

1 **Selection of roosting habitat by male *Myotis* bats in a boreal forest**

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21 **Abstract**

22 Male little brown bat (*Myotis lucifugus* (Le Conte, 1831)) and northern long-eared bat (*Myotis*
23 *septentrionalis* (Trouessart, 1897)), often roost under exfoliating bark, within the trunks and
24 cavities of trees during summer. Current lack of knowledge about the roosting ecology of these
25 species in boreal forest limits our understanding of how they may be affected by logging. The
26 main objective was to identify tree and forest stand features that were selected by bats for
27 roosting within a balsam fir (*Abies balsamea* [L.]Miller)-paper birch (*Betula papyrifera*
28 Marshall) forest of Quebec (Canada). Over three years, we captured and fitted radio-transmitters
29 to 22 individual bats to locate their roost trees for seven to 14 days following release. We
30 measured tree and forest stand features in the field and using Light Detection and Ranging
31 (LiDAR) technology. Roost trees were compared to random trees using generalized linear mixed
32 models. Male *Myotis* bats selected larger and taller snags, within stands containing a higher
33 proportion of canopy gaps and a larger number of snags compared to random trees. Vegetation
34 clumps of 0.1 ha containing a minimum of 10 snags with a Diameter at Breast Height (DBH) \geq
35 10 cm should be maintained to preserve roosting habitat that is used by male *Myotis* bats in
36 balsam fir-paper birch forests.

37 Key words: boreal forest, habitat selection, LiDAR, little brown bat, *Myotis lucifugus*, *Myotis*
38 *septentrionalis*, northern long-eared bat, Quebec, roost tree, snags

39

40 **Résumé**

41 La petite chauve-souris brune (*Myotis lucifugus* (Le Conte, 1831)) et la chauve-souris nordique
42 (*Myotis septentrionalis* (Trouessart, 1897)), se perchent souvent sous l'écorce exfoliante, à
43 l'intérieur des troncs et des cavités d'arbres durant l'été. Le manque actuel de connaissances sur
44 l'écologie de perchage de ces espèces dans la forêt boréale limite notre compréhension sur la
45 façon dont elles peuvent être affectées par l'exploitation forestière. L'objectif principal était
46 d'identifier les caractéristiques des arbres et des peuplements forestiers qui étaient sélectionnés
47 par les chauves-souris pour se percher au sein de la sapinière (*Abies balsamea* [L.]Miller) à
48 boulot blanc (*Betula papyrifera* Marshall) du Québec (Canada). Durant trois ans, nous avons
49 capturé et équipé 22 chauves-souris de radio-émetteurs pour localiser leurs arbres-gîtes durant
50 sept à 14 jours après relâche. Nous avons mesuré les caractéristiques des arbres et du peuplement
51 sur le terrain et en utilisant la technologie LiDAR (Light Detection and Ranging). Les arbres-
52 gîtes ont été comparés à des arbres aléatoires en utilisant des modèles mixtes linéaires
53 généralisés. Les chauves-souris mâles du genre *Myotis* ont choisi des chicots plus larges et plus
54 hauts au sein de peuplements contenant une plus grande proportion de trouées et un plus grand
55 nombre de chicots, comparativement aux arbres aléatoires. Des parcelles de végétation de 0,1 ha
56 comprenant un minimum de 10 chicots avec un Diamètre à Hauteur de Poitrine (DHP) ≥ 10 cm
57 devraient être maintenues afin de préserver les sites de perchages des chauves-souris mâles du
58 genre *Myotis* au sein des sapinières à bouleau blanc.

59 Mots clés: arbre-gîte, chicots, chauve-souris nordique, forêt boréale, LiDAR, *Myotis lucifugus*,
60 *Myotis septentrionalis*, petite chauve-souris brune, Québec, sélection d'habitat

61

62 **Introduction**

63 Nearly half of known bat species worldwide use trees as roosts for at least part of the year (Kunz
64 and Lumsden 2007). Bats use trees as shelters, protection against predators, for social interactions
65 (O'Shea and Bogan 2003), and as a likely means of reducing thermoregulation costs (Smith and
66 Racey 2005; Boyles 2007). Roosting habitat is thus an important component of bat ecology that
67 is sometimes limiting (O'Donnell and Sedgeley 1999; Kunz and Lumsden 2007), especially under
68 the effects of anthropogenic disturbances, such as logging (Campbell et al. 1996; Loeb and
69 O'Keefe 2011). Indeed, logging has been recognized as a major threat to bats worldwide (Hutson
70 et al. 2001). Forest management influences tree size and tree mortality rates, as well as stand
71 species composition, stand density and stand age, such that management prescriptions are likely
72 to affect both the availability of trees that are used as roosts by bats, as well as their surrounding
73 environment (Guldin et al. 2007).

74 The increasing attention that bat roosting ecology has received over the last three decades
75 indicates that roost selection depends upon a broad range of requirements (Kalcounis-Rueppell et
76 al. 2005) at various habitat scales (Miles et al. 2006; Boland et al. 2009; Fleming et al. 2013).
77 Features such as tree decay (Parsons et al. 2003; Baker and Lacki 2006), tree height and tree
78 diameter (Lacki and Baker 2003) can influence selection by bats. At the stand scale, proportion of
79 canopy gaps (Loeb and O'Keefe 2011) and the availability of nearby snags are also important
80 features of bat habitat selection (Arnett and Hayes 2009). Recent research also suggests that bats
81 use networks of roost trees (Johnson et al. 2012), although advantages associated with these
82 networks remain unclear (Broders et al. 2006; Reckardt and Kerth 2007).

