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

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Abstract

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

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


**Introduction**

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

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

The little brown bat (*Myotis lucifugus* (Le Conte, 1831)) and the northern long-eared bat (*Myotis septentrionalis* (Trouessart, 1897)) are two insectivorous cavity-roosting bats that were common
throughout the north-eastern boreal forests of Canada prior to the appearance of White Nose Syndrome (WNS; Blehert et al. 2009). Since its discovery in 2006 in New York State, WNS has caused mass mortality of hibernating bats throughout eastern North America (Dzal et al. 2010; Moosman et al. 2013) and is predicted to lead to regional extinctions of the little brown bat (Frick et al. 2010). Both *Myotis* bats are known to roost under exfoliating bark, inside crevices, or within the cavities of large trees during summer (Parsons et al. 2003; Jung et al. 2004; Garroway and Broders 2008). Roost selection by these species has been well documented for females and in temperate forests (Barclay and Kurta 2007), but few studies have investigated roost selection by males and within the Boreal Shield ecozone (Broders and Forbes 2004; Jung et al. 2004).

Moreover, no study to date has investigated the habitat requirements of cavity-roosting bats, such as *Myotis* bats, in the Province of Quebec (Canada). This lack of knowledge prevents the adaptation of forest management practices that favour habitat conservation of *Myotis* bats. Considering that direct WNS-associated mortality cannot yet be mitigated in North America, an appropriate strategy would be to reduce the influence of other anthropogenic disturbances to preserve the natural habitat of the bats. This requires greater knowledge of *Myotis* roosting habitats, particularly in the case of males, which remain largely underrepresented in habitat selection studies.

We hypothesize *a priori* the tree and forest stand features that might be selected by both *Myotis* bats, based on a review of 34 published manuscripts on roost selection by cavity-roosting bats in North America. We predict that *Myotis* bats select roosts in taller and larger trees with advanced decay stages and that these possess a higher percentage of remaining bark compared to random trees (Parsons et al. 2003; Kalcounis-Rueppell et al. 2005; Perry and Thill 2007). We also predict that roost trees that are selected by *Myotis* bats are surrounded by lower vegetation cover, a higher proportion of canopy gaps, and a larger number of snags compared to random trees.
As suggested by Brigham et al. (1997), a higher proportion of canopy gaps should also provide greater exposure to sunlight and limit daily thermoregulation costs (Lacki et al. 2013; Johnson and Lacki 2014).

**Materials and methods**

**Study area**

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

**Capture and tracking**

We captured bats from mid-June to mid-August 2011, 2012 and 2013, using 10 mist nets (Avinet Inc., Dryden, NY, USA). We placed mist nets from 2100 to 0100 along trails, close to ponds and forest stands, and changed their locations after two consecutive nights to increase capture success. We weighed each captured individual and identified it to species. We visually determined reproductive status (reproductive or not reproductive) and age classes (adult or juvenile), following the methodology described in Kunz and Parsons (2009). We glued radio transmitters (Model LB-2X, Holohil Systems Limited, Carp, ON, Canada) onto the trimmed
interscapular fur of adult bats that weighed more than 6 g, using non-toxic surgical adhesive (Skin-Bond, Smith and Nephew United, Memphis, TN, USA). We tracked released individuals on a daily basis, using a three-element Yagi antenna and receiver system (ATSR4500S model, Advanced Telemetry Systems, Isanti, MN, USA). We located their roost trees by homing in until the transmitter fell off. Because of the risk of WNS transmission, we decontaminated every item that was used during manipulations with a fungicide (Clinicide®, Bimeda-MTC Animal Health Inc., Cambridge, ON), following the National White-Nose Syndrome Decontamination Protocol that was provided by the United States Fish and Wildlife Service (USFWS). We followed ASM guidelines for research on live mammals and the Animal Committee Care of Laval University approved all of the above described procedures and manipulations (License number # 2011064).

