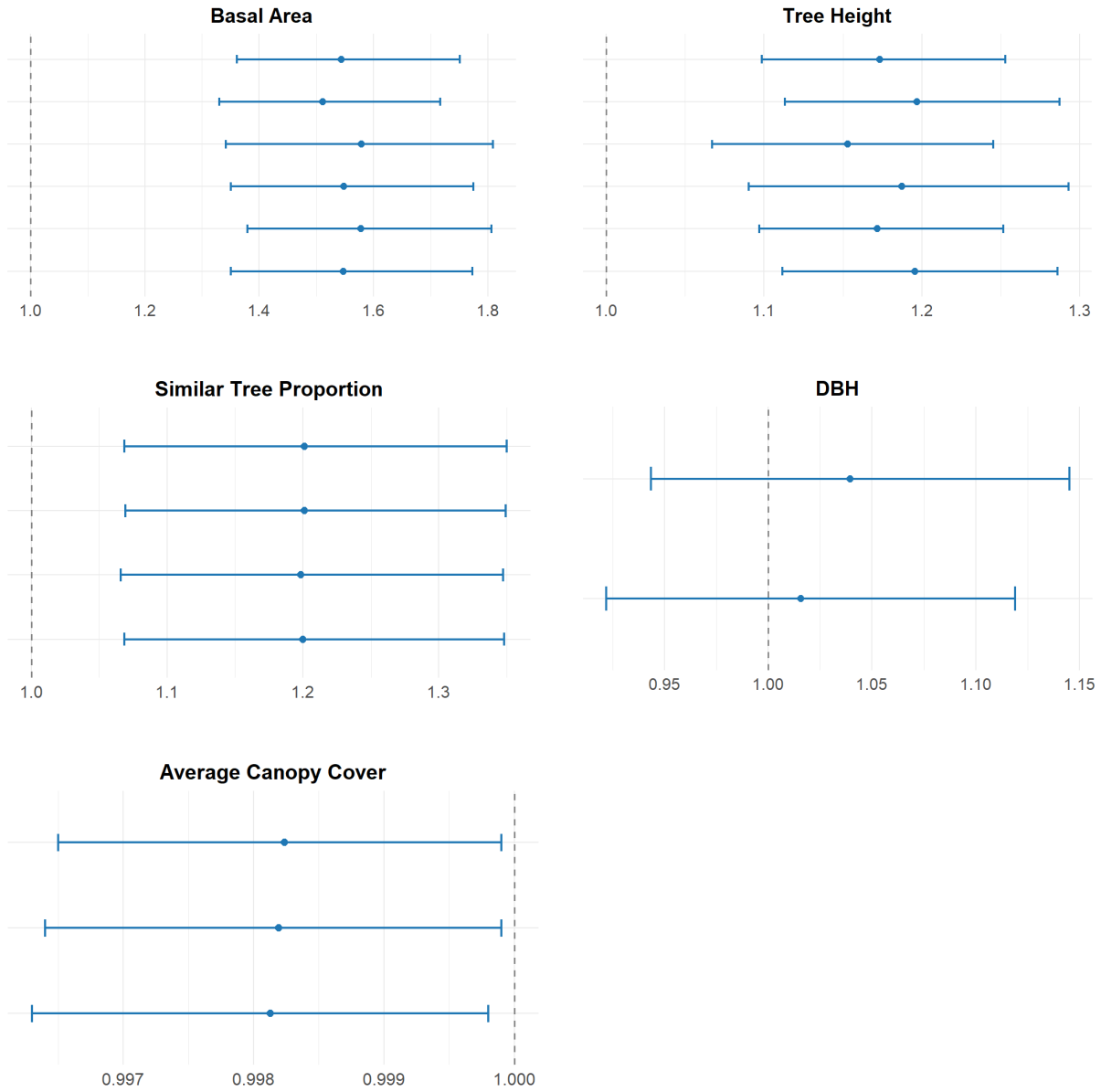
Figure 4. Estimates and 85% confidence intervals for odds ratios for different patch (basal area and similar tree proportion) and tree-level (tree height, DBH, average canopy cover) features influencing roost selection by northern myotis, summer 2022-2023, northeastern Montana. Different estimates come from competing models (Table 6). 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.

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