Thermoregulatory ecology of a solitary bat, *Myotis evotis*, roosting in rock crevices

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Summary

1. Most studies of the thermoregulatory ecology of bats have been limited to laboratory experiments or studies of individuals roosting in artificial structures.

2. We investigated the interaction between thermoregulatory behaviour and roost choice in reproductive female Western Long-Eared Bats, *Myotis evotis* (H. Allen), roosting solitarily in natural rock crevices. The study was conducted in the badlands of the South Saskatchewan River Valley, Alberta, Canada, during 1997 and 1998.

3. Individuals used torpor every day and the amount of time spent in torpor was primarily influenced by the amount of time available to do so. Minimum body temperature was influenced by ambient temperature, although the form of this relationship differed between pregnant and lactating females. Pregnant females used deep torpor more frequently than lactating females.

4. All individuals roosted in rock crevices but pregnant and lactating females chose roosts that were different in structure and thermal characteristics. Pregnant females chose horizontal roosts that cooled at night but warmed quickly during the day, thus allowing passive rewarming from torpor. Lactating females chose vertical roosts that stayed warm at night when non-volant pups were present, thereby minimizing thermoregulatory costs to the young.

5. The behaviours observed are adaptive, but differ from those of other temperate-zone insectivorous bats that have been studied in the past. This highlights the importance of studying free-ranging animals living in natural habitat if we are to have an accurate view of thermoregulatory strategies and the importance of roost characteristics for roost-site selection.

Key-words: Chiroptera, natural roosts, reproduction, thermoregulation, torpor

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Introduction

To survive and reproduce, animals must balance energy use with energy accumulation. Female mammals experience their highest energy demands during pregnancy and lactation (Gittleman & Thompson 1988) and temperate-zone insectivorous bats experience particularly high energy demands owing to their small size, an expensive mode of locomotion (Kurta *et al*. 1989a) and a short breeding season. Reproductive female bats may adjust to high energy demands and variable prey availability by modifying their thermoregulatory and/or roosting behaviour (Hamilton & Barclay 1994).

Torpor is a facultative energy-saving strategy used by some mammals and birds (Wang & Wolowyk 1988). Torpid individuals accrue significant energy savings relative to individuals that maintain high body temper-

atures (T_b) (Studier & O'Farrell 1976; Geiser 1993; Webb, Speakman & Racey 1993; Song & Geiser 1997), and even small reductions in T_b may result in substantial energy savings (Studier 1981; Webb *et al*. 1993). However, entry into torpor results in reduced rates of embryonic development and prolonged gestation in some bats (Racey 1973; Racey & Swift 1981; Audet & Fenton 1988; Lewis 1993). Milk production is also reduced at low T_b and may delay weaning (Tuttle 1976; Wilde, Knight & Racey 1999). Delays in parturition or weaning result in delayed self-sufficiency of young which may be particularly detrimental for temperate-latitude bats because the foraging season is short and starvation over the winter during hibernation is thought to be a major source of mortality (Kurta 1986). Female Big Brown Bats (*Eptesicus fuscus*) appear to avoid using torpor, particularly during lactation (Audet & Fenton 1988; Hamilton & Barclay 1994; Grinevitch, Holroyd & Barclay 1995). Higher ambient temperatures (T_a) during lactation may reduce the energetic benefits of torpor, making

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it less profitable relative to the costs of slowed juvenile growth.

Bats spend a significant proportion of their lives roosting (Kunz 1982; Lewis 1996). Roosts typically provide relatively stable microclimates and protection from predation and adverse weather (Kunz 1982; Hamilton & Barclay 1994; Lewis 1996; Sedgeley 2001). Considering the energetic costs of reproduction, the influence of temperature on foetal and juvenile growth rates, and the thermal lability of temperate insectivorous bats, choosing roosts with an appropriate microclimate should be important (Kunz 1982; Hamilton & Barclay 1994; Lewis 1996). Reproductive females should choose warm roosts to reduce thermoregulatory costs while facilitating foetal and juvenile growth (Hamilton & Barclay 1994). The choice of roosts may be particularly important for bats that live in small colonies or are solitary, as they are less able to take advantage of the benefits of metabolic heat accumulation due to clustering than those roosting in large maternity colonies. In addition, roost choice may differ between pregnant females and those with prevolant juveniles with poor thermoregulatory abilities.

