

Thermoregulation and roosting behaviour of reproductive and nonreproductive female western long-eared bats (*Myotis evotis*) in the Rocky Mountains of Alberta

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Abstract: Entering torpor can yield significant energy savings for temperate-zone bats but can be costly for reproductive females by slowing fetal development and reducing milk production. We studied western long-eared bats (*Myotis evotis* (H. Allen, 1864)) in the Rocky Mountains of Alberta to test the hypothesis that different costs of torpor result in different patterns of thermoregulation and roosting behaviour for reproductive and nonreproductive females. We radio-tracked bats to monitor body temperatures and locate roosts. We took roost measurements and inserted temperature data loggers to measure roost microclimate. Bats entered torpor frequently, but nonreproductive females spent longer periods in torpor, had lower minimum body temperatures, and entered deep torpor more often than reproductive females did, supporting the hypothesis that entering torpor is more costly for reproductive individuals. Roosts were located mainly in rock fields on steep, open, south-facing slopes. Reproductive females roosted in crevices between rocks located above or on the surface of the ground. Roosts warmed rapidly and reached warm daytime temperatures. Females roosted alone during pregnancy but formed small colonies within roosts during lactation when ambient conditions were cooler. Clustering may reduce thermoregulatory costs for both adults and young. Nonreproductive females roosted mainly alone in crevices in the ground. These roosts had cooler, more stable microclimates, allowing females to enter deeper bouts of torpor and remain torpid longer.

Résumé : L'entrée en torpeur peut représenter des économies importantes d'énergie chez les chauves-souris de la zone tempérée, mais elle peut s'avérer coûteuse pour les femelles reproductrices en ralentissant le développement des foetus et en réduisant la production de lait. Nous avons étudié le murin à grandes oreilles (*Myotis evotis* (H. Allen, 1864)) dans les montagnes Rocheuses de l'Alberta afin d'évaluer l'hypothèse selon laquelle les coûts différents associés à la torpeur chez les femelles reproductrices et non reproductrices entraînent des patrons différents de thermorégulation et de comportement sur les perchoirs. Nous avons suivi des chauves-souris par radio pour déterminer leur température corporelle et pour trouver leurs perchoirs. Nous avons mesuré les perchoirs et installé des enregistreuses à température pour déterminer le microclimat des perchoirs. Les chauves-souris entrent fréquemment en torpeur, mais les femelles non reproductrices passent plus de temps en torpeur, ont des températures corporelles minimales plus basses et entrent en torpeur profonde plus souvent que les femelles reproductrices; cela appuie l'hypothèse selon laquelle l'entrée en torpeur est plus coûteuse pour les individus reproducteurs. Les perchoirs se situent principalement dans les champs de pierre sur les pentes abruptes, ouvertes et orientées vers le sud. Les femelles reproductrices se perchent dans les crevasses entre les pierres situées au-dessus ou au ras du sol. Les perchoirs se réchauffent rapidement et atteignent des températures chaudes durant la journée. Les femelles se perchent seules durant leur grossesse, mais elles forment de petits groupes durant l'allaitement à un moment où les températures sont plus fraîches. Ce regroupement peut réduire les coûts de la thermorégulation tant chez les adultes que chez les jeunes. Les femelles non reproductrices se perchent principalement seules dans des crevasses dans le sol. Ces perchoirs ont des climats frais et plus stables, ce qui permet aux femelles d'entrer dans des épisodes plus profonds de torpeur et de rester en torpeur plus longtemps.

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Introduction

Meeting daily energy requirements can be challenging for small-bodied endotherms (Peters 1983; Schmidt-Nielsen 1997), particularly those in unpredictable environments or

those that depend on unpredictable food sources. To escape energetic constraints, many small birds and mammals can enter torpor by reducing their body temperature below normothermic levels (Wang and Wolowyk 1988). There is a curvilinear relationship between body temperature (T_b) and metabolic rate during torpor in thermoconforming endotherms such that every 10 °C reduction in T_b roughly halves the metabolic rate, resulting in substantial energy savings (Prothero and Jurgens 1986; Wang and Wolowyk 1988). Temperate-zone insectivorous bats are extremely thermolabile and can effectively control energy savings by regulating the frequency, depth, and duration of torpor

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bouts (Audet and Fenton 1988; Wang and Wolowyk 1988; Speakman and Thomas 2003). Given the energetic benefits of torpor, one might predict that bats would use heterothermy invariably during periods of inactivity. However, different patterns of daily torpor may arise when the costs of entering torpor are not equal among individuals.

Entering torpor can delay reproduction by female bats by slowing fetal development (Racey 1973) and reducing milk production (Wilde et al. 1995, 1999). Young that are born and weaned later during summer are less likely to survive hibernation (Ransome 1989), resulting in a fitness cost for reproductive bats that enter torpor. Furthermore, females that give birth later have less time to accumulate fat reserves prior to hibernation, which may affect their own overwinter survival (Beer and Richards 1956; Pagels 1975). Therefore, pregnant and lactating females should use less torpor than nonreproductive females. This appears to be the case (Audet and Fenton 1988; Hamilton and Barclay 1994), although these studies examined bats living in buildings and may not reflect the thermoregulatory behaviour of individuals living in natural roosts (Chruszcz and Barclay 2002; Lausen and Barclay 2006; Willis 2006). Lausen and Barclay (2003) compared the use of torpor between reproductive and post-lactating bats, but to date no study of bats in natural roosts has compared reproductive and nonreproductive females.

Reproductive endotherms that remain homeothermic must compensate for the costs of reproduction by increasing daily energy intake or reducing energy expenditure (Racey and Entwistle 2000). Although there is some evidence that reproductive female bats increase foraging activity as lactation progresses (e.g., Barclay 1989), the associated increase in flight costs may be prohibitive. A more economical solution would be to minimize thermoregulatory costs within day roosts, where bats spend most of their time. The thermal characteristics of roosts are determined by extrinsic habitat features (e.g., slope aspect, canopy cover) and intrinsic structural features (e.g., roost depth, opening dimensions; Vonhof and Barclay 1997; Lausen and Barclay 2003). For example, shallow rock crevices that are poorly buffered from environmental conditions have a warmer but more variable microclimate than deep, well-buffered crevices (Lausen and Barclay 2003). By selecting roosts that provide microclimates within their thermoneutral zone, bats can passively maintain warm, stable body temperatures (Speakman and Thomas 2003). Bats may also cluster with other individuals within a roost to minimize thermoregulatory costs. Clustered bats retain metabolic heat better than solitary individuals (Trune and Slobodchikoff 1976; Roverud and Chappell 1991), and the trapped heat may also elevate the temperature of the roost (Burnett and August 1981).

We investigated how the costs and benefits of using torpor can result in different patterns of thermoregulation and roosting behaviour among temperate insectivorous bats. Specifically, we compared the behaviour of reproductive and nonreproductive females from a rock-roosting population of western long-eared bats (*Myotis evotis* (H. Allen, 1864)) in the mountains of Alberta. We predicted that reproductive females would use torpor less than nonreproductive females, and compensate by selecting roosts with warmer microclimates and (or) clustering with more individuals.

