Social thermoregulation exerts more influence than microclimate on forest roost preferences by a cavity-dwelling bat

Craig K. R. Willis · R. Mark Brigham

Abstract Nest or roost temperature (T_{roost}) is thought to impact reproductive fitness in many endotherms but few studies have directly tested the hypothesis that naturally occurring variability in nest or roost microclimate is large enough to affect reproductive success. We conducted a field experiment to test whether roost selection by cavity-dwelling, reproductive female big brown bats (*Eptesicus fuscus*) is more strongly influenced by roost microclimate or a physical characteristic of roosts that facilitates social thermoregulation (i.e., cavity volume). We quantified spatial variability in T_{roost} within different-sized, unoccupied cavities and also recorded T_{roost} in occupied vs unoccupied roost trees. We used equations relating energy use and ambient temperature for big brown bats to calculate values of daily energy expenditure from T_{roost} data because energy is a currency that likely affects reproductive fitness. We found no difference between maximum and minimum T_{roost}, spatial variability in T_{roost}, or predicted energy expenditure in more-preferred vs less-preferred roosts. However, there was a significant difference between T_{roost} and predicted energy expenditure when we compared occupied vs unoccupied roosts. The presence of bats increased T_{roost} by as much as 7°C, and there was a significant positive correlation between the number of bats occupying a roost, maximum daily T_{roost}, and energy savings. We calculate that, on average, a normothermic individual would save about 6.5 kJ/day (roughly 9% of the daily energy budget) by roosting in an occupied cavity relative to roosting alone and that savings may increase to 40 kJ/day (about 53% of the energy budget) for an individual roosting in a group of 45 bats. Our findings suggest that variability in microclimate among potential roost or nest sites may be less important to some cavity-dwelling endotherms than has been suggested in previous studies. Our results reinforce the importance of sociality and social thermoregulation to the roosting ecology of forest-living bats and socially roosting or nesting endotherms in general.

Keywords Chiroptera · Energetics · Roost selection · Huddling

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Introduction

Decisions made by animals about where to shelter while resting and rearing young have obvious implications for reproductive fitness. Microclimate has commonly been suggested as a criterion underlying the preferences of endotherms for some nest or roost sites over others and has been linked to habitat preferences in many species (e.g., Entwistle et al. 1997; Nelson and Martin 1999; Martin 2001; Sedgeley 2001; Wiebe 2001; Russell et al. 2002; Hartman and Oring 2003; Willis and Brigham 2005). Among birds and mammals, however, few field studies

have directly tested whether natural differences in roost or nest temperature between preferred and less-preferred sites are large enough to influence reproductive success. Some studies which have compared microclimates have uncovered unexpected results. For example, Lloyd and Martin (2004) found that differences in microclimate at preferred nest sites of Chestnut-collared Longspurs (*Calcarius ornatus*) were likely detrimental in terms of fitness as nestlings raised in preferred, high-temperature sites grew more slowly and reached a smaller final size. Wiebe (2001) tested the microclimate hypothesis for tree-cavity nesting Northern Flickers (*Colaptes auratus*) and found a weak effect of nest temperature on clutch size. However, there was no effect of microclimate on the numbers of eggs hatched or nestlings fledged, which means that differences in clutch size did not directly translate into fitness differences. Wiebe (2001) argued that low thermal conductance resulting from a large body size, coupled with biparental care in flickers, could mitigate their energetic and, therefore, microclimate requirements. In these and other systems, it could also be that differences in microclimate between potentially available nest or roost structures are insufficient to result in differential reproductive success (Wiebe 2001).

In contrast to Northern Flickers, cavity-roosting temperate bats are small bodied, and females, alone, provide parental care. Many insectivorous bats use torpor to save energy during inclement weather and/or periods with reduced prey availability even during summer (Audet and Fenton 1988; Hamilton and Barclay 1994; Chruszcz and Barclay 2002; Lausen and Barclay 2003; Turbill et al. 2003a, b; Willis et al. 2006a). However, reproductive females appear to face strong selection pressure to remain warm because cold roost temperatures (T_{roost}) and torpor slow the development of prenatal and juvenile bats (Racey 1973; Racey and Swift 1981; Tuttle and Stevenson 1982; Wilde et al. 1999). Thus, while torpor results in energy savings for females, it can negatively impact juvenile overwinter survival and mother/offspring fitness (Kunz 1987; Thomas et al. 1990). A small body size coupled with uniparental care means that thermal constraints faced by reproductive females are likely extreme. Therefore, as a group, cavity-roosting bats are well suited to testing hypotheses about microclimate as a motivating factor for habitat selection. Recent studies demonstrate that female bats do employ torpor while reproductive but they are more likely to express deep torpor during pregnancy relative to lactation, possibly due to higher thermoregulatory costs and reduced foraging efficiency while pregnant (Kerth et al. 2001a; Chruszcz and Barclay 2002; Lausen and Barclay 2003; Willis 2006). Outside of winter, lactation is the period during which temperate bats likely face the most pronounced energetic bottleneck because of high costs of milk production (Kurta et al. 1989, 1990). This means that, if bats can save energy by selecting roosts with favorable microclimates, they would be expected to do so during lactation when they likely face the greatest challenge to balancing energy budgets.

Roosts represent critical habitat for many bat populations, and most of the roughly 1,000 species use trees or other plants as roosts (Kunz and Lumsden 2003). Therefore, understanding roost requirements of forest-dwelling bats is critical to understanding their behavior and ecology. A standard presence–absence paradigm is typically used to study roost selection by forest bats where individuals are radiotracked to roost sites and features of roost trees (e.g., height, diameter at breast height (DBH), canopy cover, etc.) are compared to those of randomly selected presumably nonroost trees (e.g., Vonhof and Barclay 1996; Brigham et al. 1997; Sedgeley and O'Donnell 1999; Broders and Forbes 2004; Willis and Brigham 2005). A meta-analysis of these studies indicated that, in general, cavity-living bats prefer relatively tall trees of large diameter in areas of forest with an open canopy and high density of snags (Kalcounis-Rüppell et al. 2005). Most of the roost vs nonroost studies of forest-living bats have proposed that at least some of the statistically significant features differentiating roost from random trees correlate with T_{roost}. To date, however, few have tested this hypothesis by measuring T_{roost}, and fewer still have tested whether differences in roost microclimate are large enough to affect a currency relevant to fitness, such as energy use (but see Kalcounis and Brigham 1998; Sedgeley 2001; Willis and Brigham 2005). Entwistle et al. (1997) studied *Plecotus auritus* roosting in buildings and found that, on average, attic roosts were about 1°C warmer than nonroost attics and that this temperature difference would result in energy savings of about 1 kJ/day (4% of the roosting energy budget). In one of the few studies to assess microclimate differences between tree cavities available to bats, Sedgeley (2001) working in a New Zealand forest found significant temperature differences between roost and nonroost sites large enough to influence energy use by *Chalinolobus tuberculatus*. However, it remains unclear if natural variability in microclimate between different potential roost sites in forests is consistently large enough to affect energy expenditure. We propose that, for many cavity-roosting bats, the benefits of social thermoregulation may be more important than benefits associated with differences in microclimate between different potential roost cavities. The presence of multiple animals can warm the microenvironment significantly, and clustering can reduce thermal conductance or heat loss (e.g., Fleming 1980, 1985; Burnett and August 1981; Roverud and Chappell 1991; Hayes et al. 1992). Thus, social thermoregulation likely exerts a strong influence on energy expenditure.

