

Thermoregulation and roost selection by reproductive female big brown bats (*Eptesicus fuscus*) roosting in rock crevices

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Abstract

A free-ranging maternity colony of big brown bats *Eptesicus fuscus* roosting in rock crevices along the South Saskatchewan River in south-eastern Alberta, Canada, was studied to understand better the discrepancy that exists in the literature regarding torpor use by reproductive female bats. Using radio-telemetry, thermoregulatory patterns and roost microclimate were recorded for pregnant, lactating and post-lactating females. Relative torpor use is described in several ways: the proportion of days on which torpor was used, depth, minimum body temperature, time spent in torpor, and a comprehensive torpor unit (degree-min). Pregnant and lactating female *E. fuscus* used torpor to the same extent overall (degree-min), but pregnant bats used torpor less frequently and with more time in deep torpor. Torpor was used to the greatest extent after weaning (post-lactation). Evidence is presented that the cost : benefit ratio for deep and prolonged periods of torpor may be highest during lactation. Microclimates of rock-crevice roosts mirrored the use of torpor throughout reproduction by bats. Lactation roosts (deeper, larger opening size) were more thermally stable and remained warmer at night compared to the shallow roosts used by pregnant and post-lactating females. It is shown that conclusions about relative use of torpor can differ depending on the units of comparison, necessitating measurement of all aspects of torpor (depth, duration and frequency). Comprehensive measurements, individual-based normothermic temperatures, and a definition of torpor that accounts for all energy savings, allow a more accurate depiction of patterns and facilitates inter-study comparisons.

Key words: Chiroptera, reproduction, rock crevices, roost microclimate, roost selection, torpor, *Eptesicus fuscus*

INTRODUCTION

The ability to enter torpor as a means of conserving energy and water occurs in a few species of birds and various mammals (Wang & Wolowyk, 1988). Use of torpor during reproduction, however, is relatively uncommon, presumably because of the costs associated with a lowered metabolic rate (McClure, 1987). In addition to decreased escape and vigilance capabilities, and diminished body heat transfer from mother to offspring (Cossins & Bowler, 1987), reproductive female mammals experience costs of prolonged gestation (Racey, 1973; Lewis, 1993), and reduced milk production (Wilde, Kerr *et al.*, 1995), which could retard juvenile growth. Despite such costs, some birds use torpor during incubation if energy intake is low (Calder & Booser, 1973), and some marsupials use torpor during pregnancy, but not lactation (Geiser & Masters, 1994).

Many species of small bats can enter torpor (e.g. McNab, 1969; Kurta, Johnson & Kunz, 1987; Webb, Speakman & Racey, 1993; Hamilton & Barclay, 1994; Chruszcz & Barclay, 2002), although there are relatively

few field studies of individuals in natural roosts. The extent of torpor use during reproduction is also unclear, as some studies of reproductive females in buildings report little or no use of torpor, especially during lactation (e.g. Audet & Fenton, 1988), while others, studying bats in natural roosts, report extensive use of torpor throughout pregnancy and lactation (e.g. Chruszcz & Barclay, 2002). This may be the result of differences among species, but part of the discrepancy is because of variation in the definition of torpor, and to differences in the methods used to quantify it (Barclay, Lausen & Hollis, 2001). Some mammals also display different thermoregulatory patterns in captivity *vs* in the field (Geiser *et al.*, 2000), suggesting that selection of roost micro-climate is important in determining the use of torpor under natural conditions.

The goals of our study were to determine the use of torpor by free-ranging reproductive female bats roosting in natural sites, and how use of torpor and roost selection vary throughout reproduction. We predicted that because of the fitness costs associated with torpor, i.e. increased gestation length (Racey, 1973) and reduced milk production (Wilde, Kerr *et al.*, 1995), torpor should be used less during pregnancy and lactation than during the post-reproductive period. Female big brown bats *Eptesicus fuscus* in our

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study area select roosts in rock crevices based on aspect and roost dimensions, and select different attributes during each reproductive stage (Lausen & Barclay, 2002). Based on this and other roosting studies (Vaughan & O'Shea, 1976; Sedgeley, 2001; Chruszcz & Barclay, 2002), we predicted that rock crevice roosts vary in microclimate and that individuals select roosts appropriate for their thermoregulatory strategy.

Because torpor has been defined and described in numerous ways (Barclay, Lausen *et al.*, 2001), we also wanted to establish a method that would best describe torpor patterns. Use of conservative definitions of torpor (e.g. Michener, 1992; Hickey & Fenton, 1996), together with species-specific, rather than individual-specific, normothermic body temperatures have probably resulted in an underestimation of the use of torpor in some studies. This was addressed by determining normothermic temperatures for each individual, measuring all aspects of torpor (depth, duration and frequency), and defining torpor in a biologically relevant manner that would facilitate comparisons with other studies, populations and species. Because advances in technology allow for automated continuous collection of body temperature data, it is possible to collect torpor data throughout the day with relative ease. This was not feasible in many earlier field studies, and therefore a comprehensive description of torpor patterns was not always possible. Our aim was to determine whether comparisons based on a single measure of torpor (e.g. frequency), yield different conclusions to comparisons based on a comprehensive description of torpor (depth, duration and frequency).

METHODS

Study species and study site

Eptesicus fuscus is widespread across much of North America. Individuals weigh *c.* 18 g and feed on flying insects. Parturition occurs in late June or early July, and in western North America most females give birth to 1 young. During the summer, adult females roost in maternity colonies averaging fewer than 100 individuals (van Zyll de Jong, 1985). The maternity colony of *E. fuscus* studied consisted of *c.* 34 adult females. Natural roost sites for this species include rock crevices and tree hollows, but *E. fuscus* is also 1 of the most common species found in buildings (van Zyll de Jong, 1985).