Few studies have examined the interaction between thermoregulation and roost choice in free-ranging bats, especially in natural roost sites (see Arlettaz *et al.* 2000 for a winter study). Research has been limited to laboratory experiments (Studier & O'Farrell 1972; Kurta 1986; Kurta *et al.* 1987; Kurta & Kunz 1988) and studies of bats roosting in human-made structures (Audet & Fenton 1988; Hamilton & Barclay 1994; Grinevitch *et al.* 1995; Entwistle, Racey & Speakman 1997). Because captive animals often do not behave like their free-ranging counterparts (Geiser *et al.* 2000), and because of inherent differences between the structural and thermal characteristics of artificial and natural roosts, examination of behavioural patterns in naturally roosting bats is a necessary complement to the studies mentioned above. We thus studied the thermoregulatory ecology of reproductive female Long-Eared Bats, *Myotis evotis* (H. Allen), roosting solitarily in natural roosts in southeastern Alberta. Specifically, we addressed the impact of reproductive condition and T_a on the use of torpor and roost site selection.

Materials and methods

STUDY SITE AND SPECIES

Our research was conducted from May to August 1997 and 1998 in the South Saskatchewan River Valley about 20 km south of the town of Bindloss, Alberta, Canada (50°73′ N, 110°56′ W, elevation 700 m). The river valley is bordered by steep sandstone cliffs inundated with drainage gullies (or coulees) eroded into the sandstone, and is referred to as 'badlands'. Reproductive female *M. evotis* roost in the coulees in sandstone boulders that lie above the more permeable surrounding sandstone. Most roost alone, but they are occasionally found in small groups of up to three individuals. Individuals forage in and around clusters of Cottonwood trees (*Populus deltoides* Marsh) at the edge of the river (Holloway & Barclay 2000).

Myotis evotis inhabits much of temperate western North America (Manning & Jones 1989) and in our study area it is the second most abundant bat species, making up 30% of captures along the river (Holloway & Barclay 2000). All reproductive females captured before 1 July ($N = 11$) were pregnant and all but three of those captured after 1 July ($N = 15$) were lactating. Therefore, May and June are referred to as the pregnancy period, and July and the first week of August as the lactation period. *Myotis evotis* is a slow, manoeuvrable flier and can take prey from vegetation (gleaning) as well as prey in flight (hawking; Faure & Barclay 1994). In our study area *M. evotis* is the only gleaning species. Lepidoptera are the principal prey, but Coleoptera and Diptera are also consumed (Barclay 1991; Holloway & Barclay 2000).

CAPTURE

Bats were captured in mist nets at various positions within riparian Cottonwood stands. The reproductive condition of all captured females (i.e. pregnancy, lactation and postlactation; Racey 1988), as well as mass (Sartorius PT600 Balance, ±0·1 g; Sartorius AG, Goettingen, Germany) and age (subadult or adult) were determined. Age was determined by examining the cartilaginous gap between the diaphysis of the metacarpal and proximal phalanx (Anthony 1988).

To find roosts and monitor T_b, temperature-sensitive radio-transmitters (Holohil Systems Ltd, Carp, ON) weighing either 0·54 g (1997) or 0·56 g (1998) were attached to reproductive females. The fur between the shoulder blades was trimmed and the transmitters glued to the skin using Skinbond® surgical adhesive (Canadian Howmedica, Guelph, Ontario, e.g. Hamilton & Barclay 1994).