**Habitat variables**

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

We determined tree species, percent of remaining bark on trunks, and tree decay classes (Imbeau and Desrochers 2002). In class (1) trees are alive with ≥ 95 % of foliage, showing no sign of deterioration; (2) senescent trees where remaining foliage is between ≥ 20 % and < 95 %; (3) senescent trees with < 20 % foliage remaining; (4) recently dead trees with firm bark cover, 0 % green foliage and small twigs still remaining; (5) no dead foliage present, no small twigs; (6) loose bark cover, broken top, height still more than 50 % of what is observed on trees with same
DBH (Diameter at Breast Height, 1.3 m); (7) broken top with height less than 50 % of what is observed on trees with same DBH. Illustrations of decay classes (from 1 to 7) from Imbeau and Desrochers (2002) are provided in Figure 1. We measured tree height using a clinometer and tree DBH using a DBH tape.

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

**Light detection and ranging imagery**

We have used airborne LiDAR (Light Detection and Ranging) to improve estimates of stand scale variables such as mean canopy height, proportion of canopy gaps, and insolation levels. Airborne LiDAR uses a laser beam to scan a complete scene from a fixed-wing aircraft (Suárez et al. 2005). It provides a three-dimensional point cloud that can be processed to extract landscape features such as elevation, slope, canopy height, tree density or light penetration. LiDAR has
many applications in forestry (Dubayah and Drake 2000; Suárez et al. 2005) and has recently been used for detailed characterization of bat habitats (Jung et al. 2012; Yang et al. 2013).

Airborne LiDAR survey was performed in August 2011 using an Optech ALTM 3100 sensor that was flown at 1000 m above the terrain with a 100 kHz pulse rate, wavelength of 1046 nm, a divergence of 0.25 mrad, and with a maximal scan angle of 17° from the Nadir. Flight line overlap was 50%, and final median density was about five points per square meter. The point cloud that we obtained was then converted to a surface model representing ground and vegetation, which we refer to as the Digital Surface Model (DSM). Identification of ground returns was carried out by the provider and triangulated to create a Digital Terrain Model (DTM). Subtraction of DTM from DSM yielded a Canopy Height Model (CHM), which we used as a representation of the canopy (Vazirabad and Karslioglu 2010). We derived mean stand height, proportion of canopy gaps, and mean insolation levels within 2 m and 16 m radius buffers around each tree from the LiDAR (Table 1). We defined canopy gaps as being greater than 2 m², with a tree height that was two-thirds lower than the surrounding mean canopy height. Insolation level refers here to the theoretical amount of solar radiation energy (expressed in megajoule) received by each roost tree or random location during a day (MJ/m²/day). We simulated DSM mean insolation for June and July 2011, from 0600 to 2000, at 47°17′60″N, using SAGA (System for Automated Geoscientific Analyses) GIS (Kumar et al. 1997).

Statistical analyses

We considered trees rather than individual bats as our sampling units and pooled the data from both species of bats to examine roost selection at the genus level, to overcome issues of limited sample sizes (n = 14 roosts for the little brown bat, n = 26 roosts for the northern long-eared bat; Table 1). We examined differences between selected roost trees and random trees using Generalized Linear Mixed Models (GLMM, lme4 package, R Development Core Team 2013).
with a binomial distribution and a logit link function. We based maximum likelihood estimation of our parameters on an Adaptive Gaussian Quadrature approximation. We assumed that a potential source of variation in roost selection could be attributed to individual bats. We therefore included individual bat IDs as a random effect in our GLMMs (Bolker et al. 2009). The “random effect” term here refers to a latent variable from which we wanted to estimate the potential variance component. If the variance that was associated with individuals does not vary consistently across treatments, (i) the random effect term should approach 0, (ii) its inclusion should not improve the model fit (and subsequently lower the AICc), and (iii) the model residual variance should stay unchanged, compared to a GLM including only fixed effects. To overcome the problem of combining two bat species with potential differences in roost selection into the same model, we included species codes (“MYLU” for little brown bat, “MYSE” for northern long-eared bat) as a fixed factor in our GLMMs. This categorical variable allows model building with an intercept for each species and a common slope for our variables of interest, which we believe, would be the best compromise between a model by species with a limited number of samples and a model that pools both species of bats.

