Roost selection by male northern long-eared bats (*Myotis septentrionalis*) at their western range edge

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ABSTRACT

Conservation in multi-use landscapes requires identifying and conserving critical resources for imperiled species because those resources may otherwise be destroyed or degraded by human activity. Summer day-roost sites are critical resources for bats, so conserving roost sites is thus an important component of many bat conservation plans. We used VHF telemetry to identify and characterize summer day-roost selection by male northern long-eared bats (*Myotis septentrionalis*) at the western edge of their range in South Dakota, USA. We tracked 18 bats to

43 tree roosts and used an information theoretic approach to determine the relative importance of tree- and plot-level characteristics on roost site selection. Bats selected roost trees that were larger in diameter, more decayed, closer to more snags, and under denser canopy than other trees available on the landscape. Protecting large-diameter snags within intact forest is important for the conservation of this federally threatened species, particularly along the western edge of its range where it may be subject to range contraction and local extinction. Protecting short (≤ 3 m) snags in particular may be a low-risk, high-reward strategy for conservation of resources important to male northern long-eared bats.

Key words: bats, Black Hills, Chiroptera, forest management, habitat use, peripheral populations, ponderosa pine (Pinus ponderosa), radiotelemetry

INTRODUCTION

Habitat degradation by humans is a leading cause of extinction and population declines for species globally (Dobson et al. 1997; Halpern et al. 2008; Hansen et al. 2013). Less than 15% of Earth's land surface falls within a protected area, and less than half of that area is free from human development, agriculture, livestock grazing, light pollution, and transportation infrastructure (Jones et al. 2018). Even in relatively undisturbed areas, land uses other than conservation of nature—such as wildfire prevention, livestock grazing, recreation, and extraction of timber and other forest products—are the norm rather than the exception. Conservation measures targeting these multi-use landscapes are thus vital for conserving species (Kremen and Merenlender 2018).

Some species and populations are at greater risk from human pressure than others. For example, species that use only one or a few resources of a particular type (e.g., food, nest sites) may be especially susceptible to loss of that resource (Safi and Kerth 2004; Sagot and Chaverri 2015). Typically, populations at range edges are also more prone to local extinction and have lower growth rates, so loss of critical resources (i.e., resources required for species persistence) at range edges should be more likely to trigger range contraction relative to more interior populations (Yackulic et al. 2011). Additionally, populations at range edges are often of conservation concern even when they are common or geographically widespread because political boundaries isolate peripheral populations within management units that do not consider larger populations in neighboring political jurisdictions (Hunter and Hutchinson 1994; Lesica and Allendorf 1995).

Successful conservation in multi-use landscapes often requires the identification of critical resources for species of conservation concern so that the supply of those critical resources can be maintained or increased. Day-roosts appear to be critical resources for many bats, providing shelter from predators and environmental stressors (Fenton et al. 1994; Solick and Barclay 2006), communal sites for social interactions (Willis and Brigham 2004), and secure places to raise young (Kunz 1982). Bats spend most of their time in day-roosts, alone or in groups of up to millions of individuals, depending on sex and species. Patterns of bat abundance and distribution are correlated with roost availability (Humphrey 1975), and declines in reproductive success have been documented when pregnant or lactating bats are experimentally excluded from preferred roosts (Brigham and Fenton 1986). Because day-roosts are so important for bats, measures to conserve roosts feature prominently in bat conservation plans. Resource managers seeking to conserve bats while managing landscapes for multiple uses could benefit from knowledge of roost characteristics that promotes bat roost conservation, particularly for populations at range edges.

