

1 Running header: *Myotis septentrionalis* roost selection

2 **Roost selection by male northern long-eared bats (*Myotis***  
3 ***septentrionalis*) in a managed fire-adapted forest**

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16

17 **Abstract:** Wildlife conservation in multi-use landscapes requires identifying and conserving  
18 critical resources that may otherwise be destroyed or degraded by human activity. Summer day-  
19 roost sites are critical resources for bats, so conserving roost sites is a focus of many bat  
20 conservation plans. Studies quantifying day-roost characteristics typically focus on female bats  
21 due to their much stronger influence on reproductive success, but large areas of species' ranges  
22 can be occupied predominantly by male bats due to sexual segregation. We used VHF telemetry  
23 to identify and characterize summer day-roost selection by male northern long-eared bats (*Myotis*  
24 *septentrionalis*) in a ponderosa pine (*Pinus ponderosa*) forest in South Dakota, USA. We tracked  
25 18 bats to 43 tree roosts and used an information-theoretic approach to determine the relative  
26 importance of tree- and plot-level characteristics on roost site selection. Bats selected roost trees  
27 that were larger in diameter, more decayed, and under denser canopy than other trees available  
28 on the landscape. Much like studies of female northern long-eared bats have shown, protecting  
29 large-diameter snags within intact forest is important for the conservation of male northern long-  
30 eared bats. Unlike female-specific studies, however, many roosts in our study (39.5%) were  
31 located in short ( $\leq 3$  m) snags. Protecting short snags may be a low-risk, high-reward strategy for  
32 conservation of resources important to male northern long-eared bats. Other tree-roosting bat  
33 species in fire-prone forests may benefit from forest management practices that promote these  
34 tree characteristics, particularly in high-elevation areas where populations largely consist of  
35 males.

36

37 **Key words:** Black Hills, Chiroptera, forest management, habitat use, prescribed fire, ponderosa  
38 pine (*Pinus ponderosa*), radiotelemetry

39

40 **1. Introduction**

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

50 In multi-use landscapes, successful conservation often requires the identification of  
51 critical resources for species of conservation concern so that the supply of those critical resources  
52 can be maintained or increased. Day-roosts appear to be critical resources for many bats,  
53 providing shelter from predators and environmental stressors (Fenton et al., 1994; Solick and  
54 Barclay, 2006), communal sites for social interactions (Willis and Brigham, 2004), and secure  
55 places to raise young (Kunz, 1982). Bats spend most of their time in day-roosts, alone or in  
56 groups of up to millions of individuals, depending on sex, species, and reproductive status.  
57 Patterns of bat abundance and distribution are correlated with roost availability (Humphrey,  
58 1975), and declines in reproductive success have been documented when pregnant or lactating  
59 bats are experimentally excluded from preferred roosts (Brigham and Fenton, 1986). Because  
60 day-roosts are so important for bats, measures to conserve roosts feature prominently in bat  
61 conservation plans. Resource managers seeking to conserve bats while managing landscapes for  
62 multiple uses benefit from knowledge that promotes bat roost conservation.

63           We evaluated day-roost selection by male northern long-eared bats (*Myotis*  
64 *septentrionalis*) in a ponderosa pine (*Pinus ponderosa*) forest in the Black Hills of South Dakota,  
65 USA. Our study population inhabits a managed fire-adapted forest at the western edge of this  
66 species' range. Northern long-eared bats inhabit much of the eastern United States and southern  
67 Canada (Caceres and Barclay, 2000), but are increasingly threatened by white nose syndrome  
68 and have been protected in the United States under the Endangered Species Act since 2015 and  
69 in Canada under the Species at Risk Act since 2014. Throughout their range, northern long-eared  
70 bats roost almost exclusively in tree cavities and under sloughing bark within intact forest (Lacki  
71 et al., 2009), and forage within forests or at forest edges (Henderson and Broders, 2008; Owen et  
72 al., 2003; Patriquin and Barclay, 2003).