Data were collected from May to August 2000 in the South Saskatchewan River Valley (50°38' N, 110°11' W; 620 m a.s.l.) *c.* 25 km south-east of the hamlet of Bindloss, AB, Canada. The terrain consists of eroded sandstone cliffs in the valley (badlands) with flat grasslands above. There are no buildings within 5 km of the study area, and with the exception of several clusters of cottonwoods *Populus* spp. found close to the river's edge, the study area is devoid of trees. The climate is arid (9.8 cm rainfall 1 June–26 August 2000). Mean daily minimum and maximum ambient temperatures (T_{amb}) during the study period were 9.7/24.1 °C in June, 15.3/31.3 °C in July, and 13.7/28.8 °C in August.

Captures and radio-telemetry

Bats were captured with mist-nets and adults distinguished from juveniles by examining the finger joints for ossification (Anthony, 1988). Females were classified as non-reproductive, pregnant, lactating or post-lactating (Racey, 1988). By gently palpating the abdomen, pregnancy could be detected, and was confirmed by recapture of all but 2 bats later in the season. Lactation was confirmed by expressing milk from enlarged teats. Post-lactating females had hair re-growth around the periphery of the teats, and milk could not be expressed. A numbered, coloured plastic split-band was placed onto 1 forearm of each individual for identification.

To locate roosts and monitor skin temperature, 0.7 g temperature-sensitive radio-transmitters (Holohil Systems, Carp, ON, Canada) were attached to the dorsal fur of reproductive females using Skinbond[®] surgical adhesive (Smith and Nephew United, Inc., Largo, FL, U.S.A.). As recommended by Aldridge & Brigham (1988), transmitter mass was < 5% of bat body mass. Using a Merlin 12 receiver (Custom Electronics, Nokomis, FL, U.S.A.), roosts were located during the day on each day an individual carried an active tag. Roosts were accessed by climbing, or using ladders or ropes. Roosts were observed at emergence to confirm exit(s) and to count bats.

Skin temperature (T_{skin}) of bats was recorded using a LOTEK SRX 400 (Lotek Engineering Inc., Newmarket, ON, Canada) scanning receiver, which recorded bat temperatures every 10 min. The receiver recorded the amount of time necessary for the transmitter to produce 3 pulses, and used transmitter-specific calibration curves supplied by the manufacturer to determine T_{skin} . Skin temperature measured using these methods accurately reflects core body temperature (T_b ; Audet & Thomas, 1996; Barclay, Kalcounis *et al.*, 1996).

Crevices

All rock crevices were classified into 3 categories based on shape: crack, slab (thin outer wall), and hole/tube (eroded hollow). Roosts were classified as pregnancy, lactation or post-lactation roosts depending on the reproductive condition of the bats using them.

Once a roost was located, a nearby crevice was randomly selected that was similar in aspect (within 10°), but differed in depth and/or opening size. Temperature was measured in roosts and randomly selected crevices, as well as ambient conditions, using 2 types of dataloggers: Thermochron iButtons[®], Model DS1921 (± 0.5 °C, Dallas Semiconductor Corp., Dallas, TX, U.S.A.) and HOBO Loggers[®] (± 0.7 °C, Onset Computer Corp., Pocasset, MA, U.S.A.). Two HOBO Loggers[®] were encased in solar radiation shields to record ambient temperature. Roost sensors or sensor cables were placed as far into crevices as possible, and where bats had been roosting, if this position was known. To eliminate the potential problem of bats roosting on sensors, data during the period when bats occupied a roost were not used for

statistical analyses. All sensors recorded conditions every 10 min.

To test whether roost structure influenced microclimate, temperatures were compared for roosts facing the same direction but differing in type (slab, crack, hole/tube). To control for ambient conditions such as wind, temperature and cloud cover, all measurements were collected on the same day.

Most bats roosted on the north-west side of the river, but from 11–29 July we placed dataloggers into crevices located on the south-east side of the river as well. Each crevice was similar in opening shape and crevice type (slab, tube/hole, crack) to a roost on the north-west side of the river which also had a datalogger placed inside; these 2 crevices were a 'pair' for statistical purposes. From 30 July to 20 August bats roosted on both sides of the river and again temperature dataloggers were placed into roosts (pairs) of similar shape and size on opposite sides of the river. Roosts included in these observations had been occupied at some point during the study.

Statistical analyses and defining terms

To describe microclimate, the 24-hour period was divided into 2 parts: we called bat emergence to civil morning twilight 'night', and civil twilight until emergence 'day'. Time to reach maximum temperature is the number of min after sunrise the roost took to reach maximum temperature. For statistical analyses, 4 readings of T_{amb} and crevice temperatures were used for each bat-day: (1) maximum night temperature (MXNT) usually occurred near the time of emergence; (2) minimum night temperature (MNNT) occurred near civil morning twilight; (3) minimum day temperature (MNDT) occurred near sunrise; (4) maximum day temperature (MXDT) occurred at some point during the day.

To account for individual bat differences, normothermic T_{skin} was determined for each bat. This is referred to as its active temperature (T_{act}), and was determined by recording T_{skin} within 10 min before emergence of a bat to forage each night. The lowest of these recordings was used to represent a slightly conservative but realistic measure of the normothermic T_{skin} of each bat. T_{skin} before emergence was used to determine T_{act} , as this was the temperature at which bats were warm enough to fly. If the temperature of a bat dropped $\leq 10^\circ\text{C}$ below T_{act} , this was termed shallow torpor, and if the temperature of a bat dropped $> 10^\circ\text{C}$ below T_{act} , this was deep torpor (as defined by Hamilton & Barclay, 1994; Grinevitch, Holroyd & Barclay, 1995).

A 'bat-day' was defined as starting at morning twilight (civil), or when the bat returned to the roost for the last time, and ending when the bat emerged to forage that night. Because energy savings can be accrued even when animals enter in to and out of torpor without an intervening steady-state period (Hiebert, 1990), a bout of torpor was defined as a drop in T_{skin} below T_{act} that lasted for 20 min or more. A bat-day on which a bat experienced at least 1 bout of torpor is referred to as a torpor-day. This also applied to deep-torpor-days. For a bat-day to be used in

all other measures of torpor, T_{skin} had to be recorded for a minimum of 10 h beginning no later than 09:00. If no bouts of torpor were observed, the bat-day was deemed a non-torpor-day. Only bat-days where ≥ 15 h of T_{skin} were recorded were used for calculating degree-min of torpor (see below). Because of the different requirements for each measure of torpor, not all bat-days could be used in all calculations of torpor.

