

## PHYSIOLOGICAL AND ECOLOGICAL ASPECTS OF ROOST SELECTION BY REPRODUCTIVE FEMALE HOARY BATS (*LASIURUS CINEREUS*)

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Most recent research on the roosting habits of temperate, forest-living bats has focused on species that use enclosed cavities, but less has been done to address roosting by foliage-living species, which are assumed to have more flexible roost requirements. Numerous studies have suggested that bats select roosts on the basis of microclimate, yet few have tested this hypothesis empirically and none have addressed the use of foliage roosts in this context. We used radiotelemetry to locate roost sites of reproductive female hoary bats (*Lasiurus cinereus*) then compared a variety of physical features of these trees with randomly selected nonroost trees. We also recorded ambient temperature and wind speed at roost and nonroost sites to test the hypothesis that physical features associated with foliage roosts provide energetic benefits. Hoary bats selected roost sites on the southeast side of mature white spruce trees (*Picea glauca*;  $\bar{X}$  orientation  $158.6 \pm 6.3^\circ$  SSE). Roost trees were more likely than random trees to be the same height as the surrounding forest canopy; had less canopy cover facing out from the tree in the direction of the roost branch; and had lower forest density on their southeast side. Wind speed was significantly lower at roost sites compared with opposite sides of the same trees, presumably due to increased protection from prevailing west winds. Incorporating an estimate of convective cooling due to wind, we predicted daily thermal energy expenditure for normothermic bats and found that selected roost sites provided statistically significant energy savings (up to  $1.60 \pm 0.99$  kJ/day) relative to the predicted expenditures if bats had roosted on the opposite sides of trees. Our results provide direct evidence that hoary bats select forest roosts on the basis of microclimate and suggest that roost requirements of foliage-roosting species may be more specific than has been previously assumed.

Key words: AIC, Chiroptera, convective cooling, foliage, forest, hoary bats, *Lasiurus cinereus*, roosting

Selection of specific roost or nest sites can result in fitness benefits for animals by providing shelter from the weather, places to rear young, protection from predators, and opportunities for mating (Alcock 2001). For many species, microclimate may be an important factor influencing roost or nest site selection (Hartman and Oring 2003; Kalcounis and Brigham 1998; Kerth et al. 2001; Sedgeley 2001; Wiebe 2001). Selection pressure associated with microclimate should be especially pronounced for endotherms in the temperate zones. Despite warm afternoon ambient temperatures ( $T_a$ ) in temperate regions during summer,  $T_a$  may fall well below thermal neutrality for many species at night and in the early morning, particularly at the beginning and end of the warm season. The issue of roost microclimate may be especially important for

nocturnal animals like bats. Summer nights are short at high latitudes and bats may be confined to roost sites for long periods without access to food or water. Under these circumstances, selecting roosts with specific microclimate conditions may be important for maintaining positive energy budgets.

Microchiropteran bats are heterothermic endotherms and can exploit torpor during summer, presumably to balance energy budgets during periods of inclement weather and reduced prey availability (Chruszcz and Barclay 2002; Lausen and Barclay 2003; Turbill et al. 2003). However, reproductive female bats, which provide the only direct parental care investment, are predicted to face intense selection pressure to roost in relatively warm sites. Cold roost temperatures and the use of torpor slow the development of prenatal and juvenile bats (Racey and Swift 1981; Tuttle and Stevenson 1982; Wilde et al. 1999), which has implications for overwinter survival and, therefore, fitness of mother and offspring (Kunz 1987; Thomas et al. 1990). Recent evidence demonstrates that female bats use torpor while raising young, but they are more likely to select the warmest possible roosts (Kerth et al. 2001) and avoid torpor use (especially deep

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torpor—Chruszcz and Barclay 2002; Hamilton and Barclay 1994) during lactation relative to pregnancy (Willis, in press). The energetic costs of lactation are high for bats (Kurta et al. 1989, 1990), so any thermoregulatory benefit achieved through roost selection is likely important for balancing the energy budget. Therefore, selection of roosts on the basis of microclimate should be more pronounced during lactation than during other times of year.

Recent studies have begun to address the roosting requirements of forest-living bats (Barclay and Brigham 1996; Brigham et al. 1997; Kalcounis and Brigham 1998; O'Donnell and Sedgely 1999; Sedgely and O'Donnell 1999; Vonhof and Barclay 1996; reviewed in Kunz and Lumsden 2003). Typically these studies involve tracking radiotagged bats to roost sites and comparing physical characteristics between roost trees and randomly selected, nonroost trees (Hutchinson and Lacki 2000; Mager and Nelson 2001; Sedgely and O'Donnell 1999; Vonhof and Barclay 1996). Most of these studies speculate that some structural features that differentiate roost from nonroost trees, (e.g., tree height, stem diameter, canopy cover) correlate with ambient temperature, but few have tested this hypothesis by measuring microclimate conditions (Kalcounis and Brigham 1998; Sedgely 2001).

Individuals of most temperate forest-dwelling bat species hibernate for the winter and roost in enclosed cavities during summer. Females of these species raise their young in groups, buffered from the elements within tree hollows or beneath exfoliating bark (Nagorsen and Brigham 1993). In these species, selection pressure for females to avoid torpor while raising young should be intense because juvenile overwinter survival is positively correlated with body mass at weaning and at onset of hibernation (Kunz 1987; Thomas et al. 1990). If juveniles do not accumulate sufficient fat stores during their 1st summer, there is a low probability they will survive the winter. Hoary bats (*Lasiurus cinereus*) are among the small number of temperate bat species that raise their young, solitarily, in the open foliage of trees and migrate to avoid cold winters (Koehler 1991; Shump and Shump 1982). Thus, they may face more extreme weather conditions than most temperate bats during summer, but possibly experience warmer conditions during winter. A dense pelage helps to insulate them against cold  $T_a$  (Shump and Shump 1980), and their migratory overwintering strategy may relax selection pressure for rapid offspring growth rates relative to hibernating bats (Koehler and Barclay 2000). They also have been observed to use torpor during lactation (Hickey and Fenton 1996; Koehler 1991; Willis, in press), although preliminary data suggest that they use torpor much less during lactation than during pregnancy (Willis, in press). This leads to the prediction that hoary bats may not expend energy to seek out roost sites on the basis of the thermal environment. Differences between potential open foliage sites may be minimal, and the consequences of cold roosts for mother and offspring fitness may be less than those for cavity roosting, hibernating species. To date, however, there have been no detailed studies of the roosting ecology of hoary bats in forests, although a few anecdotal reports exist (Constantine 1966; Kalcounis 1994). Furthermore, no study has provided direct

evidence that any bat species selects foliage roosts on the basis of microclimate.

Our specific objectives were to test the hypothesis that reproductive female hoary bats select roost sites with physical features that differentiate roosts from randomly available trees; to test the hypothesis that microclimate at roost sites differs from that at nonroost sites; and to model thermoregulatory energy expenditure and test the hypothesis that the selection of specific roost sites provides energetic benefits for reproductive female bats.