73           At our study site and other high-elevation areas in the Black Hills, male bats are much  
74 more common than females (Choate and Anderson, 1997; Cryan et al., 2000). Sexual segregation  
75 driven by elevation or temperature is widespread among bats, and is believed to be driven by  
76 differences in energy requirements that allow males to inhabit areas that are colder or have less  
77 prey (Barclay, 1991; Ford et al., 2002; Senior et al., 2005). Male northern long-eared bats are  
78 therefore likely to occupy substantially different habitat than females, but range-wide  
79 conservation for the species is informed predominantly by studies focusing on female bats (J.  
80 Alston, unpublished data). Forest managers in male-dominated areas may therefore rely on  
81 incomplete information to conserve the majority of bats within their jurisdictions. Our study  
82 provides managers in such areas with information to appropriately guide management in male-  
83 dominated areas and supplement the existing wealth of information on female habitat use.

84           To evaluate factors driving roost selection, we tracked adult male northern long-eared  
85 bats to day-roosts and quantified characteristics of both used and available roost trees using

86 variables easily measured by forest and wildlife managers. We evaluated these data using an  
87 information-theoretic approach to select the best models from a suite of candidate models. We  
88 hypothesized that in this managed forest, bats primarily select roost trees with characteristics that  
89 promote cavity formation (e.g., tree size and amount of decay), the number of nearby roosts (e.g.,  
90 plot-level tree and snag density), and thermal characteristics suitable for behavioral  
91 thermoregulation (e.g., canopy cover and orientation in relation to sunlight).

92

## 93 **2. Methods**

### 94 2.1. Study Area

95 We conducted our study during the summers of 2017 and 2018 on Jewel Cave National  
96 Monument (43° 45' N, 103° 45' W) and surrounding areas of Black Hills National Forest, 16 km  
97 west of Custer, South Dakota, USA. In this area, mean monthly summer high temperatures range  
98 between 22 – 27°C and mean monthly summer precipitation ranges between 60 – 80 mm  
99 (Western Regional Climate Center, 2018). Open ponderosa pine forests dominate our study site,  
100 with Rocky Mountain juniper (*Juniperus scopulorum*) and quaking aspen (*Populus tremuloides*)  
101 occurring locally. In our local study area, forests form a heterogenous mosaic with northern  
102 mixed-grass prairie where a large stand-replacing fire occurred in 2000. A large cave system and  
103 several smaller caves lie underground at our study site, and there is substantial topographic relief  
104 on the landscape in the form of intersecting canyon systems and rock outcrops.

105 Forests in this landscape are intensively managed. Black Hills National Forest typically  
106 uses even-aged management techniques other than clear-cutting (e.g., two-step shelterwood  
107 harvest). Stand harvest rotations are 120 years on average, but selective cutting occurs at 10- to  
108 20-year intervals to harvest mature trees and thin the understory. Aside from large severe

109 wildfires, the forest self-regenerates and does not require planting. Forest management on private  
110 lands generally also follow this formula but thinning intervals vary (B. Phillips, personal  
111 communication). Forests on Jewel Cave National Monument are managed for resource  
112 preservation, primarily using prescribed fire.