Torpor has been defined and quantified in many ways (Barclay, Lausen *et al.*, 2001). In an attempt to best describe thermoregulatory patterns, we present proportion of bat-days in which torpor was used (frequency), min in torpor, minimum T_{skin} , frequency and duration of shallow vs deep torpor, and area under the T_{act} line on a T_{skin} vs time graph (degree-min). This latter method combines both depth and duration of torpor and summates all drops in T_{skin} (Barclay, Lausen *et al.*, 2001). Because even small drops in T_b (Studier, 1981; Webb *et al.*, 1993) and short bouts of torpor (Schmidt-Nielsen, 1990) can result in significant energy savings, this method of quantifying torpor better reflects the energy savings. By examining all measures of torpor, a better understanding of the use of torpor should emerge.

The use of torpor was monitored in pregnant (11 individuals, 79 bat-days), lactating (9, 50) and post-lactating (11, 84) *E. fuscus*, for a total of 213 bat-days. Some individuals were used during > 1 reproductive stage. To ensure independency of data in statistical tests, the individual was nested in reproductive stage where possible. Where this was not possible, data were removed so that each individual was used only once.

For the T_{skin} data recorded for each of 158 bat-days (20 individual bats), the generalized cross validation method was used to create a non-parametric smoothing spline (SAS version 7.0 for Windows). Values were interpolated for each 0.5 min period, subtracted from the T_{act} of the bat, and multiplied by the 0.5 min interval. In doing so, the area between the T_{act} line and the T_{skin} curve (i.e. $T_{act} - T_{skin}$ differential multiplied by time) was calculated. This number is called degree-min, as it encompasses both depth and duration of torpor (Fig. 1).

Data were transformed (e.g. \log_{10} , squared, cubed, square root) to meet assumptions of normality and variance homogeneity. An alpha value of 0.05 was used and means \pm SE presented. Kruskal–Wallis, *t*-tests, ANOVAS, ANCOVAs, and regressions were performed using SYSTAT 7.0.1 for Windows. χ^2 tests were performed using Statistix 4.1. Yates correction factor was used for all χ^2 tests with 1 degree of freedom (Zar, 1984). Multiple comparison following Kruskal–Wallis was performed as outlined in Siegel & Castellan (1988).

RESULTS

Captures

As the season progressed, fewer unbanded *E. fuscus* were captured in association with roosts, and radio-tracked individuals roosted together regularly. It was therefore

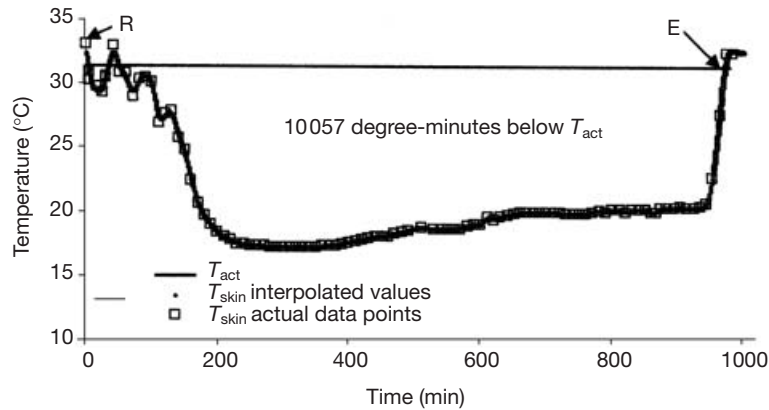


Fig. 1. Use of torpor by a pregnant *Eptesicus fuscus* on 25 June: R, when the bat returned to the roost; E, time of emergence; straight line, active temperature for this bat; curve, T_{skin} throughout the bat-day; squares, temperature readings taken every 10 min; interpolated values are every 0.5 min. Area between the lines (measure of torpor), is 10 057 degree-min.

concluded that the bats followed during this study formed one maternity colony. Radio-transmitters were attached to 23 adult females (some females were tagged more than once during different reproductive stages). Eleven were attached to pregnant females, and all but two were recaptured and their pregnancy confirmed. Eleven lactating females were tagged, two of which became post-lactating during the life of the transmitter, as confirmed by recapture. Eleven post-lactating bats were radio-tagged. The last radio-transmitters were attached on 20 August and these bats (along with untagged big brown bats) were still in the area on 26 August when the study ended.

Ambient temperature and thermoregulation

The study period was divided into three parts based on the reproductive condition of the majority of bats in the colony: pregnancy (6–30 June), lactation (1–30 July), post-lactation (31 July–25 August). Mean minimum and maximum ambient temperatures (T_{amb}) for these periods were $10 \pm 1^\circ\text{C}$ and $24 \pm 1^\circ\text{C}$, $15 \pm 1^\circ\text{C}$ and $31 \pm 1^\circ\text{C}$, and $14 \pm 1^\circ\text{C}$ and $29 \pm 1^\circ\text{C}$, respectively. These means differed significantly (ANOVA, minimum T_{amb} , $F_{2,78} = 15.3$, $P < 0.001$; maximum T_{amb} , $F_{2,78} = 16.0$, $P < 0.001$), with the pregnancy period significantly cooler than the lactation (Tukey's pairwise comparison $P < 0.001$) and post-lactation ($P < 0.001$) periods.