We verified the presence of outliers and potential leverage effects, over-dispersion (coeff. > 1), and multicollinearity before interpreting our GLMM results. We decided to exclude from our analyses the number of snags that had DBH ≥ 20 cm, together with stand basal area and mean stand canopy height variables, to avoid strong correlations (r ≥ 0.7; Dormann et al. 2013) between variables (i.e., stand basal area vs tree DBH; proportion of canopy gaps vs mean canopy height; snags with DBH ≥ 10 cm vs snags with DBH ≥ 20 cm). We also decided not to include decay classes (1 to 7) in our statistical analyses to avoid model over fitting, given the limited number of samples (n roost trees = 40; n random trees = 40).
We used the second-order Akaike’s information criterion for small samples (AICc) to rank the candidate set of models according to our predictions (AICcmodavg package, R Development Core Team 2013). All of the variables that were included in the candidate set of models had been selected *a priori* (Burnham and Anderson 2002). To represent roosting habitat selection by bats at various spatial scales, we constructed three subsets of candidate models for a total of 20 alternative models (Table 2). The first set combined only stand feature variables. The second set combined both stand and tree feature variables, while the third set combined only tree feature variables (Table 2). We calculated Δ AICc values (Δi) and Akaike weights (ωi) to determine the relative importance of the candidate set of models from the best explanatory model (Δi = 0). Models were considered equivalent when they had a Δi ≤ 2 (Burnham and Anderson 2002). For each variable that was included in the best models, we calculated the odds ratio (and 95 % CI) by applying an inverse logarithm transformation to the model estimates (β). We calculated the relative-importance weights of each variable appearing in the 95 % confidence set of models (Burnham and Anderson 2002). We calculated a prediction curve for each estimate from the GLMM with the lowest AICc (Figure 2) and used these predictions to make recommendations for forest management.

**Results**

**Captures and telemetry**

Because of extreme sex ratio or capture bias, we only captured male *Myotis* bats at a mean mist net height of 2.5 m ± 1.3 m (mean ± SD; range: 0.5 to 5.5 m) from the ground. From a total of 22 captured males, we found five individuals roosting alone or in small groups in human habitations and six individuals were not recovered. Of the 11 successfully tracked individuals, we had six little brown bats (8.0 g ± 1.1 g; range: 6.8 to 9.4 g) and five northern long-eared bats (7.0 g ± 0.5
g; range: 6.1 to 7.3 g) in 2011. For both species, we found 5 ± 2 roost trees (range: 3 to 7) per individual bat, during a mean tracking period of 9 days ± 2 days (range: 7 to 14 days). Bats switched roost trees about every 2 days ± 1 day (range: 1 to 6 days). We found 40 roost trees and identified the exact position of the roost sites within trees for 18 cases. *Myotis* bats selected roosts at a mean height of 4.9 m ± 2 m (range: 1.5 to 8 m) and with a mean direction of 226° ± 50° (range: 110 to 292°), indicating a preference for southwestern exposures (n = 18 roost trees).