113

## 114 2.2. Capture and VHF Telemetry

115 We used mist nets to capture bats over permanent and semi-permanent water sources  
116 (e.g., springs, stock tanks, and stock ponds). In summer (Jun–Aug) 2017 and 2018, we netted 20  
117 and 49 nights at 15 water sources. Mist netting sites were distributed throughout our study area,  
118 and all were in or near large burned areas and harvested areas. We opened mist nets at civil  
119 sunset and closed them after five hours and during inclement weather. We affixed VHF  
120 transmitters (0.28 g LB-2X model – Holohil Systems Ltd., Carp, ON, Canada; 0.25 g model –  
121 Blackburn, Nacogdoches, TX, USA) between the scapulae of adult male northern long-eared  
122 bats with latex surgical adhesive (Osto-Bond, Montreal Ostomy, Montreal, QC, Canada). In our  
123 study area and others in the region (Cryan et al. 2000), sex ratios are overwhelmingly male.  
124 Because patterns of roost selection can differ between male and female bats (Boland et al., 2009;  
125 Elmore et al., 2004; Hein et al., 2008; Perry and Thill, 2007), we targeted males specifically.  
126 Additionally, the roosting habits of male bats are less studied than those of females—only 2 of  
127 the 14 peer-reviewed studies on roost selection of northern long-eared bats provide data on  
128 males, and 11 out of 111 peer-reviewed studies on roost selection of cavity-roosting bats in  
129 general provide data on males (J. Alston, unpublished data). All transmitters weighed <5% of the  
130 mass of the bat (Aldridge and Brigham, 1988). We tracked bats to roosts each day transmitters  
131 were active using handheld VHF receivers (R-1000 model, Communication Specialists Inc.,

132 Orange, CA, USA) equipped with flexible H antennae (RA-23K model, Telonics Inc., Mesa, AZ,  
133 USA). All tracking was conducted on foot. All protocols were approved by the University of  
134 Wyoming and National Park Service Animal Care and Use Committees and met guidelines  
135 approved by the American Society of Mammalogists (Sikes et al., 2016).

136

### 137 2.3. Roost Characterization

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

149

### 150 2.4. Statistical Analysis

151 To quantify differences between roost trees used by northern long-eared bats and the 200  
152 randomly sampled available roost trees, we used the R statistical software environment (R Core  
153 Team, 2018) to build binomial-family generalized linear models. Because we were unable to  
154 confirm that available roost trees were never used by bats, our analyses should be interpreted

155 within the context of the use-availability resource selection framework (Beyer et al., 2010;  
156 Johnson et al., 2006; Manly et al., 2007). We employed an information-theoretic approach using  
157 Akaike's Information Criterion adjusted for small sample sizes ( $AIC_c$ ) to compare competing  
158 models (Burnham and Anderson, 2002) using the 'MuMIn' package (Barton, 2018). We  
159 calculated  $AIC_c$  values and model weights ( $w_i$ ) for all possible combinations of a maximum of 8  
160 predictors (one variable for each 5 observations) in our set of candidate models to prevent biased  
161 coefficient estimates and unreliable confidence interval coverage (Vittinghoff and McCulloch,  
162 2007). Predictors with variance inflation factors (VIFs)  $> 10$  were removed from consideration in  
163 our global model to reduce problems associated with multicollinearity (Kutner, 2005). Because  
164 no model had a  $w_i > 0.90$ , we averaged model coefficients for all models with cumulative  $w_i >$   
165 0.95 using the full-averaging method to obtain a final averaged model (Burnham and Anderson,  
166 2002). Finally, we validated our averaged model using area under the receiver operating  
167 characteristic curve (AUC; Manel et al., 2001; Swets, 1988).

168

### 169 **3. Results**

170 We located  $2.4 \pm 0.3$  (range: 1-5) roost trees per bat during our study, for a total of 44  
171 roosts used on 59 days by 18 bats. Aside from one roost in a rock crevice, bats roosted  
172 exclusively in ponderosa pines, either in cavities or under loose bark. Thirty-six out of 43 tree  
173 roosts (83.7%) occurred in dead trees (hereafter termed "snags"). Seventeen of 43 (39.5%) roosts  
174 that we located occurred in broken-off snags  $\leq 3$  m in height. Bats typically roosted in the same  
175 patch of contiguous forest for the active life of the transmitter. Bats roosted  $790 \pm 90$  m (range:  
176 55 – 2,530 m) from the sites at which they were captured.