Depth of torpor

Individual T_{skin} fell as much as 24.6°C below T_{act} in pregnancy (mean = $8.6 \pm 0.9^\circ\text{C}$, $n = 73$ torpor-days), 17.7°C below T_{act} in lactation (mean = $5.4 \pm 0.6^\circ\text{C}$, $n = 44$), and 22.9°C below T_{act} in post-lactation (mean = $8.5 \pm 0.4^\circ\text{C}$, $n = 58$). Mean minimum T_{skin} for pregnant, lactating and post-lactating individuals were $27.0 \pm 0.8^\circ\text{C}$, $29.0 \pm 0.6^\circ\text{C}$, and $26.3 \pm 0.7^\circ\text{C}$, respectively (Fig. 2). Minimum T_{skin} differed significantly among reproductive stages (ANOVA, $F_{2,144} = 4.7$, $P < 0.05$); post-lactating and pregnant bats had signi-

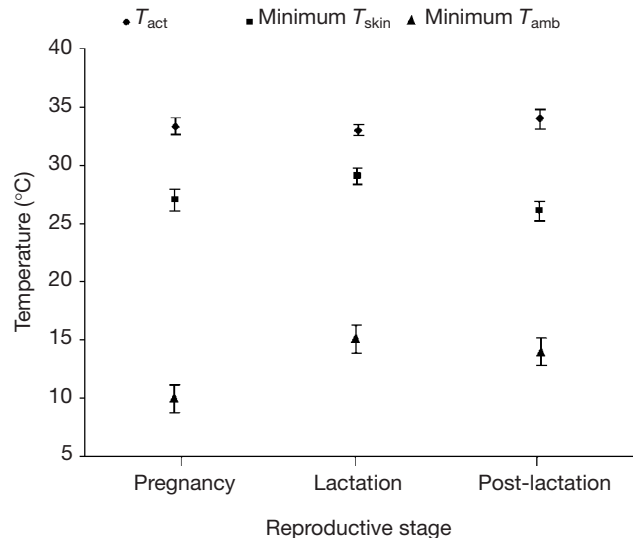


Fig. 2. Mean (\pm SE) active body and minimum body temperature of reproductive *Eptesicus fuscus*, and mean minimum T_{amb} . Sample sizes for pregnancy, lactation and post-lactation were 11, 9, and 11 individuals; 84, 50 and 85 bat-days; 25, 30 and 26 bat-days, respectively.

ficantly lower mean minimum T_{skin} than did lactating bats (Tukey's pairwise comparison $P < 0.05$). Individual nested in stage ($F_{28,144} = 5.9$, $P < 0.001$) was included in the model as individuals were monitored over several bat-days. Mean minimum T_{skin} of post-lactating bats approached T_{amb} more closely than that of pregnant bats (ANOVA, $F_{2,144} = 6.2$, $P < 0.01$, Tukey's pairwise comparison $P < 0.01$; Fig. 2), despite pregnant bats experiencing a significantly colder T_{amb} . While the mean minimum T_{skin} of post-lactating bats also approached T_{amb} more closely than that of lactating bats, the difference was not significant ($P = 0.06$). To understand the effect T_{amb} had on minimum T_{skin} , an ANCOVA was used with T_{amb} as a covariate. When variation resulting from T_{amb} was accounted for in this way, post-lactating females lowered their T_{skin} significantly more than

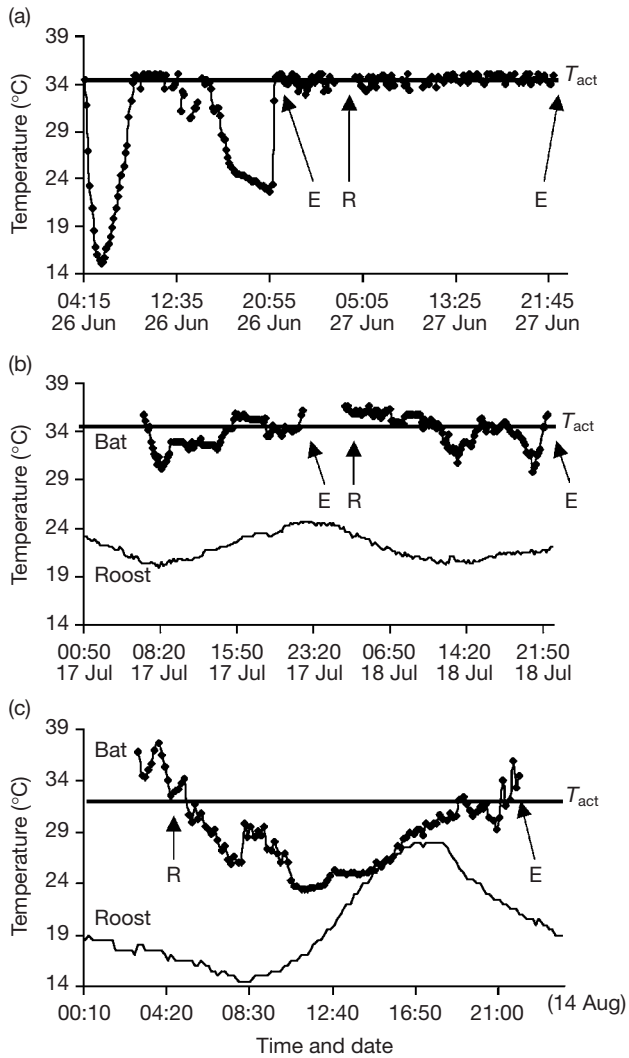


Fig. 3. Examples of thermoregulation by female *Eptesicus fuscus*: (a) pregnant; (b) lactating; (c) post-lactating. Temperature readings were taken every 10 min while the bats were in the roost. Straight line, active temperature (T_{act}); arrows, emergence (E) and return (R). Roost temperature is shown in (b) and (c), but was unavailable for (a). Note passive re-warming in (c).

pregnant or lactating females ($F_{2,141} = 6.8$, $P < 0.001$, Tukey's pairwise comparison $P < 0.05$). There was also an interaction between stage and T_{amb} ($F_{2,141} = 5.8$, $P < 0.01$); minimum T_{skin} of lactating females did not decrease with decreasing T_{amb} , while T_{skin} of pregnant and post-lactating females did.

Frequency of torpor

Individuals frequently had a bout of torpor in the morning and another in the evening (Fig. 3 (a) 26 June, (c) 17–18 July). Pregnant bats used torpor on 43 (75%) bat-days, lactating bats on 44 (88%) bat-days, and post-lactating bats on 49 (92%) bat-days. This is a significant difference in frequency of torpor ($\chi^2 = 12.1$, d.f. = 2, $P < 0.05$).