We evaluated day-roost selection by northern long-eared bats (*Myotis septentrionalis*) in a ponderosa pine forest in the Black Hills of South Dakota, USA. Our study population inhabits an intensively logged landscape at the western edge of this species' range. Northern long-eared bats inhabit much of the eastern United States and southern Canada (Caceres and Barclay 2000), but are increasingly threatened by white nose syndrome and have thus been protected under the Endangered Species Act since 2015. Throughout their range, northern long-eared bats roost almost exclusively in tree cavities and under sloughing bark within intact forest (Lacki et al. 2009), and forage within forests or at forest edges (Owen et al. 2003; Patriquin and Barclay 2003; Henderson and Broders 2008). At our study site and other high elevation areas in the Black Hills, males are much more common than females (Choate and Anderson 1997; Cryan et al. 2000), and are thus important for maintaining bat populations in these areas.

To evaluate factors driving roost selection, we tracked adult male northern long-eared bats to day-roosts and quantified characteristics of both used and available roost trees using variables easily measured by forest managers. We evaluated these data using an information-theoretic approach to select the best models from a suite of candidate models. We hypothesized that in this intensively logged ecosystem, bats primarily select roost trees with characteristics that promote cavity formation (e.g., tree size and amount of decay) and thermal characteristics suitable for behavioral thermoregulation (e.g., canopy cover and orientation in relation to sunlight).

MATERIALS AND METHODS

Study Area. We conducted our study during the summers of 2017 and 2018 on Jewel Cave National Monument (43˚ 45' N, 103˚ 45' W) and surrounding areas of Black Hills National Forest, 16 km west of Custer, South Dakota, USA. In this area, mean monthly summer high temperatures range between 22 – 27˚ C and mean monthly summer precipitation ranges between 60 – 80 mm (Western Regional Climate Center 2018). Open ponderosa pine (*Pinus ponderosa*) forests dominate our study site, with Rocky Mountain juniper (*Juniperus scopulorum*) and quaking aspen (*Populus tremuloides*) occurring locally. Forests are actively managed to prevent wildfire, and those managed by the US Forest Service and private landowners also undergo intensive logging. Forests form a heterogeneous mosaic with northern mixed-grass prairie where a large stand-replacing fire occurred in our study area in 2000. A large cave system and several smaller caves lie underground at our study site, and there is substantial topographic relief on the landscape in the form of intersecting canyon systems and rock outcrops.

Capture and VHF Telemetry. We used mist nets to capture bats over permanent and semi-permanent water sources (e.g., springs, stock tanks, and stock ponds). In summer (Jun–Aug) 2017 and 2018, we netted 20 and 49 nights at 9 and 15 water sources, respectively. We opened mist nets at civil sunset and closed them after five hours and during inclement weather. We affixed VHF transmitters (LB-2X model .28 g – Holohil Systems Ltd., Carp, ON, Canada; .25 g model – Blackburn, Nacogdoches, TX, USA) between the scapulae of adult male northern long-eared bats with latex surgical adhesive (Osto-Bond, Montreal Ostomy, Montreal, QC, Canada). In our study area and others in the regions (Cryan et al. 2000), sex ratios are biased heavily toward males. Because patterns of roost selection differ between male and female bats (Elmore et al. 2004; Hein et al. 2008), we targeted males specifically. Additionally, the roosting habits of male bats are less studied than those of females—only 2 of the 14 peer-reviewed studies on roost selection of northern long-eared bats focus on males, and 11 out of 111 peer-reviewed studies on roost selection of bats in general focus on males (J. Alston, unpublished data). All transmitters weighed <5% of the mass of the bat (Aldridge and Brigham 1988). We tracked bats to roosts each day transmitters were active. All protocols were approved by the University of Wyoming and National Park Service Animal Care and Use Committees and met guidelines approved by the American Society of Mammalogists (Sikes 2016).

Roost Characterization. To characterize roosts, we collected data for each roost and randomly sampled potential roost trees in our study area. We identified potential roost trees by generating a sample of 200 random points within 2.53 km (the farthest distance we located a bat roosting from its capture site during our study) of sites where we captured northern long-eared bats and selecting the nearest potential roost tree at a random bearing from each point. We defined potential roost trees as live trees >20 cm in diameter or any dead tree with a visible defect (e.g. sloughing bark or cavities) sufficiently large for a bat to roost within. For each tree and plot, we measured characteristics that may influence roost suitability (Table 1). We measured vegetation characteristics at two spatial scales: 1) individual trees, and 2) a 706.86 m^2 (15 m radius) plot around the tree. We also measured topographic variables at the plot scale.

