Roost selection by the solitary, foliage-roosting hoary bat (*Lasiurus cinereus*) during lactation

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Abstract: Nests, roosts, and dens are an important facet of life for many animals and often provide refuge from weather and predators. Reproduction, particularly lactation, is energetically expensive. Many small mammals form maternity colonies in sheltered locations, which provides protection for offspring and mitigates the cost of staying warm. However, lasiurine bats give birth in roosts that superficially appear to offer relatively little thermal buffer. Given the consequences of a cold environment on offspring growth and the high energetic demand of thermoregulating and lactating concurrently, choosing roosts with certain microclimatic properties would be beneficial. We investigated the influence of microclimate on roost selection by lactating hoary bats (*Lasiurus cinereus* (Beauvois, 1796)), a solitary foliage-roosting species. We found that roosts chosen by bats offered shelter from the wind and exposure to sunlight, and consistently had an opening that faced south. We suggest that lactating *L. cinereus* choose roosts based largely on a microclimate that reduces convective cooling and increases radiant heating, thereby mitigating the cost of thermoregulation and promoting rapid growth of offspring.

Key words: hoary bat, lactation, *Lasiurus cinereus*, microclimate, roosting ecology, roost selection.

Résumé : Les nids, les perchoirs et les terriers représentent des aspects importants de la vie de nombreux animaux et fournissent souvent un refuge contre le climat et les prédateurs. La reproduction, et en particulier l'allaitement, ont un coût énergétique élevé. Plusieurs petits mammifères forment des colonies de maternité dans des sites abrités qui procurent une protection aux petits et réduisent les coûts du maintien de la chaleur. Cependant, les chauves-souris lasiurinées donnent naissance dans des perchoirs qui, au premier abord, semblent fournir un tampon thermique relativement faible. Compte tenu des conséquences d'un environnement froid sur la croissance des rejetons et des exigences énergétiques importantes conjointes de l'allaitement et de la thermorégulation, il leur serait avantageux de choisir des perchoirs avec certaines propriétés microclimatiques. Nous examinons l'influence du microclimat sur le choix du perchoir chez des chauves-souris cendrées (*Lasiurus cinereus* (Beauvois, 1796)), une espèce solitaire qui se perche dans le feuillage. Nous observons que les perchoirs choisis par les chauves-souris offrent un abri contre le vent et l'exposition à la lumière solaire et qu'ils possèdent invariablement une ouverture donnant sur le sud. Nous croyons que les *L. cinereus* qui allaitent choisissent leur perchoir en grande partie en fonction du microclimat qui réduit le refroidissement par convection et augmente le réchauffement par radiation, ce qui diminue les coûts de la thermorégulation et favorise la croissance rapide des rejetons.

Mots-clés : chauve-souris cendrée, allaitement, *Lasiurus cinereus*, microclimat, écologie du perchage, sélection des perchoirs.

[Traduit par la Rédaction]

Introduction

Roosts are important resources that provide shelter from ambient conditions (e.g., Kalcounis and Brigham 1998; Chruszcz and Barclay 2002), protection from predators (Fenton et al. 1994), a place to raise young (McCracken et al. 2006), and an arena for social interaction in gregarious species (e.g., Willis and Brigham 2004; Garroway and Broders 2007). Because roosts are important in so many aspects of life and are critical to reproductive success (Wiebe 2001; Kunz and Lumsden 2003), roost use is not indiscriminate but depends on a number of factors related to life history and biology. Bats roost in a wide variety of structures, both natural, such as caves and trees, and anthropogenic, such as buildings and bridges (Kunz and Lumsden 2003). Many studies examining the criteria bats use to select roosts have found strong selection for a number of habitat characteristics (Kunz and Lumsden 2003; Kalcounis-Rüppell et al. 2005). For example, forest-dwelling bats have preferences based on landscape features, such as proximity to water and foraging areas (Elmore et al. 2004; Limpert et al. 2007), forest density and age class (Crampton and Barclay 1998; Arnett and Hayes 2009), and linear features for orientation (Verboom and Huitema 1997; Hein et al. 2008; Perry et al. 2008; O'Keefe et al. 2009). Also influential are characteristics of the roost itself, such as tree species and height (Kalcounis and Brigham

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1998; Perry and Thill 2007), and crevice depth and aspect (Chruszcz and Barclay 2002; Lausen and Barclay 2002, 2003). Early studies focused mainly on measuring gross physical attributes, but attention has also been placed on the importance of microclimate (Hamilton and Barclay 1994; Kerth et al. 2001; Chruszcz and Barclay 2002; Willis and Brigham 2005).