There was no significant difference between lactating and post-lactating bats ($\chi^2 = 0.18$, d.f. = 1, $P > 0.5$), and when they were combined and compared to pregnant bats, there was a significant difference ($\chi^2 = 5.2$, d.f. = 1, $P < 0.05$), indicating that lactating and post-lactating bats used torpor more often than pregnant bats did. Lactating bats used deep torpor less often (4/44, 9%) than other females (pregnant: 13/43, 30%; post-lactating: 13/49, 27%; $\chi^2 = 5.3$, d.f. = 1, $P < 0.05$).

Duration of torpor

A different picture emerged when time in torpor rather than frequency of torpor was analysed. The amount of time spent in torpor per bat-day differed with reproductive stage (ANOVA, $F_{2,143} = 4.6$, $P < 0.05$), with post-lactating females ($n = 54$ bat-days) in torpor significantly longer than pregnant bats ($n = 73$ bat-days; Tukey's pairwise comparison $P < 0.05$) or lactating bats ($n = 46$ bat-days; $P < 0.05$). When we included T_{amb} as a covariate in the analysis, post-lactating females spent significantly more time in torpor (reproductive stage, $F_{2,140} = 4.6$, $P < 0.05$) than pregnant (Tukey's pairwise comparison $P < 0.001$) or lactating bats ($P < 0.01$). There was also a significant interaction between stage and minimum day T_{amb} ($F_{2,140} = 5.9$, $P < 0.01$), with pregnant and post-lactating females spending longer in torpor in colder T_{amb} , but lactating females using a similar amount of torpor regardless of T_{amb} . Individuals at the same stage of reproduction also varied significantly ($F_{27,140} = 3.2$, $P < 0.001$). Time in shallow torpor did not differ among reproductive stages (ANOVA, $F_{2,106} = 1.3$, $P > 0.05$), while time in deep torpor did differ (Kruskal–Wallis = 6.8, d.f. = 2, $P < 0.05$; pregnant $n = 34$ torpor-days, mean = 184 ± 61 min/bat-day; lactating $n = 40$, mean = 21 ± 14 ; post-lactating $n = 29$, mean = 79 ± 29). All two-way comparisons were significant; pregnant females were in deep torpor longer per bat-day than post-lactating females, who spent more time in deep torpor than lactating females.

Comprehensive measure of torpor

Finally, use of torpor was quantified by combining both depth and duration into one unit, degree-min. One hundred and fifty-eight bat-days (64 pregnancy bat-days, 42 lactation bat-days, 52 post-lactation bat-days) were used. Degree-min varied significantly (Fig. 4) with reproductive stage (ANOVA $F_{2,131} = 3.5$, $P < 0.05$). Post-lactating *E. fuscus* had significantly more degree-min of torpor than lactating females (Tukey's pairwise comparison $P < 0.05$). When T_{amb} was included as a covariate to account for its influence ($F_{1,128} = 27.7$, $P < 0.001$), post-lactating females used significantly ($F_{24,128} = 2.7$, $P < 0.001$) more torpor than pregnant (Tukey's pairwise comparison $P < 0.001$) or lactating bats ($P < 0.01$). Again there was a significant interaction between stage and minimum day T_{amb} ($F_{2,124} = 9.4$, $P < 0.001$), with pregnant and

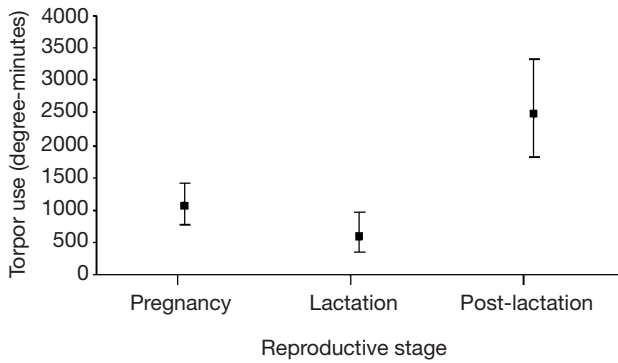


Fig. 4. Mean (\pm SE) degree-min of torpor use by pregnant, lactating, and post-lactating *Eptesicus fuscus*.

post-lactating females using more torpor in colder T_{amb} , but lactating females using a similar amount of torpor regardless of T_{amb} .

Torpor summary

Measures of torpor use produced different results. The discrepancy was primarily with respect to the use of torpor during lactation. When all aspects of torpor (depth, duration, frequency) were considered together, pregnant and lactating bats used torpor to the same extent, but with different thermoregulatory patterns. Lactating bats used torpor frequently but spent the least amount of time in deep torpor, while pregnant females used torpor less often but spent the most time in deep torpor. After weaning took place, females used torpor more extensively. When frequency of torpor alone was considered, it was concluded that lactating females used the same amount of torpor as post-lactating individuals, and more than pregnant bats.

Crevices

Microclimate varied depending on roost structure (Fig. 5). Deep, thick-walled crevices retained heat and roost temperature was less variable (Fig. 5a) than in shallow, thin-walled roosts (Fig. 5b) in which roost temperature fluctuated with T_{amb} , and reached temperatures in excess of T_{amb} (Fig. 5c). Microclimate for 13 roosts on the north-west side of the river were compared: slabs ($n = 4$), cracks ($n = 5$) and holes/tubes ($n = 4$). ANCOVA was used to determine whether crevice type (i.e. slab, crack, hole/tube) influenced maximum day temperature and time to reach maximum temperature, with opening area as a covariate. Opening size did not explain a significant portion of the variation ($F_{1,9} = 0.48$, $P > 0.05$). For maximum day temperature, type explained a significant amount of variation ($F_{2,9} = 8.86$, $P < 0.01$). Slab roosts had significantly higher maximum temperatures compared to crack roosts (Tukey's pairwise comparison $P < 0.01$) and hole/tube roosts ($P < 0.05$). Type of roost did not