Statistical Analysis. To quantify differences between roost trees used by northern long-eared bats and randomly sampled available roost trees, we used the R statistical software environment (R Core Team 2018) to build binomial-family generalized linear models in a use-availability sampling design (Manly et al. 2007). We employed an information theoretic approach using Akaike's Information Criterion adjusted for small sample sizes (AIC_c) to compare competing models (Burnham et al. 2002) using the 'MuMIn' package (Barton 2018). We calculated AIC_c values and model weights (w_i) for all possible combinations of a maximum of 8 predictors (one variable for each 5 observations) in our set of candidate models to prevent bias and unreliable confidence interval coverage (Vittinghoff and McCulloch 2007). Predictors with variance inflation factors > 10 were removed from consideration in our global model to reduce problems associated with multicollinearity (Kutner 2005). We averaged model coefficients for all models with cumulative $w_i > .95$ (Burnham et al. 2002). Finally, we validated our averaged model using area under the receiver operating characteristic curve (AUC; Swets 1988; Manel et al. 2001).

RESULTS

We located 44 roosts used by 18 bats during our study. Aside from one roost in a rock crevice, bats roosted exclusively in ponderosa pines, either in cavities or under loose bark. Thirty-six out of 43 tree roosts (83.7%) occurred in snags. We found 2.4 ± 0.3 (range: 1-5) roost trees per bat. Bats typically roosted in the same patch of contiguous forest for the active life of the transmitter. Bats roosted 790 ± 90 m (range: 55 – 2,530 m) from the sites at which they were captured.

Our global model distinguishing used roost trees from available roost trees incorporated DBH, tree height, decay class (*sensu* Maser et al. 1979), slope, aspect (split into two components—eastness and southness), percent bark remaining, plot tree density, plot snag density, plot canopy cover, and interaction terms between slope and eastness and slope and southness. The global model provided an adequate fit to the data (le Cessie-van Houwelingen-Copas-Hosmer global goodness of fit test; z = 0.806, p = 0.420). Our averaged model indicated that DBH, decay class, snag density, and canopy cover were important variables (Table 2). Significant averaged model coefficients, confidence intervals, and scaled and unscaled odds ratios are reported in Table 2. Mean differences between used and available roost trees among significant variables are reported in Table 3. Predictive performance of the averaged model was high (AUC = 0.924).

Four variables (DBH, decay class, plot snag density, and canopy cover) were all positively related to roost selection (Fig. 1; Supplementary Data SD1). For each 5 cm increase in DBH, odds of selection increased by 61% (CI: 21-113%). For each 1 unit increase in decay class, odds of selection increased by 111% (CI: 47-203%). For each additional snag within a 15 m radius of the roost tree, odds of selection increased by 12% (CI: 3-22%). For each additional 10% increase in canopy cover, the odds of selection increased by 126% (CI: 55-230%).

Discussion

Northern long-eared bats primarily selected roosts in trees with characteristics that promote cavity formation. At the tree level, northern long-eared bats selected for large diameter trees with substantial decay. This corroborates previous work on northern long-eared bats (Jung et al. 2004; Rojas et al. 2017) and is intuitive because large trees with more decay have more roost structures (i.e., cavities and loose bark) for bats to use (Reynolds et al. 1985). This is particularly true of ponderosa pines, which can produce large amounts of resin to defend against localized physical injury (Lewinsohn et al. 1991; Kane and Kolb 2010) and therefore tend to develop cavities only when they are scarred or dead. In intensively logged landscapes like the Black Hills, cavities are found overwhelmingly in snags because most trees are harvested before they reach ages at which cavities typically form.