177 Our global model distinguishing used roost trees from available roost trees incorporated  
178 DBH, tree height, decay class, slope, aspect (split into two components—eastness and  
179 southness), percent bark remaining, plot tree density, plot snag density, plot canopy cover, and  
180 interaction terms between slope and eastness and slope and southness. The snag variable was  
181 removed from consideration so that no variable in the global model had a VIF >10. The global  
182 model provided an adequate fit to the data (le Cessie-van Houwelingen-Copas-Hosmer global  
183 goodness of fit test;  $z = 0.805$ ,  $p = 0.421$ ). Our averaged model (incorporating 104 models in our  
184 confidence set; Table A.2) indicated that DBH, decay class, and canopy cover were important  
185 variables (Table 2). Significant ( $p < 0.05$ ) averaged model coefficients, confidence intervals, and  
186 scaled and unscaled odds ratios are reported in Table 3. Mean differences between used and  
187 available roost trees among our variables of interest are reported in Table 4. Predictive  
188 performance of the averaged model was very high (AUC = 0.924).

189 Three variables (DBH, decay class, and canopy cover) were positively related to roost  
190 selection (Fig. 1; Table 2). For each 5 cm increase in DBH, odds of selection increased by 61%  
191 (95% CI: 21-113%). Use was greater than availability at all diameters >37 cm. For each 1 unit  
192 increase in decay class, odds of selection increased by 111% (95% CI: 47-203%). Use was  
193 generally greater than availability for decay classes >2. For each additional 10% increase in  
194 canopy cover, the odds of selection increased by 126% (95% CI: 55-230%). Use was greater  
195 than availability at all canopy cover levels >19%.

196

#### 197 **4. Discussion**

198 Male northern long-eared bats primarily selected roosts in trees with characteristics that  
199 promote cavity formation. At the level of individual trees, bats selected for large-diameter trees

200 with substantial decay. This corroborates previous work on northern long-eared bats (Jung et al.,  
201 2004; Rojas et al., 2017) and is intuitive because large trees with more decay have more roost  
202 structures (i.e., cavities and loose bark) for bats to use (Reynolds et al., 1985). This is particularly  
203 true of ponderosa pines, which can produce large amounts of resin to defend against physical  
204 injury (Kane and Kolb, 2010; Lewinsohn et al., 1991) and therefore tend to develop cavities only  
205 when they are scarred or dead. In intensively managed landscapes like the Black Hills, cavities  
206 are found overwhelmingly in snags because most trees are harvested before they reach ages at  
207 which cavities typically form.

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

220 Of the variables we considered that may influence thermal characteristics of roosts, only  
221 canopy cover influenced roost selection significantly. Trees were more likely to be used as roosts  
222 as surrounding canopy cover increased, and use was greater than availability at all canopy cover

223 levels >19%. Although many snags were available within our study area in open areas burned by  
224 a severe wildfire in 2000, bats in our study rarely used those snags, instead selecting snags in the  
225 interior of forest stands with live canopy. Forty out of 43 (93.0%) roosts were within intact forest  
226 stands with live canopy, and all roosts were within 50 m of intact forest stands. Bats may prefer  
227 these areas because canopy cover creates cooler environments, but they may also simply prefer  
228 to be immediately near forested areas where they forage (Henderson and Broders, 2008; Owen et  
229 al., 2003; Patriquin and Barclay, 2003). Either way, stand-replacing fire likely poses risks to  
230 local populations of northern long-eared bats at the western edge of its range, where severe  
231 wildfire is increasingly prevalent due to climate change (Westerling et al., 2006). Clearcutting  
232 also poses risks to local populations of northern long-eared bats in these areas, even if snags are  
233 retained. Selective logging that leaves some level of canopy cover remaining would ensure that  
234 snag retention is effective for bat roost conservation.

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

246 fires. Bats may instead depend on snag-generating processes that operate at more local scales and  
247 over longer intervals to create suitable roosts.