## MATERIALS AND METHODS

All procedures were approved by the University of Regina President's Committee on Animal care in accordance with guidelines set by the Canadian Council for Animal Care and the American Society of Mammalogists (<http://www.mammalogy.org/committees/index.asp>). We conducted fieldwork over 3 summers from May to August 2000–2002, in Cypress Hills Provincial Park, Saskatchewan, Canada (49°34'N, 109°53'W). The Cypress Hills extend about 50 km in an east–west orientation, at between about 1,170 m and 1,375 m, and are the most elevated area on the Canadian prairies. Vegetation in the region consists of about 50% grassland, 45% woodland, and 5% wetland (Sauchyn 1993). Woodland vegetation is characterized by lodgepole pine (*Pinus contorta*) forest in dry, high elevation areas and white spruce (*Picea glauca*) forest with more substantial understory in lower lying, wetter areas (Sauchyn 1993). Trembling aspen (*Populus tremuloides*) predominate at middle elevations but can be found throughout the study area (Sauchyn 1993). This site is ideal for addressing hypotheses about the influence of microclimate on roost selection by bats because it is characterized by dramatic seasonal and diurnal temperature variation. Snowstorms as late as early June are not uncommon, and midsummer temperatures, during a single 24-h period, can vary from  $>30^{\circ}\text{C}$  in the afternoon to near  $0^{\circ}\text{C}$  at night.

We captured bats in mist nets set near foraging areas. Body mass was recorded for all females, and their reproductive status was assessed. We used gentle palpation of the abdomen to discern pregnancy and expression of milk or the presence of bare patches around the nipples to indicate lactation. We distinguished volant juveniles from adults based on fusion of the phalangeal epiphyses (Anthony 1988). Reproductive females and a few juveniles were outfitted with numbered, plastic, split-ring forearm bands and 1.05 g or 0.75 g radiotransmitters (BD-2T and BD-2AT, respectively, Holohil Systems Ltd., Carp, Ontario, Canada). Dorsal fur between the scapulae was trimmed, and transmitters were affixed to the exposed skin using surgical cement (Skin-Bond, Smith and Nephew United, Largo, Florida). The mean body mass of radiotagged bats was  $27.8 \pm 5.8$  g (range: 20.1–34.5 g) and transmitter mass represented less than 5% of each bat's body mass (Aldridge and Brigham 1988). We released bats within several h of capture and tracked them to their roosts using hand-held telemetry receivers (R-1000, Communication Specialists Inc., Orange, California) and 5-element yagi antennas (AF Antronics, Inc., Urbana, Illinois). Once a roost tree was located, we used binoculars to locate the branch and specific point on the branch where the bat was roosting. By observing bats at roosts on as many days as possible, we were able to determine parturition dates for pregnant bats and count the number of young with each female.

We recorded tree species and status (living or dead) for each roost tree. We measured 7 physical characteristics of roost trees that we hypothesized could influence roost microclimate or that had been measured in previous studies of forest-roosting bats (Barclay and Brigham 1996; Hutchinson and Lacki 2000; Kalcounis and Brigham

1998; Mager and Nelson 2001; Sedgely and O'Donnell 1999; Vonhof and Barclay 1996). Specifically, we recorded tree height, roost height, diameter at breast height (DBH), compass orientation of the roost branch relative to the trunk of the tree (corrected for true north), percentage canopy cover, and distance to nearest tree with a DBH > 9.5 cm. We also assigned a canopy level score for each tree based on whether the top of each roost tree was even with (1), above (2), or below (3) the surrounding forest canopy within about 20 m of the roost tree. Heights were measured using a clinometer. Percentage canopy closure was estimated from a position directly below the roost site, looking straight up, facing away from the tree in the direction of the roost branch. This value was defined as the percentage of an observer's circular field of view, centered on the roost site, which contained limbs and foliage that would block overhead sunlight from reaching the roost. Before making an estimate, we noted the position of branches and foliage below the height of the roost and excluded these from the estimate. In all cases, 2 observers estimated percentage canopy cover independently and the mean was calculated. At each roost tree we randomly selected a compass bearing and a distance between 50 and 100 m. The tree with DBH > 9.5 cm closest to this random point was used for pairwise comparison with the roost tree. With the exception of roost height, we measured the same set of variables for random trees as for roost trees. The distance limits of 50 and 100 m were selected to avoid overlap between roost and random plots (see below) and to ensure that both sites were in the same forest stand. For percentage canopy values at nonroost trees we randomly selected a compass orientation relative to the trunk of the tree from which to make our estimate.

To assess the density of forest in the vicinity of roost and random trees we defined a 0.045-ha circular plot centered on the focal tree (roost or random). Within this plot we recorded the distance and compass orientation (later corrected for true north) between the focal tree and all trees of DBH > 9.5 cm. A DBH of 9.5 cm was selected as a minimum size because trees of this diameter were never as tall as the roost branches on which we found hoary bats and, thus, likely had little impact on the degree of forest clutter experienced by bats. We counted the number of trees within roost and random plots to quantify 6 different variables for subsequent analyses: total number of trees of all species, total number of spruce trees, number of trees of all species and number of spruce trees that fell within 30° (i.e., ±15°) of the roost branch orientation, and the number of trees and number of spruce trees that fell within 30° of a southeast orientation (i.e., 135°). We differentiated between all trees and spruce trees in these counts because spruce trees were typically taller than the 3 other species present, particularly trembling aspen, which rarely reached the height at which hoary bats roosted. Thus, we hypothesized that spruce trees would have the greatest impact on the degree of forest clutter experienced by bats at their roost sites. An angle of 30° from roost branches and due southeast were chosen based on the hypothesis that bats might select roosts that maximize morning sun exposure and provide an open flyway leading out from the roost branch.

Previous studies of roost selection by forest-dwelling bats, and wildlife habitat use in general, have relied on stepwise logistic regression to identify continuous and categorical independent variables that best predict a dichotomous categorical response variable (in the case of bats, roost trees versus randomly selected trees—Brigham et al. 1997; Hutchinson and Lacki 2000; Sedgely and O'Donnell 1999). This stepwise logistic regression approach is problematic because arbitrary alpha levels (e.g.,  $P = 0.1$ ,  $P = 0.15$ ) are used to remove variables from the analysis during backward elimination. A null hypothesis testing approach is prone to errors because there is high risk of eliminating biologically significant variables, even with a relatively

high alpha level (e.g.,  $P = 0.15$  or  $0.20$ —Hosmer and Lemeshow 1989). Thus, the same dataset can result in dramatically different conclusions with a slight adjustment of alpha at any step of elimination. Anderson et al. (2000) proposed an information-theoretic approach as an alternative to null hypothesis testing. Their method makes use of the Akaike information criterion (AIC) to rank a series of candidate models, which are defined a priori. We used  $AIC_c$ , a value of AIC corrected for small sample sizes (Anderson et al. 2000), to evaluate candidate logistic regression models that differentiated roost trees from randomly selected trees. In the model building process we used 11 of the 13 measured or calculated variables of roost and random trees outlined above (compass orientation and roost height were excluded because they did not apply to random trees). We performed correlation analyses to ensure that no pairs of variables were highly correlated (Pearson  $r > 0.70$ ). None were eliminated on this basis, so we included all 11 variables in an initial logistic regression. We used a very high alpha value ( $P > 0.35$ ) as an exclusion criterion to ensure that biologically significant variables were not removed (Hosmer and Lemeshow 1989). This preliminary exclusion step left 5 variables in the global model: distance to nearest neighbor, percentage canopy cover, canopy level score, number of trees within 30° of southeast, and number of spruce within 30° of southeast. Thirty-two subset candidate models (i.e., different combinations of the 5 variables included in the global model) were then ranked based on their  $AIC_c$  scores and AIC weights ( $w_i$ ), with lowest scores and highest weights representing the best models. AIC weight is the probability that the candidate model is the true model given the entire subset of potential models. We also calculated each variable's relative importance value. This is the sum of AIC weights for all models in which a given variable occurs and indicates the importance of a particular independent variable for differentiating the response variable (Burnham and Anderson 1992).