MONITORING AMBIENT AND BODY TEMPERATURES

A HOBO®-TEMP data logger (Model HTEA-37 + 46, Onset Computer Corporation, Bourne, MA) was used to continuously record T_a in the shade every 10 min. The logger was positioned 1·5 m above the ground. The T_b of radio-tagged bats was monitored every 10 minutes from the time they returned to their roost after foraging until they emerged again the following evening. Temperatures of roosting bats were determined manually using a Merlin 12 receiver (Custom Electronics, Nokomis, FL) with a five-element yagi antenna. The time taken for a transmitter to emit 10 pulses (averaged over 3 sets of 10) was measured and these values were compared to transmitter-specific calibration curves (provided by the manufacturer) to determine skin temperatures. Skin temperature measured this way
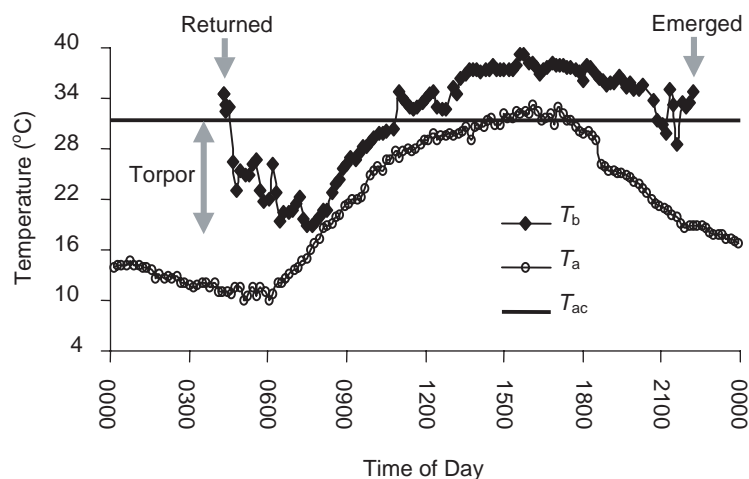
Fig. 1. A typical daily temperature profile from a pregnant *M. evotis*, 25 May 1998. T_b is body temperature of the bat, T_a is ambient temperature, T_{ac} is active temperature of the bat (i.e. the lowest T_b of the bat at the time of emergence out of all of the days that it held its transmitter). The female can enter torpor when $T_a < T_{ac}$ and is in torpor when $T_b < T_{ac}$.
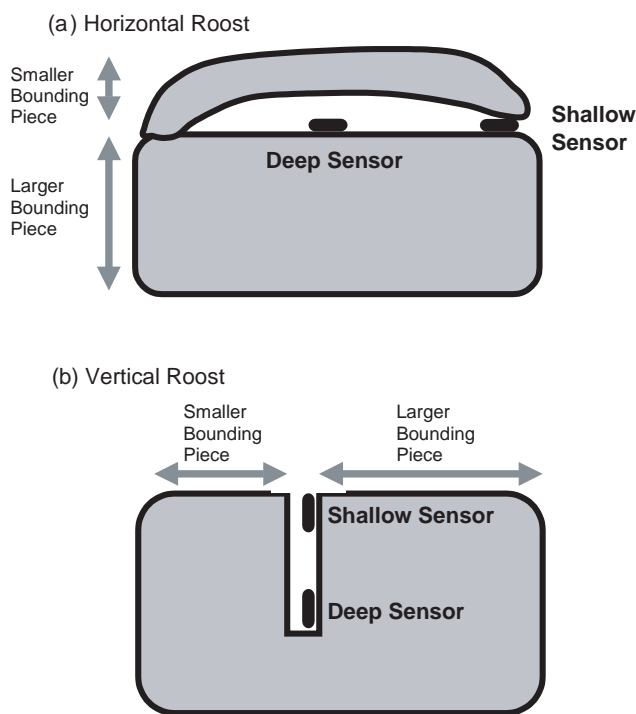
Fig. 2. Schematic cross-section of two types of roosts used by pregnant and lactating *M. evotis*. (a) Pregnant females roosted in horizontal crevices under flakes of rock that weathered off the surface of cemented sandstone boulders. (b) Lactating females roosted in vertical crevices where the cemented sandstone boulder had split in two. Also shown are the various positions where HOBO®-TEMP data loggers were placed.

accurately reflects core body temperature (T_b) in active and torpid bats (Audet & Thomas 1996; Barclay *et al*. 1996). A LOTEK SRX 400 (Lotek Engineering Inc., Newmarket, ON) scanning receiver was also used to monitor T_b values automatically while we were away from the study area.

The definitions of torpor and deep torpor described by Grinevitch *et al*. (1995) and Hamilton & Barclay (1994) were used. An individual was in torpor if its T_b fell below its active temperature (T_{ac}, i.e. the lowest T_b recorded for the individual immediately before it emerged to forage, during the period that it held its transmitter; Fig. 1). A bat was in deep torpor if its T_b fell below its T_{ac} by at least 10 °C. The time available for the bat to use torpor was defined as the amount of time when T_a was lower than the bat's T_{ac} (Fig. 1).

The time spent in torpor by pregnant and lactating females was compared using ANCOVA with minimum T_a during torpor, foraging time the night before, and time available for torpor as covariates. Reproductive condition (i.e. pregnant or lactating) and individual nested within reproductive condition were class variables. Individual nested within reproductive condition was considered as a random effect and individual was included in the model to account for repeated measures (i.e. data from the same individual taken over several days).

CHARACTERIZATION OF ROOSTS

Pregnant and lactating females used structurally different roosts (Fig. 2). These differences were quantified in a number of ways. First, roost crevices were grouped as having their longest dimension either vertical or horizontal to the ground. Second, the minimum width of the rock on either side of the roost cavity was measured. This provided two measures: one of the larger bounding piece of rock and one of the smaller bounding piece of rock. Because the data were not normal, Mann–Whitney *U*-tests were used to compare these measures between roosts chosen by pregnant and lactating females.