Methods

Study species and area

Myotis evotis occupies much of western North America. Individuals weigh 5–8 g (Manning and Jones 1989) and feed by taking insects from the air or from vegetation (gleaning; Faure and Barclay 1994). During the summer, *M. evotis* roosts in crevices and cavities of snags, stumps, boulders, and rock outcrops, as well as in caves, mines, and man-made structures (Manning and Jones 1989; Vonhof and Barclay 1997; Holloway 1998; Waldien et al. 2000; Chruszcz and Barclay 2002; Rancourt et al. 2005). Adults typically roost alone in natural roosts, although small maternity groups (2–14 individuals) have been reported (Vonhof and Barclay 1997; Holloway 1998; Waldien et al. 2000; Chruszcz and Barclay 2002; Rancourt et al. 2005). Female *M. evotis* bear a single pup during summer and are solely involved in rearing it before the onset of hibernation.

We collected data from June to August 2002 in the Kananaskis (51°00'N, 115°05'W) and Sheep River (50°39'N, 114°39'W) valleys in the foothills of the Rocky Mountains of southwestern Alberta, Canada. Both sites consist of a river surrounded by modest peaks (elevation 1350–2500 m). Extensive lodgepole pine (*Pinus contorta* Dougl. ex Loud.) and mixed aspen–pine (primarily trembling aspen, *Populus tremuloides* Michx.) forests cover the valley bottoms and mountain ridges, while sheer cliffs, talus slopes, and boulder fields occupy the steeper regions. Warm days and cold nights characterize summers at these sites. Long-term averages of daily minimum/maximum temperatures are 4.5/18.2 °C (June), 6.6/21.5 °C (July), and 6.1/21.1 °C (August) for Kananaskis, and 2.3/18.3 °C (June), 4.1/21.1 °C (July), and 3.7/21.0 °C (August) for Sheep River. Freezing temperatures are recorded each month, and sites receive 32–35 cm of precipitation (including snow), on average, each summer (Environment Canada 2000).

Captures and radiotelemetry

We caught bats in harp traps and mist nets placed across forest trails. Individuals were identified to gender and marked with coloured, numbered plastic split-rings on the forearm. Adults were distinguished from juveniles (young-of-the-year) by the degree of epiphysial fusion at the finger joints (Anthony 1988). We examined adult females for reproductive condition (pregnant, lactating, post-lactating, or nonreproductive; Racey 1988). Females in late pregnancy possessed an obviously distended abdomen and palpable embryo. Lactation was distinguished from post-lactation by expressing milk from swollen teats. Females lacking these characteristics were considered nonreproductive. We exclusively captured pregnant females ($n = 11$) between 22 June and 22 July and lactating bats ($n = 11$) on or after 22 July. Therefore, we refer to 22 June – 22 July as the pregnancy period, and 23 July – 31 August as the lactation period. Animals were cared for in accordance with the principles and guidelines of the Canadian Council on Animal Care.

We used radiotelemetry to locate roosts and monitor skin temperatures for pregnant, lactating, and nonreproductive adult females. We trimmed interscapular fur and glued temperature-sensitive radio transmitters (Holohil Systems Ltd., Carp, Ontario) weighing 0.5 g to the exposed skin us-

ing Skinbond® surgical adhesive (Smith and Nephew United Inc., Largo, Florida). Bats were held for 30 min to let the glue set and were released at the site of capture. We tracked individuals daily, using a Merlin 12 receiver (Custom Electronics, Nokomis, Florida), during the battery life of the transmitter or until the transmitter fell off.

Ambient and body temperature

We measured ambient temperature (T_a) every 10 min using Thermocron iButtons® ($\pm 1^\circ\text{C}$, Dallas Semiconductor Corp., Dallas, Texas) and HOBO® (Onset Computer Corp., Pocasset, Massachusetts) data loggers placed in solar radiation shields located at the University of Calgary Barrier Lake Field Station in the Kananaskis Valley and the University of Calgary R.B. Miller Field Station in the Sheep River Valley. Both stations are centrally located in the study areas.

To determine the body temperature (T_b , measured as skin temperature, T_{sk}) of radio-tagged individuals, a Lotek SRX_400 scanning receiver (Lotek Wireless Inc., Newmarket, Ontario) monitored and recorded T_{sk} every 10 min after a bat entered its roost during morning until it emerged to forage at night. Several studies of bats and small birds have demonstrated a strong correlation between T_{sk} , recorded by external transmitters, and core T_b (Audet and Thomas 1996; Barclay et al. 1996; Brigham et al. 2000). However, this relationship can be influenced by T_a , roosting behaviour, and the physiological state of the animal (i.e., torpid, normothermic, actively rewarming; Willis and Brigham 2003). Despite these limitations, the small size of *M. evotis* likely helped minimize the potential discrepancy between T_{sk} and core T_b . In addition, implanted transmitters are impractical for small bats because the reception range of small internal transmitters is too small for wide-ranging animals.

We defined torpor and deep torpor as in some previous studies (Hamilton and Barclay 1994; Grinevitch et al. 1995; Barclay et al. 2001; Chruszcz and Barclay 2002; Lausen and Barclay 2003). A bat was torpid when its T_{sk} dropped below its active temperature (T_{act}), defined as the lowest T_{sk} of an individual recorded immediately (i.e., <10 min) before it emerged to forage, during the period the transmitter remained on the bat. A bat was in deep torpor if its T_{sk} dropped more than 10°C below its T_{act} . The time available for torpor was defined as the number of minutes that T_a fell below T_{act} while a bat was in the roost. We quantified the thermoregulatory behaviour of females by calculating the proportion of bat-days during which torpor occurred (frequency) and the length of time spent in torpor and deep torpor per day. We analyzed minimum and maximum T_{sk} and time spent in torpor and deep torpor using ANOVAs with reproductive condition as the main effect. We included individual (nested within reproductive condition) to account for repeated measures. For analyses of time spent in torpor and deep torpor, we included the time available for torpor as a covariate.

Properties of roosts and roost habitat

We measured several variables for each roost we located using radiotelemetry. We determined percent canopy cover using a densiometer held above the roost, averaging readings obtained for each of four directions (N, S, E, and W) and

multiplying by 1.04. We measured the aspect of the slope in which the roost was located using a compass, and the percent slope using a clinometer. Roosts were classified as pregnancy, lactation, or nonreproductive depending on the reproductive condition of the bats using them. Roosts were located in either rock crevices or cavities. Crevice roosts consisted of a narrow fissure bounded by two layers of rock substrate, whereas cavity roosts were formed by an aggregation of three or more rocks.

We measured roost opening dimensions (maximum length and width) and shape (rectangle, triangle, etc.), maximum roost depth, and roost aspect. The opening dimensions and shape for each roost were used to calculate opening area and roost volume for statistical analyses. We also noted whether roosts were located on or under the surface of the ground, protected or unprotected from precipitation, and oriented vertically or horizontally in relation to the ground.