*Microclimate measurements.*—During the 2000 and 2002 field seasons, once roost trees were located, we climbed the trees and affixed small (1.5 cm diameter, 0.5 cm width) temperature dataloggers (accurate to ±0.5°C, iButton, Dallas Semiconductor, Dallas, Texas) so that they hung 5–10 cm below the roost branch and, horizontally, within 30 cm of the radiotagged bat. To place them in position, dataloggers were affixed to a length of monofilament fishing line and tossed out onto the roost branch. Adult female bats never flew from roosts during this process. Ambient temperature ( $T_a$ ) was recorded every h throughout the study. For comparison, we also affixed a datalogger to a branch on the opposite side of the tree from the roost site (hereafter, opposite sites). Opposite sites were the same height, and same approximate distance (within ±20 cm) from the trunk as roost sites. Radiant heating likely had little effect on our measure of  $T_a$  because all dataloggers were shaded by surrounding foliage. The reflective metal casing of the dataloggers also minimized radiant heating.

When possible, during 2001 and 2002, we recorded wind speeds at roost sites and opposite sites, and in open air at the same height, using a hand-held anemometer accurate to 0.1 m/s (factory calibrated, Kestrel 2000, Nielsen Kellerman, Chester, Pennsylvania). Within several days after a bat abandoned its roost site, we climbed the tree and affixed the anemometer to a 3-m pole. The anemometer was then positioned beneath the roost or opposite branch within 10–20 cm of the temperature datalogger so that the impeller faced directly into the wind stream, in a position that matched that of a roosting bat. The anemometer was held in place for 5 min at each location and the maximum wind speed during that 5-min period was recorded. At each roost tree, the order of measurement for roosts, opposite sites, and the open air was randomized. Wind speed measurements were taken once per tree, opportunistically between mid-July and late August. No more than 3 trees were measured on any given day. Consistently high winds

are typical of the Cypress Hills in summer, and for safety reasons we only climbed trees on moderately windy days (open-air wind speed <3.5 m/s). Thus, our measurements of wind speed likely underestimate the severity of conditions experienced by bats at their roost sites.

*Modeling thermoregulatory energy expenditure.*—Cryan and Wolf (2003) reported oxygen consumption by female hoary bats at different  $T_a$ . Based on their data, the linear relationship between resting mass-specific metabolic rate (MR) and  $T_a$  is

$$\text{MR} = -0.849(T_a) + 35.01 \quad (1)$$

where MR is a value in mW/g ( $r^2 = 0.71$ ,  $P < 0.001$ ). We used this equation to calculate thermoregulatory energy expenditure at  $T_a$  values we recorded at roost and opposite sites (temperature model).

We also predicted thermoregulatory energy costs given convective heat loss resulting from wind exposure at roost and opposite sites (convective cooling model). For this 2nd model we calculated convective heat loss as suggested by Bakken and Kunz (1988):

$$\text{Convective Heat Transfer} = H(T_{\text{fur}} - T_a). \quad (2)$$

$T_{\text{fur}}$  represents the animal's fur temperature and  $H$  is convective conductance for a sphere. This is given by

$$H = 6.84(\text{SA})(\text{Vol}^{1/3})^{-0.4}(\text{Wind Speed})^{0.6} \quad (3)$$

where SA = surface area ( $\text{m}^2$ ), Vol = volume ( $\text{m}^3$ ), and wind speed is measured in m/s (Bakken and Kunz 1988). Following Bakken and Kunz (1988), we assumed an average hoary bat was a sphere of radius 60 mm to simplify calculation of the rate of heat transfer. We used the mean wind speeds recorded at roost and opposite sites. The equation relating thermoregulatory energy expenditure and  $T_a$ , given convective cooling, becomes

$$\text{MR} = (-0.849[T_a] + 35.01) + H(T_{\text{fur}} - T_a). \quad (4)$$

Willis and Brigham (2003) reported that the average resting normothermic skin temperature ( $T_{\text{sk}}$ ) of free-ranging hoary bats was about 34°C. To calculate  $T_{\text{fur}}$  we corrected this  $T_{\text{sk}}$  value based on the insulative value of a hoary bat's pelage ( $0.32^\circ\text{C W}^{-1} \text{m}^{-2}$ , Shump and Shump 1980) at different rates of heat production (i.e., based on the MR predicted for a given  $T_a$ ).

We calculated  $T_a$  for both temperature and convective cooling models by averaging hourly roost temperatures recorded over 2-week periods during early lactation (June 15–30 2002) and late lactation (July 15–30, 2002). To account for foraging time when bats were away from the roost, we excluded temperatures recorded for 2 h starting near dusk (2200 and 2300 h). Thus, both models predict metabolic rates for 22 h of an average 24-h period. Based on our radio tracking observations, 2 h away from the roost at night during lactation is a reasonable estimate. Nights are short and  $T_a$  drops rapidly in the Cypress Hills following sunset (to <10°C and often near freezing), so foraging typically lasts for only a short time. For both models, we assumed that hoary bats had a mass of 32 g, the mean for lactating females captured during the study. Data on metabolic rates of torpid female hoary bats are not available, so we did not model energy expenditure during torpor.

*Statistical analyses.*—All analyses were performed using Systat Version 9 (SPSS Inc., 1998). We used repeated measures analysis of variance (ANOVA) to compare temperature profiles of roost versus opposite sites and analysis of covariance (ANCOVA) to compare wind speeds, with open-air wind speed as a covariate. We used paired  $t$ -tests to compare predicted daily energy expenditure between roost and opposite sites. Values are reported as means  $\pm$  SD unless stated otherwise. Orientations of roost branches were compared with a random circular distribution using Rayleigh's test (Zar 1999). For null hypothesis testing we assessed significance at  $P < 0.05$ .

## RESULTS

*Radiotracking.*—We radiotracked 21 reproductive females (3 in 2000, 9 in 2001, and 9 in 2002) and 4 volant juveniles (1 in 2000 and 3 in 2002) to a total of 32 maternity roost sites (1 individual was tracked in both 2000 and 2001). Despite spending long periods visually searching roost trees for the specific roost site, 5 of 25 lactating female bats could not be directly observed in the trees to which we tracked them. The 20 bats that were directly visible from the ground all had 2 young. Only 3 pregnant bats were captured prior to parturition (1 in 2001 and 2 in 2002).

*Physical features.*—All roost sites were at elevations below 1,200 m, where white spruce is most abundant. All roosts but 1 were found in the foliage of living white spruce trees. The single exception was a small trembling aspen tree (DBH < 10 cm) used by a lactating bat on 18 July 2001. The bat only used this tree on the day immediately following capture and her prevolant young were not present. On 19 July 2001, she and 2 pups used a white spruce tree about 200 m away and were observed there on 14 subsequent days. Therefore, we excluded the aspen tree from analyses of roost characteristics and included the white spruce maternity roost. To avoid pseudo-replication, we only included the 1st roost found for each individual during lactation in our analyses of roost characteristics. We excluded trees from the analysis if we were unable to visually locate the actual roost site in the tree. This left a sample of 19 roost trees for our analysis.

Bats typically roosted about 2 m away from the trunk of the tree on branches characterized by an umbrella of dense foliage above the roost site. Roost branches were  $12.7 \pm 3.4$  m above the ground, with an orientation of  $158.6 \pm 6.3^\circ$  SSE. Roost orientations differed significantly from a random circular distribution (Fig. 1,  $z = 7.8$ ,  $P < 0.001$ ,  $n = 19$ ).

Five of eleven variables that we measured were included in  $\text{AIC}_c$  calculations based on a preliminary logistic regression analysis (Table 1). Three of 33 candidate models of the global model were within 0.5  $\text{AIC}_c$  units of each other, which suggests that these models best distinguish roost trees from random trees (Table 2). The following variables were included in the 3 top-ranked models: percentage canopy cover, canopy level score, number of trees within  $30^\circ$  of the southeast side of the focal tree, and number of spruce trees within  $30^\circ$  of the southeast side of the focal tree. Of these, percentage canopy cover and canopy level score had the highest importance values (Fig. 2). This indicates that these variables are most important for distinguishing roost from random trees. The sum of AIC weights for the top 3 models was 0.605, which means there is a 60.5% chance that these models are true predictors of the response variable.