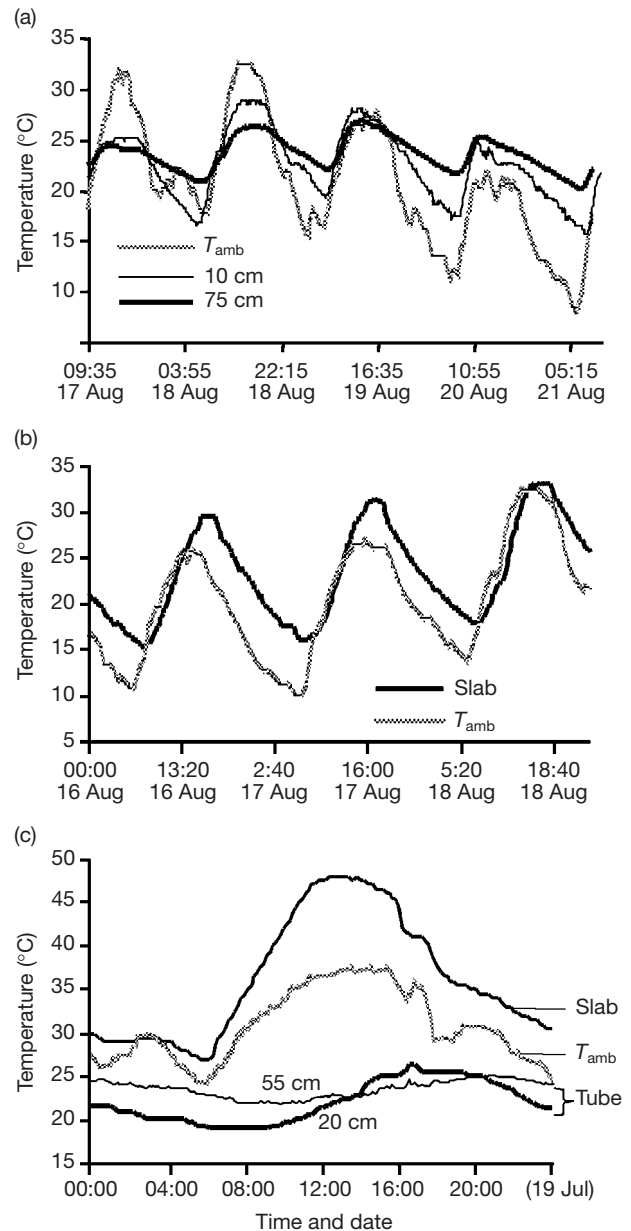


Fig. 5. Temperatures inside roosts of *Eptesicus fuscus*: (a) a deep erosion-tube; (b) a shallow, thin-walled slab-roost; (c) a comparison of the two roost types. Roosts were unoccupied. Deep roosts had shallow and deep sensors, and depths of the sensors are indicated (a) and (c).

explain the variation in time to maximum temperature ($F_{2,9} = 0.33$, $P > 0.05$).

Seventy-two rock-crevice roosts used by the *E. fuscus* maternity colony were identified and microclimate was measured in 37 of them, as well as in 15 randomly selected rock crevices. The effect of depth and opening size on crevice microclimate was determined by performing multiple linear regression analyses (with step-wise elimination) using the appropriate T_{amb} as a covariate in each model (Table 1). Separate linear regressions were performed for maximum (MXDT) and minimum day

Table 1. Results of multivariate regression analyses of crevice microclimate properties. Minimum night temperatures (MNNT), minimum day temperatures (MNDT), maximum day temperatures (MXDT), maximum night temperatures (MXNT), daily ranges of crevice temperatures (CRNG), and times to reach maximum roost temperature (MINS) were independent variables. In each regression model the appropriate ambient temperature (T_{amb}), roost depth and roost opening size were included. The results of step-wise elimination, and the final regression model are presented

	Test statistic	<i>P</i>	<i>R</i> ²
MNNT = 8.4 + 0.03(depth) + 0.7(T_{amb})			
Regression	$F_{2,49} = 16$	< 0.001	0.39
Constant	$t = 4.3$	< 0.001	
Depth	$t = 2.1$	0.042	
T_{amb}	$t = 5.1$	< 0.001	
MNDT = 7.8 + 0.03(depth) + 0.7(T_{amb})			
Regression	$F_{2,49} = 17$	< 0.001	0.41
Constant	$t = 4.1$	< 0.001	
Depth	$t = 2.0$	0.046	
T_{amb}	$t = 5.3$	< 0.001	
MXDT = 15 - 0.05(depth) - 0.008(open. size) + 0.6(T_{amb})			
Regression	$F_{3,48} = 8.7$	< 0.001	0.36
Constant	$t = 2.8$	0.007	
Depth	$t = -2.1$	0.039	
Opening size	$t = -2.0$	0.046	
T_{amb}	$t = 3.5$	0.001	
MXNT = 10 - 0.005(open. size) + 0.7(T_{amb})			
Regression	$F_{2,49} = 42$	< 0.001	0.63
Constant	$t = 6.1$	< 0.001	
Opening size	$t = -2.6$	0.011	
T_{amb}	$t = 8.5$	< 0.001	
CRNG = 6.6 - 0.08(depth) - 0.4(range T_{amb})			
Regression	$F_{2,49} = 6.1$	0.004	0.19
Constant	$t = 1.9$	0.064	
Depth	$t = -2.7$	0.032	
Range T_{amb}	$t = 2.2$	0.032	
MINS = 515 + 2.1(depth)			
Regression	$F_{1,50} = 8.9$	0.004	0.15
Constant	$t = 14.7$	< 0.001	
Depth	$t = 3.0$	0.004	

(MNDT) and night (MXNT, MNNT) temperatures, time to reach maximum crevice temperature (MINS), and crevice temperature range (CRNG). The deeper the crevice, the cooler it remained during the day (MXDT and MINS), the warmer it stayed at night (MNNT) and at dawn (MNDT), and the less its temperature fluctuated (CRNG). The smaller the opening size, the warmer the crevice during the day (MXDT), and after sundown (MXNT; Table 1).