In 1998 (using roosts found during the 1997 field season) HOBO®-TEMP data loggers were placed into roosts used by pregnant (horizontal) and lactating (vertical) bats. Temperatures were monitored simultaneously in a randomly chosen pregnancy and a lactation roost, and six pairs of roosts were used consecutively throughout the summer. Loggers remained in each pair of roosts for 10–12 days and recorded temperatures every 10 min. Loggers were placed in two positions in each roost: deep (~15–30 cm from the roost opening) and shallow (~3 cm from the roost opening; Fig. 2). In both vertical and horizontal roosts, the deep position was used by bats when observed in the roosts. Bats were not necessarily in the monitored roosts at the same time sensors were present, although all roosts had been used previously. At no time did roost temperatures indicate that a bat roosted in contact with the sensor.

Mean daytime temperatures were calculated as the mean of all temperatures between the average return time and average emergence time of all bats during the period in question (i.e. pregnancy or lactation) for both types of roosts. Similarly, mean night-time temperatures were the mean of all temperatures between the average emergence time and the average return time of

all bats during the period in question. Daily (24 h) maximum and minimum temperatures, and temperature range for each roost were also determined. The temperature regimes of roosts used by pregnant (horizontal) and lactating (vertical) females were compared. The temperature recorded from the deep position in this analysis was used because it was the position females roosted in. Mean day and night temperatures, daily maximum and minimum temperatures, and daily temperature range were analysed separately using ANCOVA, with the corresponding measure of T_a as a covariate. Period of the season (i.e. pregnancy or lactation), roost-type (i.e. horizontal or vertical) and roost-pair (i.e. 1–6) were class variables. Roost-pair was included in the models to account for repeated measures.

If temperature varies within a roost, bats can potentially select the temperature most appropriate for their thermoregulatory requirements. To assess the range of conditions available to bats within roosts, horizontal and vertical roosts were analysed separately. Temperatures (deep *vs* shallow) were compared using analysis of variance (ANOVA).

All analyses were performed using SAS Version 7·0, Statistix for Windows, or Systat Version 5·0. Means are presented ± SE. An alpha value of 0·05 was used except for pairwise comparisons where alpha values were corrected using the sequential Bonferroni procedure (Rice 1989).

Results

Twenty-three adult female *M. evotis* were captured over the two field seasons, some more than once. Data from various subsets of these bats were used, depending on whether the bat in question had a transmitter attached to it, the reproductive condition of the individual and the analysis being performed.

Aldridge & Brigham (1988) suggested that transmitters should be kept less than 5% of an individual's body mass. In this study, using the smallest transmitters available, transmitter mass ranged from 5·9% to 8·9% of bat mass (mean = 7·3 ± 0·1%, $N = 34$). However, foraging behaviour and reproductive success were not influenced by the application of radio-transmitters

(Chruszcz 1999). For example, individuals foraged all night whether they carried a radio-transmitter or not and bats gained mass whether carrying a transmitter or not.

USE OF TORPOR

Daytime T_b of 10 pregnant and 7 lactating females was monitored over the two field seasons. Mean minimum T_b of pregnant and lactating females was 18·4 ± 0·9 °C and 23·9 ± 0·8 °C, respectively, and mean active temperatures (T_{ac}) of pregnant and lactating females were 27·61 ± 0·5 °C and 31·3 ± 0·4 °C, respectively. Minimum T_b was always below T_{ac} and was within 3 °C of T_{ac} on only 8 of 52 bat-days. The lowest T_b recorded for any radio-tagged bat was 10·7 °C for a pregnant female on 25 June 1997. Every bat used torpor every day. However, pregnant females used deep torpor more frequently (71% of 38 bat-days) than lactating females did (37% of 27 bat-days, *G*-test: $G = 7·38$, $P < 0·01$). T_a in our study area ranged from –0·7 °C to 43·5 °C over the two field seasons and fell below 10 °C on 39 days.

The time spent in torpor was compared using data from six pregnant ($N = 15$ bat-days) and six lactating ($N = 19$ bat-days) females. The model explained a significant proportion of the variation in torpor time (Table 1). The use of torpor varied among individuals (within each reproductive condition) and there was a significant interaction between foraging time and individual bat, but the most important factor influencing the use of torpor was the amount of time available to use it. As the time available for torpor increased, time in torpor increased (Fig. 3). Reproductive condition did not significantly influence time spent in torpor.