The big brown bat (*Eptesicus fuscus*) is a common vespertilionid that ranges from southern Canada to north-west South America (Kurta and Baker 1990). In our study area, female big brown bats form maternity groups in hollow trembling aspen trees (*Populus tremuloides*) and conform to a fission–fusion colony structure (Willis and Brigham 2004). Bats switch roost trees about every 2 days throughout the summer but remain loyal to roosting areas of forest, reusing the same trees within and between years (Kalcounis and Brigham 1998; Willis and Brigham 2004). The colony of bats in an area of forest is usually divided among multiple trees, and groups of bats do not necessarily switch roosts together. Indeed, one function of roost switching in this system may be to break up colony subgroups and to allow opportunities for day–roost associations between more different individuals within the larger colony (Willis and Brigham 2004). Sharing of day roosts is strongly influenced by preferences of individuals for each other or active associations (Willis and Brigham 2004). However, sharing may also be influenced by passive associations if multiple bats select the same roosts at the same time because of preferences for roost characteristics such as microclimate. The presence–absence protocol described above has little value for identifying roost preferences in our study system because bats appear to use all potential trembling aspen tree cavities in their roosting area as they switch from tree to tree (Kalcounis and Brigham 1998; Willis and Brigham 2004). Willis et al. (2006b) used a different approach incorporating the length of time that bats used individual trees and the sizes of roosting groups to show that bats prefer tree cavities with relatively large volumes. Specifically, bats used trees with crevice openings (long vertical openings in the trunks of trees; hereafter referred to as crevices) or multiple circular holes in the trunk more often than predicted based on the availability of those trees, and trees with just a single circular opening less often than expected. Trees with crevices and multiple holes had cavities with large internal volumes, whereas single-hole trees had much smaller cavities. Moreover, the size of roosting groups was positively correlated with cavity volume (Willis et al. 2006b).

Our aim was to better understand the importance of microclimate for roost or nest-site selection in endotherms by studying the roosting ecology of big brown bats. We tested three hypotheses to account for the preference of this species for large-volume cavities: (1) Large cavities are warmer than other cavities; (2) large cavities provide greater spatial variation in T_{roost} at any given time so that bats can move inside the roost to remain as close to thermoneutrality as possible (Vaughan and O'Shea 1976; Willis 2006); or (3) large cavities allow for larger clusters of bats which would increase T_{roost} and reduce energy costs

(Roverud and Chappell 1991). We tested these hypotheses using a simple field experiment in which we recorded T_{roost} at different positions within occupied and vacant tree-roost cavities. By itself, temperature reveals little about reproductive fitness implications of preferred roost sites, so we used the relationship between metabolic rate and ambient temperature (T_a) in big brown bats to model the energy use of bats exposed to microclimate conditions in different roosts. While the use of energy is not a direct measure of fitness, maintaining a balanced energy budget (on some timescale) is crucial for survival and reproduction. Therefore, predictions about energy expenditure may strengthen inferences about the implications of preferred roosts for survival and reproductive success (Willis and Brigham 2005).

Materials and methods

The University of Regina President's Committee on Animal Care approved all protocols, which met guidelines set by the Canadian Council for Animal Care. We conducted fieldwork in Cypress Hills Provincial Park, Saskatchewan, Canada (49°34′ N, 109°53′ W) between 1 June and 20 August 2000–2002. Details of the study area are described by Willis and Brigham (2004). We captured big brown bats in mist nets as they emerged from their roost trees and, occasionally, when they were foraging. We did not net at roost sites more frequently than once every 7 days (mean = 15.6±8.5, range=7–30 days) to avoid undue disturbance. Males were rarely captured in the study area (two males were caught at foraging areas, and none was captured during roost tree netting sessions over the course of the study), and thus all the data we report are for adult females. We identified pregnant females by gently palpating the abdomen. Expression of milk or bare patches around the nipples was taken to indicate lactation. Based on the reproductive status of the majority of bats captured at roosts, we divided each year of the study into early pregnancy, pregnancy, and lactation periods. In each year, we defined the start of the pregnancy period by the first capture of a palpably pregnant bat (12–18 June) and the start of lactation by the first capture of a lactating bat (6–16 July). We designated the first period as early pregnancy because at this time of the year, females likely carried embryos too small for us to detect.

We distinguished adults from volant young based on fusion of the phalangeal epiphyses (Anthony 1988). We outfitted adult females with numbered, plastic, split-ring forearm bands (4 mm diameter, National Band and Tag, Newport, KY, USA) and 0.7 g radio transmitters (BD-2T, Holohil Systems, ON, Canada). We trimmed a small area of dorsal fur and attached transmitters to the skin between the

scapulae using surgical adhesive (Skin-Bond, Smith and Nephew United, Largo, FL, USA). Transmitter mass did not exceed 5% of a bat's body mass (Aldridge and Brigham 1988). We released bats within several hours of capture and tracked them to roosts on as many days as possible using hand-held telemetry receivers (R-1000, Communication Specialists, Orange, CA, USA) and five-element Yagi antennas (AF Antronics, Urbana, IL, USA). We watched roost trees at dusk to confirm the presence of bats and count the number that emerged. We used heavy gauge wire to measure the internal dimensions of vacant roost cavities and, from these dimensions, calculated cavity volume as described by Willis et al. (2006b).