In temperate regions, individuals are subject to highly variable weather conditions throughout the day and season, and thermal characteristics of a roost may be particularly important. Many small mammals, including bats, use torpor, a physiological state in which body temperature (T_b) and metabolic rate are lowered resulting in energy savings (Wang and Wolowyk 1988). However, prolonged gestation (Racey 1982), reduced lactation rates (Glazier 1985; Wilde et al. 1999), and slowed postnatal growth (Kunz and Hood 2000) are costs associated with low body temperature and result in less torpor expression in reproductive females (Racey 1982; Geiser 1996). Therefore, many temperate-zone bats form maternity colonies in warm, thermally stable roosts, such as buildings (e.g., Lausen and Barclay 2006) and tree cavities (e.g., Kalcounis 1994), which mitigates the costs of maintaining high T_b during lactation.

Not all temperate-region bats occupy sheltered roosts while reproductive. Lasiurines (genus *Lasiurus* Gray, 1831) are migratory bats that roost almost invariably in foliage, including during the reproductive period (e.g., Webster et al. 1980; Shump and Shump 1982a, 1982b; Wilkins 1987; Kurta and Lehr 1995). Although roosts of these species occur in a relatively ubiquitous, homogeneous resource compared with that available to cave-, crevice-, and bark-roosting species, there is still evidence of active roost-selection. Eastern red bats (*Lasiurus borealis* (Müller, 1776)) and seminole bats (*Lasiurus seminolus* (Rhoads, 1895)) roost close to open, linear features, such as trails and corridors (Limpert et al. 2007; Hein et al. 2008; O'Keefe et al. 2009), likely because the relatively fast flight and limited maneuverability of lasiurines (Farney and Fleharty 1969; Norberg and Rayner 1987) favour open areas for foraging and locomotion (Barclay 1985). Hoary bats (*Lasiurus cinereus* (Beauvois, 1796)) and *L. seminolus* roost in thick, tall trees in old-growth forest (Perry and Thill 2007; Perry et al. 2008). If active roost selection occurs in nonreproductive lasiurines, one can expect the increased energy demand of reproductive individuals to result in more stringent selection criteria that reflect thermal requirements during lactation. Only one study to date has assessed roost selection in reproductive lasiurines specifically from a microclimatic perspective, and it found that *L. cinereus* preferred the lee side of trees in a coniferous forest, ostensibly for the benefits of decreased convective cooling (Willis and Brigham 2005). Another proposed criterion for roost selection by bats in general is exposure to sunlight based on the benefits of radiant heating (Geiser and Drury 2003), but this has rarely been tested beyond inferences made from roost aspect and temperatures recorded within roosts (Kalcounis and Brigham 1998; Lausen and Barclay 2002, 2003).

We investigated roost selection in reproductive female *L. cinereus*, with a focus on microclimate variables on two spatial scales (the roost tree and the immediate surrounding habitat). We hypothesized that microclimate is the principal determinant of roost selection in lactating *L. cinereus*. In par-

ticular, we predicted that they select roosts protected from wind to minimize convective heat loss (Willis and Brigham 2005), and open to sunlight to benefit from the effects of radiant heat during rewarming from torpor and maintenance of high body temperatures (Bakken and Kunz 1988; Geiser and Drury 2003). We also predicted that because *L. cinereus* is a relatively large, fast, and less maneuverable species in flight (Farney and Fleharty 1969; Barclay 1985; Norberg and Rayner 1987), roost choice reflects the benefit of adjacent flyways, and roosts along edges and open linear features would be favoured.

