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Day roost characteristics of northern long-eared bats (*Myotis septentrionalis*) in relation to female reproductive status[1]

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Abstract: In summer, females of most temperate bat species aggregate at maternity roosts, during which time females gestate, give birth, and wean offspring. These activities make the presence of suitable roosts critical for population persistence. Many studies have identified important roost tree characteristics by comparing roost trees to random trees. However, if bats select trees that facilitate either torpor use or maintenance of normothermic body temperatures relative to the energetic demands of reproduction, then it follows that roost tree characteristics may vary similarly. We compared variation in roost tree and site selection by lactating northern long-eared bats to the pre- and post-lactation periods. Scores from 2 principal components were the best predictors of the variation in roost selection. Relative to pre- and post-lactation periods lactating bat roost sites had a high and relatively open dominant canopy with low tree density (both coniferous and deciduous) and roost sites were situated high in tall trees. Our result demonstrates that when managing for bat roost trees, within-season variation in roost tree use should be considered.
Keywords: *Chiroptera*, day roost, Nova Scotia, roost selection, roost tree, tree cavity.

Résumé : Durant l'été, les femelles de la plupart des espèces tempérées de chauve-souris se regroupent dans des colonies de maternité pour la gestation, la mise bas et le sevrage des jeunes. Ces activités rendent essentielle la présence de dortoirs adéquats pour la persistance des populations. Plusieurs études ont identifié des caractéristiques importantes des arbres dortoirs en les comparant avec des arbres choisis au hasard. Cependant, si les chauves-souris sélectionnent les arbres qui facilitent soit l'utilisation de la torpeur ou le maintien de températures corporelles normothermiques en fonction des demandes énergétiques de la reproduction, les caractéristiques des arbres choisis peuvent varier en conséquence. Nous avons comparé les variations dans la sélection des arbres et des sites de repos chez les femelles du vespertilion nordique entre les périodes avant, pendant et après, la lactation. Deux composantes principales offraient les meilleures prédictions de la variation dans la sélection des dortoirs. En comparaison avec les périodes d'avant et d'après la lactation, les sites de repos des chauve-souris en lactation présentaient des canopées dominantes hautes et relativement ouvertes avec une faible densité d'arbres (conifères et feuillus) et les dortoirs étaient situés en hauteur dans les grands arbres. Nos résultats démontrent qu'il faut tenir compte de la variation saisonnière du choix des sites de repos dans la gestion des arbres dortoirs chez les chauves-souris.
Mots-clés : arbre dortoir, cavité arboricole, *Chiroptera*, Nouvelle-Écosse, perchoir de jour, sélection du site de repos.

Nomenclature: Farrer, 1995; Wilson & Reeder, 2005.

Introduction

Beginning in late spring and continuing through early autumn, females of most temperate bat species aggregate in roosting groups ranging from a few to several hundred individuals. Within these groups offspring are gestated and nursed until weaned (Kunz & Lumsden, 2003). These roost sites are presumably critical for population persistence as they provide a microclimate suitable for offspring development and act as a centre for social interactions (Wilde, Knight & Racey, 1999; Kerth *et al.*, 2003). Accordingly, it is important to understand how bats use roosts if these features are to be maintained in a landscape.

Roost-tree and site-level characteristics that either facilitate the use of torpor or reduce the costs of maintaining normothermic body temperature may be selected depending upon the energetic demands of reproduction. For example, reproductive individuals may select warm roosts because low temperatures may delay gestation (Racey & Swift, 1981) and decrease milk production (Wilde *et al.*, 1995; Wilde, Knight & Racey, 1999). Alternatively, pregnant individuals may sometimes select cooler roosts to facilitate entering torpor and reduce the added energetic costs of flight associated with carrying and nourishing a foetus (Kerth, Weissmann & Konig, 2001) or possibly to delay parturition until environmental conditions and resources are favourable for meeting the added energetic demands associated with lactation (Willis, Brigham & Geiser, 2006).