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

262

## 263 **5. Conclusions**

264         Forest managers require actionable knowledge to guide conservation, and our results  
265 indicate that conserving large-diameter snags within intact forest stands is one such action that  
266 can be taken to conserve male northern long-eared bats in wildfire-prone coniferous forests.  
267 Short ( $\leq 3$  m) snags in particular represent a low-risk, high-reward resource to target for  
268 preservation in male-biased, high-elevation populations of this species. For federally threatened

269 northern long-eared bats, conserving these snags at the western edge of their range may prevent  
270 range contraction and local extinction. Similar patterns may hold true for other cavity-roosting  
271 bat species in wildfire-prone coniferous forests, like those found throughout western North  
272 America. Further study on roost selection by male bats represents an underappreciated  
273 conservation research opportunity that may be particularly valuable for high-elevation bat  
274 populations. Although bats face danger from many threats unrelated to roosts (e.g., white nose  
275 syndrome, wind energy development, etc.), roost conservation remains an important tool for bat  
276 conservation in the face of such threats.

277

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288

## 289 **Appendix A: Supplementary Data**

290 **Table A.1.** *A priori* rationales for including variables of interest in the global model.

291

292 **Table A.2.** Candidate models,  $\Delta$ AIC values, and model weights ( $w_i$ ) used to determine model-  
293 averaged coefficients.

294

295 **Fig. A.1.** Density plots of significant variables in the averaged model. Use was generally great  
296 than availability at all decay classes  $> 2$ , and greater than availability for all DBHs  $>37$  and all  
297 canopy cover levels  $>19\%$ .

298

### 299 **Data Availability**

300 Data and R code used in analysis have been archived on *Zenodo*. They can be located using the  
301 following link: <https://zenodo.org/record/2727206#.XNY-iKR7k2w>.

302

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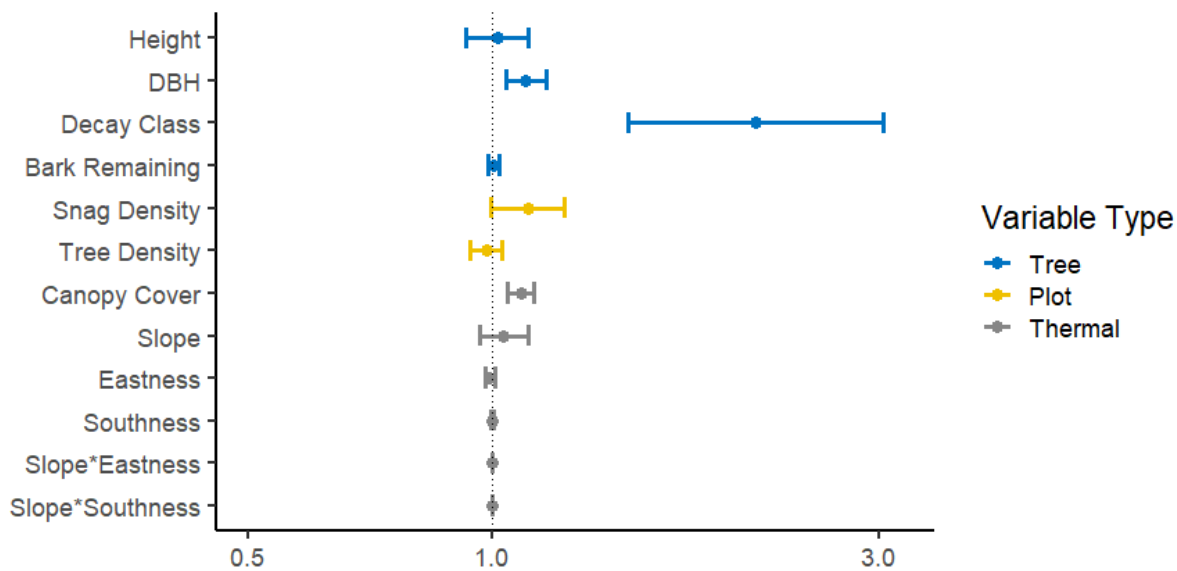
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443

444 **Figure Legends**

445 **Fig. 1.** Unscaled odds ratios associated with each variable in the averaged roost selection model.

446 Error bars represent 95% confidence intervals.



447

448 **Table 1.** Variables measured at used and available summer day-roosts of male northern long-eared bats (*Myotis septentrionalis*) in the  
 449 Black Hills of South Dakota, 2017–2018.