We analyzed qualitative measures (roost type, on or under ground, orientation, protection) using χ^2 tests with reproductive condition as the conditional variable. For contingency tables that contained cells with expected values <5, we grouped pregnancy and lactation roosts into a single category (reproductive roosts). We analyzed canopy cover, percent slope, and roost dimensions using single-factor ANOVAs with reproductive condition as the main effect. We compared circular data (slope and roost aspect) among pregnancy, lactation, and nonreproductive roosts using the nonparametric statistical procedure outlined by Fisher (1993, p. 115). This procedure uses a test statistic that is normally evaluated using the χ^2 distribution. However, because our sample included <25 pregnancy and lactation roosts, we evaluated the test statistic against a distribution generated from random permutations of the sample data. We present mean directions \pm circular standard error (Fisher 1993).

We inserted HOBO and Thermocron iButton temperature data loggers 15–30 cm from the roost opening or, when possible, where the bat had been seen roosting. Data loggers were inserted 3–5 days after the roost had been occupied by a bat, and bats did not reoccupy roosts while data loggers were present. Data loggers recorded temperatures every 10 min for 3–7 days (mean = 4.6 ± 0.2 days).

To compare the thermal properties of roosts used by bats in different reproductive classes, we used five measures of roost temperature (T_r): mean daytime and nighttime temperatures, daily maximum and minimum temperatures, and daily temperature range. Mean daytime temperature was calculated as the mean of all temperatures recorded between the average return time and the average emergence time of all bats during the reproductive period in question (i.e., pregnancy or lactation). Similarly, mean nighttime temperature was the mean of all temperatures recorded between the average emergence time and the average return time of all bats during each reproductive period.

We analyzed roost temperature data using general linear models. Specifically, we tested for differences in mean daytime and nighttime T_r , daily maximum and minimum T_r , and daily T_r range, with reproductive class of the roost and individual roost (nested within reproductive class) as main effects. We included the appropriate measure of T_a (mean daytime or nighttime T_a , daily maximum or minimum T_a , or

Table 1. Results of one-way ANOVAs comparing ambient temperature (T_a ; °C) during the pregnancy and lactation periods of *Myotis evotis* in the study area.

Variable	Reproductive period ($F_{[1,45]}$)	Means \pm SE	
		Pregnancy	Lactation
Mean daytime T_a	21.4***	21.7 \pm 1.3	14.3 \pm 0.7
Mean nighttime T_a	10.2**	11.5 \pm 1.0	8.1 \pm 0.5
Daily maximum T_a	23.7***	29.4 \pm 1.4	21.4 \pm 1.5
Daily minimum T_a	8.58**	7.5 \pm 1.0	4.6 \pm 0.5
Daily T_a range	11.5**	21.7 \pm 1.2	16.9 \pm 1.3

Note: **, $P < 0.01$; ***, $P < 0.001$.

daily T_a range) as a covariate to control for variation during the summer.

We confirmed the presence and number of adult bats in roosts by observing roosts during the early morning (i.e., when bats were in deep torpor), by counting bats exiting at dusk, or by trapping emerging bats at roosts with mist nets. After 24 August (when volant pups were first captured), we determined the number of adults within lactation roosts by trapping.

We performed ANOVA, ANCOVA, general linear models, and regression using SAS® 8.0 (SAS Institute Inc., Cary, North Carolina), Kruskal–Wallis tests using SYSTAT® 10.2 (Systat Software Inc., Richmond, California), and χ^2 tests using Statistix 4.1 (Analytical Software, Tallahassee, Florida). We applied Yates' correction factor to χ^2 tests with one degree of freedom (Zar 1984). We used a type I error rate of 0.05 and present least squares means \pm standard error.

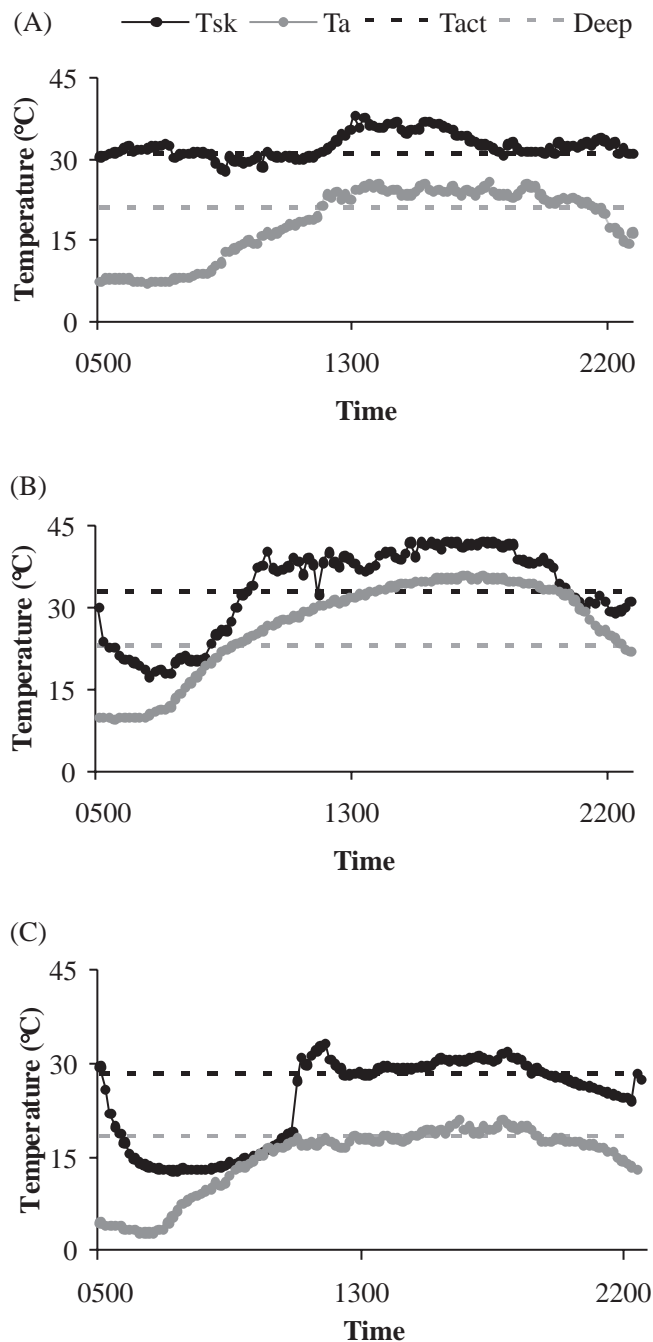
Results

During 2002, we captured 58 *M. evotis* (34 females, 24 males). Sixty-eight percent of females ($n = 23$) were reproductive: 11 were pregnant, 11 were lactating, and 1 was post-lactating. We attached radio transmitters to 6 pregnant, 6 lactating, and 8 nonreproductive females. We also radio-tracked and located roosts for an additional 4 reproductive females (1 pregnant, 3 lactating) from July to August 2001 as part of a preliminary study. Two individuals from 2001 were recaptured while pregnant during 2002 and were radio-tracked again. Of the nonreproductive females radio-tracked in 2002, 2 were tracked during the pregnancy period and 6 were tracked during the lactation period. Each individual was radio-tracked for 1 to 9 days (mean = 4.5 ± 0.4 days).