In mid-May 2002, before bats returned to the study area for the summer, we climbed trees and inserted temperature dataloggers (iButton Thermocron, Dallas Semiconductor, Dallas, TX, USA), suspended on monofilament line, into 19 roost trees identified during the previous 2 years. All trees were located within one <2 km^2 roosting area of forest (roosting area 1, see Willis and Brigham 2004). To sample a range of cavity volumes, we placed dataloggers in nine trees with crevice openings, five trees with multiple holes, and five trees with just a single hole. To standardize datalogger placement, we drilled 2.5-cm-diameter holes into roost trees within 15 cm of the top and 15 cm of the bottom of roost cavities. For cavities less than 45 cm in height, only one centrally placed hole was drilled into the roost. For cavities greater than 80 cm in height, we drilled a third hole, halfway between the top and bottom holes, and for a few long cavities (>1.5 m), four holes were drilled at evenly spaced intervals along the trunk. A datalogger was inserted into each opening so that it hung inside the cavity, 1 cm below the hole, in contact with the inner wall of the cavity. We confirmed the position of each datalogger inside the cavity by sight and also by touch through the drilled hole. We inserted tight-fitting corks into each hole to minimize changes to the thermal properties of cavities. This procedure did not alter the roosting behavior of bats, and roosting groups continued to reuse trees with and without dataloggers. Dataloggers were programmed to record T_{roost} every hour for the duration of the summer. All roost cavities were at least 1–5 m below the forest canopy and were shaded by overhead foliage for much of the day, so direct sunlight was unlikely to influence T_{roost} measurements. We checked trees outfitted with dataloggers about once per week from the ground to ensure that dataloggers and corks remained in place. We also climbed each tree twice in July and August to check the dataloggers. An additional data-logger was placed in a shaded location central to all the roost trees to record T_{a}.

For calculations of microclimate variability and to predict thermoregulatory energy expenditure in cavities of different volume, we excluded data for days when we knew

trees were occupied based on radiotracking data or direct observations. We used the data from occupied trees to determine if the presence of bats affected T_{roost}. We observed trees to which we did not track bats at dusk to confirm they were vacant but it was not possible to check each tree every day. Therefore, some trees classified as "unoccupied" may have been used as roosts by non-radiotagged bats. However, during 2002, we radiotracked at least three individuals every day of the study, and even on days when as many as eight bats were tracked, the colony never used more than three different roost trees from among the tens to hundreds of potential roosts in the roosting area. Furthermore, on all days that we recorded T_{roost}, we could account for all the radiotagged bats in the study area. Therefore, we are confident that we rarely, if ever, misclassified occupied trees as unoccupied.

For each datalogger, we calculated hourly average T_{roost} for 2-week periods during pregnancy (15–30 June 2002) and lactation (15–30 July 2002). Based on these values, we determined the daily maximum and minimum T_{roost} for each cavity. To test the hypothesis that large cavities have more spatially variable microclimates, we also calculated the absolute value of the maximum difference in T_{roost} within each tree for each hour of the day, for trees outfitted with multiple dataloggers. The sum of these values for each tree during pregnancy and lactation (see below) was plotted against cavity volume to assess whether the microclimate in large cavities was more variable.

We also used T_{roost} data to calculate normothermic or resting metabolic rates (RMR) and torpid metabolic rates (TMR) based on equations relating mass-specific RMR and TMR with T_{a} for big brown bats (Willis et al. 2005):

$$\text{RMR} = 84.71 - 2.94\,T_{\text{a}}\ \text{mW g}^{-1} \qquad (1)$$

$$\text{LogTMR} = 0.054 T_{\text{a}} - 0.887\,\text{mW g}^{-1} \qquad (2)$$

We used these equations to calculate the metabolic rate of a bat for every hour during the same 2 weeks of the pregnancy period and 2 weeks of the lactation period as for our T_{roost} calculations above. We averaged metabolic rate values for each hour of the day and calculated standard errors for each hourly average to account for T_{roost} measurement error in our MR estimates. For trees with more than one datalogger, we determined the minimum average metabolic rate for each hour of the day. For example, during part of the day, one datalogger at the top of a cavity may have recorded the warmest T_{roost} resulting in a low RMR, whereas later in the day, the bottom datalogger may have recorded a warmer T_{roost} and consequently low RMR. Therefore, we selected the minimum hourly average RMR and TMR values for our analyses based on the assumption that bats would select microclimates that

minimize energy costs. For both RMR and TMR, we calculated the sum of minimum hourly average values to determine the daily energy expenditure predicted for a bat in each roost tree. To quantify upper and lower error values for each daily RMR and TMR estimate, we also calculated the sums of each hourly RMR ± 1 SE.

For simplicity, we did not model metabolic costs during warming and cooling but assumed that bats remained either completely normothermic or completely torpid. We also assumed that bats remained in their roosts for 24-h periods. Nights are short at this latitude during summer, and big brown bats in the Cypress Hills forage for only a few hours each night (Arbuthnott and Brigham 2007). In addition, adult bats come and go from day roosts during the short activity period, and nonvolant pups remain in roosts all night during the lactation period. Therefore, we based our analyses on 24-h temperature profiles during both lactation and pregnancy to allow for direct comparison between these reproductive periods and because 24-h temperature profiles are important in the context of energy use for adults that return to roosts throughout the short foraging period and for pups (although thermal energy costs for pups will differ from those of adults). We assumed that pregnant bats had a body mass of 22.2 g, and lactating bats had a mass of 19.6 g, the average masses of individuals captured during each reproductive period. During the afternoon, the hourly average maximum T_{roost} used to calculate RMR was occasionally greater than 26.7°C, the lower critical temperature of the thermoneutral zone for big brown bats (Willis et al. 2005). Above this T_{roost}, we assumed that RMR was equal to basal metabolic rate (6.31 mW g^{-1}, Willis et al. 2005).

During the pregnancy period, we collected T_{roost} data from 7 of 19 trees in which we placed dataloggers because a number of the dataloggers could not be recovered after becoming detached from the fishing line. Therefore, we do not have a large enough sample size to compare T_{roost} or predicted RMR and TMR among the three roost types during pregnancy. However, the seven remaining cavities varied widely in volume, from 0.0054 m^3 (5.4 l) to 0.1145 m^3 (114.5 l), which did allow us to compare energy use over the complete range of available cavity volumes. We checked dataloggers more frequently during lactation, and T_{roost} data were recorded from 14 of 19 trees during this period, which ranged in volume from 0.0017 to 0.1145 m^3.