*Microclimate measurements.*—There were no significant differences in average daily temperature profiles between 5 roost and opposite sites during early lactation (15–30 June, Fig. 3A,  $F = 3.5$ ,  $df = 1, 8$ ,  $P = 0.10$ ) or 8 roost and opposite sites during late lactation (15–30 July, Fig. 3B,  $F = 1.9$ ,  $df = 1, 14$ ,  $P = 0.19$ ). However, there was a nonsignificant tendency for roost sites to be warmer (up to 1.5°C) in the late morning and afternoon (Fig. 3).

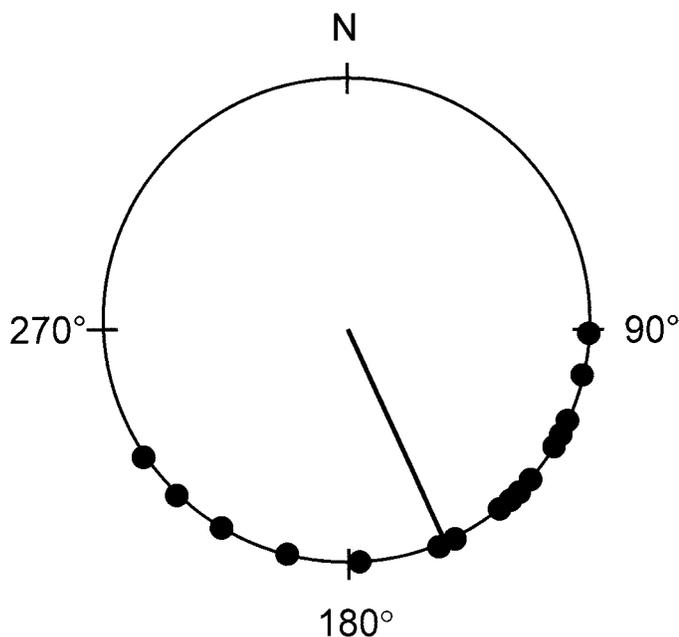


FIG. 1.—Compass orientations (corrected for true north) of branches used as roosts by 19 reproductive female hoary bats (*Lasiurus cinereus*) in Saskatchewan, Canada. A few of the roost points overlap so only 16 points appear. The solid line indicates the mean direction.

Wind speeds recorded at 16 trees were significantly lower at roost sites ( $1.0 \pm 0.4$  m/s) than at opposite sites ( $1.6 \pm 0.7$  m/s;  $F = 8.9$ ,  $df. = 1, 1, 29$ ,  $P = 0.006$ ; adjusted for the significant covariate, open-air wind speed:  $2.7 \pm 0.8$  m/s;  $F = 8.9$ ,  $df. = 1, 1, 29$ ,  $P = 0.006$ ). Despite the fact that wind speeds were measured on 11 different days over 2 years, opposite sites had higher wind speeds than roosts every time measurements were taken.

*Predicted thermoregulatory energy expenditure.*—Average hourly temperatures at roost or opposite sites were never greater than the lower critical temperature of female hoary bats

(about  $31^{\circ}\text{C}$ —Cryan and Wolf 2003). During early lactation there was a measurable difference between predicted thermoregulatory energy expenditure at roost and opposite sites based on the temperature model ( $1.02 \pm 0.94$  kJ/day), but the effect was not statistically significant (Fig. 4A,  $t = -2.6$ ,  $P = 0.06$ ,  $df. = 4$ ). However, when heat loss due to the wind was considered using the convective cooling model, there was a significant difference ( $1.60 \pm 0.99$  kJ/day) between roost and opposite sites (Fig. 4A,  $t = -3.6$ ,  $P = 0.02$ ,  $df. = 4$ ). The same pattern was observed during late lactation. There was no significant difference ( $0.67 \pm 0.99$  kJ/day) between roost and opposite sites based on modeling temperature alone (Fig. 4B,  $t = -2.2$ ,  $P = 0.07$ ,  $df. = 7$ ), but there was a significant difference ( $1.24 \pm 0.93$  kJ/day) when convective cooling was considered (Fig. 4B,  $t = -3.8$ ,  $P < 0.007$ ,  $df. = 7$ ).

## DISCUSSION

We found that lactating female hoary bats selected roost sites on southeast facing branches of living white spruce trees. Roost sites were sheltered by a dense umbrella of overhanging foliage that likely concealed bats from visual predators and could influence microclimate, as has been observed for other foliage-roosting species (Veilleux et al. 2003). The characteristics that best differentiated roost trees from random trees were a lower canopy cover in the direction of the roost branch and a greater likelihood of the roost trees being roughly equal in height to the surrounding forest canopy. Roost trees were also characterized by a reduced forest density, generally, and spruce tree density, specifically, in a wedge-shaped spatial pattern southeast of the tree. The physical features associated with roost trees likely affect microclimate. A southeast orientation, reduced canopy closure, and reduced forest density in a southeast direction could all increase sun exposure, and therefore radiant heating, especially during the cool morning hours. We were not able to measure radiant heating, but this source of energy could help reduce energetic costs if bats avoid torpor. When bats enter torpor, radiant heating could also help them arouse passively at

TABLE 1.—Characteristic features of trees ( $n = 19$ ) selected as roosts by reproductive female hoary bats and paired, randomly selected trees.  $P$  values are based on results of a preliminary logistic regression analysis comparing roost trees and random trees. Variables that met our exclusion criterion ( $P < 0.35$ ) in the preliminary analysis are indicated by an asterisk and were included in subsequent analyses.

	Tree height (m)	Diameter at breast height (cm)	Number of trees/0.045 ha plot <sup>a</sup>	Number of spruce/0.045 ha plot <sup>a</sup>	Number of trees within 30° of branch <sup>b</sup>	Number of spruce within 30° of branch <sup>b</sup>	Distance to nearest neighbor (cm)	Canopy cover (%)	Canopy level score (1–3) <sup>c</sup>	Number of trees within 30° of southeast <sup>d</sup>	Number of spruce within 30° of southeast <sup>d</sup>
Roost trees											
$\bar{X}$	21.6	43.5	31.6	23.6	2.1	1.5	228.5	40.7	1.1	2.1	1.8
$SD$	4.82	11.21	11.08	7.64	2.47	1.74	142.91	18.76	0.32	1.89	1.80
Random trees											
$\bar{X}$	20.9	42.7	28.7	17.4	2.4	1.5	182.7	62.6	1.8	3.7	2.1
$SD$	5.5	17.48	17.63	9.60	1.84	1.18	128.90	23.62	0.83	3.08	2.20
$P$ value	0.81	0.56	0.80	0.86	0.64	0.61	0.21*	0.09*	0.05*	0.25*	0.21*

<sup>a</sup> 0.045-ha plot centered on the roost or random tree.

<sup>b</sup> 30° wedge centered on the roost branch orientation.

<sup>c</sup> A score of 1–3 indicating whether the top of the roost or random tree was even with (1), above (2), or below (3) the surrounding forest canopy.

<sup>d</sup> 30° wedge facing southeast from the roost or random tree.