We compared mean daytime, mean nighttime, daily maximum, and daily minimum T_a and daily range in T_a during pregnancy ($n = 11$ days) and lactation ($n = 36$ days) using one-way ANOVAs. Ambient temperatures were significantly warmer, and the daily T_a range significantly greater, during the pregnancy period (Table 1).

Bats displayed two distinct thermoregulatory patterns. Pregnant and lactating females either maintained a relatively high T_{sk} , with occasional bouts of shallow torpor (14 of 32 days; Fig. 1A), or became torpid in the morning and passively rewarmed with the heat of the day to an active T_{sk} (18 of 32 days; Fig. 1B). In contrast, nonreproductive females nearly always (25 of 26 roost-days) became torpid, and their morning bouts of torpor were typically longer and deeper

Fig. 1. Examples of thermoregulatory patterns used by *Myotis evotis*: (A) maintenance of a high T_{sk} by a lactating female on 19 July; (B) torpor by a pregnant female on 10 July; and (C) torpor by a nonreproductive female on 21 July. Temperatures were recorded every 10 min from a bat's return to the roost until emergence. Note the passive rewarming and shallow torpor prior to emergence in B and C. T_{sk} , bat's skin temperature; T_a , ambient temperature; T_{act} , bat's active temperature; Deep, temperature below which deep torpor occurred.



than those of reproductive females (Fig. 1C). This represents a significant difference in the thermoregulatory strategies practiced by reproductive and nonreproductive females ($\chi^2 = 9.48$, $df = 1$, $P < 0.001$). Furthermore, on days when both reproductive and nonreproductive females carried trans-

Table 2. Mean minimum and maximum skin temperature (T_{sk}) and mean active temperature (T_{act}) ($^{\circ}\text{C}$; $\pm\text{SE}$) for pregnant, lactating, and nonreproductive *M. evotis*.

Variable	Pregnant ($n = 18$)	Lactating ($n = 14$)	Nonreproductive ($n = 25$)
Minimum T_{sk}	21.6 \pm 1.62	21.1 \pm 1.68	15.8 \pm 1.04
Maximum T_{sk}	36.8 \pm 1.29	38.1 \pm 1.11	36.0 \pm 0.97
T_{act}	26.6 \pm 2.23	30.2 \pm 1.39	27.9 \pm 1.18

Note: Sample sizes for T_{act} were 5, 6, and 7 individuals for pregnant, lactating, and nonreproductive *M. evotis*, respectively.

mitters ($n = 17$), thermoregulatory patterns differed 41% of the time, demonstrating that torpor use was not determined solely by ambient conditions. In both patterns, females frequently preceded emergence with a short, shallow bout of torpor (33 of 57 days), which coincided with a drop in T_a , and then actively rewarmed just prior to emergence (e.g., Fig. 1C).

We compared the mean minimum and maximum T_{sk} and T_{act} of pregnant ($n = 5$ bats, 18 bat-days), lactating ($n = 6$, 14 bat-days), and nonreproductive female ($n = 7$, 25 bat-days) *M. evotis* (Table 2). Minimum T_{sk} varied significantly ($F_{[15,35]} = 8.29$, $r^2 = 0.78$, $P < 0.001$), with reproductive condition ($F_{[2,35]} = 18.71$, $P < 0.001$) and individual ($F_{[13,35]} = 5.44$, $P < 0.001$) explaining much of the variation. Minimum T_{sk} 's for pregnant and lactating females were significantly higher than those for nonreproductive females (Tukey's test, $P < 0.05$). Maximum T_{sk} also varied significantly ($F_{[15,35]} = 2.56$, $r^2 = 0.52$, $P < 0.05$), with the greatest variation explained by individual ($F_{[13,35]} = 2.86$, $P < 0.01$). Maximum T_{sk} did not vary significantly by reproductive condition ($F_{[2,35]} = 1.10$, $P > 0.05$). Active temperature did not differ significantly among reproductive classes ($F_{[2,17]} = 1.41$, $r^2 = 0.16$, $P > 0.05$).

Bats entered daily torpor frequently during the study period, irrespective of reproductive condition ($\chi^2 = 3.94$, $\text{df} = 2$, $P > 0.05$). Pregnant females entered torpor slightly less often (83% of 24 bat-days) than lactating (91% of 22 bat-days) and nonreproductive females (97% of 39 bat-days). The frequency with which bats entered deep torpor depended on reproductive condition ($\chi^2 = 7.12$, $\text{df} = 2$, $P < 0.05$). Pregnant and lactating females entered deep torpor less frequently (33% and 32% of bat-days, respectively) than nonreproductive females (61%).

The amount of time a female *M. evotis* spent in torpor per day varied significantly ($F_{[18,38]} = 5.64$, $P < 0.001$). Females in different reproductive conditions differed in the amount of time they spent in torpor ($F_{[2,38]} = 6.70$, $P < 0.01$). Pregnant and lactating females did not differ, but both spent less time in torpor than nonreproductive females (Tukey's test). Individuals differed ($F_{[15,38]} = 2.41$, $P < 0.05$) and the time spent in torpor increased as the time available increased ($F_{[1,38]} = 31.44$, $P < 0.001$). The amount of time spent in deep torpor also varied significantly ($F_{[15,13]} = 5.43$, $P = 0.03$), with reproductive condition influencing duration ($F_{[2,13]} = 6.83$, $P = 0.02$). Pregnant and lactating females did not differ, but both spent less time in deep torpor than nonreproductive females did (Tukey's test). The time available for torpor also influenced the time spent in deep torpor

($F_{[1,13]} = 12.85$, $P = 0.043$), but individuals did not differ ($F_{[11,13]} = 3.88$, $P > 0.05$).

We located 9 roosts in 2001 and 70 roosts in 2002. Roosts were located in rock structures, with the exception of 6 roosts, used by 2 pregnant females, that were located in standing dead trees. These roosts were in tall, large-diameter trees (5 *Picea glauca* (Moench) Voss and 1 *Pinus contorta*) under exfoliating bark and were not included in our analyses. The same 2 females also occupied rock roosts.

Of the 73 rock roosts, 92% were used only once. One roost was used on two separate occasions during the same year: once by a lactating female and once by a nonreproductive female. Another roost was also used on two occasions during the same year: first by a pregnant female and then by both a lactating and a nonreproductive female. Two roosts were used in both years, but by different individuals in different reproductive states each year.

We located roosts in nine rock fields located along river valleys and mountain slopes (elevation 1353–1698 m, mean = 1543.3 \pm 82.8 m). Rock fields were patchily distributed in the environment and were separated by broad expanses of forest. Females switched roosts frequently (mean = 3.5 \pm 1.3 roosts/bat, range 1–6 roosts/bat), but movements were largely confined within a single rock field and the distance between consecutive roosts was relatively short (i.e., average approximately 50 m). Females occupied each roost for an average of 1.2 \pm 0.5 consecutive days (range 1–4 days).

Canopy cover and percent slope of roost sites did not differ significantly among reproductive classes ($F_{[2,68]} > 0.53$, $P > 0.05$ in each case). Roosts were located on steep slopes in relatively open habitats (Table 3), receiving only moderate shade from overhanging trees and shrubs. Bats roosted primarily on south-facing slopes (93% of 71 roosts; $\chi^2 = 30.1$, $\text{df} = 1$, $P < 0.001$). Slope aspect did not differ significantly among roosts used by pregnant, lactating, and nonreproductive bats (permutation test, $Y = 0.89$, 500 permutations, $P > 0.05$).