Data for 10 pregnant ($N = 29$ bat-days) and 6 lactating ($N = 24$ bat-days) females were used to test the influence of T_a on minimum T_b of roosting females. There was no significant relationship between T_a and minimum T_b for pregnant females (least squares regression: $F_{1,27} = 1·12$, $r^2 = 0·04$, $P > 0·2$, Fig. 4a). However, examination of the data showed two distinct groups of points: regulating bats and conforming bats (Fig. 4a). The regulating group consisted of 5 of the 10 females, with 2 bats represented on two different days ($N = 7$ bat-days). Three of the five regulating females also belonged to the conformer group. The data in the regulating group came from 1997 and 1998 and spanned most of the pregnancy period, occurring from 4 to 28 June. The mean ± SE minimum T_b of regulating females was 25·0 ± 0·3 °C. On the days in question these females maintained T_b independent of ambient conditions. Nevertheless, the mean minimum T_b for this group was still below the corresponding mean T_{ac} (27·3 ± 1·0 °C), and the bats were in torpor as each minimum T_b was below the T_{ac} of the individual that it was obtained from, although by only a few degrees.

Table 1. Results of the model describing torpor time in solitarily roosting *M. evotis* in the badlands of southeastern Alberta

Source	r^2	df	F	P
Model	0·88	21,12	4·08	0·008
Reproductive condition		1,12	2·42	0·147
Bat (reproductive condition)*		6,12	3·58	0·029
Time available		1,12	21·96	<0·001
Foraging time†		1,12	0·04	0·849
T_a		1,12	0·28	0·609
Foraging time × bat (reproductive condition)?		7,12	3·96	0·019

*Individual bat nested within reproductive condition.
†The amount of time spent foraging the night before torpor time was measured.
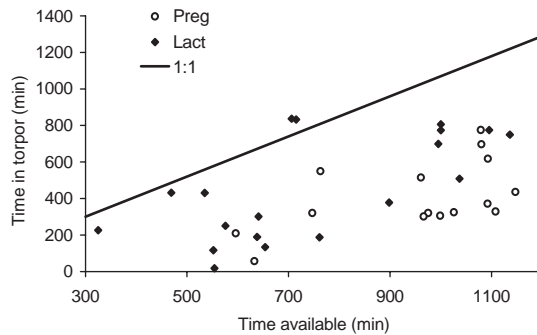
Fig. 3. The effect of time available for torpor on the amount of time spent in torpor by reproductive female *M. evotis*. Twelve females were used in this analysis ($N = 34$ bat-days). The solid line indicates torpor time = time available. The regression line for these data is: torpor time = 0·65 time available – 202·3. Two points lie above the solid line likely because actual time available (based on roost temperature) is longer than that recorded based on ambient temperature.
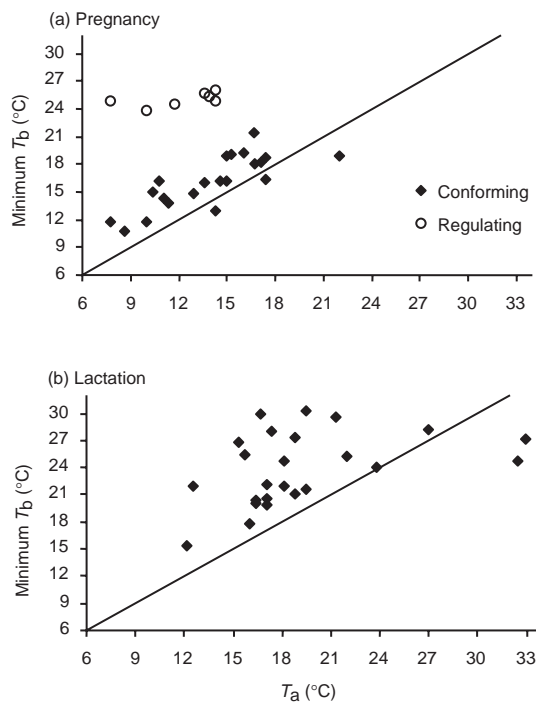
Fig. 4. The relationship between ambient temperature (T_a) and minimum body temperature (T_b) in (a) pregnant and (b) lactating female *M. evotis*. Ten pregnant females ($N = 28$ bat-days) and six lactating females ($N = 24$ bat-days) were used in these analyses. The solid lines indicate minimum $T_b = T_a$. In (a) the regression is significant only when regulators are removed from the data set. The corresponding regression equation is $T_b = 0·66T_a + 6·93$. In (b) the regression is significant and has an equation of $T_b = 0·32T_a + 17·81$. Some of the points lie below the solid line likely because roost temperature was lower than ambient temperature.