**Tree characteristics and stand composition**

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

At the stand scale, roost trees were primarily located in mixed stands that were dominated by conifers (57.5 %, n = 23) or in conifer stands (40 %, n = 16), but rarely in deciduous stands (2.5 %, n = 1). Random locations were also located in mixed stands that were dominated by conifers (50 %, n = 20), in conifer stands (42.5 %, n = 17), and in deciduous stands (7.5 %, n = 3). The main source of disturbance was clear-cutting in bat-selected stands (78 %, n = 21) and random locations (68 %, n = 21). With respect to stand composition, we found that balsam fir dominated bat-selected stands (76.8 %, n = 456) and random locations (76 %, n = 377), followed by black and white spruce (bat-selected: 13.1 %, n = 78; random: 13.1 %, n = 65), paper birch (bat-selected: 9.8 %, n = 58; random: 9.1 %, n = 45), and trembling aspen (*Populus tremuloides* Michaux; bat-selected: 0.3 %, n = 2; random: 1.8 %, n = 9). When we considered tree decay
classes (Figure 1), male *Myotis* bats selected roost trees in stands that contained a high proportion of snags in classes 6 (bat-selected: 14.2 %, \( n = 14 \); random: 5.6 %, \( n = 45 \)) and 7 (bat-selected: 13.4 %, \( n = 133 \); random: 4 %, \( n = 32 \)), together with a few living trees of class 3 (bat-selected: 38.8 %, \( n = 386 \); random: 64.2 %, \( n = 519 \)).

**Generalized linear mixed model ranking**

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

**Discussion**

Since bat species was of low relative importance weight in the 95 % confidence set of models, we suggest that males of both species showed overlap in roosting habitat requirements, at least for the variables that we tested. Similar results including *Myotis* bats were reported by Cryan et al. (2001), and Jung et al. (2004), but contradict those found by Broders and Forbes (2004) in temperate Nordic forest. In light of these results, we are confident that the benefits of pooling the two species to increase our sample size outweighed the subsequent loss of information. The
variance explained by the random effect was close to 0 (with a standard deviation of $1.02 \times 10^{-08}$), indicating that variation among individuals was not greater than would be expected according to random variation. Including this random effect only penalized our best model AICc, suggesting that this parameter was not ecologically meaningful (Arnold 2010).

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

In conifer-dominated stands of the balsam fir-paper birch forest, solitary males of both bat species roosted under loose bark of balsam fir (i.e., the dominant tree species) and in white spruce snags. This behavior was also observed by Broders and Forbes (2004) and Jung et al. (2004). The only living trees that were used by male *Myotis* bats were senescent paper birches with less than 20% remaining foliage (decay class 3; Figure 1) in which individuals found roosts under the exfoliating bark. Dead trees with broken tops, loose bark cover, and height less than 50% of what is observed for adjacent trees with the same DBH (decay class 6; Figure 1) were mostly used by male *Myotis* bats. More advanced decay stages lead to smaller trees with less remaining bark (Imbeau and Desrochers 2002), which makes them less suitable for cavity-roosting bats such as *Myotis* species (Barclay and Mark Brigham 2001; Vonhof and Gwilliam 2007). At decay class 6, trees were probably tall enough to be both visible and accessible for bats (Kalcounis-Rueppell et al. 2005; Barclay and Kurta 2007; Garroway and Broders 2008) and possessed sufficient remaining bark to provide available shelter (Parsons et al. 2003; Perry and Thill 2007).
Although the percentage of remaining bark was included in the second best model, it was of low relative importance. We believe that measuring the percentage of exfoliating bark rather than the percentage of remaining bark would lead to better results. Living paper birches provide a good example of this assertion: although 100% of the bark remained on the trunks, this species differed from other living tree species (such as balsam fir and spruces) by the presence of exfoliating bark, which made them suitable for male *Myotis* bats.

Male *Myotis* bats selected slightly larger trees compared to random trees. Male bats are usually solitary roosters, so that they do not necessarily require large cavities in which to rest compared to lactating females (Psyllakis and Brigham 2006; Willis et al. 2006; Park and Broders 2012).