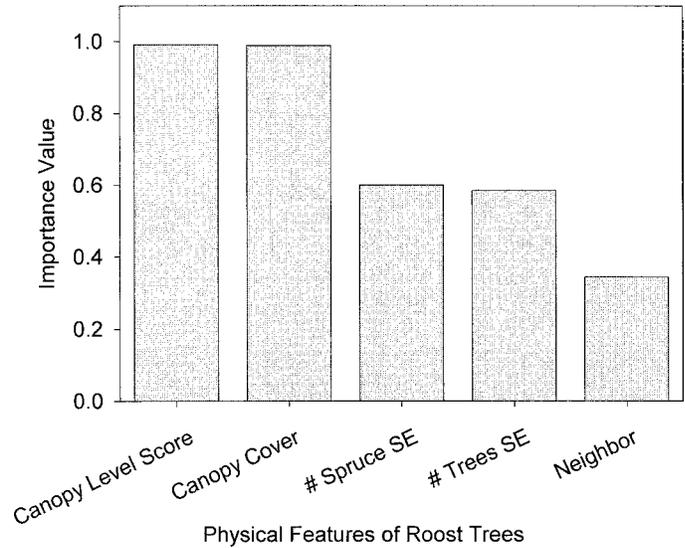
**TABLE 2.**—Akaike information criterion (AIC) results for the best 5 of 33 candidate models differentiating trees selected as roosts by reproductive female hoary bats and randomly selected trees. Each candidate model was a different combination of 5 variables measured for roost and random trees. The AIC score describes how well the candidate models differentiate roost versus random sites.  $AIC_c$  = AIC score corrected for a small sample size.  $\Delta_i$  = the difference in AIC scores between different candidate models, with the best model given a value of 0.  $w_i$  = AIC weight, which is the probability that the model is the true model given the entire set of candidate models.

Model variables	$AIC_c$	$\Delta_i$	$w_i$
Canopy cover, canopy level score, <sup>a</sup> No. of trees within 30° of southeast <sup>b</sup>	27.901	0.000	0.216183
Canopy cover, canopy level score, <sup>a</sup> No. of spruce within 30° of southeast <sup>b</sup>	27.911	0.010	0.215105
Canopy cover, canopy level score, <sup>a</sup> No. of trees within 30° of southeast, No. of spruce within 30° of southeast <sup>b</sup>	28.343	0.441	0.173386
Distance to nearest neighbor, canopy cover, canopy level score, <sup>a</sup> No. of spruce within 30° of southeast <sup>b</sup>	28.951	1.049	0.127935
Distance to nearest neighbor, canopy cover, canopy level score, <sup>a</sup> No. of trees within 30° of southeast <sup>b</sup>	29.327	1.425	0.106008
Global model (includes all 5 variables; included for comparison)	30.014	2.113	0.075173

<sup>a</sup> A score of 1–3 indicating whether the top of the roost or random tree was even with (1), above (2), or below (3) the surrounding forest canopy.  
<sup>b</sup> 30° wedge facing southeast from the roost or random tree.

a fraction of the cost of active arousal (Geiser and Drury 2003; Geiser et al. 2004). Further work with larger sample sizes incorporating measurements of solar radiation in addition to  $T_a$  is important to further clarifying the influence of microclimate on roost selection in foliage-roosting species.

We did not detect statistically significant differences in air temperature between roost sites and sites on the opposite sides of roost trees. However, there was a highly significant difference in wind speed between roost sites and opposite sites. Furthermore, roost wind speeds were lower than at opposite sites every time measurements were taken. The southeast orientation of roost sites should reduce wind exposure, given that the prevailing winds are typically from the west in southwestern Saskatchewan (Environment Canada 2003). The significant difference in wind speed that we observed between roost and opposite sites supports this hypothesis. An even height relative to surrounding canopy could also be important because roosting in trees that emerge above the canopy could result in greater wind exposure. At the landscape scale, selection of white spruce over other tree species may reflect the relative abundance of spruce at lower elevations in the Cypress Hills. Wind intensity may be greater at high elevations where aspen and lodgepole pine predominate. Several studies of avian nesting behavior have assessed the importance of wind exposure (e.g., Hartman and Oring 2003; Walsberg 1986; Wolf and Walsberg 1996). Hartman and Oring (2003) found that horned larks (*Eremophila alpestris*) orient their nests in a direction that provides them not only with increased shade in the hottest part of the day but reduced wind exposure as well. Convective cooling may be an important

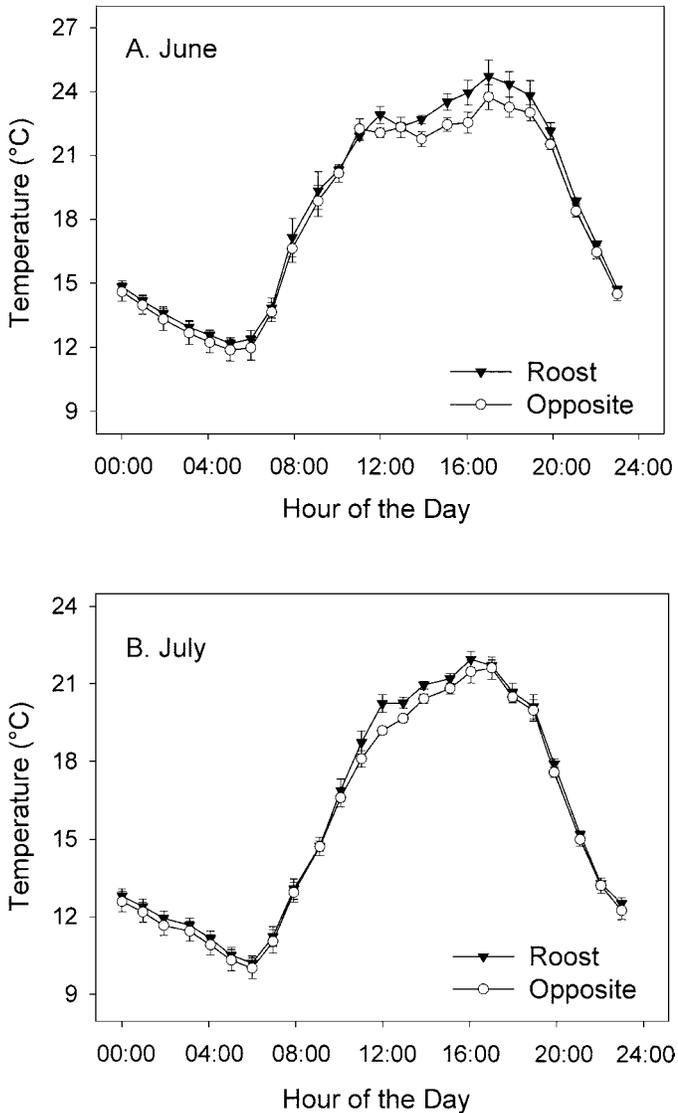


**FIG. 2.**—Importance values for the 5 variables included in the global model for Akaike information criterion (AIC) analysis. Values for each variable represent the sum of AIC weights ( $w_i$ ) for all models in which the variable occurs and indicates the relative importance of that variable in predicting the response variable.  $w_i$  is the probability that a candidate model is the true model, given the full set of candidate models. Canopy level score is a score of 1–3 indicating whether the focal tree (roost or random) was even with (1), above (2), or below (3) the surrounding forest; canopy cover refers to percentage canopy closure facing in the direction of the roost branch; number of spruce SE and number of trees SE refer to the number of spruce trees and number of trees of all species, respectively, within a 30° wedge to the southeast of the focal tree; and neighbor refers to the distance between the focal tree and the nearest neighboring tree.

factor influencing roost or nest site selection for many birds and foliage-roosting bat species.