Eighty-one percent of 69 roosts were on or under the surface of the ground. Of the remaining roosts, none were >1 m off the ground. Reproductive female bats tended to roost above or on the surface of the ground (72% of 39 roosts), whereas nonreproductive females roosted mainly underground (61% of 28 roosts; $\chi^2 = 5.81$, $\text{df} = 1$, $P < 0.05$).

Females roosted mainly in distinct crevices (62% of 69 roosts) created between adjoining boulders or in fissures within boulder or bedrock substrate. Thirty-eight percent of roosts were located in obscure cavities formed by piles of loose boulders or talus stones. Roost type did not differ significantly ($\chi^2 = 0.69$, $\text{df} = 2$, $P > 0.05$) among pregnancy, lactation, and nonreproductive roosts.

There were no differences in roost dimensions ($F_{[2,68]} > 0.7$, $P > 0.05$ in all cases) or roost aspect among reproductive classes (permutation test, $Y = 1.20$, 500 permutations, $P > 0.05$). Reproductive roosts faced south more often than expected for a random distribution (80% of 40 roosts; $\chi^2 = 6.65$, $\text{df} = 1$, $P < 0.05$), but nonreproductive roosts did not face any particular direction (39% of 31 roosts faced north, 61% faced south; $\chi^2 = 0.41$, $\text{df} = 1$, $P > 0.05$).

The orientation of the longest roost dimension in relation to the ground was primarily vertical (i.e., between 45° and

Table 3. Quantitative measures (means \pm SE) of roosts used by pregnant, lactating, and nonreproductive *M. evotis*; differences among reproductive conditions are not significant for any variable.

Reproductive condition	<i>n</i>	Canopy cover (%)	Percent slope (%)	Slope aspect (°)	Roost aspect (°)	Roost opening area (cm ²)	Roost depth (cm)	Roost volume (cm ³)
Pregnant	23	16.8 \pm 4.9	66.0 \pm 4.3	165.4 \pm 6.9	151.2 \pm 7.6	34.6 \pm 9.0	20.4 \pm 2.5	696.6 \pm 221.7
Lactating	17	21.6 \pm 3.8	57.0 \pm 5.3	157.6 \pm 8.3	173.0 \pm 14.0	77.3 \pm 34.7	23.8 \pm 2.5	1790.6 \pm 1001.9
Nonreproductive	29	14.3 \pm 3.6	60.4 \pm 5.4	151.3 \pm 6.7	135.6 \pm 9.9	43.8 \pm 11.5	26.5 \pm 5.1	1145.5 \pm 375.0
All bats	69	17.3 \pm 2.5	61.4 \pm 3.1	167.4 \pm 4.4	179.9 \pm 6.3	46.6 \pm 7.9	23.7 \pm 2.2	1083.9 \pm 225.3

Table 4. Analyses of general linear models comparing thermal properties of roosts (roost temperature, T_r) used by pregnant, lactating, and nonreproductive *M. evotis*; the corresponding measure of T_a was included as a covariate.

Variable	Fit of overall model	Reproductive class	Roost (reproductive class)	T_a	Reproductive class $\times T_a$
Mean daytime T_r	$F_{[38,163]} = 64.88^{***}$	$F_{[2,163]} = 2.77$	$F_{[33,163]} = 12.41^{***}$	$F_{[1,163]} = 338.42^{***}$	$F_{[2,163]} = 4.74$
Mean nighttime T_r	$F_{[38,168]} = 19.90^{***}$	$F_{[2,168]} = 4.39^*$	$F_{[33,168]} = 5.51^{***}$	$F_{[1,168]} = 134.01^{***}$	$F_{[2,168]} = 5.16^{**}$
Daily maximum T_r	$F_{[38,164]} = 64.93^{***}$	$F_{[2,164]} = 6.34^{**}$	$F_{[33,164]} = 17.46^{***}$	$F_{[1,164]} = 296.04^{***}$	$F_{[2,164]} = 5.76^{**}$
Daily minimum T_r	$F_{[36,164]} = 12.80^{***}$	$F_{[2,164]} = 12.50^{***}$	$F_{[33,164]} = 4.59^{***}$	$F_{[1,164]} = 55.74^{***}$	—
Daily T_r range	$F_{[36,164]} = 25.25^{***}$	$F_{[2,164]} = 21.52^{***}$	$F_{[33,164]} = 17.25^{***}$	$F_{[1,164]} = 105.35^{***}$	—

Note: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; —, not applicable.

135°; 84% of 69 roosts) and did not differ among reproductive classes ($\chi^2 = 1.90$, $df = 2$, $P > 0.05$). Most roosts were protected from precipitation (87%) by overhanging rocks or vegetation. Nonreproductive females always occupied protected roosts, whereas only 77% of 40 roosts used by reproductive females were protected. This represents a significant difference between reproductive and nonreproductive roosts ($\chi^2 = 7.50$, $df = 1$, $P < 0.01$).

Thermal properties differed among 7 pregnancy ($n = 32$ roost-days), 10 lactation (47 roost-days), and 19 nonreproductive (86 roost-days) roosts used by female *M. evotis*. General linear models explained a significant amount of the variation in each temperature measure (Table 4). In each analysis, T_r varied significantly among individual roosts and increased significantly with increases in the corresponding measure of T_a . Mean daytime and daily maximum T_r 's (Figs. 2A, 3A) were often higher than the corresponding measures of T_a (i.e., above the 1:1 line), indicating that roosts amplified warm ambient conditions. Mean nighttime and daily minimum T_r 's (Figs. 2B, 3B) were higher and daily ranges in T_r were narrower than the corresponding measures of T_a , indicating that roosts were also buffered against cool ambient conditions.

Mean daytime, mean nighttime, and daily maximum T_r 's were significantly influenced by an interaction between reproductive class and T_a (Table 4). Comparison of partial regression coefficients (Table 5) indicated that mean daytime and nighttime T_r 's for pregnancy and lactation roosts increased similarly with T_a and were more influenced by T_a than were the same measures for nonreproductive roosts. This meant that at high T_a 's, nonreproductive roosts were cooler than pregnancy or lactation roosts (Fig. 2). In contrast, coefficients for daily maximum T_r 's were more similar between lactation and nonreproductive roosts and increased significantly faster with T_a than did those for pregnancy roosts.