Materials and methods

Study species

Lasiurus cinereus is a relatively large (mean = 27 g; Shump and Shump 1982b), insectivorous bat (Vespertilionidae) common in Canada. It is widespread, found throughout most of North America, southward through Central America, and into Argentina and Chile (Shump and Shump 1982b). However, it is a migratory species with individuals moving between summer birthing grounds and overwintering grounds. *Lasiurus cinereus* typically arrives in our study area in early June and gives birth during mid- to late June (Koehler and Barclay 2000). Unlike most other bats, *L. cinereus* is monoestrus but produces twins (Barclay and Harder 2003) and gives birth alone among the foliage of tree branches (Koehler and Barclay 2000). Families begin to migrate out of our study area in mid- to late August (Barclay 1984). Nonreproductive, resident *L. cinereus* are not known to occur in our study area. *Lasiurus cinereus* is not known to use long-term torpor, but instead uses daily torpor as a means of energy conservation (Shump and Shump 1982b; Cryan and Wolf 2003).

Study site

We conducted our study near the University of Manitoba Field Station at Delta Marsh, Manitoba, Canada (50°11′02.44″N, 98°22′55.15″W). Delta Marsh is located at the southern end of Lake Manitoba and consists of wet meadows, open ponds, and narrow channels (Barclay 1984). We searched for roosting *L. cinereus* along a narrow (mean width of 80 m) forested dune ridge bordered by Lake Manitoba to the north and marsh to the south, as well as in woodlots of various sizes in the surrounding area. All sites consisted mainly of deciduous trees, including Manitoba maple (*Acer negundo* L.), bur oak (*Quercus macrocarpa* Michx.), green ash (*Fraxinus pennsylvanica* Marsh.), cottonwood (*Populus deltoides* Bartr. ex Marsh.), and peach-leaved willow (*Salix amygdaloides* Anderss.). The combination of trees and marsh provides ideal roosting and foraging habitat for *L. cinereus*. Reproductive female *L. cinereus* return to this site annually to give birth (Koehler and Barclay 2000).

We used binoculars at ground level to visually locate roosting bats among the foliage. To minimize biases in our search effort, we searched for roosting bats along edges of available forest stands and along transects through the middle of stands. We accessed families using a portable tower, constructed from interlocking sections of aluminium TV tower, and captured them with a modified bucket trap (Kunz and Kurta 1988). To avoid pseudoreplication, we used only the

first roost in which we found a family in our statistical analyses (Willis and Brigham 2005). However, analysing the data using all roosts did not change our conclusions.

Roost characteristics

We examined two variables thought to affect roost microclimate, protection from wind and exposure to sunlight. After a family vacated its roost owing to our disturbance, we measured mean wind speed ($\pm$0.1 m/s) and mean light intensity ($\pm$0.1 lx) in the exact position we found the family, in a randomly chosen potential roost, and in the open. For potential roosts, we identified a point at a random direction and distance (between 25 and 100 m) from each occupied roost. We restricted the distance to ensure the potential roost was outside the area directly surrounding the roost tree but within the same stand. The spot closest to the current roost's height ($\pm$1 m) within the foliage above the random point was the potential roost and the corresponding tree was used as a paired random roost tree. In the event that there was no obvious tree to use or the tree was <10 cm in diameter, we used the next random distance and direction generated. We recorded light intensity in an open field within 200 m of the occupied and potential roosts and over the same time period as the roost and potential roost. We took open wind readings at a height of 5 m in an area at least 100 m from any tree or other structure, and all three readings (i.e., roost, random, and open) occurred within 30 min. We used an anemometer (Kestrel 3000; Kestrel Meters, Sylvan Lake, Michigan, USA) to measure mean wind speed over a 5 min period. Because wind in our study area is predominantly from the north (Environment Canada 2010), we took all wind measurements under conditions of northerly winds and with the anemometer oriented to face directly into the prevailing wind. To more directly assess the degree of radiant heating, we used relative light intensity as a proxy, recorded every 5 min for four consecutive days with a light-sensitive pendant data logger (HOBO model UA-002-08; Onset Computer Corporation, Bourne, Massachusetts, USA). We could not monitor temperatures in roosts because the effect of radiant heat on sensors exposed to sunlight results in equivocal readings (Bakken and Kunz 1988).