At the onset of post-lactation (30 July), females began roosting on both sides of the river (having roosted only on the north-west side during pregnancy and lactation). Crevices on the two sides of the river differed in microclimate. Crevices on the north-west side were significantly warmer at 09:00 than those on the south-east side (ANCOVA; side of river, $F_{1,33} = 37.2$, $P < 0.001$). This difference was not influenced by the time of year (before 30 July vs after 30 July; $F_{1,33} < 0.1$, $P > 0.5$), or pair (i.e. similar crevices on either side of the river were one pair; $F_{6,33} = 1.52$, $P > 0.05$). Comparisons on different days were controlled for by including

Table 2. Results of ANCOVA models describing microclimate of *E. fuscus* roosts: maximum day temperature (MXDT), minimum day temperature (MNDT), maximum night temperature (MXNT), minimum night temperature (MNNT), time to reach maximum temperature (MINS), crevice temperature range (CRNG), and temperature elevation above minimum T_{amb} (ELEV). Stage (i.e. pregnancy, lactation, post-lactation) was a categorical variable in all ANCOVAs and represented the reproductive stage during which the roosts were used. T_{amb} was initially included as a covariate in all models. Asterisks indicate models in which roost microclimate differed significantly among reproductive stages

	Source	<i>F</i>	<i>P</i>
MXDT	Stage	$F_{2,33} = 0.08$	0.971
	T_{amb}	$F_{1,33} = 4.70$	0.041
MNDT	Stage	$F_{2,33} = 3.64$	0.037*
	T_{amb}	$F_{1,33} = 4.23$	0.047
MXNT	Stage	$F_{2,33} = 4.82$	0.015*
	T_{amb}	$F_{1,33} = 11.4$	0.002
MNNT	Stage	$F_{2,33} = 2.87$	0.071
	T_{amb}	$F_{1,33} = 4.91$	0.034
MINS	Stage	$F_{2,33} = 4.29$	0.002*
	MXDT	$F_{1,33} = 9.08$	0.005
CRNG	Stage	$F_{2,34} = 0.57$	0.573
ELEV	Stage	$F_{2,33} = 0.94$	0.400
	T_{amb}	$F_{1,33} = 5.77$	0.022

maximum and minimum T_{amb} as covariates in the model (maximum T_{amb} , $F_{1,33} = 3.67$, $P = 0.06$; minimum T_{amb} , $F_{1,33} = 22.03$, $P < 0.001$). MXDT in crevices on opposite sides of the river was not significantly different ($F_{1,33} = 1.86$, $P > 0.05$), nor was MINS ($F_{1,35} = 1.67$, $P > 0.05$).

Pregnancy, lactation and post-lactation roosts differed significantly in microclimate (Table 2). At dawn (Tukey's pairwise comparison $P < 0.05$) and at time of emergence ($P < 0.05$), lactation roosts were significantly warmer than pregnancy roosts, and they took significantly longer to reach maximum temperature ($P < 0.05$). Post-lactation roosts were significantly warmer than pregnancy roosts at time of emergence ($P < 0.05$).

DISCUSSION

Thermoregulation

As predicted, pregnant and lactating bats used torpor (degree-min) less than post-lactating females did. This supports the results of previous studies that found limited use of torpor during some part of the reproductive period (e.g. Brigham, 1992; Geiser & Masters, 1994), probably because of a high cost : benefit ratio. During post-lactation, females reached significantly lower minimum T_{skin} than during lactation, despite experiencing similar T_{amb} . Likewise, pregnant and post-lactating females achieved similar minimum T_{skin} despite significantly colder T_{amb} during pregnancy. Post-lactating females spent less time in deep torpor (per torpor-day) than pregnant individuals did, but their T_{skin} more closely approached T_{amb} , and they were torpid on a greater proportion of bat-days. This suggests that during post-lactation, greater use of torpor

reduced the energy lost to the surroundings, and females saved energy as they prepared for hibernation. Pregnant females probably experienced significant heat loss to their cold surroundings, increasing the benefits of deep torpor.

Previous thermoregulatory studies on bats have produced conflicting results regarding the use of torpor during reproduction. Laboratory vs field studies, varying definitions, and restrictive measures of torpor, have contributed to the mixed conclusions. For example, one laboratory study (Studier & O'Farrell, 1972) found lactating little brown bats *Myotis lucifugus* achieved lower body temperatures compared to pregnant and post-lactating bats, while another study (Kurta, Johnson *et al.*, 1987) concluded that reproductive and post-reproductive *M. lucifugus* did not use torpor despite recording twofold decreases in oxygen consumption from active levels. Field studies of *E. fuscus* have produced similar discrepancies; Audet & Fenton (1988) found infrequent use of torpor by lactating bats compared to pregnant and non-reproductive *E. fuscus*, but Hamilton & Barclay (1994) reported more frequent use of torpor by lactating *E. fuscus*, although torpor was usually shallow.

Use of torpor by lactating female mammals is especially confusing. Generally, torpor does not occur during lactation (e.g. Geiser & Masters, 1994), although extensive use of torpor by lactating females occurs in some species of bats (e.g. Studier & O'Farrell, 1972; Chruszcz & Barclay, 2002). Because patterns of torpor in laboratory studies often do not coincide with those in field studies, and because laboratory studies can underestimate use and depth of torpor (Geiser *et al.*, 2000), it is important to study animals under natural conditions. We found that although mean torpor use (degree-min) was similar during pregnancy and lactation, the pattern of torpor use was not. Differing ambient conditions and behavioural responses probably contributed to these differences. Lactating females in our study experienced warmer T_{amb} and would therefore have experienced less heat loss to their environment, compared to pregnant females. Despite this, lactating females used torpor more frequently than pregnant bats did, but torpor was shallower. Warm T_{amb} did not limit the depth of torpor during lactation, because post-lactating bats were exposed to similar warm T_{amb} but used deeper torpor. This suggests that deep torpor is particularly costly during lactation. This is supported by the fact that lactating females did not increase their use or depth of torpor when T_{amb} dropped, while pregnant and post-lactating females did. Instead, lactating females defended a higher T_{skin} when T_{amb} was low, perhaps maintaining a sufficient rate of milk secretion (Wilde, Knight & Racey, 1999) and minimizing the costs of arousal to nurse pups (Lovegrove, Kortner & Geiser, 1999). On the other hand, lactating females did not decrease use or depth of torpor when T_{amb} rose, as pregnant and post-lactating females did. This suggests that shallow torpor is an important energy-saving strategy for lactating females who put large amounts of energy into milk production (Kurta, Bell *et al.*, 1989; Wilde, Knight *et al.*, 1999).