83 The little brown bat (*Myotis lucifugus* (Le Conte, 1831)) and the northern long-eared bat (*Myotis*
84 *septentrionalis* (Trouessart, 1897)) are two insectivorous cavity-roosting bats that were common

85 throughout the north-eastern boreal forests of Canada prior to the appearance of White Nose
86 Syndrome (WNS; Blehert et al. 2009). Since its discovery in 2006 in New York State, WNS has
87 caused mass mortality of hibernating bats throughout eastern North America (Dzal et al. 2010;
88 Moosman et al. 2013) and is predicted to lead to regional extinctions of the little brown bat (Frick
89 et al. 2010). Both *Myotis* bats are known to roost under exfoliating bark, inside crevices, or
90 within the cavities of large trees during summer (Parsons et al. 2003; Jung et al. 2004; Garroway
91 and Broders 2008). Roost selection by these species has been well documented for females and in
92 temperate forests (Barclay and Kurta 2007), but few studies have investigated roost selection by
93 males and within the Boreal Shield ecozone (Broders and Forbes 2004; Jung et al. 2004).
94 Moreover, no study to date has investigated the habitat requirements of cavity-roosting bats, such
95 as *Myotis* bats, in the Province of Quebec (Canada). This lack of knowledge prevents the
96 adaptation of forest management practices that favour habitat conservation of *Myotis* bats.
97 Considering that direct WNS-associated mortality cannot yet be mitigated in North America, an
98 appropriate strategy would be to reduce the influence of other anthropogenic disturbances to
99 preserve the natural habitat of the bats. This requires greater knowledge of *Myotis* roosting
100 habitats, particularly in the case of males, which remain largely underrepresented in habitat
101 selection studies.

102 We hypothesize *a priori* the tree and forest stand features that might be selected by both *Myotis*
103 bats, based on a review of 34 published manuscripts on roost selection by cavity-roosting bats in
104 North America. We predict that *Myotis* bats select roosts in taller and larger trees with advanced
105 decay stages and that these possess a higher percentage of remaining bark compared to random
106 trees (Parsons et al. 2003; Kalcounis-Rueppell et al. 2005; Perry and Thill 2007). We also predict
107 that roost trees that are selected by *Myotis* bats are surrounded by lower vegetation cover, a
108 higher proportion of canopy gaps, and a larger number of snags compared to random trees

109 (Broders and Forbes 2004; Arnett and Hayes 2009; Loeb and O'Keefe 2011). As suggested by
110 Brigham et al. (1997), a higher proportion of canopy gaps should also provide greater exposure to
111 sunlight and limit daily thermoregulation costs (Lacki et al. 2013; Johnson and Lacki 2014).

112 **Materials and methods**

113 **Study area**

114 We studied roosting behavior of bats at the Montmorency Research Forest (47°19'N, 71°07'W),
115 which is located 70 km north of Quebec City, within the balsam fir (*Abies balsamea* [L.]Miller)-
116 paper birch (*Betula papyrifera* Marshall) bioclimatic domain. With an average elevation of 850 m
117 asl, climatic conditions in the region are considered cold and wet, with an average summer (May
118 to September) temperature of $11.4\text{ }^{\circ}\text{C} \pm 3.3\text{ }^{\circ}\text{C}$ (mean \pm SD; range: 4.0 to 16.4 $^{\circ}\text{C}$) and
119 precipitation of $128.0\text{ mm} \pm 49.2\text{ mm}$ (range: 44.5 to 267 mm). The boreal forest alternates
120 between mixed and coniferous stands, which rarely exceed 90 years of age. The forest is actively
121 managed by clear cuts, partial cuts and shelter wood cutting. Natural disturbances are mainly
122 caused by outbreaks of spruce budworm (*Choristoneura fumiferana* (Clemens)) and tree decay,
123 thereby creating a patchy mosaic of forest structures.

124 **Capture and tracking**

125 We captured bats from mid-June to mid-August 2011, 2012 and 2013, using 10 mist nets (Avinet
126 Inc., Dryden, NY, USA). We placed mist nets from 2100 to 0100 along trails, close to ponds and
127 forest stands, and changed their locations after two consecutive nights to increase capture
128 success. We weighed each captured individual and identified it to species. We visually
129 determined reproductive status (reproductive or not reproductive) and age classes (adult or
130 juvenile), following the methodology described in Kunz and Parsons (2009). We glued radio
131 transmitters (Model LB-2X, Holohil Systems Limited, Carp, ON, Canada) onto the trimmed

132 interscapular fur of adult bats that weighed more than 6 g, using non-toxic surgical adhesive
133 (Skin-Bond, Smith and Nephew United, Memphis, TN, USA). We tracked released individuals
134 on a daily basis, using a three-element Yagi antenna and receiver system (ATSR4500S model,
135 Advanced Telemetry Systems, Isanti, MN, USA). We located their roost trees by homing in until
136 the transmitter fell off. Because of the risk of WNS transmission, we decontaminated every item
137 that was used during manipulations with a fungicide (Clinicide®, Bimeda-MTC Animal Health
138 Inc., Cambridge, ON), following the National White-Nose Syndrome Decontamination Protocol
139 that was provided by the United States Fish and Wildlife Service (USFWS). We followed ASM
140 guidelines for research on live mammals and the Animal Committee Care of Laval University
141 approved all of the above described procedures and manipulations (License number # 2011064).

142 **Habitat variables**

143 We georeferenced roost trees with a Trimble GeoXM Global Positioning System (GPS) receiver
144 (Trimble Navigation, Sunnyvale, CA). For comparative purposes, we selected a random location
145 for each roost tree. We determined each random location by taking a random distance (from 32 to
146 250 m) and a random bearing (from 0 to 360°) from each roost tree. Comparisons at the stand
147 scale were done between roosts and random locations. For comparisons at the tree scale, we took
148 the closest living or closest dead tree from each random location, matching the corresponding
149 roost tree (i.e., alive or dead).

150 We determined tree species, percent of remaining bark on trunks, and tree decay classes (Imbeau
151 and Desrochers 2002). In class (1) trees are alive with ≥ 95 % of foliage, showing no sign of
152 deterioration; (2) senescent trees where remaining foliage is between ≥ 20 % and < 95 %; (3)
153 senescent trees with < 20 % foliage remaining; (4) recently dead trees with firm bark cover, 0 %
154 green foliage and small twigs still remaining; (5) no dead foliage present, no small twigs; (6)
155 loose bark cover, broken top, height still more than 50 % of what is observed on trees with same

156 DBH (Diameter at Breast Height, 1.3 m); (7) broken top with height less than 50 % of what is
157 observed on trees with same DBH. Illustrations of decay classes (from 1 to 7) from Imbeau and
158 Desrochers (2002) are provided in Figure 1. We measured tree height using a clinometer and tree
159 DBH using a DBH tape.