To determine if *L. cinereus* in our study area chose roosts based on tree or landscape features, we compared a number of physical characteristics of the tree and surrounding landscape, with an emphasis on variables that might affect microclimate (i.e., physical characteristics of the roost tree or surrounding vegetation that may block sunlight or wind from penetrating the roost). For each tree, we measured tree species, height, diameter at breast height (DBH), and canopy-level score (below (0), level with (1), or above (2) the surrounding vegetation). The position of the roost within the tree affects microclimate, thus to determine if bats actively chose the location of their roost within the tree, we recorded roost height, roost aspect, and distance relative to the tree trunk at breast height, and canopy cover above the roost (mean of two values obtained by two researchers using a densiometer). We also measured the degree and direction of canopy openings around the roost, which included areas within 20 m of the roost that lacked trees taller than 1 m below roost height (i.e., those that could affect wind and sunlight in the roost). For landscape analysis, we recorded the DBH,

species, and direction and distance from the roost of all neighbouring trees at or above roost height within a 0.045 ha circular plot centred on the roost. We did not record trees more than 1 m below roost height because we assumed the effect on microclimate and access to be trivial. From these data, we also calculated total basal area (m^2) in the plot and basal area of trees south and north of the roost. To determine if bats preferred a specific species of roost tree, we used the point-centred quarter sampling method to determine the relative density of available tree species and compared this with the proportion of tree species used as roosts (Cottam et al. 1953; Dahdouh-Guebas and Koedam 2006).

Statistical analysis

To confirm all data met assumptions of normality, we used Kolmogorov–Smironov goodness-of-fit tests and visually inspected data against normal distributions using quantile–quantile (Q–Q) plots. We used analysis of covariance (ANCOVA) to compare mean 5 min wind speeds at roost and random trees with open wind-speed as a covariate. To compare mean light intensity between roosts and random roosts, we used values from the single day with the highest total available light (as recorded by the data logger in the open field) in an ANCOVA with available (i.e., open) light as a covariate. Bats typically used torpor in the early morning during our study (Klug 2011). To further assess the potential for roost selection based on radiant heating available during rewarming from early morning torpor, we used an ANCOVA to compare light intensity between roosts and random trees during the first 4 h after sunrise, with available light as a covariate. We used Rayleigh's (Z) circular statistics tests to compare mean aspect and exposure of roost and random trees, and χ^2 tests (χ^2) to compare the proportion of trees with adjacent, open areas between roost and random trees.

For analysis of tree and landscape characteristics, we used an information–theoretic approach (i.e., Akaike information criterion, AIC) to construct and compare models describing roost selection by *L. cinereus*. We measured or calculated 26 variables describing tree or landscape properties. Roost height was not used for analysis because height of prospective roosts was determined by the height of the paired, actual roost. Before constructing models for AIC analysis, we eliminated highly correlated variables ($r > 0.70$) and performed an initial logistic regression with an arbitrarily high α value ($P = 0.35$) to further reduce the number of variables but retain those that may be biologically important. We included the remaining variables in our candidate models. We constructed 63 candidate models, containing one-, two-, and three-way combinations of the variables of interest, and ranked them according to their AIC_c values and weights (w_i), the best models being those with the lowest AIC_c and highest w_i. The AIC_c value is the AIC value corrected for small sample size and w_i is a normalized value reflecting the probability the given model is correct given the entire subset of candidate models (Burnham and Anderson 2002). We also calculated the relative importance value of each variable by summing the w_i of all models in which the variable appeared. To analyse tree-species data, we compared the proportion of tree species used as roosts with the relative density of each species calculated from the point-centred transect data using a χ^2 test. We performed all statistical analyses using R ver-