Conservation actions targeting northern long-eared bats should include preservation of large snags whenever possible. Our study demonstrated that northern long-eared bats select large-diameter snags (>37 cm), and large diameter snags also tend to remain standing longer than thinner snags (Bull 1983; Chambers and Mast 2014). These snags need not be tall—short (≤ 3 m) snags are important resources for male northern long-eared bats as well. Seventeen of 43 (39.5%) roosts that we located occurred in broken-off snags ≤ 3 m in height. These are important resources and are likely more vulnerable to loss during prescribed fire activities than other potential roost trees. Snags are often intentionally removed during forest management activities because of hazards posed to forest management personnel (e.g., loggers and firefighters) and the general public. However, these short snags pose less danger to forest management personnel and the public than taller snags, and their preservation is therefore a realistic and actionable step toward bat conservation.

Within plots, snag density predicted roost selection. This is often true of tree-roosting bats (Weller and Zabel 2001; Bernardos et al. 2004; Kalcounis□Rüppell et al. 2005), and researchers have generally attributed this to selection for areas in which individuals can readily switch roosts. We believe, however, that snag density may be an artifact of spatial autocorrelation between snags on the landscape. Many of the processes that create snags are spatially autocorrelated (e.g., wildfire, insect outbreaks, disease, and windstorms; Marcot 2017), and if bats select snags as roost sites, selection for high snag density may be an inevitable (but non-biologically driven) correlation. Follow-up analysis confirmed that plots centered around snags contained more snags than plots centered around live trees (Wilcoxon signed-rank test; $W = 9{,}338$; $p < .0001$). However, areas of dense snags are prime targets for conservation to promote bat populations regardless of whether bats select for snag density *per se* because they contain more snags per unit of area.

Of the variables we considered that may influence thermal characteristics of roosts, only canopy cover influenced roost selection significantly. Trees were more likely to be used as roosts as surrounding canopy cover increased, and use was greater than availability at all canopy cover levels >19%. In a landscape that is largely burned, 40 out of 43 (93.0%) roosts were within or immediately bordering intact forest stands with live canopy, and all roosts were within 50 m of intact forest stands. Though many snags were available at our study site in areas burned by a severe wildfire in 2000, northern long-eared bats use those snags rarely, instead preferring snags in the interior of forest stands with live canopy. Bats may prefer these areas because canopy cover creates cooler environments, but they may also simply prefer to be immediately near forested areas where they forage (Owen et al. 2003; Patriquin and Barclay 2003; Henderson and Broders 2008). Either way, stand-replacing fire likely poses risks to local populations of northern long-eared bats at the western edge of its range, where severe wildfire is increasingly prevalent due to climate change (Westerling et al. 2006). Clearcutting also poses risks to local populations of northern long-eared bats in these areas, even if snags are retained. Selective logging that leaves some level of canopy cover remaining would ensure that snag retention is effective for bat conservation.

Dynamics of regional disturbance may be important when evaluating local-scale factors that influence roost selection (O'Keefe and Loeb 2017). The ponderosa-dominated landscape where we conducted our research is substantially different than other landscapes (i.e., deciduous and mixed forests in the eastern United States) where roost selection by northern long-eared bats has been studied. Although many of the factors driving roost selection appear to be similar among areas, the processes that create roosts may be fundamentally different in different areas. Snags in ponderosa pine forests are often generated in large pulses by severe wildfire and mountain pine beetles (*Dendroctonus ponderosae*), but the long-term ramifications of these resource pulses for bats are not well understood. Severe wildfire appears to create snags that are largely unused by bats. Mountain pine beetle outbreaks may do the same if beetle-induced mortality reduces or eliminates canopy cover over large areas, or if outbreaks lead to more severe fires. Northern long-eared bats may instead depend on snag-generating processes that operate at more local scales and over longer intervals to create suitable roosts.