Minimum T_r and daily T_r range differed significantly among reproductive classes (Table 4). Pregnancy roosts had

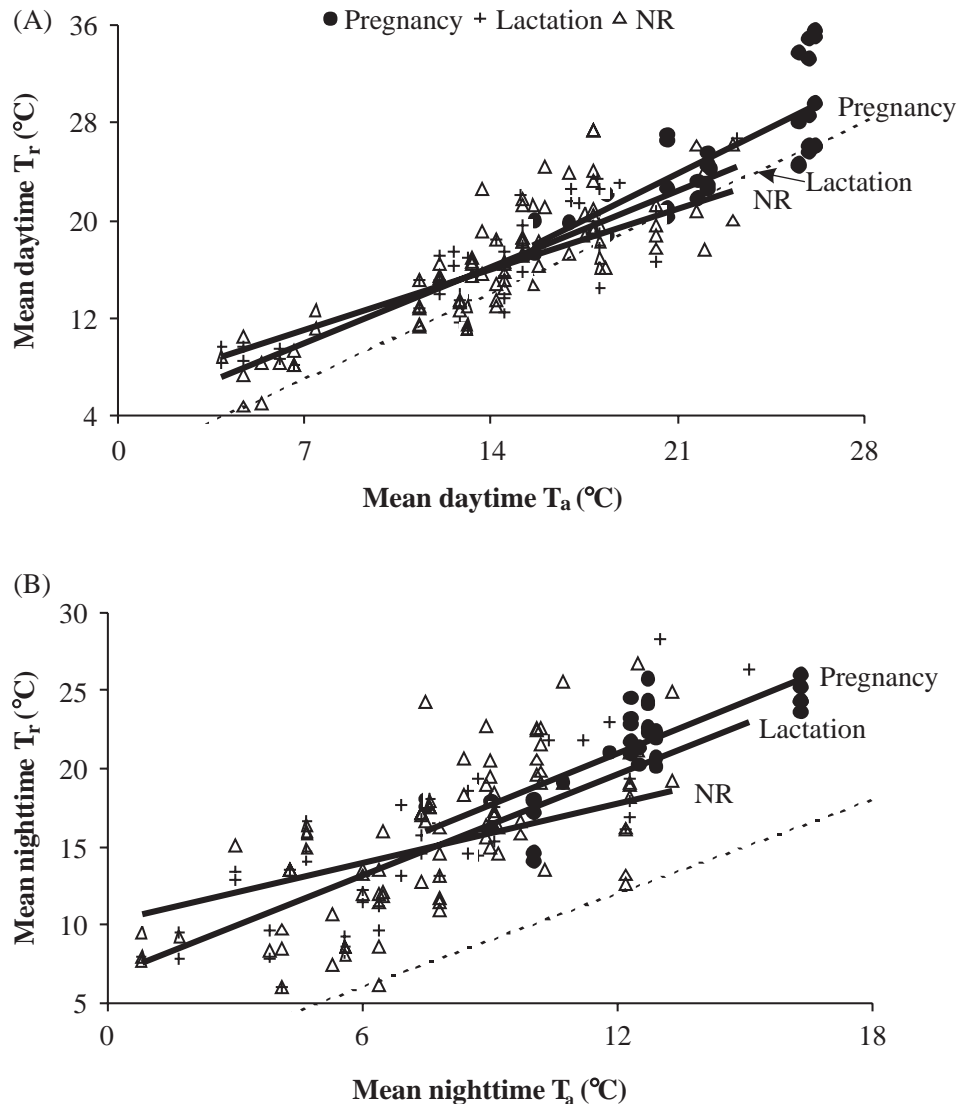
the highest minimum T_r 's (Fig. 3B) and experienced the greatest daily fluctuations in T_r (Tukey's tests, $P < 0.05$). Minimum T_r 's were similar between lactation and nonreproductive roosts (Tukey's test, $P > 0.05$), but daily T_r range was significantly greater in lactation roosts (Tukey's test, $P < 0.05$).

The rate at which roosts warm may be important to bats, so we also compared the number of minutes after sunrise before roosts reached their maximum temperature each day. Analysis of a general linear model ($F_{[35,165]} = 6.22$, $r^2 = 0.63$, $P < 0.001$) detected significant influences of reproductive class ($F_{[2,165]} = 11.06$, $P < 0.001$), individual roost ($F_{[32,165]} = 5.52$, $P < 0.001$), and T_a ($F_{[1,165]} = 14.46$, $P < 0.001$). Pregnancy roosts ($n = 31$ roost-days) warmed significantly faster (least-squares mean \pm SE = 559.4 \pm 22.1 min) than lactation (48 roost-days; 682.6 \pm 12.2 min) or nonreproductive roosts (90 roost-days; 671.0 \pm 9.3 min) (Tukey's test, $P < 0.001$ in both comparisons). All roosts reached maximum temperatures more quickly on days with higher maximum T_a 's.

To test whether differences between pregnancy and lactation roosts resulted from differences in T_a during the two reproductive periods, we compared temperatures for 5 pregnancy roosts ($n = 17$ roost-days), recorded during the lactation period, with temperatures for 10 lactating roosts (47 roost-days; Table 6). Thermal properties of pregnancy and lactation roosts did not differ significantly during the lactation period, although they did differ significantly among individual roosts (nested within reproductive class).

We compared the numbers of adult females occupying pregnancy ($n = 18$ roost-days), lactation (17 roost-days), and nonreproductive (23 roost-days) roosts using a Kruskal–Wallis test. There was significant variation in group size (Kruskal–Wallis = 28.0, $df = 2$, $P < 0.001$), with females forming larger groups in lactation roosts (mean = 3.06 \pm 0.32 bats) than in pregnancy (1.28 \pm 0.31 bats) or nonreproductive (1.04 \pm 0.29 bats) roosts. We did not find a significant relationship between the number of bats occupying a

Fig. 2. (A) Mean daytime temperature of roosts (T_r) used by pregnant ($r^2 = 0.60$), lactating ($r^2 = 0.72$), and nonreproductive (NR; $r^2 = 0.68$) *M. evotis* in relation to mean daytime T_a . (B) Mean nighttime T_r for pregnancy ($r^2 = 0.65$), lactation ($r^2 = 0.65$), and nonreproductive ($r^2 = 0.48$) roosts in relation to mean nighttime T_a . The dashed line represents a 1:1 relationship.



roost and the T_a when bats arrived at that roost (regression, $t_{[0.05,35]} = 0.27$, $r^2 = 0.002$, $P > 0.05$). To determine whether there was a relationship between group size and the thermoregulatory behaviour of bats within roosts, we used regression analysis. We analyzed the effect of group size on the minimum T_{sk} , the proportion of time spent in torpor, and the proportion of time spent in deep torpor by individuals for 36 roost-days. Minimum T_{sk} increased significantly and the proportion of time spent in torpor or deep torpor decreased significantly for individuals as the number of bats within roosts increased (regression, $t_{[0.05,35]} > 2.61$, $r^2 > 0.17$, $P < 0.001$ for all models).