160 At the stand scale, we estimated lateral vegetation cover in each cardinal direction, using a
161 vegetation profile board at 2 m and 16 m distances from each (roost and random) tree (Table 1).
162 The maximum distance of 16 m around each tree corresponds to a 0.1 ha plot. We performed
163 angle count sampling (plotless point-sampling) of the surrounding trees using a wedge prism
164 (with a basal area factor of 2). For each tree selected by the wedge prism, we recorded tree
165 species, decay class and tree DBH. We determined dominant tree species, stand type (coniferous,
166 mixed, or deciduous), stand basal area, the number of snags with $DBH \geq 10$ cm, and the number
167 of snags with $DBH \geq 20$ cm from these counts. We performed all habitat measurements at roost
168 sites after September to minimize disturbance to the bats. We also imported our selected bat roost
169 and random tree locations into ArcGIS (version 10.1, Environmental Systems Research Institute,
170 Redlands, CA) to extract the origin of stand disturbance at each location from digitized eco-forest
171 maps of the Montmorency Research Forest, which were provided by the Ministère des Forêts, de
172 la Faune et des Parcs (MFFP).

173 **Light detection and ranging imagery**

174 We have used airborne LiDAR (Light Detection and Ranging) to improve estimates of stand
175 scale variables such as mean canopy height, proportion of canopy gaps, and insolation levels.
176 Airborne LiDAR uses a laser beam to scan a complete scene from a fixed-wing aircraft (Suárez et
177 al. 2005). It provides a three-dimensional point cloud that can be processed to extract landscape
178 features such as elevation, slope, canopy height, tree density or light penetration. LiDAR has

179 many applications in forestry (Dubayah and Drake 2000; Suárez et al. 2005) and has recently
180 been used for detailed characterization of bat habitats (Jung et al. 2012; Yang et al. 2013).
181 Airborne LiDAR survey was performed in August 2011 using an Optech ALTM 3100 sensor that
182 was flown at 1000 m above the terrain with a 100 kHz pulse rate, wavelength of 1046 nm, a
183 divergence of 0.25 mrad, and with a maximal scan angle of 17° from the Nadir. Flight line
184 overlap was 50 %, and final median density was about five points per square meter. The point
185 cloud that we obtained was then converted to a surface model representing ground and
186 vegetation, which we refer to as the Digital Surface Model (DSM). Identification of ground
187 returns was carried out by the provider and triangulated to create a Digital Terrain Model (DTM).
188 Subtraction of DTM from DSM yielded a Canopy Height Model (CHM), which we used as a
189 representation of the canopy (Vazirabad and Kararlioglu 2010). We derived mean stand height,
190 proportion of canopy gaps, and mean insolation levels within 2 m and 16 m radius buffers around
191 each tree from the LiDAR (Table 1). We defined canopy gaps as being greater than 2 m², with a
192 tree height that was two-thirds lower than the surrounding mean canopy height. Insolation level
193 refers here to the theoretical amount of solar radiation energy (expressed in megajoule) received
194 by each roost tree or random location during a day (MJ/m²/day). We simulated DSM mean
195 insolation for June and July 2011, from 0600 to 2000, at 47°17'60"N, using SAGA (System for
196 Automated Geoscientific Analyses) GIS (Kumar et al. 1997).

197 **Statistical analyses**

198 We considered trees rather than individual bats as our sampling units and pooled the data from
199 both species of bats to examine roost selection at the genus level, to overcome issues of limited
200 sample sizes ($n = 14$ roosts for the little brown bat, $n = 26$ roosts for the northern long-eared bat;
201 Table 1). We examined differences between selected roost trees and random trees using
202 Generalized Linear Mixed Models (GLMM, *lme4* package, R Development Core Team 2013)

203 with a binomial distribution and a logit link function. We based maximum likelihood estimation
204 of our parameters on an Adaptive Gaussian Quadrature approximation. We assumed that a
205 potential source of variation in roost selection could be attributed to individual bats. We therefore
206 included individual bat IDs as a random effect in our GLMMs (Bolker et al. 2009). The “random
207 effect” term here refers to a latent variable from which we wanted to estimate the potential
208 variance component. If the variance that was associated with individuals does not vary
209 consistently across treatments, (i) the random effect term should approach 0, (ii) its inclusion
210 should not improve the model fit (and subsequently lower the AICc), and (iii) the model residual
211 variance should stay unchanged, compared to a GLM including only fixed effects. To overcome
212 the problem of combining two bat species with potential differences in roost selection into the
213 same model, we included species codes (“MYLU” for little brown bat, “MYSE” for northern
214 long-eared bat) as a fixed factor in our GLMMs. This categorical variable allows model building
215 with an intercept for each species and a common slope for our variables of interest, which we
216 believe, would be the best compromise between a model by species with a limited number of
217 samples and a model that pools both species of bats.

218 We verified the presence of outliers and potential leverage effects, over-dispersion (coeff. > 1),
219 and multicollinearity before interpreting our GLMM results. We decided to exclude from our
220 analyses the number of snags that had $DBH \geq 20$ cm, together with stand basal area and mean
221 stand canopy height variables, to avoid strong correlations ($r \geq 0.7$; Dormann et al. 2013)
222 between variables (i.e., stand basal area vs tree DBH; proportion of canopy gaps vs mean canopy
223 height; snags with $DBH \geq 10$ cm vs snags with $DBH \geq 20$ cm). We also decided not to include
224 decay classes (1 to 7) in our statistical analyses to avoid model over fitting, given the limited
225 number of samples (n roost trees = 40; n random trees = 40).