There is accumulating evidence that the social interactions between individuals at maternity roosts conform to the fission–fusion social model and may provide important fitness benefits (Kerth & Konig, 1999; O'Donnell, 2000; Vonhof, Whitehead & Fenton, 2004; Willis &

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Brigham, 2004; Garroway & Broders, 2007). Within the fission–fusion social setting, colony members roost in multiple roost trees on a given day and switch roost trees often (Kerth & Konig, 1999; O'Donnell, 2000; Vonhof, Whitehead & Fenton, 2004; Willis & Brigham, 2004). Therefore, it may also be important to manage for a large network of suitable roosts for the maintenance of a colony.

To examine trends in roost selection by forest-dwelling bats Kalcounis-Rüppell, Pysllakis, and Brigham (2005) performed a meta-analysis of literature examining bat roost selection. They found that in general both foliage- and cavity-roosting species roosted in tall trees with a large diameter at breast height that were located in stands with a high density of snags. Cavity-roosting bats selected trees in open canopy stands that were closer to water relative to those selected by foliage-roosting species. Significantly less well understood is whether, given that forest bats tend to select these features, there are any preferences that are manifested based upon reproductive status. Energetic constraints (Gittleman & Thompson, 1988) and social group cohesion (Garroway & Broders, 2007) vary with reproductive stage, and so it seems likely that roost characteristics could co-vary during the reproductive season reflecting these constraints.

Despite the potential for variation in roost-tree selection by temperate bats, few studies have examined intra-annual variation in roost-tree and site-level characteristics. To our knowledge, only Veilleux, Whitaker, and Veilleux (2004) have investigated intra-annual variation in roost tree and site characteristics. They showed that the characteristics of day roosts selected by foliage-roosting female eastern pipistrelles (*Perimyotis subflavus*) vary with "reproductive season" and the putative energetic constraints associated with reproductive periods. Other studies have looked at roost microclimate variation in relation to reproductive period (rock-crevice roosting *Eptesicus fuscus* and *Myotis evotis*; Chrusczc & Barclay, 2002; Lausen & Barclay, 2002; cavity roosting *M. bechsteinii* and *E. fuscus*; Kerth, Weissmann & Konig, 2001; Willis, Voss & Brigham, 2006), and those too have shown that reproductive bats (at varying stages) select different roost microclimates than bats during non-reproductive periods. However, it is often difficult to measure the microclimatic characteristics of cavities used by forest-roosting bats, so it is important to have easily measured external characteristics from which to judge the suitability of a tree and site as a bat roost.

We hypothesized that for female temperate bats to maximize energy efficiency during the different stages of reproduction, roost-tree and site-level characteristics they select should vary similarly among the different stages. This is because of the variation in 1) energetic constraints associated with the various stages of reproduction and 2) the fitness benefits of torpor during these stages. To assess our hypothesis we tested the prediction that externally measurable roost characteristics associated with the lactation period would be distinguishable from those used both before and after the lactation period. To do this we assessed variation in roost-tree selection by female northern long-eared bats (*M. septentrionalis*) in relation to reproductive season in Nova Scotia, Canada. Northern long-eared bats are forest dependent for roosting and foraging and typically roost in cavities or under loose bark (Broders & Forbes, 2004; Broders *et al*., 2006). In Nova Scotia, maternity roosts are composed of members from multiple non-randomly assorting fission–fusion social groups (Garroway & Broders, 2007).

Methods

We conducted field work at Dollar Lake Provincial Park (44° 55' N, 63° 19' W) in Nova Scotia, Canada from 1 June to 31 August 2005. Bats were trapped along forested trails using harp traps (Austbat Research Equipment, Lower Plenty, Victoria, Australia) and at roost trees using modified harp traps placed over cavity exits (Kunz & Kurta, 1988). Reproductive status of females was classified as pregnant (based upon gentle stomach palpation), lactating (bare patches around nipples or presence of milk), or no evidence of reproduction. Radio-transmitters (0.39 g, Model LB-2NT, Holohil Systems Limited, Carp, Ontario, Canada) were glued (Skinbond, Smith and Nephew United Inc., Largo, Florida, USA) to a subset of captured females to locate roost trees. Tagged bats were tracked to roost trees with a radio receiver (HR 2000 Osprey VHF Receiver, H.A.B.I.T. Research Limited, Victoria, British Columbia, Canada) and a 3-element Yagi antenna (AF Antronics, Urbana, Illinois, USA) on a daily basis until the transmitters fell off.