We report values as means ± 1 SD unless otherwise specified. For all tests, cavity volume data were log-transformed to meet normality assumptions of parametric tests. Where ANOVA was significant, we used Tukey's multiple comparison tests to ascertain differences between means. ANCOVAs, with cavity volume as a covariate, were used to test for differences between minimum predicted RMR and TMR for bats in different roost types. The

significance of all null hypothesis tests was assessed at an alpha value of 0.05.

Results

Unoccupied roost trees

Unoccupied roost trees had relatively stable microclimates relative to outside T_a (Fig. 1). For trees with more than one datalogger, average daily T_{roost} maxima and minima were significantly colder during pregnancy (max.=21.7±1.8°C; min.=12.5±0.6°C, n=7) compared to lactation (max.=22.9± 1.0°C, n=10, ANCOVA, $F_{1,1,14}$=5.6, P=0.03; min=14.0± 0.7°C, $F_{1,1,14}$=26.5, P<0.001), but there was no effect of cavity volume on maximum (ANCOVA, $F_{1,1,14}$=1.5, P=0.24) or minimum T_{roost} ($F_{1,1,14}$=0.14, P=0.71). For trees outfitted with more than one datalogger, we also calculated the maximum difference in T_{roost} recorded by all the dataloggers in the cavity. Surprisingly, there was no relationship between maximum T_{roost} difference and cavity volume during pregnancy (linear regression, R^2=0.15, n=7, P=0.39) or lactation (R^2=0.001, n=10, P=0.94), which means that larger cavities did not have greater spatial variability in microclimate.

During pregnancy, there was no relationship between log-transformed cavity volume and minimum RMR (Fig. 2a, R^2=0.08, n=7, P=0.27) or TMR (Fig. 2b, R^2= 0.29, n=7, P=0.12). Similarly, during lactation, cavity volume or roost type did not influence predicted energy
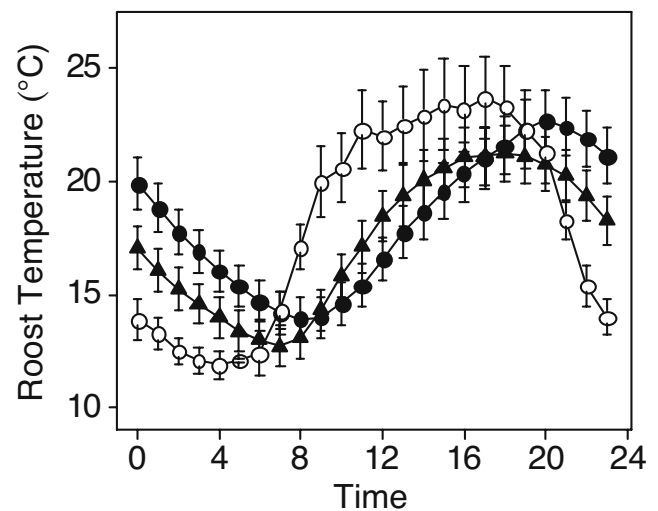
Fig. 1 Mean hourly roost temperatures measured using two dataloggers placed within 15 cm of the top and 15 cm of the bottom of a cavity in one roost tree (*filled symbols*). Outside ambient temperature is shown by *empty circles*. Values represent means ± SE for each hour of the day for a 2-week period during lactation (15–30 July 2002)
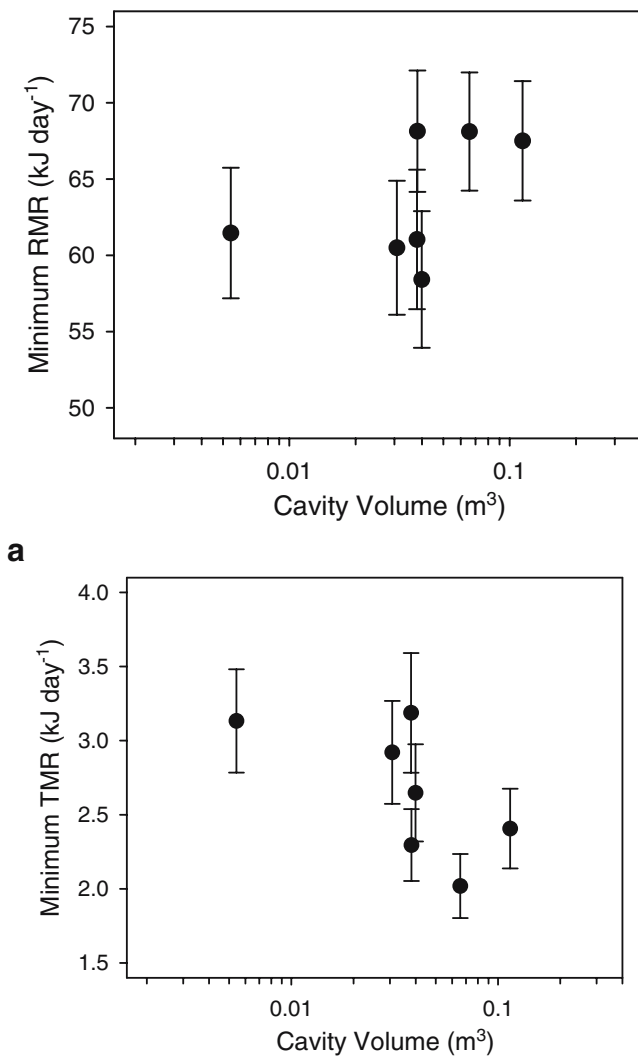
a

b

Fig. 2 Scatterplots of cavity volume vs predicted RMR (**a**) and TMR (**b**) based on maximum and minimum roost temperature profiles (see "Materials and methods" section), respectively. Temperature data were recorded in roost trees during the pregnancy period (15–30 June 2002). Error bars represent ±1 SE calculated based on variation in temperature on different days

use. There was no difference between minimum RMR predicted for nine crevice trees vs five multiple- and single-hole trees (Fig. 3a, ANCOVA, $F_{1,1,11}=0.09$, $P=0.78$), and cavity volume did not affect minimum RMR (Fig. 3a, $F_{1,1,11}=0.02$, $P=0.89$). Similarly, roost type (Fig. 3b, ANCOVA, $F_{1,1,11}=0.11$, $P=0.74$) and cavity volume (Fig. 3b, $F_{1,1,11}=0.95$, $P=0.35$) did not affect TMR.