226 We used the second-order Akaike's information criterion for small samples (AICc) to rank the
227 candidate set of models according to our predictions (*AICcmodavg* package, R Development
228 Core Team 2013). All of the variables that were included in the candidate set of models had been
229 selected *a priori* (Burnham and Anderson 2002). To represent roosting habitat selection by bats
230 at various spatial scales, we constructed three subsets of candidate models for a total of 20
231 alternative models (Table 2). The first set combined only stand feature variables. The second set
232 combined both stand and tree feature variables, while the third set combined only tree feature
233 variables (Table 2). We calculated Δ AICc values (Δ_i) and Akaike weights (ω_i) to determine the
234 relative importance of the candidate set of models from the best explanatory model ($\Delta_i = 0$).
235 Models were considered equivalent when they had a $\Delta_i \leq 2$ (Burnham and Anderson 2002). For
236 each variable that was included in the best models, we calculated the odds ratio (and 95 % CI) by
237 applying an inverse logarithm transformation to the model estimates (β). We calculated the
238 relative-importance weights of each variable appearing in the 95 % confidence set of models
239 (Burnham and Anderson 2002). We calculated a prediction curve for each estimate from the
240 GLMM with the lowest AICc (Figure 2) and used these predictions to make recommendations for
241 forest management.

242 **Results**

243 **Captures and telemetry**

244 Because of extreme sex ratio or capture bias, we only captured male *Myotis* bats at a mean mist
245 net height of $2.5 \text{ m} \pm 1.3 \text{ m}$ (mean \pm SD; range: 0.5 to 5.5 m) from the ground. From a total of 22
246 captured males, we found five individuals roosting alone or in small groups in human habitations
247 and six individuals were not recovered. Of the 11 successfully tracked individuals, we had six
248 little brown bats ($8.0 \text{ g} \pm 1.1 \text{ g}$; range: 6.8 to 9.4 g) and five northern long-eared bats ($7.0 \text{ g} \pm 0.5$

249 g; range: 6.1 to 7.3 g) in 2011. For both species, we found 5 ± 2 roost trees (range: 3 to 7) per
250 individual bat, during a mean tracking period of $9 \text{ days} \pm 2 \text{ days}$ (range: 7 to 14 days). Bats
251 switched roost trees about every $2 \text{ days} \pm 1 \text{ day}$ (range: 1 to 6 days). We found 40 roost trees and
252 identified the exact position of the roost sites within trees for 18 cases. *Myotis* bats selected roosts
253 at a mean height of $4.9 \text{ m} \pm 2 \text{ m}$ (range: 1.5 to 8 m) and with a mean direction of $226^\circ \pm 50^\circ$
254 (range: 110 to 292°), indicating a preference for southwestern exposures ($n = 18$ roost trees).

255 **Tree characteristics and stand composition**

256 Among the 40 roost trees that were selected by male *Myotis* species, 32 (80 %) were balsam fir,
257 five (12.5 %) were paper birch, and three (7.5 %) were white spruce (*Picea glauca* [Moench]
258 Voss). Of these 40 roost trees, 36 (90 %) were snags and the remaining four (10 %) were living
259 paper birches (Figure 1). The random trees included 35 (87.5 %) balsam fir, 4 (10 %) paper birch,
260 and 1 (2.5 %) black spruce (*Picea mariana* Miller BSP). Regarding tree decay classes, we found
261 that male *Myotis* bats roosted primarily on class 6 snags, with 25 (62.5 %) roosts. Class 6 snags
262 were only represented by 14 (35 %) random trees (Figure 1).

263 At the stand scale, roost trees were primarily located in mixed stands that were dominated by
264 conifers (57.5 %, $n = 23$) or in conifer stands (40 %, $n = 16$), but rarely in deciduous stands (2.5
265 %, $n = 1$). Random locations were also located in mixed stands that were dominated by conifers
266 (50 %, $n = 20$), in conifer stands (42.5 %, $n = 17$), and in deciduous stands (7.5 %, $n = 3$). The
267 main source of disturbance was clear-cutting in bat-selected stands (78 %, $n = 21$) and random
268 locations (68 %, $n = 21$). With respect to stand composition, we found that balsam fir dominated
269 bat-selected stands (76.8 %, $n = 456$) and random locations (76 %, $n = 377$), followed by black
270 and white spruce (bat-selected: 13.1 %, $n = 78$; random: 13.1 %, $n = 65$), paper birch (bat-
271 selected: 9.8 %, $n = 58$; random: 9.1 %, $n = 45$), and trembling aspen (*Populus tremuloides*
272 Michaux; bat-selected: 0.3 %, $n = 2$; random: 1.8 %, $n = 9$). When we considered tree decay

273 classes (Figure 1), male *Myotis* bats selected roost trees in stands that contained a high proportion
274 of snags in classes 6 (bat-selected: 14.2 %, $n = 14$; random: 5.6 %, $n = 45$) and 7 (bat-selected:
275 13.4 %, $n = 133$; random: 4 %, $n = 32$), together with a few living trees of class 3 (bat-selected:
276 38.8 %, $n = 386$; random: 64.2 %, $n = 519$).

277 **Generalized linear mixed model ranking**

278 The best model (AICc weight = 0.66) that explained differences between random trees and
279 selected trees by male *Myotis* bats included five variables (Table 2): number of snags with DBH
280 ≥ 10 cm (relative importance weight = 1.00), tree height (0.98), tree DBH (0.97), proportion of
281 canopy gaps at 2 m (0.95), and bat species (0.26). The random effect variance was 1.05×10^{-16} ,
282 with a standard deviation of 1.02×10^{-08} . At the tree scale, the odds of selecting larger and taller
283 trees were respectively 1.28 (95 % CI: $1.08 \leq \beta \leq 1.50$) and 1.50 (95 % CI: $1.12 \leq \beta \leq 2.00$) times
284 more likely than random (Table 3). At the stand scale, the odds of selecting a tree with a higher
285 percentage of canopy gaps was 1.04 (95% CI: $1.01 \leq \beta \leq 1.07$) times more likely than random
286 (Table 3). Every additional snag with a DBH ≥ 10 cm that was found near a roost tree increased
287 the odds that male *Myotis* bats would select this habitat by 1.51 (95 % CI: $1.21 \leq \beta \leq 1.88$; Table
288 3). Means and standard errors for all of the aforementioned variables are shown in Table 1.