Unlike the regulating group, T_b of females in the conforming group dropped to near T_a (Fig. 4a). The conforming group included data from 8 of the 10 pregnant females, with 7 individuals represented more than once ($N = 22$ bat-days). The mean ± SE minimum T_b of the conforming group was 16·1 ± 0·6 °C. T_a had

a significant, positive influence on minimum T_b for conforming females (least squares regression: $F_{1,19} = 33·13$, $r^2 = 0·64$, $P < 0·001$).

Finally, there was also a significant positive relationship between T_a and minimum T_b for lactating females (least squares regression: $F_{1,23} = 4·56$, $r^2 = 0·17$, $P < 0·05$, Fig. 4b). There were no obvious groups of regulating or conforming lactating females.

CHARACTERIZATION OF ROOSTS

Reproductive females roosted in sandstone boulders and were typically solitary; on a few occasions two or three individuals were observed emerging from a roost. Individuals switched roosts regularly, rarely using the same roost for more than four days. Pregnant females primarily used horizontal roosts (11 of 13) whereas lactating females used roosts that were in a vertical plane relative to the ground (7 of 8, *G*-test: $G = 10·65$, $P < 0·005$).

Horizontal roosts were under flakes of rock weathering off the surface of boulders, while vertical roosts were crevices in boulders that had split in half. The width of the smaller bounding piece of rock was significantly smaller in roosts used by pregnant females compared with those used by lactating females (Mann–Whitney *U*-test: $U = 99$, $P < 0·001$, Fig. 2). However, the width of the larger bounding piece of rock did not differ between roosts used by pregnant and lactating females (Mann–Whitney *U*-test: $U = 63$, $P > 0·4$). Because the smaller bounding rock layer was thinner in roosts used by pregnant females, pregnant females had less rock buffering them against the surrounding ambient conditions than lactating females had.

Differences in temperature between roosts used by pregnant and lactating females were assessed, using roost-type (vertical or horizontal), period of the season (pregnancy or lactation), T_a and roost-pair as the main effects. Each analysis involved six pairs of roosts ($N = 63$ nights for night-time means and $N = 62$ days for the other four analyses). All five models (for mean daytime and night-time roost temperatures, daily maximum and minimum roost temperatures, and daily roost temperature range) explained a significant proportion of the variation in the data (ANCOVA, $P < 0·001$) and T_a was the most important factor contributing to the variation in each case. Temperatures within roosts were moderate relative to T_a. Mean night-time roost and minimum roost temperatures were higher and roost temperature ranges and maximum roost temperatures were lower than the corresponding ambient conditions. Thus, roosts were buffered against external temperatures.

Period of the season significantly influenced all of the models except roost temperature range. Roosts were warmer during the lactation than the pregnancy period. Mean daytime roost temperature was significantly influenced by the interaction between roost-type and period of the season ($F_{1,105} = 4·80$, $P < 0·05$).

During the pregnancy period, horizontal roosts were warmer than vertical roosts, while during lactation there was no significant difference between roost-types. Mean night-time roost temperature was significantly influenced by roost-type as vertical roosts stayed significantly warmer than horizontal roosts ($F_{1,108} = 27 \cdot 92$, $P < 0 \cdot 001$). Daily roost temperature range was influenced by the interaction between roost-type and period of the season ($F_{1,109} = 58 \cdot 52$, $P < 0 \cdot 001$). Horizontal roosts had significantly greater temperature fluctuations than vertical roosts during both periods, although the difference between roost-types was reduced during the lactation period. Vertical roosts were more buffered against T_a than horizontal roosts were. Daily maximum roost temperature was influenced by the interaction between roost-type and period of the season ($F_{1,110} = 23 \cdot 03$, $P < 0 \cdot 001$). Horizontal roosts had significantly greater maximum temperatures than vertical roosts during the pregnancy period, but there was no significant difference between roost-types during lactation. Daily minimum roost temperature was influenced by roost-type as temperature was significantly greater in vertical roosts than in horizontal roosts ($F_{1,111} = 17 \cdot 51$, $P < 0 \cdot 001$). In summary, roost temperatures were influenced by, but were more moderate than, ambient temperatures; vertical roosts were more buffered against ambient temperatures than horizontal roosts; during the pregnancy period horizontal roosts were warmer than vertical roosts during the day; and throughout the season vertical roosts were warmer than horizontal roosts at night.