When no bats were known to be roosting within roost trees we measured roost tree and site characteristics for a 0.1-ha plot (17.8 m radius) centred on roost trees. The variables measured were chosen for their potential influence on roost microclimate and structural characteristics of the surrounding forest (*e.g.*, clutter) that may influence roost selection. We measured tree height with a clinometer (model PM-5/1520, Suunto, Finland) and canopy closure (average of 4 cardinal directions measured from the base of the roost tree) using a spherical densiometer (model-A, Forest Densiometers, Bartlesville, Oklahoma, USA). Dominant canopy height was calculated from the average of 5 trees judged to be representative of the dominant canopy within the plot. Canopy height relative to roost height was calculated as the distance between the dominant canopy height and the roost entrance. We also measured roost-tree diameter at breast height (dbh) and the distance to the nearest tree as tall as the roost within a 180° arc centred on the roost entrance and counted the number of deciduous trees, coniferous trees (stems higher than 2 m), and potential roost (defined as trees decay class ≥ 2 with evidence of defects; *sensu* Broders & Forbes, 2004) trees within the plot. Finally, we included a variable for the total number of trees within the plot.

We used a logistic regression analysis and coded trees used during the lactation period (from first evidence of lactation to capture of the first volant juvenile) as 1 and trees used during the non-lactation period (pre- and post-lactation) as 0. To test whether bat roosts are associated with multiple tree and site-level characteristics, principal components were constructed using a correlation-matrix-based principal components analysis. Principal component scores were used as independent variables within the logistic regression analysis (Aguilera, Escabias & Valderrama, 2006). We included components with eigenvalues > 1 as variables within the logistic regression model because components with values below 1 explain less variation than single variables (Kaiser, 1960). The dependent variable was permuted (keeping the number of trees in each category constant), and parameter estimates were calculated 999 times. Components were considered to have a significant effect if the parameter estimate was greater than 97.5% or less than 2.5% (2-tailed test) of permuted values and the 95% confidence interval of the parameter estimate did not overlap zero. Goodness of fit was assessed using Hosmer and Lemeshow's goodness of fit test and McFadden's rho^2 (Hosmer & Lemeshow, 2000). McFadden's rho^2 values are interpreted similarly to the linear regression R^2; however, values tend to be lower (Hosmer & Lemeshow, 2000), with values between 0.20 and 0.40 indicating that a high proportion of variation in the data is explained by the model (Hensher & Johnson, 1981). Variables highly correlated (loadings < –0.5 and > 0.5; arbitrarily chosen) on important components were considered to have important effects. Because this research was based on 1 y of data we consider it somewhat preliminary and exploratory. All analyses were conducted with S-PLUS software (Insightful, Seattle, Washington, USA.).

Results

We recorded tree and site measurements for 44 day-roost trees (pre- and post lactation $n = 22$, lactation $n = 22$; Table I). Tree species used included red maple (*Acer rubrum*; $n = 20$), eastern hemlock (*Tsuga canadensis*; n=15), yellow birch (*Betula alleghaniensis*; $n = 4$), red spruce (*Picea rubens*; $n = 2$), sugar maple (*A. saccharum*; $n = 2$), and white birch (*B. papyrifera*; $n = 1$). Eight of the 22 trees used during pre-/post-lactation periods and 9 used during the lactation period were snags (completely dead trees). The remaining 14 and 13 trees used during the pre-/post-lactation and lactation period, respectively, were living trees with defects.

Five principal components explaining 87% of the variance in the data were included as variables in the logistic regression analysis. Component 1 ($\beta_{component1}$: 1.664, 95% CI: 1.01, 2.32, $P = 0.024$) and component 2 ($\beta_{component2}$: –1.478, 95% CI: –0.05, –2.91, $P = 0.012$) had significant effects in the logistic regression analysis. Hosmer and Lemeshow's goodness of fit test indicated that the model adequately fit the data ($P = 0.416$).