289 **Discussion**

290 Since bat species was of low relative importance weight in the 95 % confidence set of models, we
291 suggest that males of both species showed overlap in roosting habitat requirements, at least for
292 the variables that we tested. Similar results including *Myotis* bats were reported by Cryan et al.
293 (2001), and Jung et al. (2004), but contradict those found by Broders and Forbes (2004) in
294 temperate Nordic forest. In light of these results, we are confident that the benefits of pooling the
295 two species to increase our sample size outweighed the subsequent loss of information. The

296 variance explained by the random effect was close to 0 (with a standard deviation of 1.02×10^{-08}),
297 indicating that variation among individuals was not greater than would be expected according to
298 random variation. Including this random effect only penalized our best model AICc, suggesting
299 that this parameter was not ecologically meaningful (Arnold 2010).

300 Selection of roosting habitat requirements by male *Myotis* bat species operated at both tree and
301 stand scales. Similar results were reported by (Miles et al. 2006). Male little brown bats and male
302 northern long-eared bats selected larger and taller snags compared to those selected at random.
303 They preferred to roost in stands with a higher proportion of canopy gaps, and with a larger
304 number of surrounding snags (with DBH ≥ 10 cm) nearby, when compared to random locations.
305 These results are consistent with other studies in North America (Lacki and Baker 2003;
306 Kalcounis-Rueppell et al. 2005).

307 In conifer-dominated stands of the balsam fir-paper birch forest, solitary males of both bat
308 species roosted under loose bark of balsam fir (i.e., the dominant tree species) and in white spruce
309 snags. This behavior was also observed by Broders and Forbes (2004) and Jung et al. (2004). The
310 only living trees that were used by male *Myotis* bats were senescent paper birches with less than
311 20 % remaining foliage (decay class 3; Figure 1) in which individuals found roosts under the
312 exfoliating bark. Dead trees with broken tops, loose bark cover, and height less than 50 % of
313 what is observed for adjacent trees with the same DBH (decay class 6; Figure 1) were mostly
314 used by male *Myotis* bats. More advanced decay stages lead to smaller trees with less remaining
315 bark (Imbeau and Desrochers 2002), which makes them less suitable for cavity-roosting bats such
316 as *Myotis* species (Barclay and Mark Brigham 2001; Vonhof and Gwilliam 2007). At decay class
317 6, trees were probably tall enough to be both visible and accessible for bats (Kalcounis-Rueppell
318 et al. 2005; Barclay and Kurta 2007; Garroway and Broders 2008) and possessed sufficient
319 remaining bark to provide available shelter (Parsons et al. 2003; Perry and Thill 2007).

320 Although the percentage of remaining bark was included in the second best model, it was of low
321 relative importance. We believe that measuring the percentage of exfoliating bark rather than the
322 percentage of remaining bark would lead to better results. Living paper birches provide a good
323 example of this assertion: although 100 % of the bark remained on the trunks, this species
324 differed from other living tree species (such as balsam fir and spruces) by the presence of
325 exfoliating bark, which made them suitable for male *Myotis* bats.

326 Male *Myotis* bats selected slightly larger trees compared to random trees. Male bats are usually
327 solitary roosters, so that they do not necessarily require large cavities in which to rest compared
328 to lactating females (Psyllakis and Brigham 2006; Willis et al. 2006; Park and Broders 2012).
329 Lacki and Schwierjohann (2001), and Perry and Thill (2007) found that male bats used small
330 diameter trees (mean DBH < 15 cm) to roost. Similarly, Broders and Forbes (2004) found that the
331 DBH of trees that were selected by male *Myotis* bats in conifer-dominated stands were less than
332 20 cm. Within the managed balsam fir-paper birch stands of the Montmorency Research Forest,
333 trees with DBH \geq 30 cm were rare since they represented only 2.5 % of our counts ($n = 1810$).
334 This low proportion of large trees in the forest landscape might also force male *Myotis* bats to
335 roost in trees with a small DBH. In a sugar maple (*Acer saccharum* Marshall)-yellow birch
336 (*Betula alleghaniensis* Britten) forest that was located 23 km south of our study area (Jacques-
337 Cartier National Park), male *Myotis* bats had access to bigger trees (52 % of trees with DBH \geq
338 30; $n = 227$). Male *Myotis* bats selected larger diameter roost trees ($40.3 \text{ cm} \pm 17.6 \text{ cm}$; $n = 8$)
339 compared to random ones ($27.6 \text{ cm} \pm 12.6 \text{ cm}$; $n = 8$) in this unmanaged area (Fabianek et al.
340 2011, unpublished data).

341 At the stand scale, another feature that slightly increased roost selectivity by male *Myotis* bats
342 was a high proportion of canopy gaps at 2 m around roosts. Although we predicted that trees with
343 a higher proportion of canopy gaps would lead to greater exposure to sunlight, we failed to find

344 differences between bat-selected stands and random locations with respect to mean insolation
345 levels. These results suggest that a higher proportion of canopy gap does not necessarily imply
346 greater exposure to sunlight (Canham et al. 1990) and might be linked to roost accessibility (e.g.,
347 from foraging sites) instead (Loeb and O’Keefe 2011). Solar radiation through forest canopy is a
348 highly variable and complex phenomenon, which varies with size and location of canopy gaps,
349 and according to stand species composition, slope and the angle of solar incidence, among other
350 factors (Ni et al. 1997; Hardy et al. 2004). Furthermore, male *Myotis* bats might be less limited
351 by thermoregulation costs and might thus seek for cooler roosts, since they undergo torpor more
352 frequently and for a longer duration than do reproductive females (Hamilton and Barclay 1994;
353 Grinevitch et al. 1995; Cryan and Wolf 2003; Johnson and Lacki 2014).