Variation in thermal conditions within roosts used by pregnant (horizontal roosts) and lactating females (vertical roosts) was examined by comparing temperatures between the deep and shallow positions in horizontal roosts (three roosts, $N = 28$ days), and in vertical roosts (six roosts, $N = 62$ days). In all 10 ANOVAS, the dependent variable varied among roosts, indicating that the thermal regimes of roosts differed. Position did not play a significant role in any of the five ANOVAS comparing the deep and shallow positions of horizontal roosts. However, position did play a significant role in four of the five ANOVAS comparing the deep and shallow position of vertical roosts. Mean night-time temperature was significantly higher in the deep position than in the shallow position ($F_{1,112} = 75 \cdot 07$, $P < 0 \cdot 001$), as was daily minimum temperature ($F_{1,112} = 93 \cdot 60$, $P < 0 \cdot 001$). Conversely, daily maximum temperature was higher in the shallow position ($F_{1,112} = 62 \cdot 38$, $P < 0 \cdot 001$), as was daily temperature range ($F_{1,112} = 224 \cdot 71$, $P < 0 \cdot 001$). In other words, bats in horizontal roosts had little choice of temperature conditions, while bats in vertical roosts could change their thermal environment by shifting up or down the crevice.

Discussion

The *M. evotis* studied behaved in a different way from other species of temperate-zone insectivorous bats.

Individuals roosted solitarily and used torpor every day, regardless of reproductive condition or T_a. Furthermore, the amount of time they spent in torpor was mostly determined by the amount of time available for them to do so. We suggest that roosting solitarily eliminates the buffering effect that other individuals offer, and allows rapid entry into torpor. Pregnant and lactating females chose roosts that differed in structure and thermal characteristics. These patterns of thermoregulatory and roosting behaviour may allow females to balance a unique set of energy demands to enhance reproductive success.

TORPOR

Although reproductive female *M. evotis* used torpor every day, pregnant individuals used two distinct thermoregulatory strategies. Females either maintained T_b at around 25 °C (regulating) or allowed it to fall to near ambient levels (conforming). Bats, whether regulating or conforming, regularly warmed up prior to emergence (as in Fig. 1) confirming that even regulating bats were torpid and that the pattern did not result from contact between the transmitter and rock. Although pregnant *M. evotis* conform more frequently than they regulate, females may occasionally choose to regulate T_b to reduce the fitness costs associated with reduced foetal growth rates. At T_b near 25 °C, females could still save considerable energy compared to maintaining T_b near their T_{ac} (Webb *et al.* 1993).

There was no clear dichotomy in the thermoregulatory behaviour of lactating *M. evotis*. Although there was a significant positive relationship between minimum T_b and T_a, it was not as strong as it was for conforming pregnant bats. Insect availability may be higher during lactation because T_a is higher, night length is longer and lactating females are more manoeuvrable owing to their lower mass. Foraging may thus be more profitable during lactation and females may have greater energy reserves at the end of a foraging bout compared to pregnant females. They may thus be able to avoid dropping T_b to T_a upon return to their roosts but rather fine tune T_b to their daily maintenance and production requirements.

Torpor is used infrequently during lactation in other species of bats (Vaughan & O'Shea 1976; Audet & Fenton 1988; Hamilton & Barclay 1994; Grinevitch *et al.* 1995). Although this was not the case in our study, deep torpor was used less frequently by lactating females than by pregnant females. Increased T_a during lactation limited the number of days that deep torpor was possible. This, and the fact that foraging may be more profitable during lactation, may explain the less frequent use of deep torpor by lactating females.

The consistent use of torpor by *M. evotis* in our study may be a strategy to conserve water, as well as energy. The badlands of the South Saskatchewan River Valley are semiarid, receiving an average of 16–17 cm of precipitation from May to August (Environment

Canada). Low relative humidity, particularly during lactation, may result in high levels of evaporative water loss (EWL) in *M. evotis*. In general, small bats have high surface area to volume ratios, which are enhanced by large, naked flight membranes (Webb, Speakman & Racey 1995). The rate of evaporative water loss in resting bats is high relative to similarly sized terrestrial mammals and birds (Herreid & Schmidt-Nielsen 1966; Studier 1970; Webb *et al*. 1995).

Individuals spent more than 17 h per day in their roosts without access to water. Their solitary roosting habits mean that they cannot take advantage of clustering to conserve water (Kurta *et al*. 1989b), and solitary individuals are less likely to affect the relative humidity of their roosts than are groups. Torpor significantly reduces EWL (Webb *et al*. 1995) and EWL may influence the length of torpor bouts (Thomas & Geiser 1997). During lactation, temperatures are higher and females lose water in the form of milk (Kurta *et al*. 1989b). Therefore, one explanation for the unusual finding that lactating females used torpor every day is that it helps to balance daily water budgets in a particularly dry environment.