Lacki and Schwierjohann (2001), and Perry and Thill (2007) found that male bats used small diameter trees (mean DBH < 15 cm) to roost. Similarly, Broders and Forbes (2004) found that the DBH of trees that were selected by male *Myotis* bats in conifer-dominated stands were less than 20 cm. Within the managed balsam fir-paper birch stands of the Montmorency Research Forest, trees with DBH ≥ 30 cm were rare since they represented only 2.5% of our counts (n = 1810). This low proportion of large trees in the forest landscape might also force male *Myotis* bats to roost in trees with a small DBH. In a sugar maple (*Acer saccharum* Marshall)-yellow birch (*Betula alleghaniensis* Britten) forest that was located 23 km south of our study area (Jacques-Cartier National Park), male *Myotis* bats had access to bigger trees (52% of trees with DBH ≥ 30; n = 227). Male *Myotis* bats selected larger diameter roost trees (40.3 cm ± 17.6 cm; n = 8) compared to random ones (27.6 cm ± 12.6 cm; n = 8) in this unmanaged area (Fabianek et al. 2011, unpublished data).

At the stand scale, another feature that slightly increased roost selectivity by male *Myotis* bats was a high proportion of canopy gaps at 2 m around roosts. Although we predicted that trees with a higher proportion of canopy gaps would lead to greater exposure to sunlight, we failed to find
differences between bat-selected stands and random locations with respect to mean insolation levels. These results suggest that a higher proportion of canopy gap does not necessarily imply greater exposure to sunlight (Canham et al. 1990) and might be linked to roost accessibility (e.g., from foraging sites) instead (Loeb and O’Keefe 2011). Solar radiation through forest canopy is a highly variable and complex phenomenon, which varies with size and location of canopy gaps, and according to stand species composition, slope and the angle of solar incidence, among other factors (Ni et al. 1997; Hardy et al. 2004). Furthermore, male *Myotis* bats might be less limited by thermoregulation costs and might thus seek for cooler roosts, since they undergo torpor more frequently and for a longer duration than do reproductive females (Hamilton and Barclay 1994; Grinevitch et al. 1995; Cryan and Wolf 2003; Johnson and Lacki 2014).

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

At the landscape scale, several studies found a sexual segregation in bats with females less likely to occur in stands at higher elevation (Senior et al. 2005). Cryan et al. (2000) showed an inverse
relationship between habitat elevation and the presence of reproductive female bats in South Dakota, presumably because of lower ambient temperature and lower insect availability at higher elevations (Grindal et al. 1999). Russo (2002) and Arnold (2007) obtained similar results with *Myotis daubentonii* (Kuhl, 1819) and *M. septentrionalis*, respectively. Because our study area was located at high elevation and because female bats are likely to have different roosting habits than males (Hamilton and Barclay 1994; Broders and Forbes 2004; Perry and Thill 2007), we believe that relatively cold average summer temperatures occurring at the Montmorency Research Forest were unsuitable for females, which might explain why we only captured male *Myotis* bats over three consecutive summers.