354 Among all of the roosting habitat features that we considered, the number of snags (≥ 10 cm
355 DBH) was the most important criterion for predicting roost selection by male *Myotis* bats. We
356 found that bats used a network of roost trees and switched roosts regularly. This tendency of bats
357 to switch roosts frequently is mentioned by several studies (Barclay and Kurta 2007; Reckardt
358 and Kerth 2007). The benefits of roosting in clumps of high density snags might be driven by
359 predator avoidance in the case of frequent roost-switching behavior or disturbance to roosts
360 (Sparks et al. 2003; Barclay and Kurta 2007), or perhaps simply due to the transient nature of the
361 roost trees that are used (Lee 1998; Angers et al. 2010). Of course, this hypothesis is plausible
362 only if snags around roost trees share features similar to those of the occupied trees. Indeed, our
363 stand sampling results showed respectively 3.1 times more class 6 snags and 3.8 times more
364 snags with DBH ≥ 20 cm within stands selected by male *Myotis* bats, compared to random
365 locations (Table 1).

366 At the landscape scale, several studies found a sexual segregation in bats with females less likely
367 to occur in stands at higher elevation (Senior et al. 2005). Cryan et al. (2000) showed an inverse

368 relationship between habitat elevation and the presence of reproductive female bats in South
369 Dakota, presumably because of lower ambient temperature and lower insect availability at higher
370 elevations (Grindal et al. 1999). Russo (2002) and Arnold (2007) obtained similar results with
371 *Myotis daubentonii* (Kuhl, 1819) and *M. septentrionalis*, respectively. Because our study area
372 was located at high elevation and because female bats are likely to have different roosting habits
373 than males (Hamilton and Barclay 1994; Broders and Forbes 2004; Perry and Thill 2007), we
374 believe that relatively cold average summer temperatures occurring at the Montmorency
375 Research Forest were unsuitable for females, which might explain why we only captured male
376 *Myotis* bats over three consecutive summers.

377 **Light detection and ranging**

378 We used LiDAR remote sensing to assess vegetation structure associated to roost selection by
379 male *Myotis* bats. LiDAR provided exhaustive continuous landscape measurements of the canopy
380 that allowed gap identification (i.e., proportion of canopy gaps), insolation estimation, and
381 canopy height measurement (i.e., mean canopy height) in specific sampled sites, replacing time-
382 consuming field measurements and revealing habitat associations that would have otherwise been
383 missed. To fully benefit from LiDAR high precision level, we took special care while positioning
384 the plots relative to the LiDAR scan by using a GPS with sub-meter accuracy and matching it to
385 the canopy height model. A complete airborne LiDAR coverage allows extending forest structure
386 measurements outside of the field-sampled areas to identify landscape-wide potential roosting
387 habitats, something inconceivable with field sampling methods of vegetation. LiDAR also offers
388 a snapshot in time that would allow monitoring vegetation structure dynamics (Meyer et al. 2013)
389 around *Myotis* roosting habitats through repeated scans.

390 **Recommendations for management**

391 We argue that snag retention is a simple and effective way to preserve roosting habitat for forest-
392 dwelling species such as *Myotis* bats. Although the implications of our results pertain only to the
393 ecology of male bats, we confirmed the use of large snags with intermediary state of decay that
394 were located in relatively open stands for *Myotis* bats. We conclude from our GLMM estimates
395 (Figure 2) that vegetation clumps of 0.1 ha containing a minimum of 10 snags with a DBH \geq 10
396 cm should be preserved or created through logging. We propose that partial logging with variable
397 retention management systems, to retain a maximum of class 6 and class 7 snags with DBH \geq 20
398 cm, should be considered by forest managers who are interested in promoting roosting habitat for
399 male *Myotis* bats in particular and for wildlife conservation in general.

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606

607 **Tables**

608 Table 1. Mean \pm standard errors (SE) for habitat features for random trees, trees selected by male
 609 little brown bat (MYLU; *Myotis lucifugus*, male northern long-eared bat (MYSE; *Myotis*
 610 *septentrionalis*), and combined species in the Montmorency Research Forest, Québec, Canada

Habitat feature	Random (<i>n</i> = 40)	MYSE (<i>n</i> = 26)	MYLU (<i>n</i> = 14)	Combined (<i>n</i> = 40)
Tree DBH (cm)	15.53 \pm 0.85	20.17 \pm 0.84	21.64 \pm 1.29	20.69 \pm 0.71
Tree height (m)	6.63 \pm 0.47	9.34 \pm 0.64	10.01 \pm 3.01	9.57 \pm 0.50
Percent of remaining bark (%)	0.55 \pm 0.06	0.74 \pm 0.05	0.74 \pm 0.08	0.74 \pm 0.04
Number of snags \geq 10 cm DBH (<i>n</i>)	1.93 \pm 0.41	6.73 \pm 0.91	5.79 \pm 1.05	6.40 \pm 0.69
Number of snags \geq 20 cm DBH (<i>n</i>)	0.45 \pm 0.15	1.81 \pm 0.31	1.57 \pm 0.44	1.73 \pm 0.25
Number of 6 class snags (<i>n</i>)	1.13 \pm 0.31	4.68 \pm 0.68	3.17 \pm 0.80	3.44 \pm 0.54
Proportion of canopy gaps at 2 m (%)	0.54 \pm 0.07	0.76 \pm 0.07	0.77 \pm 0.08	0.76 \pm 0.05
Proportion of canopy gaps at 16 m (%)	0.67 \pm 0.04	0.71 \pm 0.04	0.66 \pm 0.04	0.69 \pm 0.03
Lateral vegetation cover at 2 m (%)	0.88 \pm 0.03	0.80 \pm 0.04	0.80 \pm 0.05	0.80 \pm 0.03
Lateral vegetation cover at 16 m (%)	0.31 \pm 0.04	0.27 \pm 0.06	0.27 \pm 0.06	0.29 \pm 0.04
Mean canopy height at 2 m (m)	13.04 \pm 0.57	10.12 \pm 0.97	8.05 \pm 1.11	9.40 \pm 0.75
Mean canopy height at 16 m (m)	13.85 \pm 0.42	13.20 \pm 0.54	13.81 \pm 0.58	13.41 \pm 0.40
Insolation level at 2 m (MJ/m ² /day)*	452.78 \pm 3.15	446.00 \pm 7.62	454.21 \pm 5.78	448.88 \pm 5.34
Insolation level at 16 m (MJ/m ² /day)*	453.10 \pm 2.71	449.38 \pm 5.08	457.36 \pm 3.43	452.18 \pm 3.54
Stand Basal area (m ² /ha)	24.80 \pm 2.59	31.77 \pm 2.76	25.43 \pm 3.36	29.55 \pm 2.17

611 *Mean insolation level simulated every day of June and July 2011, from 0600 to 2000, at

612 47°17'60"N.