Our results highlight the importance of quantifying torpor comprehensively. If we had interpreted our results

based solely on one of the most common measures of torpor, i.e. frequency of occurrence (e.g. Audet & Fenton, 1988; Hamilton & Barclay, 1994; Grinevitch *et al.*, 1995), we would have concluded that lactating and post-lactating bats used torpor to the same extent, and more often than pregnant bats. Previous studies on *E. fuscus* used frequency of torpor and concluded that lactating females enter torpor less often or more often than pregnant females (Audet & Fenton, 1988; Hamilton & Barclay, 1994). The conclusions from these studies may have been different had other measures of torpor use been used. Relative torpor use is indicative of energy savings, determined in part by the length of time the animal is torpid, how often it uses torpor, and how low its T_b is relative to the surrounding temperature (Hudson, 1973). Some field studies of other animals (e.g. Brigham, 1992; Csada & Brigham, 1994; Kortner & Geiser, 2000) have measured torpor as merely presence or absence. We suggest that simultaneous consideration of frequency, duration and depth of torpor is necessary to facilitate meaningful conclusions and comparisons among individuals, species and studies.

Roost selection

What sets field studies of torpor apart from laboratory studies is the behavioural component of thermoregulation that only can be observed in a natural setting. Animals should select microenvironments that meet their physiological needs. For example, in cool spring weather, *Antrozous pallidus* selects thin-walled rock-crevices that fluctuate with T_{amb} , but in the summer during lactation, individuals select deeper crevices that offer more stable temperatures (Vaughan & O'Shea, 1976; Lewis, 1996). Similarly, in cool spring weather, pregnant *M. evotis* roosting in our study area use thin-walled (boulder-slab) roosts that are more responsive to T_{amb} , while thicker-walled cracks in boulders, with more stable thermal regimes, are preferred by lactating *M. evotis* in the hotter summer weather (Chruszcz & Barclay, 2002).

Our study confirms that rock crevices of different structure differ significantly in microclimate. Temperatures of deep erosion tubes fluctuated least and retained heat. Deeper crevices were more thermally stable than shallow crevices, remaining cooler during the day and warmer at night. Deep roosts provide a gradient of thermal conditions that allow for behavioural thermoregulation (Vaughan & O'Shea, 1976; Hamilton & Barclay, 1994; Chruszcz & Barclay, 2002). In our study, crevices with large openings remained cooler in the day and cooled quickly after sunset, likely due to increased airflow (see also Rosenberg, 1974).

Thermoregulatory patterns of *E. fuscus* differed significantly among reproductive stages, and individuals selected roosts to match their thermoregulatory strategy. Given that lactating and post-lactating bats used different thermoregulatory patterns despite similar T_{amb} , individuals in these groups should select different roosts. Likewise, as pregnant and post-lactating bats reached similarly low minimum T_{skin} , one would expect similar

roost selection during pregnancy and post-lactation. This is what we found. Lactation roosts were insulating, thereby trapping warmth for non-volant pups that are left behind in roosts at night. This would be conducive to juvenile growth (Humphrey, Richter & Cope, 1977; McNab, 1982). These insulating roosts also remained cool enough in the day to allow shallow torpor, which may be important to compensate for the costs of lactation (Kurta, Johnson *et al.*, 1987). Alternatively, shallow torpor in cool roosts during the day may be a consequence of selecting roosts that stay warm at night for the benefit of young. Pregnant and post-lactating females used roosts that were less stable; they were cold for the first part of the day but then warmed, thereby facilitating use of deep torpor in the morning, and energy savings through passive re-warming. Using roosts that cool rapidly at night is not costly because there are no pups in the roosts and the females are out foraging.

With the onset of post-lactation, *E. fuscus* began roosting on both sides of the river. Crevices on the two sides differed in aspect (crevices on the north-west side faced south-east, and crevices on the south-east side faced south and west; Lausen & Barclay, 2002) and thus crevices on the north-west side were warmer at 09:00 than those on the south-east side, because of earlier exposure to sunlight. During pregnancy and lactation, when torpor is most costly and used least, *E. fuscus* females roosted exclusively in warm north-west-side roosts. Post-lactation coincided with increased use of torpor, facilitated by using cooler south-east-side roosts. This may allow energy savings in preparation for hibernation.

In summary, rock-roosting *E. fuscus* used torpor less during pregnancy and lactation compared with post-lactation, and the mean minimum T_{skin} of post-lactating bats most closely approached T_{amb} . This is consistent with the hypothesis that costs of torpor for reproductive females are greater than those for post-lactating females. While pregnant and lactating bats used torpor to the same extent overall (degree-min), thermoregulatory patterns differed, suggesting that the costs of using deep or prolonged periods of torpor may be highest for lactating females. Rock crevices selected as roosts by *E. fuscus* differed thermally from what was randomly available. Bats selected different types of roosts according to reproductive stage; roost microclimate reflected the thermoregulatory patterns of the bats. Our results highlight the importance of individually defined normothermic body temperatures and measuring all drops in T_b below normothermic. We have demonstrated that proportion of bat-days on which torpor occurred may not provide a comprehensive enough picture of torpor on which to base conclusions in studies of thermoregulation, and that torpor should be measured comprehensively so that meaningful comparisons can be made among thermoregulatory studies of all animals.

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