Fig. 1. Mean light intensity recorded every 10 min from sunrise to sunset in the exact locations of families of hoary bats (*Lasiurus cinereus*) within occupied roosts, versus random, prospective roost locations in Delta Marsh, Manitoba. Mean light intensity was not significantly different between occupied and prospective roosts, but bats chose locations in the foliage with less variable light levels. Thick horizontal bars represent the median. Upper and lower box limits are the 75th and 25th quartiles, respectively. Whiskers extend to the minimum and maximum values of each stage.
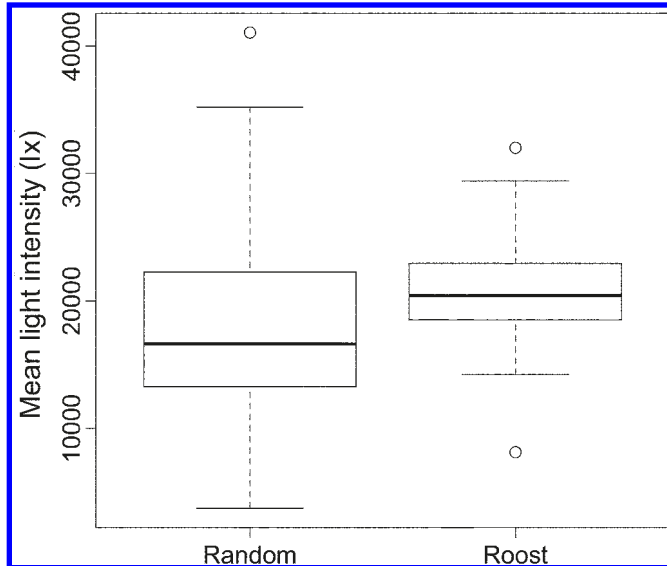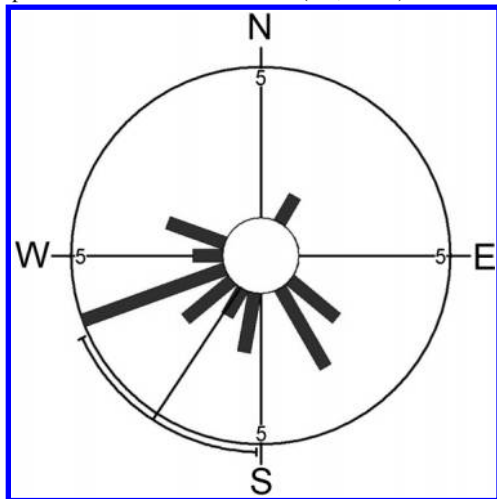

Fig. 2. Compass direction in relation to the trunk of the roost tree of 19 roosts used by lactating hoary bats (*Lasiurus cinereus*) in Delta Marsh, Manitoba. The direction was 213° ± 31.4° (mean ± SE) and differed significantly from random. The number at each cardinal direction represents the maximum count (i.e., scale) of the diagram.
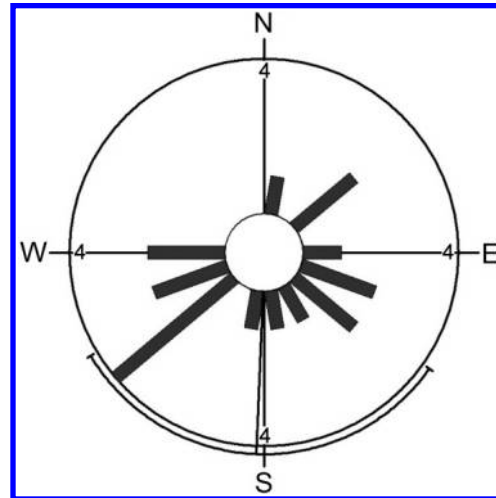

sion 2.12.2 (R Development Core Team 2011) and Oriana version 3.20 (Kovach Computing Services 2010).

Results

Over the 2 years of our study, we located 19 resident and reproductive *L. cinereus*. Roosts were located in live Manitoba maple (*n* = 8), bur oak (*n* = 7), and green ash (*n* = 4). We found multiple families in two roost trees; one bur oak was used by three different families and one Manitoba maple

Fig. 3. Compass direction of the opening of 19 roosts used by lactating hoary bats (*Lasiurus cinereus*) in Delta Marsh, Manitoba. Although not significantly different from random, in most cases (16/19) the opening faced south, with a direction of 182° ± 48.3° (mean ± SE). All roosts were exposed on one side to an open area devoid of trees of roost height or taller within 20 m. The number at each cardinal direction represents the maximum count (i.e., scale) of the diagram.

was used by two different families, but no roost tree was used by more than one family at a time. Bats roosted in bur oak more frequently than would be expected based on the relative density of this tree species (1.5%) and other available tree species (Manitoba maple = 48.9%, green ash = 33.5%, and other (e.g., willow and cottonwood) = 16.1%; $\chi^2_{[3]}$ = 52.8, P < 0.001).