613

614 Table 2. Model number, number of estimated parameters (K), differences between model AICc
 615 and those of the best model (Δi) and Akaike weights (ωi) for 20 Generalized Linear Mixed
 616 Models

# Model	K	Δi	ωi
13 Bat species + snags + gap 02 + height + DBH	7	0.00	0.66
14 Bat species + snags + gap 02 + height + DBH + bark	8	2.47	0.19
10 Bat species + snags + insolation 02 + gap 02 + height + DBH + bark	9	3.80	0.10
12 Bat species + snags + cover 02 + height + DBH	7	6.84	0.02
9 Bat species + snags + cover 02 + insolation 02 + height + DBH + bark	9	8.12	0.01
11 Bat species + snags + height + DBH + insolation 02	7	9.04	0.01
16 Bat species + snags + height + DBH	6	10.50	0.00
15 Bat species + snags + height + DBH + bark	7	12.34	0.00
5 Bat species + snags + cover 02 + insolation 02 + gap 02	7	13.55	0.00
6 Bat species + snags + insolation 02 + gap 02	6	14.25	0.00
17 Bat species + snags + DBH	5	17.49	0.00
7 Bat species + snags + gap 02	5	19.01	0.00
2 Bat species + snags + cover 16 + insolation 16 + gap 16	7	24.45	0.00
4 Bat species + snags + gap 16	5	24.46	0.00
3 Bat species + snags + insolation 16 + gap 16	6	25.13	0.00
8 Bat species + snags	4	26.21	0.00
18 Bat species + Height + DBH + bark	6	27.18	0.00
19 Bat species + DBH + bark	5	34.17	0.00
20 Bat species + DBH	4	34.94	0.00

1 Null

2 50.20 0.00

617

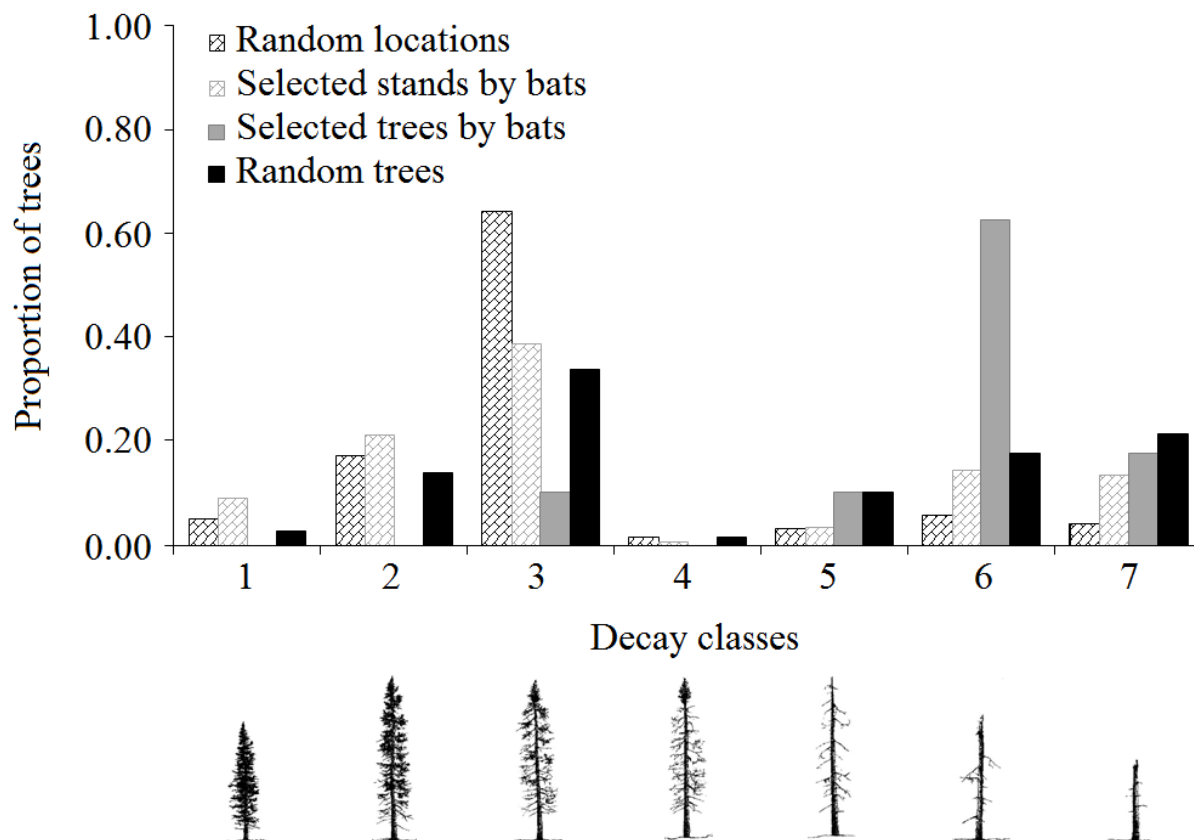
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619 Table 3. List of variables, beta coefficients (β), standard errors (SE), odd ratios and 95 %
 620 confidence intervals (CI), Z-statistics and associated P-values from the best Generalized Linear
 621 Mixed Model ($\Delta i = 0$)