Discussion

All *M. evotis* in our study entered torpor frequently, but the patterns differed between reproductive and nonreproductive females. Pregnant and lactating females either main-

tained a high T_{sk} while roosting, with occasional short bouts of shallow torpor, or allowed T_{sk} to fall and then passively rewarmed with increasing T_a . In contrast, nonreproductive females routinely entered torpor, and their periods of torpor were longer and deeper than those of reproductive bats. Reproductive females also had higher minimum T_{sk} 's. These results support the hypothesis that a trade-off exists between torpor and reproduction in bats. We suggest that as body temperature initially drops, energy savings gained by using torpor increase more rapidly than the costs of delayed reproduction. However, below a certain body temperature, further reductions yield diminishing energy savings, whereas reproductive costs likely continue to increase (Studier 1981; McNab 1982). Therefore, by entering relatively short bouts of shallow torpor, reproductive females accrue substantial energy savings (Studier 1981; Webb et al. 1993) but may minimize the costly reproductive delays associated with prolonged deep torpor. Nonreproductive females, on the other

Fig. 3. (A) Daily maximum T_r of roosts used by pregnant ($r^2 = 0.24$), lactating ($r^2 = 0.63$), and nonreproductive (NR; $r^2 = 0.68$) *M. evotis* in relation to daily maximum T_a . (B) Daily minimum T_r for pregnancy ($r^2 = 0.33$), lactation ($r^2 = 0.42$), and nonreproductive ($r^2 = 0.38$) roosts in relation to daily minimum T_a . The dashed line represents a 1:1 relationship.

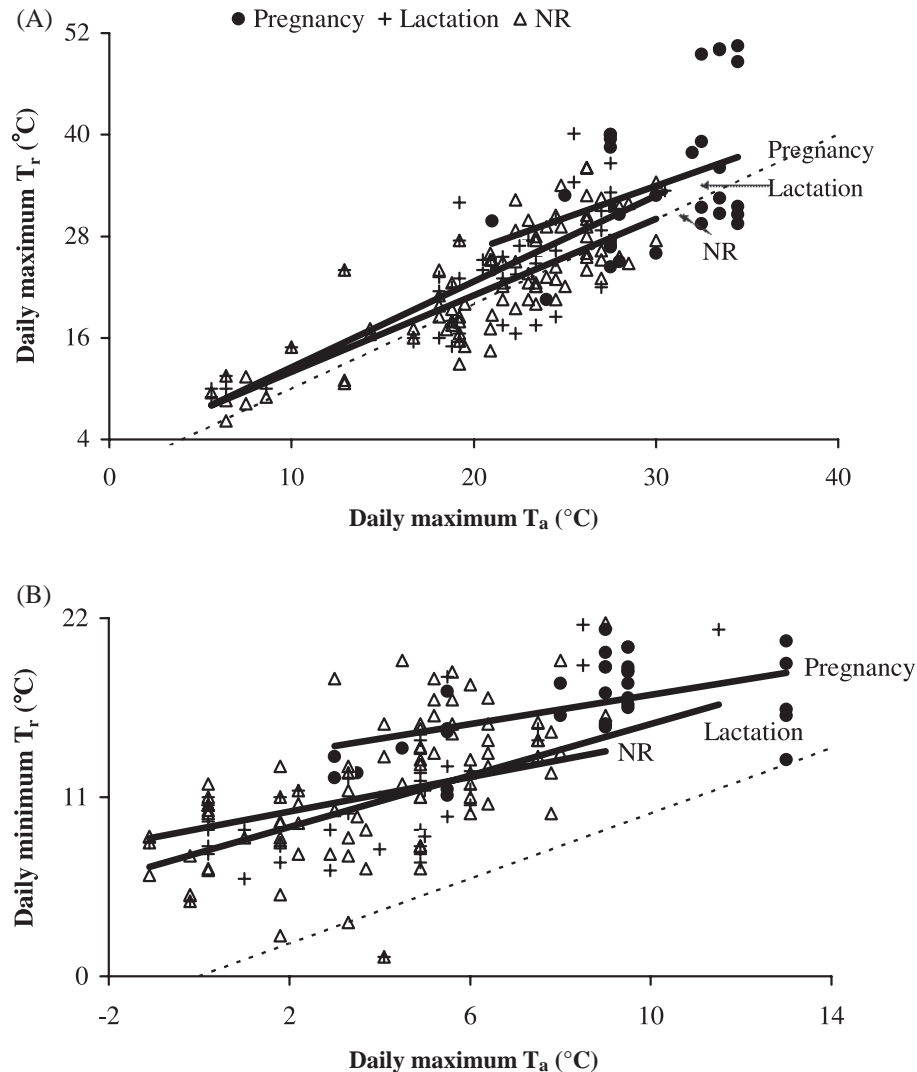


Table 5. Partial regression coefficients (mean \pm SE) describing the interaction between *M. evotis* reproductive class and T_a for roost temperature variables.

Variable	Pregnancy	Lactation	Nonreproductive
Mean daytime T_r	1.08 \pm 0.16	0.89 \pm 0.06	0.70 \pm 0.07
Mean nighttime T_r	1.10 \pm 0.19	1.07 \pm 0.11	0.64 \pm 0.10
Daily maximum T_r	0.77 \pm 0.21	1.10 \pm 0.08	0.90 \pm 0.09

Note: Boldfaced coefficients do not differ significantly from other such coefficients in the same row (comparison of slopes, $P > 0.05$). All regression coefficients differ significantly from zero ($P < 0.001$).

hand, exhibit a thermoregulatory strategy that should maximize energy conservation, indicating that they pay lower costs when torpid.

Among mammals, energy investments often vary during the reproductive cycle (Gittleman and Thompson 1988), which may favour different thermoregulatory behaviour during pregnancy and lactation. Energy demands of reproductive bats are highest during lactation (Racey and Speakman

1987; Kurta et al. 1989), but most studies of thermoregulatory behaviour of bats report minimal use of torpor, and especially deep torpor, by lactating females (Audet and Fenton 1988; Hamilton and Barclay 1994; Grinevitch et al. 1995; Chruszcz and Barclay 2002; Lausen and Barclay 2003; Willis 2006). Avoidance of torpor by lactating females has been interpreted as indicating that the reproductive costs of torpor are greater during lactation than during pregnancy (Willis 2006).

In contrast to other studies, our study showed that lactating *M. evotis* did not use torpor less than pregnant females did. Indeed, there was a tendency for longer bouts of torpor among lactating *M. evotis*. This may be a consequence of the seasonal delay in the mountains. In other regions, lactation generally occurs during midsummer, when T_a 's, and associated insect availability, are highest (e.g., Lausen and Barclay 2003). The benefits of entering torpor may be lower under such conditions (Willis 2006). In the mountains, reproduction is delayed (Solick 2004), and lactation by *M. evotis* occurs later during the summer, when conditions

Table 6. Results of ANCOVAs comparing thermal properties of roosts used by pregnant and lactating *M. evotis* during the lactation period; the corresponding measure of T_a was included as a covariate.

Variable	Fit of overall model	Reproductive class	Roost (reproductive class)	T_a
Mean daytime T_r	$F_{[15,63]} = 49.68^{***}$	$F_{[1,63]} = 3.18$	$F_{[13,63]} = 10.70^{***}$	$F_{[1,63]} = 295.38^{***}$
Mean nighttime T_r	$F_{[15,63]} = 12.50^{***}$	$F_{[1,63]} = 3.04$	$F_{[13,63]} = 2.82^{**}$	$F_{[1,63]} = 75.53^{***}$
Daily maximum T_r	$F_{[15,63]} = 48.84^{***}$	$F_{[1,63]} = 0.47$	$F_{[13,63]} = 12.59^{***}$	$F_{[1,63]} = 263.49^{***}$
Daily minimum T_r	$F_{[15,63]} = 7.45^{***}$	$F_{[1,63]} = 1.05$	$F_{[13,63]} = 2.24^*$	$F_{[1,63]} = 33.25^{***}$
Daily T_r range	$F_{[15,63]} = 13.38^{***}$	$F_{[1,63]} = 0.01$	$F_{[13,63]} = 8.15^{***}$	$F_{[1,63]} = 44.87^{***}$
Time to reach daily maximum T_r	$F_{[15,64]} = 4.84^{***}$	$F_{[1,64]} = 3.87$	$F_{[13,64]} = 3.55^{***}$	$F_{[1,64]} = 14.55^{***}$

Note: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

are cooler. To cope with the increased energy demands of foraging and thermoregulation, lactating *M. evotis* in the mountains may be forced to increase the use of daily torpor.