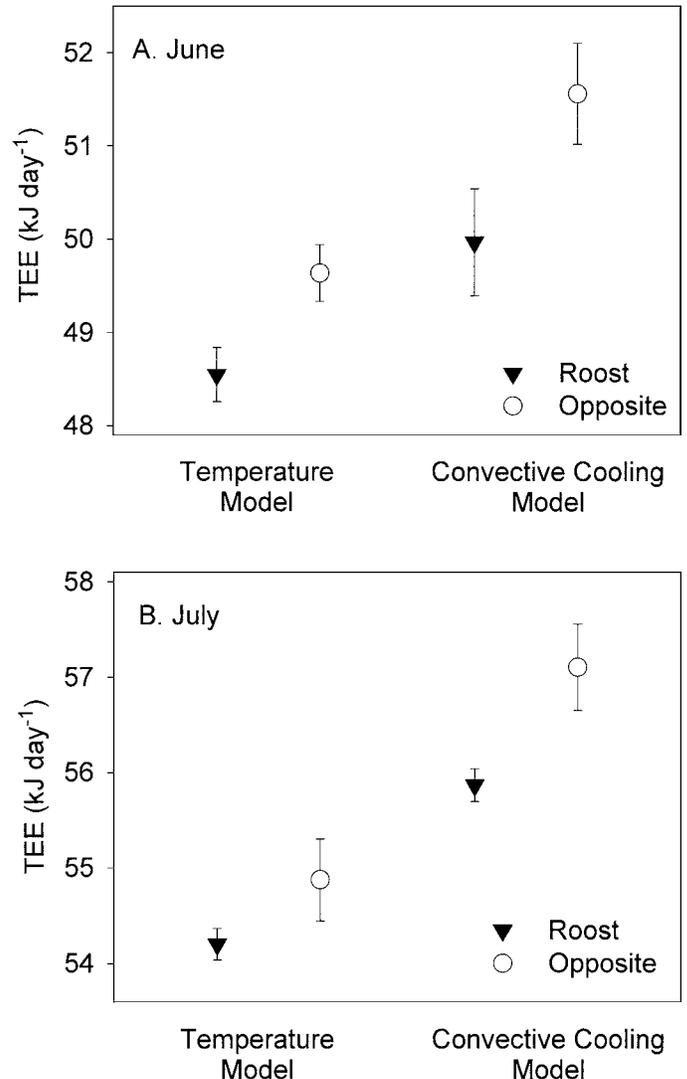
Physical features of hoary bat roost sites likely provide benefits in addition to minimizing heat loss. Reduced forest density on the southeast side of roost trees could reflect flight constraints. Hoary bats are large fast flyers with low maneuverability compared with many other forest species (Norberg and Rayner 1987). Therefore they may require a relatively open “flyway” for approaching and departing from roosts. The low tree density we observed southeast of the roost tree could represent this flyway. However, the fact that reduced forest density was oriented in a southeast direction but independent of roost branch orientation suggests that increased sun exposure may be more important than constraints on maneuverability. Woods (2002) artificially shaded free-ranging common poor-wills (*Phalanoptilus nuttallii*) to determine the influence of sun exposure on torpor patterns during hibernation. It would be interesting to take this approach with hoary bats and test the importance of the flyway concept by manipulating the degree of forest clutter and the degree of shading of hoary bat roosts.

Forest-living bats switch roost sites frequently (Kalcounis and Brigham 1998; Kurta et al. 2002; Menzel et al. 1998; Veilleux et al. 2003; Willis and Brigham 2004). Miller et al. (2003) note that virtually all studies to date have treated “roost tree,” and not “bat,” as the sampling unit (Hutchinson and



**FIG. 3.**—Average daily temperature profiles (mean °C ± SE) at roosts selected by reproductive female hoary bats (roost, closed triangles) and at sites on the opposite sides of the same trees (opposite, open circles), recorded for A) 5 trees during early lactation from 15 to 30 June 2003 and B) 8 trees during late lactation from 15 to 30 July 2003 (B).

Lacki 2000; Kalcounis and Brigham 1998; Mager and Nelson 2001; Menzel et al. 1998; Sedgely and O'Donnell 1999; Vonhof and Barclay 1996). For example, if 1 individual is tracked to 8 different trees over the life of its transmitter, while another is tracked to 2 trees, all 10 trees are treated as independent observations. Clearly, these trees are not equally independent, and results of such studies will be biased if individuals differ in their roost preferences. Pseudoreplicated studies that use this approach are still valuable from a metareplication perspective (Johnson 2002), but they may be less informative than studies that control for individual-specific preferences. Only a few bats switched roosts in our study, but, to be conservative, we only analyzed data for the 1st roost found for each individual during lactation (with the aspen tree exception).



**FIG. 4.**—Predicted daily thermoregulatory energy expenditure (TEE; mean ± SE) at roosts selected by reproductive female hoary bats (roost, closed triangles) and at sites on the opposite sides of the same trees (opposite, open circles). Values are based on temperatures recorded for A) 5 trees during early lactation from 15 to 30 June 2003 and B) 8 trees during late lactation from 15 to 30 July 2003. Values were predicted based on the temperature model of predicted thermoregulatory energy expenditure and the convective cooling model that accounted for wind exposure. See text for model equations.

*Predicted thermoregulatory energy expenditure.*—Roost sites selected by lactating hoary bats resulted in statistically significant energetic savings (up to 1.60 kJ/day) relative to sites on the opposite sides of trees. Using Bell's (1990) conversion factor, on an average day early in the 2002 lactation period, a female hoary bat would have saved the equivalent of up to 0.6 g of fresh insects (about 4 large sphinx moths, a common prey item of hoary bats in the Cypress Hills) during early lactation and 0.5 g during late lactation. This supports the conclusion that lactating hoary bats make roost selection decisions on the basis of microclimate. Based on field metabolic rate (FMR) data, free-ranging big brown bats (*Eptesicus fuscus*) expend

about 10 times basal metabolic rate (BMR) on an average day during lactation (Kurta et al. 1989). The BMR calculated by Cryan and Wolf (2003) for female hoary bats was about 14.5 kJ/day. Assuming similar rates, a free-ranging, lactating hoary bat should expend about 145 kJ/day. An energy saving of 1.60 kJ/day does not represent a large percentage of this approximate FMR. However, even small energy savings may be important to individuals facing strict energy budgets, and 1.60 kJ/day could help mother bats reduce their rate of mass loss during lactation. Furthermore, our prediction likely underestimates the energy savings afforded by roost sites because we were unable to incorporate a radiant heating component in our calculations. As mentioned above, solar radiation can have tremendous implications for energy expenditure in endotherms (Bakken and Kunz 1988; Geiser and Drury 2003; Geiser et al. 2004) and could result in considerable energy savings for hoary bats on the southeast side of roost trees.

The calculations we used to predict thermoregulatory energy expenditure simplify reality based on assumptions that may have influenced our results. One assumption was that bats do not use torpor while lactating. Hoary bats have been observed to use torpor during lactation (Hickey and Fenton 1996; Koehler 1991; Willis, in press), although preliminary data suggest they use it much less than during pregnancy (Willis, in press). In general, bats appear to avoid deep torpor during lactation presumably due to selection pressure for rapid growth of offspring (Willis, in press). This pressure is likely relaxed for hoary bats relative to other temperate species (Koehler and Barclay 2000), but their young must still reach a certain size within a finite time period before embarking on migration. Thus, it is reasonable to predict that hoary bats will avoid torpor if their roost sites help them stay warm at a reduced energetic cost.

For the purpose of modeling the energetic implications of convective cooling, we assumed that wind speed remained constant at roost and opposite sites throughout each 2-week period. Wind speed assuredly changes within and between days. We took several measures to minimize potential error resulting from this assumption. First, we did not measure wind speeds on the windiest days to avoid overestimating convective cooling. Second, we sampled a range of conditions by recording wind speed on 11 different days over 2 years, as opposed to recording all measurements on 1 day. Third, we used average wind speeds, rather than maximum values, as inputs to the convective cooling model, which is also conservative because it will underestimate cooling effects.