Variable	β	SE	Odds	95 % CI	Z	P-value
(Intercept)	-2.41	0.87				
MYSE*	0.69	0.84	1.98	0.38 – 10.23	0.82	0.41
Number of snags ≥ 10 cm DBH (<i>n</i>)	0.41	0.11	1.51	1.21 – 1.88	3.62	<0.001
Proportion of canopy gaps at 2 m (%)	0.04	0.01	1.04	1.01 – 1.07	2.96	0.003
Tree height (m)	0.40	0.15	1.50	1.12 – 2.00	2.75	0.006
Tree DBH (cm)	0.24	0.08	1.28	1.08 – 1.50	2.90	0.004

622 *MYSE = *Myotis septentrionalis* (northern long-eared bat)

623

624 **Figure captions**

625

626 Figure 1. Proportion of trees recorded during plotless point-sampling in selected stands by male

627 *Myotis* bats (996 trees), random locations (809 trees), selected roost trees by male *Myotis* bats (n

628 = 40), and random trees ($n = 40$), distributed by decay class. Illustrations of decay classes (from 1

629 to 7) are modified from Imbeau and Desrochers (2002). In class (1) trees are alive with $\geq 95\%$ of

630 foliage, showing no sign of deterioration; (2) senescent trees where remaining foliage is between

631 $\geq 20\%$ and $< 95\%$; (3) senescent trees with $< 20\%$ foliage remaining; (4) recently dead trees

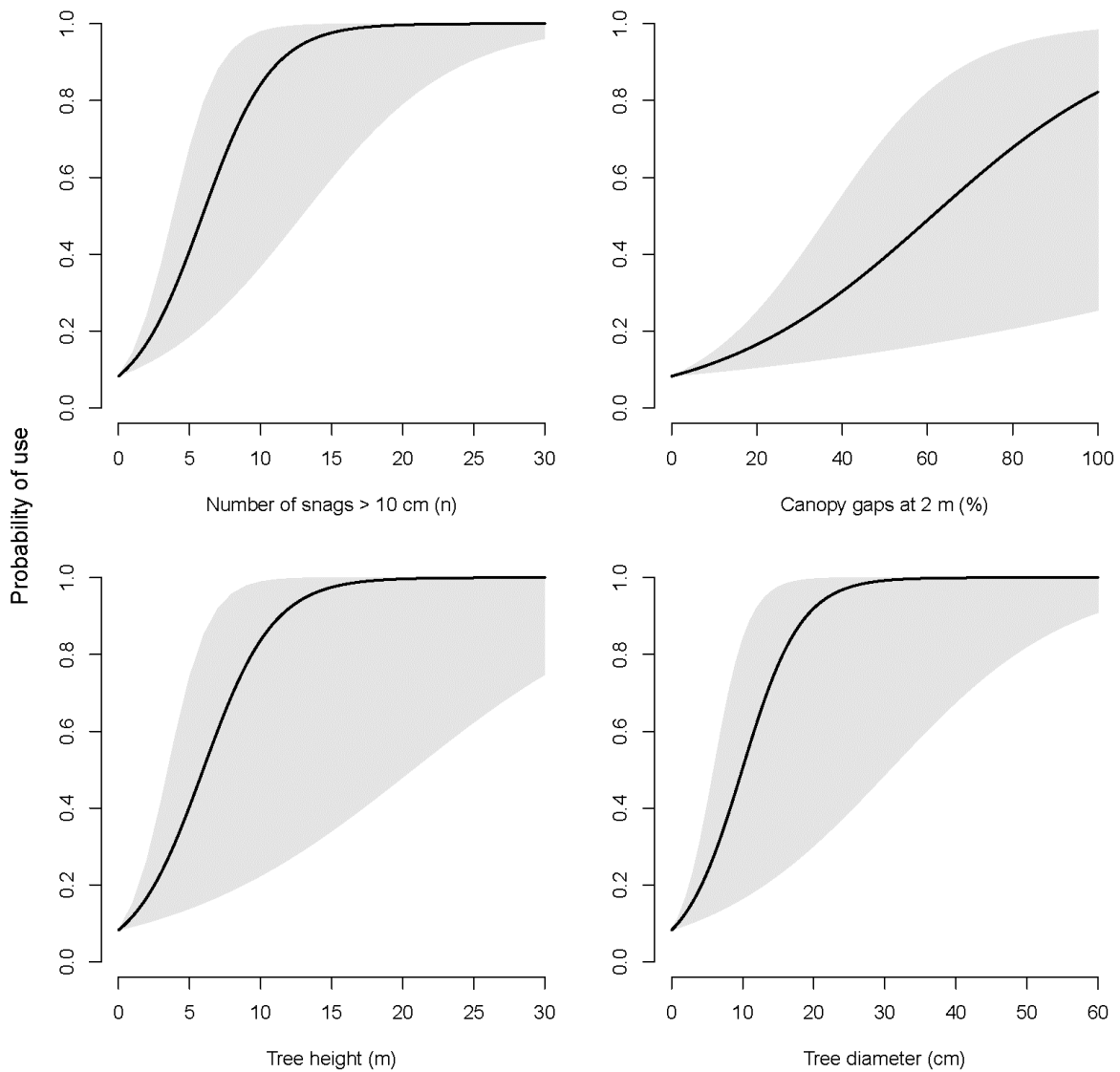
632 with firm bark cover, 0% green foliage and small twigs still remaining; (5) no dead foliage

633 present, no small twigs; (6) loose bark cover, broken top, height still more than 50% of what is

634 observed on trees with same DBH; (7) broken top with height less than 50% of what is observed

635 on trees with same DBH.

636



637

638 Figure 2. Estimated probability of use by male *Myotis* bats as a function of (A) number of snags \geq
 639 10 cm DBH (n), (B) proportion of canopy gaps (%), (C) tree height (m) and (D) tree DBH (cm).

640 Prediction curves are derived from the General Linear Mixed Model estimates with the lowest

641 AICc.