Component 1 was correlated with roost-tree height, average dominant canopy height, canopy height relative to roost height, the number of coniferous trees, and the total number of trees (Table II). The positive logistic regression parameter estimate and direction of variable correlation suggest that during the lactation period, bats are more likely to roost in taller trees with a higher dominant canopy and a greater distance between the roost and the canopy and in areas with a lower density of coniferous trees and total number of trees in general relative to pre- and post-lactation periods.

Component 2 was correlated with roost height, canopy height relative to roost height, the number of deciduous trees, and canopy cover (Table II). The negative logistic regression parameter estimate and direction of variable correlation with component 2 indicate that during the lactation period, roosts are higher in trees, closer to the dominant canopy, in areas with a lower proportion of deciduous trees, and in areas with lower canopy cover relative to pre- and post-lactation periods.

Discussion

Our results are consistent with known energetic constraints of bat biology and the results of other research that addressed this issue (Veilleux, Whitaker & Veilleux, 2004). Roost tree and site characteristics selected by female northern long-eared bats varied with the stage of reproduction. Relative to pre- and post-lactation periods, northern long-eared bat roosts were situated high in tall trees during the lactating period. Lactation-period roost-tree sites (0.1-ha plots) were characterized by a high and relatively open dominant canopy and lower tree density (both coniferous and deciduous). Roost locations during the lactation period were not affected by the distance from the nearest tree to the roost, the diameter at breast height of the roost tree, or the number of potentially suitable roost trees within the plot. Correlations between the important variables and each prin-

TABLE I. Mean (standard deviation) of northern long-eared bat (*Myotis septentrionalis*) roost tree and site characteristics measured and examined within a principal components and logistic regression analysis to determine whether trees used during the lactation period differed from those used pre- and post-lactation. ($n = 22$).

	Pre/post lactation	Lactation
Roost tree height (m)	13.4 (6.4)	22.1 (4.8)
Nearest tree as tall as roost (m)	2 (1.9)	2.4 (2.3)
Roost height (m)	8 (4.2)	16.4 (3.1)
Average dominant canopy height (m)	14.4 (4.9)	19.7 (2.0)
Canopy relative to roost (m)	7 (7)	3.7 (4)
Number of decidious trees	65 (34)	19 (16)
Number of coniferous trees	76 (52)	31 (16)
Total number of trees	108 (62)	52 (27)
Diameter at breast height of roost tree (cm)	41 (15)	43 (17)
Average canopy cover (%)	74 (32)	52 (37)
Number of potential roost trees	12 (5)	7 (4)

TABLE II. Principal component loadings and coefficients of the 2 principal components that explain intra-annual variation in roost-tree selection of northern long-eared bats (*Myotis septentrionalis*). Only variables with loadings < –0.5 or > 0.5 were considered important.

	Loadings		Coefficients	
Principal component	1	2	1	2
Roost tree height	0.62	-	0.20	0.14
Nearest tree as tall as roost	-	-	–0.20	–0.02
Roost height	-	–0.61	0.07	–0.26
Average dominant canopy height	0.88	-	0.29	0.14
Canopy relative to roost	0.54	0.66	0.18	0.28
Number of deciduous trees	-	0.69	–0.07	0.29
Number of coniferous trees	–0.85	-	–0.28	0.08
Total number of trees	–0.82	-	–0.27	0.21
Diameter at breast height of roost tree	-	-	0.01	0.17
Average canopy cover	-	0.60	0.03	0.26
Number of potential roost trees	-	-	–0.10	0.10

cipal component were in the same direction except for the variable for the distance between the roost and the canopy. The relationship between component 1 and the distance between the roost site and the dominant canopy suggest that roost sites selected by lactating bats are positively correlated with increasing distance between the dominant canopy and the roost, while the relationship between component 2 and the same variable suggests the opposite. Taken together this suggests that correlations between the principal components and this variable may not be biologically important.