Variable	Definition
DBH	Tree diameter at breast height (cm); measured with a diameter tape
Height	Tree height (m); measured with an electronic clinometer
Snag	Tree status (live/dead)
Decay Class	Stage of tree decay on ordinal scale from 1-9; higher values denote more decay ( <i>sensu</i> Maser et al., 1979)
Bark Remaining	Bark remaining on tree trunk (%); estimated visually
Canopy Cover	Average of 4 canopy cover measurements (N/E/S/W) taken 5 m from tree (%); measured with a convex spherical densiometer
Slope	Slope of 706.9-m <sup>2</sup> (15-m radius) plot centered at tree (%); measured with an electronic clinometer
Tree Density	Number of live trees in 706.9-m <sup>2</sup> plot centered at tree
Snag Density	Number of snags in 706.9-m <sup>2</sup> plot centered at tree
Eastness	Difference between aspect of 706.9-m <sup>2</sup> plot centered at tree and 90 degrees (°); measured with a compass
Southness	Difference between aspect of 706.9-m <sup>2</sup> plot centered at tree and 180 degrees (°); measured with a compass
Slope*Eastness	Interaction term between slope and eastness
Slope*Southness	Interaction term between slope and southness

450

451 **Table 2.** Coefficient estimates in the averaged model and 95% confidence intervals. Bold variables denote significance at  $\alpha = 0.05$ .

Variable	Estimate	LCL (95%)	UCL (95%)
Height	0.0133	-0.0767	0.1033
<b>DBH</b>	<b>0.0948</b>	<b>0.0382</b>	<b>0.1514</b>
<b>Decay Class</b>	<b>0.7465</b>	<b>0.3835</b>	<b>1.1094</b>
Bark Remaining	0.0033	-0.0113	0.0180
Snag Density	0.1010	-0.0039	0.2059
Tree Density	-0.0182	-0.0653	0.0289
<b>Canopy Cover</b>	<b>0.0816</b>	<b>0.0438</b>	<b>0.1195</b>
Slope	0.0323	-0.0354	0.0999
Eastness	-0.0069	-0.0207	0.0068
Southness	0.0004	-0.0041	0.0050
Slope*Eastness	0.0001	-0.0004	0.0005
Slope*Southness	0.0000	-0.0002	0.0002

452

453

454 **Table 3.** Averaged model coefficients, scaled and unscaled odds ratios (OR), and scaled lower and upper confidence limits  
 455 (UCL/LCL) for significant variables.

Variable	Coefficient	Unscaled OR	Scaled OR	Units	Scaled OR LCL (95%)	Scaled OR UCL (95%)
DBH	0.0948	1.0995	1.6065	5 cm	1.2105	2.1321
Decay Class	0.7465	2.1095	2.1095	1 unit	1.4674	3.0327
Canopy Cover	0.0816	1.0850	2.2619	10%	1.5491	3.3025

456



457 **Table 4.** Means and standard errors for variables of interest among used and available trees.

458 Bold font denotes statistically significant variables in the final averaged model.

Variable	<u>Roost</u>		<u>Available</u>	
	Mean	SE	Mean	SE
Height (m)	8.53	1.11	9.01	0.43
<b>DBH (cm)</b>	<b>35.69</b>	<b>1.57</b>	<b>30.33</b>	<b>0.69</b>
<b>Decay Class</b>	<b>4.95</b>	<b>0.33</b>	<b>3.72</b>	<b>0.18</b>
Bark Remaining (%)	74.19	4.22	69.73	2.49
Snag Density	4.74	1.03	2.12	0.23
Tree Density	19.84	2.15	10.76	1.12
<b>Canopy Cover (%)</b>	<b>36.83</b>	<b>3.02</b>	<b>14.96</b>	<b>1.39</b>
Slope (%)	16.87	1.62	11.66	0.64
Eastness (°)	76.36	8.21	93.35	3.81
Southness (°)	109.48	11.14	96.58	5.48

459