**Light detection and ranging**

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

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

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**References**


### Tables

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

<table>
<thead>
<tr>
<th>Habitat feature</th>
<th>Random ($n = 40$)</th>
<th>MYSE ($n = 26$)</th>
<th>MYLU ($n = 14$)</th>
<th>Combined ($n = 40$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree DBH (cm)</td>
<td>15.53 ± 0.85</td>
<td>20.17 ± 0.84</td>
<td>21.64 ± 1.29</td>
<td>20.69 ± 0.71</td>
</tr>
<tr>
<td>Tree height (m)</td>
<td>6.63 ± 0.47</td>
<td>9.34 ± 0.64</td>
<td>10.01 ± 3.01</td>
<td>9.57 ± 0.50</td>
</tr>
<tr>
<td>Percent of remaining bark (%)</td>
<td>0.55 ± 0.06</td>
<td>0.74 ± 0.05</td>
<td>0.74 ± 0.08</td>
<td>0.74 ± 0.04</td>
</tr>
<tr>
<td>Number of snags ≥ 10 cm DBH ($n$)</td>
<td>1.93 ± 0.41</td>
<td>6.73 ± 0.91</td>
<td>5.79 ± 1.05</td>
<td>6.40 ± 0.69</td>
</tr>
<tr>
<td>Number of snags ≥ 20 cm DBH ($n$)</td>
<td>0.45 ± 0.15</td>
<td>1.81 ± 0.31</td>
<td>1.57 ± 0.44</td>
<td>1.73 ± 0.25</td>
</tr>
<tr>
<td>Number of 6 class snags ($n$)</td>
<td>1.13 ± 0.31</td>
<td>4.68 ± 0.68</td>
<td>3.17 ± 0.80</td>
<td>3.44 ± 0.54</td>
</tr>
<tr>
<td>Proportion of canopy gaps at 2 m (%)</td>
<td>0.54 ± 0.07</td>
<td>0.76 ± 0.07</td>
<td>0.77 ± 0.08</td>
<td>0.76 ± 0.05</td>
</tr>
<tr>
<td>Proportion of canopy gaps at 16 m (%)</td>
<td>0.67 ± 0.04</td>
<td>0.71 ± 0.04</td>
<td>0.66 ± 0.04</td>
<td>0.69 ± 0.03</td>
</tr>
<tr>
<td>Lateral vegetation cover at 2 m (%)</td>
<td>0.88 ± 0.03</td>
<td>0.80 ± 0.04</td>
<td>0.80 ± 0.05</td>
<td>0.80 ± 0.03</td>
</tr>
<tr>
<td>Lateral vegetation cover at 16 m (%)</td>
<td>0.31 ± 0.04</td>
<td>0.27 ± 0.06</td>
<td>0.27 ± 0.06</td>
<td>0.29 ± 0.04</td>
</tr>
<tr>
<td>Mean canopy height at 2 m (m)</td>
<td>13.04 ± 0.57</td>
<td>10.12 ± 0.97</td>
<td>8.05 ± 1.11</td>
<td>9.40 ± 0.75</td>
</tr>
<tr>
<td>Mean canopy height at 16 m (m)</td>
<td>13.85 ± 0.42</td>
<td>13.20 ± 0.54</td>
<td>13.81 ± 0.58</td>
<td>13.41 ± 0.40</td>
</tr>
<tr>
<td>Insolation level at 2 m (MJ/m²/day)*</td>
<td>452.78 ± 3.15</td>
<td>446.00 ± 7.62</td>
<td>454.21 ± 5.78</td>
<td>448.88 ± 5.34</td>
</tr>
<tr>
<td>Insolation level at 16 m (MJ/m²/day)*</td>
<td>453.10 ± 2.71</td>
<td>449.38 ± 5.08</td>
<td>457.36 ± 3.43</td>
<td>452.18 ± 3.54</td>
</tr>
<tr>
<td>Stand Basal area (m²/ha)</td>
<td>24.80 ± 2.59</td>
<td>31.77 ± 2.76</td>
<td>25.43 ± 3.36</td>
<td>29.55 ± 2.17</td>
</tr>
</tbody>
</table>

*Mean insolation level simulated every day of June and July 2011, from 0600 to 2000, at 47°17'60"N.
Table 2. Model number, number of estimated parameters ($K$), differences between model AICc and those of the best model ($\Delta i$) and Akaike weights ($\omega_i$) for 20 Generalized Linear Mixed Models