Occupied roosts

While roost type and cavity volume had little effect on T_{roost} or calculated energy expenditure, the occupation of roost trees by bats had a pronounced effect based on a similar set of analyses and sample sizes. We radiotracked

bats to nine different roost trees that contained dataloggers on 17 days between 16 June and 12 August (i.e., some trees were reused). For both occupied and unoccupied roosts, we averaged hourly temperature values from multiple dataloggers in the same tree. This is conservative because it minimizes the influence of warming associated with the presence of bats in the roost. On all days, occupied roosts had a higher daily maximum T_{roost} than unoccupied roosts (Fig. 4, paired t test, $t=5.9$, $n=17$ days, $P<0.001$), although there was no difference in minimum temperatures (Fig. 4, $t=-0.88$, $n=17$ days, $P=0.40$). Roosting group size, based on exit counts, was not correlated with outside T_a ($R^2=0.18$), so we used a
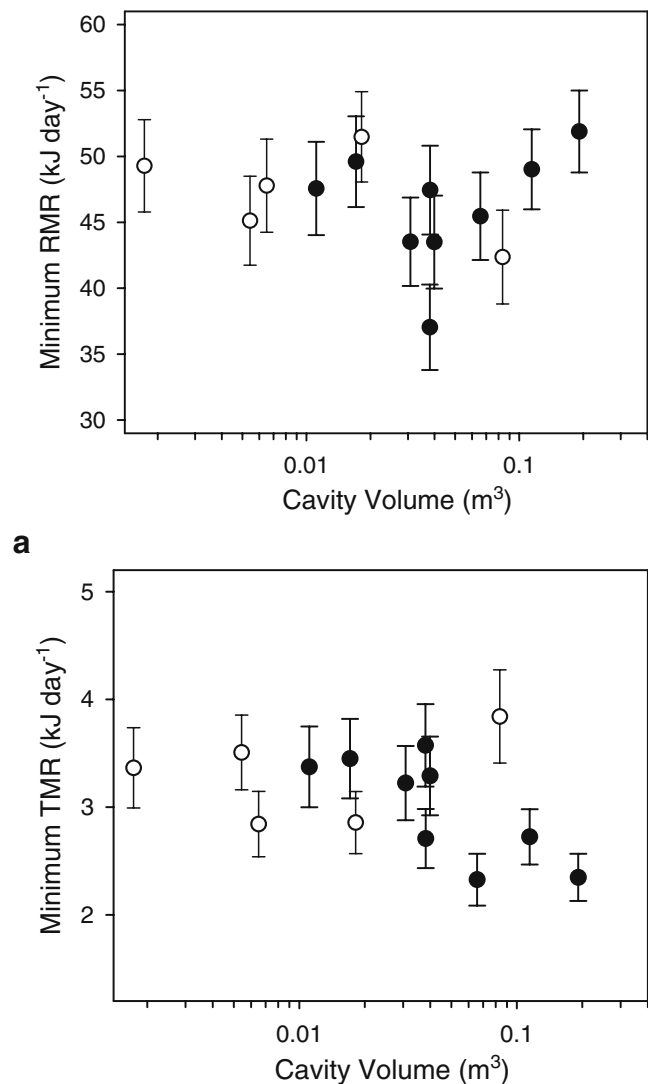

a

b

Fig. 3 Scatterplots of cavity volume vs predicted RMR (**a**) and TMR (**b**) based on maximum and minimum roost temperature profiles, respectively, recorded from roost trees during the lactation period (15–30 July 2002). *Filled circles* represent trees with crevices; *empty circles* represent trees with single or multiple holes. Error bars represent ±1 SE calculated based on variation in temperature on different days
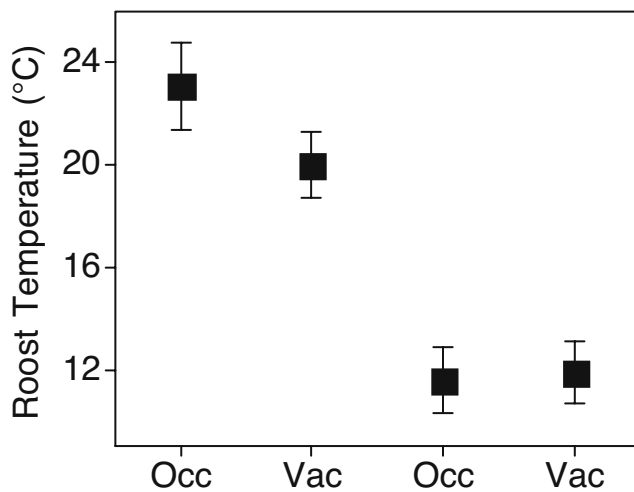
Fig. 4 Average values ± SE for maximum (*left*) and minimum (*right*) daily temperatures recorded from nine different occupied roosts (*Occ*) and 13 unoccupied roosts (*Vac*) on 17 days between 16 June and 12 August 2002

general linear model (GLM) to control for effects of T_a and test for the influence of roosting group size on maximum and minimum T_{roost} in occupied trees. The resulting model for maximum T_{roost} was highly significant ($F_{2,14}=51.5$, $R^2=0.88$, $P<0.001$). Outside T_a had a significant effect on maximum T_{roost} ($t=7.4$, $P<0.001$), but group size also had a significant effect (Fig. 5a, $t=3.0$, $P=0.009$). The minimum temperature model was also significant ($F_{2,14}=19.08$, $R^2=0.73$, $P<0.001$), and both T_a ($t=3.5$, $P=0.004$) and group size (Fig. 5b, $t=3.5$, $P=0.004$) had significant effects. Therefore, warmer outside T_a and larger group size both resulted in warmer T_{roost} daily maxima and minima.

The energetic implications of increased T_{roost} in occupied roost trees are evident from plots of RMR and TMR for 1 day, predicted from measured hourly temperatures inside an occupied tree, and the average hourly temperatures recorded inside the 13 unoccupied trees (Fig. 6). We predicted energy expenditures on 13 such days during the lactation period. When we paired occupied vs unoccupied trees by day, thus controlling for daily differences in T_a and group size, there was a significant difference between the RMR predicted for bats in occupied trees (58.7±8.9, range 19.6–109.4 kJ/day) vs the predicted RMR for bats in unoccupied trees (63.1±7.9, range=22.8–105.9 kJ/day, paired t test, $t=-2.8$, $n=13$ days, $P=0.016$). The predicted RMR for bats in occupied trees was lower than that predicted for bats in unoccupied trees on 10 of the 13 days. However, on the 3 days when RMR was equal to or greater than that predicted for occupied trees, T_a never rose above 13.5°C, and radiotagged bats could not have elevated T_{roost} via metabolic heat production because they never aroused from torpor (C.K.R. Willis, unpublished data). When we excluded these 3 days from the analysis, the effect of