Despite these assumptions, the energetic costs that we predicted are consistent with results of previous studies. The average thermoregulatory energy expenditure at roost sites predicted by our convective cooling model was  $55.87 \pm 0.49$  kJ/day, over a third of the estimate of daily energy expenditure calculated from BMR above. This is reasonable given that we have only considered thermoregulatory plus basal energy expenditure and not other metabolic costs, such as foraging and flight, lactation, and digestion, which are known to represent a large percentage of the daily energy budget in other temperate bats (Kurta et al. 1989, 1990).

Most previous studies have found that cavity roosting bats select trees that are taller and of greater DBH than randomly selected nonroost trees (Kalcounis and Brigham 1998; Vonhof and Barclay 1996), and this pattern holds for foliage-roosting eastern red bats as well (*Lasiurus borealis*—Hutchinson and Lacki 2000; Mager and Nelson 2001; Menzel et al. 1998). However, these variables did not reliably distinguish roost trees from random trees for hoary bats in our study, illustrating that features associated with habitat use in 1 area may not reflect broad criteria for habitat preferences. As suggested by Sedgeley (2001), if studies addressing roost preferences of bats, or habitat requirements of any species, are to be applied broadly in a management context, it is important to characterize preferences accurately and control for site-specific covariates like weather and climate. For studies of roost selection by bats, measuring microclimate conditions at roost sites and determining whether roosts provide energetic benefits may be a useful approach for determining the applicability of results from 1 region to another.

#### ACKNOWLEDGMENTS

We acknowledge financial support provided by the American Society of Mammalogists, Mountain Equipment Co-op, Saskatchewan Environment and Resource Management, the University of Regina, and Natural Sciences and Engineering Research Council (Canada). J. Gruver, B. Haennel, A. Kurta, M. Weisbart, members of the University of Regina Bird and Bat lab, and 2 anonymous reviewers provided helpful comments on earlier drafts of the manuscript. J. Adams, R. Fisher, Q. Fletcher, A. Karst, K. Kolar, S. Martinez, M. Ranalli, C. Voss, and M. Yaremko provided outstanding field help. We are also very grateful to P. Cryan and B. Wolf for sharing their metabolic data with us.

#### LITERATURE CITED

- ALCOCK, J. 2001. Animal behavior. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.
- ALDRIDGE, H. D. J. N., AND R. M. BRIGHAM. 1988. Load carrying and maneuverability in an insectivorous bat: a test of the 5% 'rule' of radio telemetry. *Journal of Mammalogy* 69:379–383.
- ANDERSON, D. R., K. P. BURNHAM, AND W. L. THOMPSON. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management* 64:912–923.
- ANTHONY, E. L. 1988. Age determination in bats. Pp. 47–58 in *Ecological and behavioral methods for the study of bats* (T. H. Kunz, ed.). Smithsonian Institution Press, Washington, D.C.
- BAKKEN, G. S., AND T. H. KUNZ. 1988. Microclimate methods. Pp. 303–332 in *Ecological and behavioral methods for the study of bats* (T. H. Kunz, ed.). Smithsonian Institution Press, Washington, D.C.
- BARCLAY, R. M. R., AND R. M. BRIGHAM. 1996. Proceedings of the First International Bat-Forest Interactions Symposium, Victoria, British Columbia, 19–21 October 1995, Research Branch, British Columbia Ministry of Forests Working Paper Number 23/1996. British Columbia Ministry of Forests, Victoria, British Columbia, Canada.
- BELL, G. P. 1990. Birds and mammals on an insect diet: a primer on diet composition analysis in relation to ecological energetics. *Studies in Avian Biology* 13:416–422.
- BRIGHAM, R. M., M. J. VONHOF, R. M. R. BARCLAY, AND J. C. GWILLIAM. 1997. Roosting behavior and roost-site preferences of