<table>
<thead>
<tr>
<th>#</th>
<th>Model</th>
<th>$K$</th>
<th>$\Delta i$</th>
<th>$\omega_i$</th>
</tr>
</thead>
<tbody>
<tr>
<td>13</td>
<td>Bat species + snags + gap 02 + height + DBH</td>
<td>7</td>
<td>0.00</td>
<td>0.66</td>
</tr>
<tr>
<td>14</td>
<td>Bat species + snags + gap 02 + height + DBH + bark</td>
<td>8</td>
<td>2.47</td>
<td>0.19</td>
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<tr>
<td>10</td>
<td>Bat species + snags + insolation 02 + gap 02 + height + DBH + bark</td>
<td>9</td>
<td>3.80</td>
<td>0.10</td>
</tr>
<tr>
<td>12</td>
<td>Bat species + snags + cover 02 + height + DBH</td>
<td>7</td>
<td>6.84</td>
<td>0.02</td>
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<tr>
<td>9</td>
<td>Bat species + snags + cover 02 + insolation 02 + height + DBH + bark</td>
<td>9</td>
<td>8.12</td>
<td>0.01</td>
</tr>
<tr>
<td>11</td>
<td>Bat species + snags + height + DBH + insolation 02</td>
<td>7</td>
<td>9.04</td>
<td>0.01</td>
</tr>
<tr>
<td>16</td>
<td>Bat species + snags + height + DBH</td>
<td>6</td>
<td>10.50</td>
<td>0.00</td>
</tr>
<tr>
<td>15</td>
<td>Bat species + snags + height + DBH + bark</td>
<td>7</td>
<td>12.34</td>
<td>0.00</td>
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<tr>
<td>5</td>
<td>Bat species + snags + cover 02 + insolation 02 + gap 02</td>
<td>7</td>
<td>13.55</td>
<td>0.00</td>
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<tr>
<td>6</td>
<td>Bat species + snags + insolation 02 + gap 02</td>
<td>6</td>
<td>14.25</td>
<td>0.00</td>
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<tr>
<td>17</td>
<td>Bat species + snags + DBH</td>
<td>5</td>
<td>17.49</td>
<td>0.00</td>
</tr>
<tr>
<td>7</td>
<td>Bat species + snags + gap 02</td>
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<td>19.01</td>
<td>0.00</td>
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<tr>
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<td>Bat species + snags + cover 16 + insolation 16 + gap 16</td>
<td>7</td>
<td>24.45</td>
<td>0.00</td>
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<tr>
<td>4</td>
<td>Bat species + snags + gap 16</td>
<td>5</td>
<td>24.46</td>
<td>0.00</td>
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<tr>
<td>3</td>
<td>Bat species + snags + insolation 16 + gap 16</td>
<td>6</td>
<td>25.13</td>
<td>0.00</td>
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<tr>
<td>8</td>
<td>Bat species + snags</td>
<td>4</td>
<td>26.21</td>
<td>0.00</td>
</tr>
<tr>
<td>18</td>
<td>Bat species + Height + DBH + bark</td>
<td>6</td>
<td>27.18</td>
<td>0.00</td>
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<tr>
<td>19</td>
<td>Bat species + DBH + bark</td>
<td>5</td>
<td>34.17</td>
<td>0.00</td>
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<tr>
<td>20</td>
<td>Bat species + DBH</td>
<td>4</td>
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<td>0.00</td>
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<td>618</td>
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</tbody>
</table>
Table 3. List of variables, beta coefficients (β), standard errors (SE), odd ratios and 95% confidence intervals (CI), Z-statistics and associated P-values from the best Generalized Linear Mixed Model (∆i = 0)

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

*MYSE = Myotis septentrionalis (northern long-eared bat)
Figure 1. Proportion of trees recorded during plotless point-sampling in selected stands by male *Myotis* bats (996 trees), random locations (809 trees), selected roost trees by male *Myotis* bats (*n* = 40), and random trees (*n* = 40), distributed by decay class. Illustrations of decay classes (from 1 to 7) are modified from Imbeau and Desrochers (2002). In class (1) trees are alive with ≥ 95 % of foliage, showing no sign of deterioration; (2) senescent trees where remaining foliage is between ≥ 20 % and < 95 %; (3) senescent trees with < 20 % foliage remaining; (4) recently dead trees with firm bark cover, 0 % green foliage and small twigs still remaining; (5) no dead foliage present, no small twigs; (6) loose bark cover, broken top, height still more than 50 % of what is observed on trees with same DBH; (7) broken top with height less than 50 % of what is observed on trees with same DBH.
Figure 2. Estimated probability of use by male *Myotis* bats as a function of (A) number of snags \( \geq 10 \) cm DBH \((n)\), (B) proportion of canopy gaps (%), (C) tree height (m) and (D) tree DBH (cm).

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