There are at least 2 non-exclusive plausible explanations that remain to be tested for the importance of these features to lactating bats. High roosts in tall trees that are in areas with open canopies increase exposure of the roost to the sun during the day and raise cavity temperature (McComb & Noble, 1981), possibly reducing the costs of maintaining a normothermic body temperature during lactation, when torpor would most impact offspring development and survival (Racey & Swift, 1981; Wilde *et al*., 1995; Wilde, Knight & Racey, 1999). These features may also provide air spaces with minimal clutter that allow newly volant offspring to practice flying and foraging. Offspring must be able to forage on their own shortly after being born (3 weeks for the congeneric little brown bat, *M. lucifugus*; Fenton & Barclay, 1980), so an uncluttered area for the development of flight and foraging proficiency may be important.

A number of previous studies have examined the characteristics that differentiate bat roosts from other trees, and our results support the trends from these studies (Kalcounis-Rüppell, Pysllakis & Brigham, 2005) in that we show that bats are selecting tall trees in open canopy forests. Our results, however, demonstrate that there may be another smaller scale (females and reproductive status) at which these roost features are selected and that consideration of this possibility should be incorporated into used *versus* random tree study designs. Willis *et al*. (2006) suggest (and our result supports the suggestion) that roost trees are not necessarily used equally at all times of the year and thus they should not necessarily be grouped into one category, as is often done in used *versus* random tree studies. The lactation period is the most energetically demanding time period for both mothers and offspring (Racey & Swift, 1981; Wilde *et al*., 1995; Wilde, Knight & Racey, 1999), and roost-tree and site characteristics seem to be reflected in these costs. It is therefore important to incorporate possible within-season variation in roost selection into management practices and study designs (Brigham *et al.*, 1997; Kalcounis & Brigham, 1998).

One possible consequence of less than optimal roosting conditions is depressed reproductive rates (Sedgeley & O'Donnell, 2004). Based upon a series of analyses Sedgeley and O'Donnell (2004) suggested that variable cavity microclimates used by long-tailed bats (*Chalinolobolus tuberculatus*) measured in a relatively young forest relative to more stable cavity microclimates measured in an older forest could have been an important factor among others contributing to differences in productivity between the 2 regions (O'Donnell, 2002). In the younger forest 0.24 juveniles per reproductive female were weaned and on average 0.23 juveniles survived their first year (O'Donnell & Sedgeley, 2006), whereas in the older forest with more stable cavity microclimates 0.91 juveniles per reproductive female were produced, with a first-year survival rate of 0.51 (O'Donnell, 2002).

Our data also have interesting implications for the fact that roost tree use by lactating bats was explained by multivariate principal components that are correlated with a suite of forest characteristics. First, managing for individual forest features (*e.g*., legacy trees within a harvested stand) alone may be inadequate for populations of this and likely other forest-dependent bat species to persist if roost requirements are related to multiple interdependent forest characteristics. It is therefore likely necessary to manage for multiple forest features within stands. Second, management for roost trees should explicitly account for the possibility that some roost features may be particularly important during the lactation period. For northern long-eared bats and possibly other species with similar life histories, tall trees in open stands with a high and relatively open dominant canopy are particularly important during the lactation period. These features are consistent with a subset of roost features identified as generally important for cavity-roosting bats (Kalcounis-Rüppell, Pysllakis & Brigham, 2005) and so could represent the most extreme of suitable roost requirements important during the energetically expensive lactation period and thus possibly "bottleneck" conditions. Finally, the social nature of this and other bat species adds another layer of complexity to managing forests for roost-tree maintenance that further suggests the need for stand-level management (O'Donnell, 2000; Vonhof, Whitehead & Fenton, 2004; Willis & Brigham, 2004; Garroway & Broders, 2007). Bats switch roosts often yet maintain long-term associations with specific colony members, suggesting that there may be fitness benefits to maintaining these associations; it may be necessary, therefore, to maintain a network of trees to facilitate roost switching and social interactions (O'Donnell, 2000; Vonhof, Whitehead & Fenton, 2004; Willis & Brigham, 2004; Garroway & Broders, 2007). For forest dwelling bats in general and social bat species in particular, maintaining roost areas where features important during the lactation period occur may be the minimum requirements for the maintenance of roost trees for summer bat colonies.

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