Roost selection by bats varies by sex, age class, and reproductive condition (Elmore et al. 2004; Hein et al. 2008). Studies on roost selection generally focus on females because they tend to drive reproduction, which is required to sustain populations. However, targeting roost conservation toward females exclusively may neglect resources that are important for males. Because sex ratios can be heavily biased in some areas (Cryan et al. 2000), ignoring the needs of males could leave resources that are important for most individuals inhabiting these areas unprotected. On the other hand, designing roost conservation measures on studies of males alone will leave resources that are important for females unprotected. For example, short ($\leq$ 3 m) snags are important resources for males, but they may not be for females, which aggregate in maternity colonies that require larger cavities than largely solitary males (Perry and Thill 2007). Resource managers seeking to conserve bats should take these sex differences into account when developing conservation plans and designing studies to inform those plans. In high elevation areas, males may be more important than females for sustaining local populations because there are few females in those areas.

Forest managers require actionable knowledge to guide conservation, and our results indicate that conserving large diameter snags within intact forest stands is one such action. Short ($\leq$ 3 m) snags in particular represent a low-risk, high-reward resource to target for preservation in male-biased, high elevation populations. Conserving these snags may prevent range contraction and local extinction of federally threatened northern long-eared bats. Although bats face danger from many threats unrelated to roosts (e.g., white nose syndrome, wind energy development, etc.), roost conservation remains an important tool for bat conservation in the face of such threats.

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SUPPLEMENTARY DATA

Supplementary Data SD1. Coefficient estimates in the averaged model and 95% confidence intervals. Bold variables denote significance at $\alpha = .05$.

DATA AVAILABILITY

*Data and R scripts will be archived on the lead author's personal website if this manuscript is accepted for publication by the Journal of Mammalogy.

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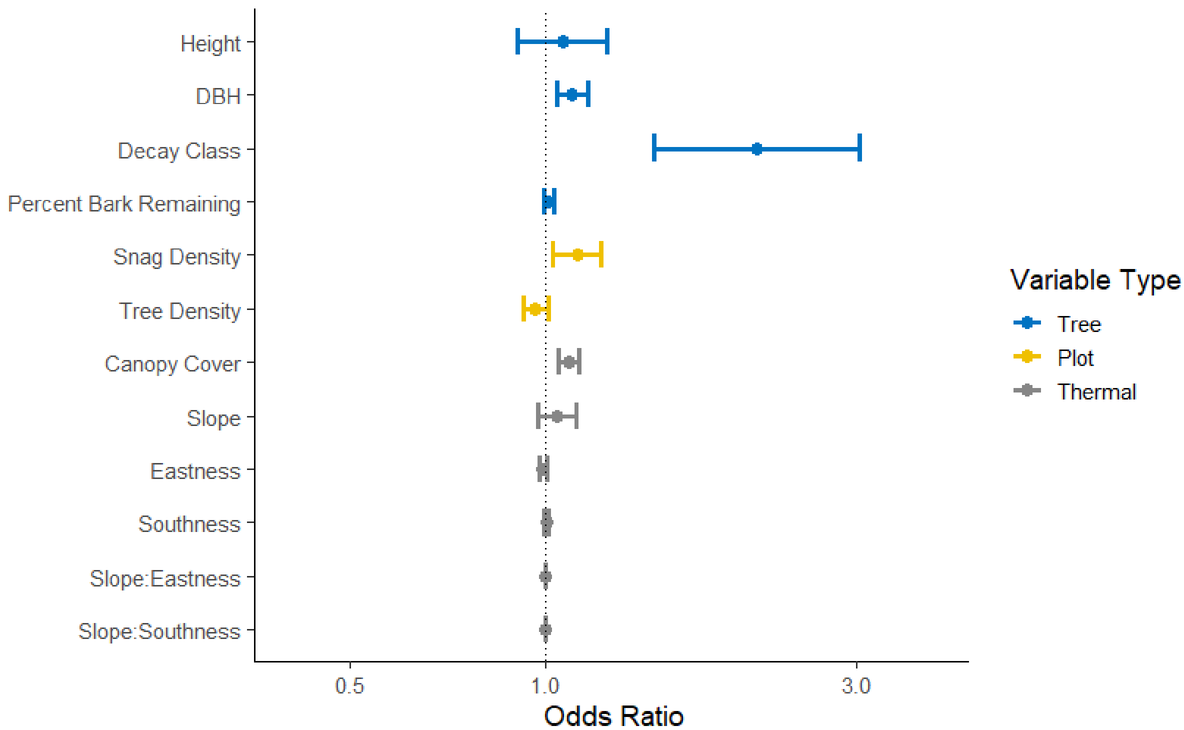
Figures