- forest-dwelling California bats (*Myotis californicus*). *Journal of Mammalogy* 78:1231–1239.
- BURNHAM, K. P., AND D. R. ANDERSON. 1992. Data-based selection of an appropriate biological model: the key to modern data analysis. Pp. 16–30 in *Wildlife 2001: populations*. Elsevier Science, London, United Kingdom.
- CHRUSZCZ, B. J., AND R. M. R. BARCLAY. 2002. Thermoregulatory ecology of a solitary bat, *Myotis evotis* roosting in rock crevices. *Functional Ecology* 16:18–26.
- CONSTANTINE, D. G. 1966. Ecological observations on lasiurine bats in Iowa. *Journal of Mammalogy* 47:34–41.
- CRYAN, P. M., AND B. O. WOLF. 2003. Sex differences in the thermoregulation and evaporative water loss of a heterothermic bat, *Lasiurus cinereus*, during its spring migration. *Journal of Experimental Biology* 206:3381–3390.
- ENVIRONMENT CANADA. 2003. Canadian climate data web site [http://www.climate.weatheroffice.ec.gc.ca/climateData/canada\\_e.html](http://www.climate.weatheroffice.ec.gc.ca/climateData/canada_e.html).
- GEISER, F., AND R. L. DRURY. 2003. Radiant heat affects thermoregulation and energy expenditure during rewarming from torpor. *Journal of Comparative Physiology, B. Biochemical, Systematic, and Environmental Physiology* 173:55–60.
- GEISER, F., R. L. DRURY, G. KÖRTNER, C. TURBILL, C. R. PAVEY, AND R. M. BRIGHAM. 2004. Passive rewarming from torpor in mammals and birds: energetic, ecological and evolutionary implications. Pp. 209–219 in *Life in the cold: evolution, mechanisms, adaptation, and application* (B. M. Barnes and H. V. Carey eds.). Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, Alaska.
- HAMILTON, I. M., AND R. M. R. BARCLAY. 1994. Patterns of daily torpor and day-roost selection by male and female big brown bats (*Eptesicus fuscus*). *Canadian Journal of Zoology* 72:744–749.
- HARTMAN, C. A., AND L. W. ORING. 2003. Orientation and microclimate of horned lark nests: the importance of shade. *Condor* 105:158–163.
- HICKEY, B. B. C., AND M. B. FENTON. 1996. Behavioural and thermoregulatory responses of female hoary bats, *Lasiurus cinereus* (Chiroptera: Vespertilionidae), to variations in prey availability. *Ecoscience* 3:414–422.
- HOSMER, D. W., AND S. LEMESHOW. 1989. *Applied logistic regression*. John Wiley & Sons, Inc., New York.
- HUTCHINSON, J. T., AND M. J. LACKI. 2000. Selection of day roosts by red bats in mixed mesophytic forests. *Journal of Wildlife Management* 64:87–94.
- JOHNSON, D. H. 2002. The importance of replication in wildlife research. *Journal of Wildlife Management* 66:919–932.
- KALCOUNIS, M. C. 1994. Selection of tree roosts by big brown (*Eptesicus fuscus*), little brown (*Myotis lucifugus*) and hoary (*Lasiurus cinereus*) bats in Cypress Hills, Saskatchewan. *Bat Research News Winter* 103.
- KALCOUNIS, M. C., AND R. M. BRIGHAM. 1998. Secondary use of aspen cavities by tree-roosting big brown bats. *Journal of Wildlife Management* 62:603–611.
- KERTH, G., K. WEISSMANN, AND B. KÖNIG. 2001. Day roost selection in female Bechstein's bats (*Myotis bechsteini*): a field experiment to determine the influence of roost temperature. *Oecologia* 126:1–9.
- KOEHLER, C. E. 1991. The reproductive ecology of the hoary bat (*Lasiurus cinereus*) and its relation to litter size variation in vespertilionid bats. M.S. thesis. University of Calgary, Calgary, Alberta, Canada.
- KOEHLER, C. E., AND R. M. R. BARCLAY. 2000. Post-natal growth and breeding biology of the hoary bat (*Lasiurus cinereus*). *Journal of Mammalogy* 81:234–244.
- KUNZ, T. H. 1987. Post-natal growth and energetics of suckling bats. Pp. 395–420 in *Recent advances in the study of bats* (M. B. Fenton, P. Racey, and J. M. V. Rayner, eds.). Cambridge University Press, Cambridge, United Kingdom.
- KUNZ, T. H., AND L. F. LUMSDEN. 2003. Ecology of cavity and foliage roosting bats. Pp. 2–90 in *Bat ecology* (T. H. Kunz and M. B. Fenton, eds.). University of Chicago Press, Chicago, Illinois.
- KURTA, A., G. P. BELL, K. A. NAGY, AND T. H. KUNZ. 1989. Energetics of pregnancy and lactation in free-ranging little brown bats (*Myotis lucifugus*). *Physiological Zoology* 62:804–818.
- KURTA, A., T. H. KUNZ, AND K. A. NAGY. 1990. Energetics and water flux of free-ranging big brown bats (*Eptesicus fuscus*) during pregnancy and lactation. *Journal of Mammalogy* 71:59–65.
- KURTA, A., S. W. MURRAY, AND D. H. MILLER. 2002. Roost selection and movement across the summer landscape. Pp. 118–129 in *The Indiana bat: biology and management of an endangered species* (A. Kurta and J. Kennedy, eds.). Bat Conservation International, Austin, Texas.
- LAUSEN, C. L., AND R. M. R. BARCLAY. 2003. Thermoregulation and roost selection by reproductive female big brown bats (*Eptesicus fuscus*) roosting in rock crevices. *Journal of Zoology (London)* 260:235–244.
- MAGER, K. J., AND T. A. NELSON. 2001. Roost-site selection by eastern red bats (*Lasiurus borealis*). *American Midland Naturalist* 145: 120–126.
- MENZEL, M. A., T. C. CARTER, B. R. CHAPMAN, AND J. LAERM. 1998. Quantitative comparison of tree roosts used by red bats (*Lasiurus borealis*) and seminole bats (*L. seminolus*). *Canadian Journal of Zoology* 76:630–634.
- MILLER, D. A., E. B. ARNETT, AND M. J. LACKI. 2003. Habitat management for forest roosting bats of North America: A critical review of habitat studies. *Wildlife Society Bulletin* 31:30–44.
- NAGORSEN, D., AND R. M. BRIGHAM. 1993. *Bats of British Columbia*. University of British Columbia Press, Vancouver, British Columbia, Canada.
- NORBERG, U. M., AND J. M. V. RAYNER. 1987. Ecological morphology of flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society of London* 316:335–477.
- O'DONNELL, C. F. J., AND J. A. SEDGELEY. 1999. Use of roosts by the long-tailed bat (*Chalinolobus tuberculatus*) in temperate rainforest in New Zealand. *Journal of Mammalogy* 80:813–923.
- RACEY, P. A., AND S. M. SWIFT. 1981. Variations in gestation length in a colony of pipistrelle bats (*Pipistrellus pipistrellus*) from year to year. *Journal of Reproduction and Fertility* 61:123–129.
- SAUCHYN, D. J. 1993. Quaternary and late Tertiary landscape evolution in the western Cypress Hills. Pp. 46–58 in *Quaternary and late Tertiary landscapes of southwestern Saskatchewan and adjacent areas*. (D. J. Sauchyn, ed.). Canadian Plains Research Centre, Regina, Saskatchewan, Canada.
- SEDGELEY, J. A. 2001. Quality of cavity microclimate as a factor influencing selection of maternity roosts by a tree-dwelling bat, *Chalinolobus tuberculatus*, in New Zealand. *Journal of Applied Ecology* 38:425–438.
- SEDGELEY, J. A., AND C. F. J. O'DONNELL. 1999. Roost selection by the long-tailed bat, *Chalinolobus tuberculatus*, in temperate New Zealand rainforest and its implications for the conservation of bats in managed forests. *Biological Conservation* 88:261–276.
- SHUMP, K. A., JR., AND A. U. SHUMP. 1980. Comparative insulation in vespertilionid bats. *Comparative Biochemistry and Physiology, A. Comparative Physiology* 66:351–354.

- SHUMP, K. A., JR., AND A. U. SHUMP. 1982. *Lasiurus cinereus*. Mammalian Species 185:1–5.
- THOMAS, D. W., M. DORAIS, AND M. J. BERGERON. 1990. Winter energy budgets and costs of arousals for hibernating little brown bats. *Journal of Mammalogy* 71:474–475.
- TURBILL, C., B. S. LAW, AND F. GEISER. 2003. Summer torpor in a free-ranging bat from subtropical Australia. *Journal of Thermal Biology* 28:223–226.
- TUTTLE, M. D., AND D. STEVENSON. 1982. Growth and survival of bats. Pp. 105–150 in *Ecology of bats* (T. H. Kunz, ed.). Plenum Press, New York.
- VEILLEUX, J. P., J. O. WHITAKER, AND S. L. VEILLEUX. 2003. Tree-roosting ecology of reproductive female eastern pipistrelles, *Pipistrellus subflavus*, in Indiana. *Journal of Mammalogy* 84:1068–1075.
- VONHOF, M. J., AND R. M. R. BARCLAY. 1996. Roost-site selection and roosting ecology of forest-dwelling bats in southern British Columbia. *Canadian Journal of Zoology* 74:1797–1805.
- WALSBERG, G. E. 1986. Thermal consequences of roost-site selection: the relative importance of three modes of heat production. *Auk* 103:1–7.
- WIEBE, K. L. 2001. Microclimate of tree cavity nests: is it important for reproductive success in northern flickers? *Auk* 118:412–421.
- WILDE, C. J., C. H. KNIGHT, AND P. A. RACEY. 1999. Influence of torpor on milk protein composition and secretion in lactating bats. *Journal of Experimental Zoology* 284:35–41.
- WILLIS, C. K. R. in press. Daily heterothermy in temperate bats using natural roosts. In *Functional and evolutionary ecology of bats: Proceedings of the 12th international bat research conference*. (Z. Akbar, G. F. McCracken, and T. H. Kunz, eds.). Oxford University Press, New York.
- WILLIS, C. K. R., AND R. M. BRIGHAM. 2003. Defining torpor in free-ranging bats: experimental evaluation of external temperature-sensitive radiotransmitters and the concept of active temperature. *Journal of Comparative Physiology, B. Biochemical, Systematic, and Environmental Physiology* 173:379–389.
- WILLIS, C. K. R., AND R. M. R. BRIGHAM. 2004. Roost switching, roost sharing and social cohesion: forest dwelling big brown bats (*Eptesicus fuscus*) conform to the fission-fusion model. *Animal Behaviour* 68:495–505.
- WOLF, B. O., AND G. E. WALSBERG. 1996. Thermal effects of radiation and wind on a small bird and implications for microsite selection. *Ecology* 77:2228–2236.
- WOODS, C. P. 2002. Ecological aspects of torpor use and winter dormancy by Common Poorwills. Ph.D. dissertation, University of Regina, Regina, Saskatchewan, Canada.
- ZAR, J. H. 1999. *Biostatistical analysis*. Prentice Hall, Inc., Upper Saddle River, New Jersey.

Submitted 20 February 2004. Accepted 8 June 2004.

Associate Editor was Ronald D. Gettinger.