ROOSTS

Buildings, cracks in the ground, caves, mines, rock crevices, loose bark, tree cavities and tree stumps in clear cuts are all used as roosting sites by *M. evotis* (Manning & Jones 1989; Vonhof & Barclay 1996, 1997). In our study, *M. evotis* roosted exclusively in the crevices of sandstone boulders. As with many other species of bats (e.g. Lewis 1996; Vonhof & Barclay 1996; Brigham *et al*. 1997), individuals switched roosts often. Despite this, individuals in different reproductive stages consistently chose different types of roosts. Pregnant females roosted in horizontal crevices, beneath flakes of rock weathering off the upper surface of the boulders. Lactating females roosted in vertical crevices that split the boulder in two.

Microclimate is important in roost site selection by bats (Vaughan & O'Shea 1976; Kunz 1982; Audet & Fenton 1988; Hamilton & Barclay 1994; Vonhof & Barclay 1997; Sedgeley 2001). Although the temperature differences between roost types were small, such differences can influence metabolic rate (Webb *et al*. 1993), production of milk (Wilde *et al*. 1999) and juvenile growth rates (Tuttle 1976). We found that although the thermal characteristics of roosts were primarily determined by T_a, roosts were nonetheless buffered against ambient conditions. Roosts were warmer than ambient at night, and daily highs and lows were less extreme than ambient highs and lows.

Passive rewarming is important to heterothermic animals (Vaughan & O'Shea 1976; Hamilton & Barclay 1994) because the most energetically costly phase of torpor is rewarming. *Myotis evotis* may choose roosts that are influenced by T_a to take advantage of passive rewarming. T_b often rose passively with T_a,

thereby eliminating the need for costly metabolic heat production.

We propose that female *M. evotis* switched from using horizontal to vertical roosts for thermoregulatory reasons. Horizontal roosts warm more rapidly than vertical roosts because of the thinner layer of rock forming the roof of horizontal roosts. Horizontal roosts also have a higher mean daytime temperature, meaning that pregnant females can maintain a relatively high T_b at minimal cost compared with the cost of roosting in a vertical roost. Although horizontal roosts cool rapidly at night, pregnant females avoid the energetic costs of this because they are out foraging. One consequence is that the roosts used during pregnancy are cold at dawn when the bats return from foraging. Individuals drop into torpor rather than maintaining a high T_b at a high cost, but then are rewarmed passively. We suggest such roosts offer the best available compromise between the costs and benefits of thermoregulation and torpor with respect to energy budget and foetal growth.

After parturition, females used vertical roosts that do not experience the large temperature fluctuations of horizontal roosts and that stay warmer at night. Non-flying juveniles, who are left in the roost while their mothers forage, can thus maintain a higher T_b than if they were left in horizontal roosts. For the first few days following parturition, juvenile bats cannot maintain T_b (Lewis 1993). Thus a warmer roost at night may allow faster growth, initially via higher T_b and subsequently, once thermoregulatory abilities have developed, by reduced costs of maintaining high T_b.

Differences in the temperature of different parts of roosts may be used for behavioural thermoregulation by bats (Vaughan & O'Shea 1976; Hamilton & Barclay 1994). We found that the thermal regime of horizontal roosts did not differ between deep and shallow positions, but it did in vertical roosts. In vertical roosts, the deep position was warmer at night on average and had more stable temperatures (lower maxima, higher minima and consequently smaller ranges) than the shallow position. There is therefore the potential for behavioural thermoregulation in vertical roosts and this may explain the greater variation in the relationship between minimum T_b and T_a in lactating compared with pregnant females. Lactating females may choose specific T_bs according to their daily energy demands, and select an appropriate position within a roost. Achieving an optimal T_b in pregnant females may be constrained as a consequence of their inability to use behavioural thermoregulation and this may lead to the tighter relationship between minimum T_bs and T_a.

Naturally roosting *M. evotis* behave unusually compared with other temperate insectivorous bats that have been studied. Their thermoregulatory behaviour, roost site selection and foraging behaviour (Chruszcz 1999) suggest that they exist on a tight energy budget. Although we cannot explicitly address the causation behind the effects described in this study, the novel

behaviour of free-ranging *M. evotis* roosting in natural habitat highlights the need to confirm laboratory results with observations of animals in the wild. Thermoregulatory behaviour of various mammals and birds differs between captive and free-ranging situations (Geiser *et al.* 2000). Further studies on other species of bats roosting in natural habitat will help determine whether the patterns described above can be applied generally to bats roosting in natural roosts, or whether they are specific to *M. evotis*.

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