Roost height ranged from 7.6 to 12.8 m (10.7 ± 1.5 m, mean ± SD). We recorded microclimate, physical, and landscape characteristics for 38 trees (19 roosts and 19 randoms). Wind speed was lower in roosts occupied by bats (0.4 ± 0.09 m/s, mean ± SE) than in potential roosts (1.0 ± 0.16 m/s) ($F_{[1,35]}$ = 10.78, P = 0.002). Although light intensity was higher at roosts (20 889 ± 1 259.3 lx, mean ± SE) than random (18 587 ± 2 152.6 lx) locations, there was no significant difference ($F_{[1,35]}$ = 0.97, P = 0.331). However, bats did choose locations in the foliage with less variable light levels than random, potential roosts ($F_{[1,36]}$ = 0.34, P = 0.028; Fig. 1). Mean light intensity during the morning did not differ between occupied and potential roosts ($F_{[1,35]}$ = 0.45, P = 0.509). Mean compass orientation of the roost in relation to the trunk of the tree at breast height was 213° ± 16.3° (mean ± SE) (Fig. 2) and differed significantly from random (Z = 5.28, P = 0.004), whereas mean compass direction of the random roosts was not significantly different from random (Z = 0.59, P = 0.561). The proportion of roosts with a side open to an area absent of trees within 20 m was higher for occupied roosts (19/19) than for potential roosts (7/19) ($\chi^2_{[1]}$ = 8.92, P = 0.003). In all cases when we observed emergence of the female at dusk (*n* = 12), bats used the open side to exit the roost. Although not significantly different than random (Z = 1.85, P = 0.158), in most cases (16/19) the opening in occupied roosts faced south (182° ± 29.1°, mean ± SE; Fig. 3).

After the Pearson's correlation tests and initial logistic re-

Table 1. Variables included in the AIC analysis comparing physical and landscape characteristics of roost trees used by lactating hoary bats (*Lasiurus cinereus*) with those of random trees in Delta Marsh, Manitoba.

Variable	Roost tree		Random tree		
	Mean	SD	Mean	SD	P^*
Tree height (m)	16.1	4.21	14.0	4.69	0.1530
Diameter at breast height (DBH; cm)	43.0	10.42	35.8	13.05	0.0762
Degrees of exposure at roost[†]	115.3	46.09	78.6	80.52	0.0986
Number of surrounding trees[‡]	8.5	4.26	11.6	4.91	0.0590
Mean DBH of surrounding trees (cm)	34.0	5.51	31.4	4.96	0.1400
Distance to closest tree in south (m)	6.5	2.70	5.7	1.99	0.3350
Basal area south of roost (m^2)	0.33	0.240	0.54	0.292	0.0366

*For the initial logistic regression, $\alpha = 0.35$.

[†]Total compass degrees from roost devoid of trees that were roost height or taller for a minimum distance of 20 m.

[‡]Trees with DBH ≥ 10 cm within a 0.045 ha (i.e., 12 m radius) circular plot centred on the roost.

Table 2. Logistic regression models comparing tree and landscape characteristics used in roost selection by lactating hoary bats (*Lasiurus cinereus*) in Delta Marsh, Manitoba, ranked by Akaike's information criterion corrected for small sample size (AIC$_c$) score and presented with AIC weight (w_i) and evidence ratio (w_1/w_i).

Model	AIC$_c$	ΔAIC$_c$	w_i	w_1/w_i
BASouth + DistTS + rExp	42.132	0.000	0.5163	
BASouth + DistTS + NTrees	44.407	2.275	0.1656	3.119
BASouth + DistTS + rDBH	47.556	5.424	0.0343	15.058
BASouth + rExp + rHeight	47.878	5.746	0.0292	17.689
BASouth + rExp	47.886	5.754	0.0291	17.760
BASouth + rDBH + rExp	47.889	5.757	0.0290	17.787
BASouth + DistTS	48.107	5.975	0.0260	19.835
BASouth + rExp + nDBH	48.342	6.210	0.0231	22.308
BASouth + DistTS + nDBH	49.068	6.936	0.0161	32.071
BASouth + DistTS + rHeight	49.709	7.577	0.0117	44.187
Global (all variables)	50.124	7.698	0.0110	46.940