occupation was even more pronounced ($t=-4.26$, $P=0.002$). A GLM relating the difference between predicted daily RMR for occupied and unoccupied roosts, group size, and T_a was significant ($R^2=0.57$, $F_{2,10}=6.7$, $P=0.01$), and group size ($t=2.4$, $P=0.04$), but not T_a ($t=0.4$, $P=0.72$), contributed significantly to the model. Moreover, group size and T_a explained most of the variation in RMR predicted for occupied roosts alone (Fig. 7, $R^2=0.94$, $F_{2,10}=73.8$, $P<0.001$). This model was significant for both independent variables (group size: $t=-3.1$, $P=0.01$; and T_a: $t=-6.6$, $P<0.001$). Taken together, our results demonstrate that roosting in a group significantly reduces RMR compared to solitary roosting, and larger group sizes and warmer outside T_a both enhance energy savings.
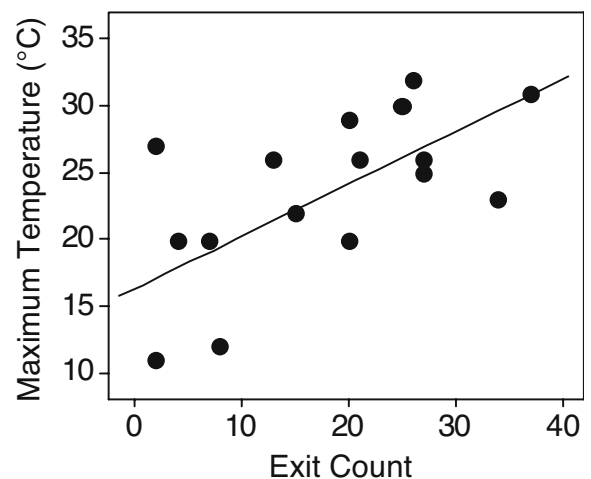
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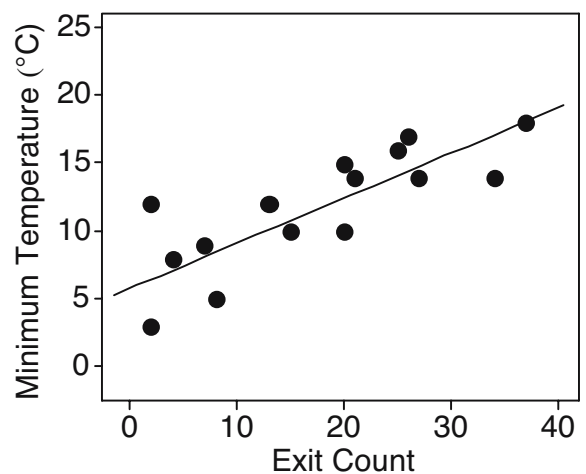
b

Fig. 5 Predicted relationships between the number of bats roosting in a tree and the maximum (**a**) and minimum (**b**) daily roost temperatures based on a general linear model (GLM) incorporating daily maximum T_a. The maximum and minimum relationships are described, respectively, by the equations: Roost Temperature = 0.19(Group Size) + 0.82(Maximum T_a) − 0.21; and Roost Temperature = 0.22(Group Size) + 0.44(Maximum T_a) − 3.1
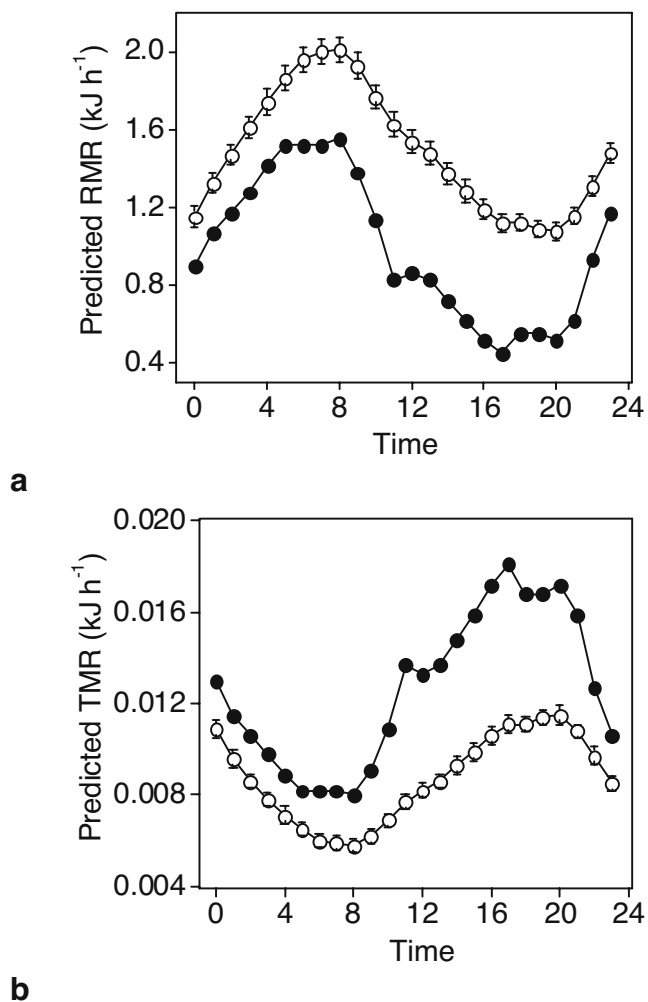
Fig. 6 Time course of predicted hourly RMR (**a**) and TMR (**b**) for 19 July 2002 based on average temperatures recorded in a roost occupied by 27 big brown bats (*filled circles*) and 13 roosts to which we did not track bats (*empty circles*, means ± SE)

Accounting for torpor, predicted TMR was higher in occupied (0.16±0.03, range: 0.02–0.34 kJ/day) vs unoccupied roosts (0.13±0.03, range 0.03–0.32 kJ/day; paired *t* test, *t*=3.3, *n*=13 days, *P*=0.007), and this pattern was consistent on all but one of the 13 days. A general linear model testing the effects of group size and maximum T_a on differences in TMR predicted for bats in occupied vs unoccupied roosts approached significance but did not account for a large percentage of the observed variation (R^2= 0.45, $F_{2,10}$=4.1, *P*=0.05). When we considered group size and T_a effects on the predicted TMR of bats in occupied roosts alone, the model was significant (R^2=0.84, $F_{2,10}$=25.7, *P*<0.001), and T_a had a significant effect (*t*= 4.5, *P*=0.01) but group size did not (*t*=1.0, *P*=0.33). Taken together, these results indicate that roosting in occupied tree hollows leads to a small increase in TMR but that the size of the roosting group has a negligible effect on this added energy cost. Thus, the cost of a slightly increased TMR in a warm, occupied roost is much smaller than the energetic benefit of a reduced RMR.