Fig. 1. Unscaled odds ratios associated with each variable in the averaged roost selection model. Error bars represent 95% confidence intervals.



404 **Table 1**. Variables measured at used and available summer day-roosts of male northern long-

405 eared bats (*Myotis septentrionalis*) in the Black Hills of South Dakota, 2017–2018.

Variable	Definition
DBH	Tree diameter at breast height (cm)
Height	Tree height (m)
Snag	Tree status (live/dead)
Decay Class	Stage of tree decay on ordinal scale
Percent Bark	Bark remaining on tree stem (%)
Canopy Cover	Average of 4 canopy cover measurements (N/E/S/W) taken 5 m from tree (%)
Slope	Slope of 706.9 m^2 (15 m radius) plot centered at tree (%)
Tree Density	Number of trees in 706.9 m^2 plot centered at tree
Snag Density	Number of snags in 706.9 m^2 plot centered at tree
Eastness	Difference between aspect of 706.9 m^2 plot centered at tree and 90 degrees (˚)
Southness	Difference between aspect of 706.9 m^2 plot centered at tree and 180 degrees (˚)
Slope:Eastness	Interaction term between slope and eastness
Slope:Southness	Interaction term between slope and southness

406

Table 2. Averaged model coefficients, confidence intervals, and scaled and unscaled odds ratios for significant variables.

Variable	Coefficient	Unscaled OR	Scaled OR	Units	Scaled OR LCL (95%)	Scaled OR UCL (95%)
DBH	0.0948	1.0994	1.6064	5 cm	1.2103	2.1321
Decay Class	0.7466	2.1098	2.1098	1 unit	1.4673	3.0337
Snag Density	0.1120	1.1185	1.1185	1 unit	1.0257	1.2196
Canopy Cover	0.0816	1.0850	2.2619	10%	1.5491	3.3026

Table 3. Means and standard errors for significant predictors among used and available trees.

	Roost		Random	
Variable	Mean	SE	Mean	SE
DBH (cm)	35.69	1.57	30.33	0.69
Decay Class	4.96	0.33	3.72	0.18
Snag Density	4.74	1.03	2.16	0.24
Canopy Cover (%)	38.30	3.14	14.96	1.39

Table SD1. Coefficient estimates in the averaged model and 95% confidence intervals. Bold variables denote significance at α = .05.

Variable	Estimate	LCL (95%)	UCL (95%)
Height	0.0590	-0.1006	0.2186
DBH	**0.0948**	**0.0382**	**0.1514**
Decay Class	**0.7466**	**0.3834**	**1.1098**
Percent Bark Remaining	0.0110	-0.0087	0.0307
Snag Density	**0.1120**	**0.0254**	**0.1985**
Tree Density	-0.0356	-0.0798	0.0087
Canopy Cover	**0.0816**	**0.0438**	**0.1195**
Slope	0.0386	-0.0288	0.1059
Eastness	-0.0101	-0.0224	0.0023
Southness	0.0016	-0.0065	0.0097
Slope:Eastness	0.0005	-0.0002	0.0012
Slope:Southness	0.0003	-0.0003	0.0009