Note: A complete description of each variable is given in Materials and methods.

gressions, seven roost variables (roost tree DBH (rDBH), roost tree height (rHeight), total degrees of roost exposure (rExp), total number of neighbouring trees (NTrees), mean DBH of neighbouring trees (nDBH), distance to closest tree south of the roost tree (DistTS), and basal area south of the roost tree (BASouth)) remained, which we included in the AIC analysis (Table 1). The highest ranked model with the lowest AIC$_c$ value (42.132) and highest w_i (0.516) contained three variables: basal area south of the roost tree (BASouth), distance to closest tree south of the roost tree (DistST), and total degrees of roost exposure (rExp) (Table 2). The AIC weight for the top-ranked model w_i (0.516) suggests that it has a high probability of being the best model given the subset of candidate models. However, the low Δ_i value of the next best model (2.275) and the evidence ratio between the top two models ($w_1/w_2 = 3.11$) suggest weak support for a single best model and that both models could be predictors of characteristics explaining roost selection in *L. cinereus* (Burnham and Anderson 2002). The two variables present in both models are basal area south of the roost and distance to closest tree in the south, and their importance values (0.921 and 0.820, respectively) suggest that these variables are key distinguishing features of roost trees compared with other trees in the landscape. Roost trees had lower southern basal

areas and greater distances to southern neighbours than random trees. The two other variables in the top-ranked models were degrees of exposure and total number of surrounding trees (importance = 0.668 and 0.211, respectively). Roost trees had more exposure and fewer neighbouring trees than randoms.

Discussion

Lactating *L. cinereus* demonstrate a finely balanced energy budget; they reduce use of torpor as offspring grow, which may increase reproductive output (Klug 2011), and they adjust the time spent foraging to meet only current energy demands (Barclay 1989). Although maternity roosts of lasiurines superficially do not appear to differ from other potential roosts on the landscape (Shump and Shump 1982*a*, 1982*b*; Kalcounis 1994; Koehler and Barclay 2000), our data suggest that lactating *L. cinereus* choose roosts with particular microclimates. Roosts typically offered shelter from wind and exposure to sunlight, which may minimize torpor use and promote rapid development of young throughout the summer.

Convection is an important avenue of heat loss (Bakken and Kunz 1988). High winds induce torpor in lactating *L. cin-*

ereus (Klug 2011) and considerably increase the cost of thermoregulation (Willis and Brigham 2005). Although the fur of *L. cinereus* has relatively high insulative value compared with that of other temperate region bat species (Shump and Shump 1980), convective heat loss in wind speeds typical of our study site and period (3.4 ± 0.04 m/s, mean ± SE; Environment Canada 2010) still resulted in favoured lee-side roosts. Given that the relative wind speed in occupied roosts is roughly half that in potential roosts at both our site and the site used by Willis and Brigham (2005; 1.6 ± 0.7 and 2.7 ± 0.8 for occupied and potential roost sites, respectively), an estimate of energy saved by roosting on the lee side of trees in our study area would likely be consistent with the 1.60 kJ/day estimated in that study. Interestingly, we did not observe bats to shift position within the roost with changing wind direction, suggesting that the costs of using torpor or spending more energy staying warm during occasional periods of southerly wind are less than the cost of frequently moving young. Conversely, we observed all nonresident bats (i.e., migrating through our study area) roosting on the lee side of trees.