Discussion

Previous work indicates that big brown bats in our study area prefer to roost in trees with the most spacious cavities accessed via crevice openings rather than circular holes (Willis et al. 2006b). Our results do not support the hypothesis that these or other physical attributes of preferred roost trees result in energetically significant benefits in terms of microclimate. Daily maximum and minimum T_{roost} were not affected by roost type or cavity volume, and there was no effect of cavity volume on spatial variability in microclimate. Furthermore, we found no relationship between roost type or cavity volume and predicted energy expenditure. Several studies have demonstrated that bat roosts in tree cavities tend to provide thermal environments that are buffered relative to outside T_a (e.g., Kalcounis and Brigham 1998; Sedgeley and O'Donnell 2004; Sedgeley 2006), and our results are consistent with these findings. On average, maximum and minimum temperatures in unoccupied tree hollows were less extreme than outside T_a (Fig. 1). However, few studies have tested the hypothesis that different tree cavities in an area differ with respect to microclimate. Sedgeley (2001) found that cavities consistently used by *C. tuberculatus* were significantly warmer than tree hollows which were never used, by about 0.5°C on average, and determined that even this
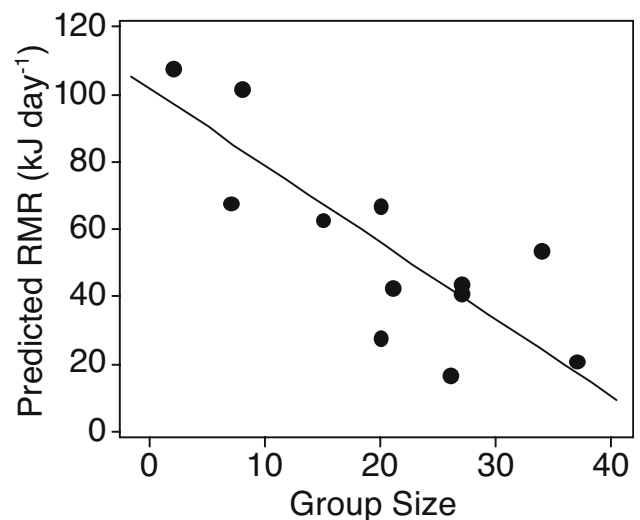

Fig. 7 Predicted relationship between the numbers of bats using the roost (*Group Size*) and RMR, calculated based on roost temperatures recorded in occupied roosts. Values are based on a general linear model analysis, which controlled for the effects of maximum daily T_a. The relationship is described by the equation: RMR = 156.8 − 0.92(Group Size) − 3.50(Maximum T_a)

small temperature difference could result in a 1.1 to 7.3% reduction in energy expenditure depending on time of the day and cavity structure. In our study area, Kalcounis and Brigham (1998) also found differences in microclimate when comparing roost cavities in trembling aspen, which are consistently used by big brown bats, to hollows in conifer snags, which are apparently never used (Kalcounis and Brigham 1998; Willis and Brigham 2004; Willis et al. 2006b). Our comparison differs from these studies in a subtle but important respect because all of the cavities we compared are used by bats at some point. The largest cavities with crevice openings are used most frequently by the largest roosting groups but all show evidence of occupation by bats. It is noteworthy that microclimate has helped explain the absence of forest-living bats from certain sites in previous studies (Kalcounis and Brigham 1998; Sedgeley 2001) but does not appear to explain their relative preferences within a pool of different types of roosts. Our data do not support the hypothesis that intrinsic differences in microclimates of available roost trees are large enough to motivate preferences for certain roosts over others.

It is possible that large-volume cavities provide thermal benefits that we were unable to measure. For example, even low levels of air turbulence can affect convective heat loss (Bakken and Kunz 1988) but we could not account for effects of turbulent airflow and convective cooling on thermal metabolism. Large-volume cavities may be characterized by high air circulation, which could allow bats to reach lower T_b more quickly during torpor and, therefore, achieve greater energy savings. We may also have failed to detect an effect of cavity volume on T_{roost} and energy expenditure due to a small sample size of unoccupied roosts. However, we sampled the complete range of available cavity volumes (from about 5 to 115 l) and, based on a similar set of analyses and sample sizes, we detected a significant effect of roost occupation and group size on T_{roost} and predicted energy use (see below). Alternative possibilities notwithstanding, our results suggest that specific thermal properties of tree cavities have a relatively minor impact on roost selection.

On the other hand, the presence of bats inside a roost cavity and the size of roosting groups had a dramatic influence on T_{roost} and energy savings. Consistent with previous work (Burnett and August 1981), roost occupation raised maximum daily T_{roost} by as much as 7°C. Based on hourly average temperatures recorded in occupied cavities, roosting with an average-sized group (19 bats), as opposed to roosting alone, would save a normothermic big brown bat about 4.4 kJ of energy on an average day during lactation. When we excluded the three unseasonably cold days during which we confirmed that radiotagged bats never emerged from bouts of deep torpor ($n=5$ bats, C.K.R. Willis, unpublished data), and thus would not have

contributed to increasing T_{roost}, the difference between predicted RMR in occupied and unoccupied roosts was roughly 6.5 kJ/day or 1.5 g of insects (an approximation based on the energy assimilation efficiency for an average insect, Bell 1990). This represents about 9% of the daily energy budget of a free-ranging individual (Kurta et al. 1990). However, predicted RMR was also significantly affected by group size and outside T_a, which means that under certain conditions, energy savings associated with roost sharing are likely to be much greater. Assuming sustained normothermia and a maximum daily T_a of 20°C, our general linear model predicts that the daily RMR of a bat roosting alone would be 1.9 times greater than that of an individual in a group of 45 bats (about 40 kJ/day or 7.3 g of insects; Bell 1990). Based on field metabolic rates (FMR) reported for lactating big brown bats (Kurta et al. 1990), this represents approximately 53% of the daily energy budget. Forty kJ/day could easily mean the difference between survival and starvation for both a mother and her offspring, which suggests a fitness benefit of social thermoregulation in this scenario.