Myotis evotis roosted primarily in rock fields on steep, south-facing slopes. Rock crevices used as roosts were typically unobstructed by vegetation, and roost openings were usually oriented vertically. Such roosts were exposed to solar radiation, and daytime roost temperatures often exceeded T_a . Most roosts were also located near or in the ground, where T_a is highest and radiative cooling is lowest (Geiger et al. 2003). As a result, roosts used by *M. evotis* warmed rapidly during the day and cooled slowly at night.

Bats within roosts experienced a variable microclimate. Roost temperatures were below the thermoneutral zone during the cool early morning and late afternoon but often surpassed T_a 's between these periods. Maintaining homeothermy within roosts with these temperature patterns would be expensive, especially during the morning when T_a is lowest. Pregnant females appeared to compensate for this by choosing roosts that warmed rapidly, thus minimizing the time spent actively maintaining T_b or the time spent in torpor. Roosts used during pregnancy also had higher daily minimum temperatures than other roosts, further reducing the costs of homeothermy.

Surprisingly, lactation roosts warmed more slowly and reached lower minimum temperatures than pregnancy roosts, despite the structural similarity of these roost types. Comparison of temperatures of pregnancy and lactation roosts during the lactation period (i.e., under the same ambient conditions) revealed similar microclimates, suggesting that thermal differences between roosts were driven by higher T_a 's during pregnancy rather than by inherent differences in roost structure. Thus, pregnant and lactating *M. evotis* sought out similar roost types despite differences in reproductive demands and external temperatures. This is unusual in comparison with other rock-roosting bat populations (*Antrozous pallidus* (Le Conte, 1856), Vaughan and O'Shea 1976; Lewis 1996; *Eptesicus fuscus* (Beauvois, 1796), Lausen and Barclay 2003), including *M. evotis* in the prairies of Alberta (Chruszcz and Barclay 2002), which exhibit seasonal shifts in roost type correlated with changing physiological needs. Given the increased demands of lactation and the increased costs of homeothermy associated with lower T_a 's, female *M. evotis* should switch to roosts with warmer, more stable microclimates after parturition. Perhaps warmer, more stable roosts than those used by pregnant females are not available in our study area.

Instead of selecting different roost types, lactating *M. evotis* achieved warm, stable T_b 's by roosting with other indi-

viduals. Bats in groups maintained higher minimum T_b 's and used torpor less, suggesting that the metabolic heat generated from clustering (and the reduced surface area) helped alleviate thermoregulatory demands. Even in small groups (e.g., 4–5 individuals), clustered bats use substantially less energy to remain warm than solitary individuals do (Trune and Slobodchikoff 1976; Hollis 2004). An additional benefit of forming groups during lactation is that nonvolant juveniles are able to remain warm, at a reduced cost, by clustering together at night when adults are foraging (Hollis 2004). In contrast to lactating females, pregnant and nonreproductive *M. evotis* tended to roost alone, although likely for different reasons. By roosting alone, nonreproductive females avoid factors that could hinder entry into torpor, such as metabolic heat buildup or disturbance from other bats. On the other hand, pregnant females may roost alone to avoid elevating T_r above lethal limits during the warmest part of the summer. Another possibility is that because of warmer roost microclimates during pregnancy, the benefits of clustering do not outweigh the costs of locating roost-mates and coordinating roosting during pregnancy (Lewis 1996).

Consistent with different thermoregulatory strategies, roosts used by reproductive and nonreproductive females differed in physical and thermal characteristics. Reproductive roosts were located mainly in rock crevices on or above the ground and were less buffered against environmental conditions than nonreproductive roosts, which were located mainly in crevices that extended into the ground. As a result, temperatures in nonreproductive roosts were more stable and thus tended to be lower at higher T_a 's than temperatures in reproductive roosts, allowing nonreproductive females to remain torpid longer and accrue greater energy savings (Speakman and Thomas 2003). Other differences in roost structure also seem to support heterothermy. Nonreproductive roosts were always sheltered from precipitation, whereas reproductive roosts were occasionally unprotected. Greater protection by overhanging rocks or vegetation may have benefited nonreproductive bats by minimizing disturbance from rain during torpor and by increasing the buffering capacity of roosts. Lastly, although nonreproductive females roosted mainly on south-facing slopes, roost openings did not face any particular direction, suggesting that these females minimized exposure to sunlight.

Given their preference for stable microclimates and greater use of torpor, why do nonreproductive females choose roosts located in the same highly exposed rock fields used by reproductive females? Roosts in less exposed areas

would be more suitable for females attempting to conserve energy by means of torpor. Rock fields on north-facing slopes and under dense canopy cover were abundant in our study area but were never used as roosting habitat. Nonreproductive females may roost on exposed slopes to take advantage of passive rewarming (Geiser and Drury 2003) and to avoid the high costs of arousal (Lovegrove et al. 1999), but they maximize torpor use by choosing roosts within slopes that have stable microclimates.

Most studies comparing torpor use between free-ranging reproductive and nonreproductive individuals (including males and post-lactating females) have focused on colonies of big brown bats, *Eptesicus fuscus*, occupying buildings (Audet and Fenton 1988; Hamilton and Barclay 1994; Grinevitch et al. 1995). Consistent with our results for *M. evotis*, reproductive female *E. fuscus* make limited use of torpor. However, *E. fuscus* entered torpor much less often than *M. evotis* in our study, suggesting that building roosts possess qualities that reduce energy demands compared with natural structures (Lausen and Barclay 2006). Lausen and Barclay (2003) investigated the thermoregulatory behaviour of *E. fuscus* roosting in natural rock crevices. Although reproductive females used torpor less than post-lactating females, all *E. fuscus* spent considerably less time in torpor than *M. evotis* in our study. Thus, the greater use of torpor by *M. evotis* may be a species-specific trait rather than a function of roost type. For example, *M. evotis* have small bodies and roost in small groups and are therefore probably under greater energy constraints than the larger, more gregarious *E. fuscus*. Chruszcz and Barclay (2002) attributed the unusually high use of torpor by *M. evotis* in the prairies of Alberta to the unique set of energy demands (i.e., solitary roosting, long foraging bouts, arid climate) faced by reproductive females in that environment. Direct comparisons among the thermoregulatory strategies of multiple species within and among environments would help determine whether the patterns reported here are unique to *M. evotis* and would help clarify the effects on torpor use of confounding factors such as body size, climate, foraging ecology, and colony size.

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