Most bats roost in cavities and experience limited or no direct exposure to sunlight (Kunz and Lumsden 2003). However, foliage-roosting bats could benefit from direct solar radiation (Bakken and Kunz 1988). The amount of energy required to arouse from torpor and maintain normothermic body temperatures is considerably reduced with radiant heat (Geiser and Drury 2003). Passive rewarming in a small marsupial (stripe-faced dunnart, *Sminthopsis macroura* (Gould, 1845); body mass 25 g) used as little as 15% of the energy required compared with active rewarming (i.e., shivering), and the metabolic rate of normothermic individuals exposed to radiant heat was almost identical to basal metabolic rate (Geiser and Drury 2003). We used light intensity within roosts of *L. cinereus* as a proxy for relative solar radiation and found considerably higher light intensities than those used by Geiser and Drury (2003; 5000 lx) in the experiment mentioned above. *Lasiurus cinereus* in roosts with sufficient solar heating could reduce the cost of remaining normothermic throughout lactation and focus energy on maintaining lactation rates. Based on the resting metabolic rate and normothermic T_b of female *L. cinereus* (Cryan and Wolf 2003), individuals spend 39.07 kJ/day remaining warm during a typical 17 h day roosting in our study area, with a mean ambient temperature of 19.8 °C; if this energy could be saved by sufficient radiant heating in the roost, it represents a large proportion (29.9%) of the estimated daily energy budget of a lactating female (145 kJ/day; Willis and Brigham 2005). Although exposure to sunlight may be inconsequential in roost selection for many bat species, our data suggest that it may impose a considerable impetus for roost selection in *L. cinereus*. Similar behaviour is observed in western long-eared myotis (*Myotis evotis* (H. Allen, 1864)) in that reproductive females choose south-facing roosts that warm quickly during the day, which aids in passive rewarming from torpor (Chruszcz and Barclay 2002; Solick and Barclay 2006). However, lactation is an exothermic process and milk production can be constrained by the ability to dissipate heat (Speakman and Krol 2010). Our data may reflect this as well, because lactating *L. cinereus* did not choose roosts with full exposure and maximum solar radiation, but opted for roosts with a narrow, less variable exposure than potential roosts.

All roosts used by *L. cinereus* had a single, south-facing opening, a characteristic found less often at random roosts. Moreover, roost trees had fewer, more distant trees to the south than random trees did. The flight characteristics of *L. cinereus* may partly explain the importance of these variables. *Lasiurus cinereus* is a relatively fast flier and is less maneuverable compared with other species of bat in North America (Farney and Fleharty 1969; Norberg and Rayner 1987), and thus prefers to forage in open areas (Barclay 1985). An open flyway for access to and from the roost is therefore beneficial. Although other lasiurines show a preference for roosts next to open, linear features (Limpert et al. 2007; Hein et al. 2008; O'Keefe et al. 2009), our data suggest the profile of the open space is less of a concern for *L. cinereus* as long as there is sufficient space to fly out of or above the surrounding canopy. In addition, the fact that all openings had a southern aspect supports the conclusion that exposure to sunlight and protection from wind are important. The preference for *L. cinereus* to roost in oaks may be explained by a preference for edge habitat (e.g., O'Keefe et al. 2009). Oaks are a moderately shade-tolerant species (Farrar 1995) and occur more often on forest edges and within gaps in the forest canopy than other tree species (MacKenzie 1982).

Generally, the ubiquity and homogeneity of trees has led to the assumption that foliage-roosting bats benefit less by choosing roosts than other forest bats do (e.g., Kunz and Lumsden 2003). However, roost selection by species that roost in caves, tree cavities, and crevices is relatively well documented compared with that of foliage-roosting species (Lacki 1996; Kunz and Lumsden 2003; Barclay and Kurta 2007). Our data support the hypothesis that reproductive, female *L. cinereus* actively choose roosts based on microclimate. Lactating bats in this study did not choose roost locations at random, but preferred roosts that provided shelter from the prevailing north wind, stable sunlight exposure, and an adjacent clearing most often to the south of the roost tree. All of these features are likely linked to the thermal benefits to lactating individuals of minimizing energy spent on thermoregulation, thus increasing the amount of energy available for lactation and increasing reproductive output and fitness. Moreover, lactating *L. cinereus* do not switch roosts often, and within and among year fidelity is high (Koehler 1991; Koehler and Barclay 2000; Willis and Brigham 2005), which suggests that one tree is not like any other and roosts are selected based on a specific set of criteria. With migratory tree-roosting bats facing population declines (Carter et al. 2003) and novel agents of mortality, such as wind turbines (Kunz et al. 2007; Arnett et al. 2008), further attention needs to be given to roost selection in these species and in developing silvicultural practices aimed at conserving known maternity sites.

Acknowledgements

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