Even the large savings we have calculated likely underestimate benefits of colonial roosting because we only account for changes in local heating. We could not quantify energy savings due to reduced surface area and thermal conductance. Hayes et al. (1992) demonstrated that thermal conductance/surface area effects accounted for about 23% of total energy savings gained by groups of five short-tailed field voles (*Microtus agrestis*) relative to individuals. Local heating accounted for 25 to 50% of total energy savings. Similarly, Roverud and Chappell (1991) found that clustering significantly reduced conductance for groups of lesser bulldog bats (*Noctilio albiventris*). Both studies are consistent with data for other taxa (e.g., Fleming 1985; Perret 1998). Individuals in groups save energy not only because they elevate the local temperature inside their roost (i.e., the benefits we have estimated) but also because their ability to reduce metabolic heat loss improves as a group. However, for big brown bats in our study system, it is likely that the local heating effects we estimated outweigh those due to surface area/conductance. For one, previous studies differentiating the two types of effects have, by necessity, relied on respirometry chambers made of materials such as glass or Perspex. Such materials conduct heat much more rapidly than a thick-walled cavity in a living tree, which means that these studies may underestimate the relative importance of local heating for free-living animals and overestimate the relative importance of surface area/conductance. Second, energetic benefits of reduced surface area drop off radically at group sizes larger than just three or four individuals in part due to the complex geometry of larger clusters of animals (Canals et al. 1989; Roverud and Chappell 1991). On the other hand,

local heating effects will continue to increase linearly with group size long after the increase in the surface area/conductance benefit has declined to negligible levels (e.g., this study). Group sizes smaller than ten are the exception rather than the rule in our study system, which means that local heating effects are likely more important for the majority of roosting groups of big brown bats. Third, estimates of surface area/conductance effects are based on the assumption that clustered animals form tightly packed, roughly spherical aggregations (e.g., Canals et al. 1989). If group-roosting animals do not form this kind of cluster, conductance is likely to be much less important than local heating. Big brown bats in our study area may form tight sphere-like clusters some of the time, perhaps during especially inclement weather. However, on the few occasions when we have observed bats inside cavities using infrared imaging, they have always lined the inside of the cavity roosting side by side as a surface of bats rather than packing into a tight ball (C.K.R. Willis and R.M. Brigham, unpublished data). Thus, the relative energetic contribution of surface area/conductance effects for bats in our system is likely much smaller than the 23% predicted by Hayes et al. (1992). In the absence of laboratory data differentiating relative contributions of local heating vs surface area/conductance effects for large groups of bats over a range of air temperatures, and without field data quantifying their clustering behavior inside roosts, it is not possible to accurately model the surface area/conductance component of energy savings. We acknowledge that these effects will contribute some energy savings beyond those we have estimated, and we stress the importance of collecting the data necessary to account for this error in future studies. However, given these arguments, our estimates based on the contribution of local heating alone provide a reasonable estimate of actual energy savings. The fact that bats will gain an added benefit due to surface area/conductance effects means that our approach is conservative and lends stronger support to our conclusion that social thermoregulation is a key factor motivating big brown bats to select large-volume tree cavities.

Our data provide evidence that social thermoregulation influences roost selection in our study system but this does not preclude the hypothesis that other factors are important, including preferences for components of microclimate other than air temperature. During early pregnancy and lactation, big brown bats in the Cypress Hills exhibited a strong preference for trees with multiple holes relative to single-hole and crevice trees (Willis et al. 2006b). Multiple-hole trees tend to have cavities with larger volumes than single-hole trees, which means that they allow more individuals to roost together. Trees with crevices have even larger cavities but the crevice openings are often more than 1 m long and may expose bats to high levels of circulating air. Bats may

prefer multiple-hole cavities during lactation (when reproductive costs are high) and early pregnancy (when T_a is cold and thermoregulatory costs are high) because trees with multiple holes provide a balance between the thermal benefits of large roosting groups and the costs of turbulent airflow in cavities with large openings. During pregnancy, thermal constraints may be relaxed if bats rely on deep torpor, so they may not necessarily aggregate passively at multiple-hole trees. Instead, individuals may opt to maintain and renew social relationships by roosting with as many different individuals in their roosting area as possible (Willis and Brigham 2004; Willis et al. 2006b). This is supported by the fact that bats exhibit the strongest preference for crevice roosts during pregnancy (Willis et al. 2006b). Other factors may influence the roost preferences of bats in our system as well. For example, large cavities allow occupancy by larger groups of bats, which may provide benefits other than reduced thermoregulatory costs if large group sizes improve the capacity of bats to transfer information about foraging areas and alternative roost sites (Kerth et al. 2001b). Roost attributes or large group sizes may reduce risk of predation (e.g., Jenkins et al. 1998) which could play a role in our system, although we have no data on predation risk for big brown bats. Humidity and evaporative water loss may also be important, particularly at high latitudes where bats are confined to roosts for long periods each day. For one, water loss could influence bats to select roost trees close to sources of fresh water (Jenkins et al. 1998). However, all roosts we studied are in close proximity to each other within a small roosting area and are effectively equidistant from the nearest fresh water source (Willis and Brigham 2004). More likely, although the roost trees of these bats are still alive, the interior of trees with large-volume cavities may be at a later stage of decay than those with smaller cavities and, thus, might provide more humid conditions. On the other hand, water loss could augment social thermoregulation benefits of large-volume cavities if the presence of large roosting groups elevates humidity. More data are needed, particularly addressing effects of roost characteristics vs roosting group sizes on evaporative water loss in natural roosts, to better understand all factors influencing roost selection. Physical characteristics of roost cavities play an important role in roost selection by other bats (e.g., Sedgeley and O'Donnell 1999) and could influence passive aggregation of bats at different types of cavities in our study area at different times of year.

Data for cavity-nesting Northern Flickers, similar to ours (Wiebe 2001), suggest that there may be insufficient natural variation in microclimate between potential nest and roost trees to provide energetic benefits large enough to impact reproductive fitness. On the other hand, the preference for relatively large cavities that allow for large groups of bats

likely influences fitness because energy savings increase with group size. Sedgeley (2001) argued that accurate determination of the roosting preferences of forest bats requires direct measurement of T_{roost} coupled with analyses quantifying physical features associated with roosts. Our results support this conclusion. It is unlikely that any of the patterns we have observed for big brown bats would have been detected using the standard presence/absence paradigm (Willis et al. 2006b). Future work addressing the influence of cavity volume and cavity entrance types on turbulent airflow, convective cooling, evaporative water loss, and other factors, such as predation risk, will improve our understanding of the roosting ecology of cavity-living bats, specifically, and cavity-using animals in general.

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