

The influence of reproductive condition and concurrent environmental factors on torpor and foraging patterns in female big brown bats (*Eptesicus fuscus*)

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Abstract Unlike many other mammals, bats in temperate regions employ short bouts of torpor throughout the reproductive period to maintain a positive energy balance. In addition to decreasing energy expenditure during the day, they typically alter foraging patterns as well. It is well known that various environmental conditions influence both torpor and foraging patterns, but studies of these factors often have focussed on one element in isolation thus it is not known how the two behaviours are collectively influencing temperate bats. The objective of our study was to assess how reproductive condition and environmental factors concurrently affect energy balance in female big brown bats (*Eptesicus fuscus*). We equipped pregnant and lactating bats in southwest Saskatchewan, Canada with temperature-sensitive radio-transmitters. While transmitters were active, skin temperature data were collected and foraging patterns were determined using triangulation. Of the various environmental and physiological parameters used to model torpor characteristics, roost type was the most important factor. Bats roosting in trees used deeper and longer torpor bouts than those roosting in buildings. Lactating bats had a tendency to forage for longer durations than pregnant bats, and often made more foraging trips. When taken together, we found that foraging duration and torpor duration were not directly related during pregnancy, but exhibited an

inverse relationship during lactation. This provides support for the hypothesis that there are physiological trade-offs for reproductive bats and suggests that how bats compensate is not entirely predictable based on current environmental conditions.

Keywords Foraging · Thermoregulation · Ecophysiology · Reproduction · Torpor · *Eptesicus fuscus*

Abbreviations

T_{sk}	Skin temperature
T_a	Ambient temperature
T_b	Body temperature
T_{onset}	Torpor onset temperature
HI	Heterothermy index
w_i	Akaike weight
AIC _c	Bias corrected akaike information criterion
LMM	Linear mixed model

Introduction

Animals must maintain an overall net positive energy balance which is typically achieved through balancing energy intake and energy expenditure. However, in some circumstances, such as during reproduction, maintaining a positive energy balance can be challenging. Small mammals often use a combination of three general strategies to obtain sufficient energy for reproduction: increased prey consumption or foraging effort, exploitation of internal or external energy sources, or reduced activity levels (Racey and Speakman 1987; Speakman 2008). Bats in temperate regions are good models for studies of energy balance strategies because they face more significant physiological constraints than those faced by most small mammals.

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Due to their size and mode of locomotion, bats cannot store more than 2–3 days' worth of fat when active (as opposed to during hibernation; Bronson 1985). The capacity to store fat is likely reduced due to the increased mass causing increased wingloading and decreased manoeuvrability (Barclay 1994; Norberg and Rayner 1987). Also, because they eat insects, they cannot store food caches to exploit during periods of low energy availability in the environment, which means that bats cannot remain inactive to decrease energy expenditure like some small terrestrial mammals (Racey and Speakman 1987). There is evidence that bats consume more energy and increase foraging effort as energy requirements during reproduction increase (e.g., Anthony and Kunz 1977; Kunz et al. 1995). However, this increase does not appear to cover the amount of energy required (McLean and Speakman 1999), which necessitates a combination of compensation strategies. One strategy employed by bats during reproduction is to reduce metabolic rate (i.e., torpor), which decreases daily energy expenditure. Thus, reproductive bats are likely to increase energy intake via foraging and/or decrease energy expenditure by entering torpor during the inactive part of the day to maintain a positive energy balance.

During torpor, metabolic rate and body temperature (T_b) are reduced which results in decreased energy expenditure through lower rates of biological/physiological process (e.g., foetal growth, milk production and body maintenance; Geiser and Ruf 1995; Speakman and Thomas 2003; Wang 1989; Racey 1973; Wilde et al. 1999). Aside from the potential negative consequences of torpor, such as a reduced immune function and an increased susceptibility to parasites and disease (Bouma et al. 2010), the benefits of this physiological process outweigh the costs as it leads to energetic savings, fat accumulation, and survival during prolonged drought and extreme ambient temperatures (T_a ; Geiser and Brigham 2012). There are several abiotic and biotic factors that have been suggested to influence whether or not an animal will employ torpor (e.g., sex, reproductive condition, food availability, T_a , roost type; Cryan and Wolf 2003; Grinevitch et al. 1995; Turbill and Geiser 2006; Doucette et al. 2012; Munn et al. 2010; Lausen and Barclay 2006). Understanding which factor(s) affect torpor expression during reproduction is important because there are potential physiological costs associated with torpor use during this time for females.

Foraging effort, typically measured as time spent flying or time away from the day roost (e.g., Chruszcz and Barclay 2003; Clark et al. 1993; Dzal and Brigham 2013), may be affected by several factors. For example, big brown bats (*Eptesicus fuscus*) eat flying insects, and insect abundance is often affected by ambient conditions such as wind, precipitation, T_a , moon phase, and time of night (e.g., Anthony et al. 1981; Beasley and Adams 1994; Benton et al. 2002;

Bryant 1975). Insect availability is likely important for determining foraging duration, but reproductive condition will also be important (Wilkinson and Barclay 1997; Grinevitch et al. 1995; Barclay 1989), likely due to different energetic requirements and changes in wingloading between and within different reproductive stages.

If individuals are in positive energy balance, we might expect them to avoid using torpor, assuming there is a cost to torpor use. However, if they are not consuming enough energy, bats will likely need to conserve energy in the short term until better foraging conditions arise. The relationship between energy consumption and conservation is predicted to be a linear one if there are no physiological costs, such as delayed parturition and slowed milk production, associated with using torpor. This means that for every additional kJ of energy consumed, less torpor should be required to maintain the balance.

The objective of our study was to assess how reproductive condition and environmental factors concurrently affect energy balance in *E. fuscus*. Factors such as minimum T_a and roost structure should also be important in describing thermoregulatory patterns because the energy required to maintain normothermy is dependent on T_a (Scholander 1955; Willis et al. 2005). Energetic requirements (Racey and Speakman 1987) and potential costs of torpor (Racey 1973; Wilde et al. 1999) differ between pregnant and lactating bats; therefore, it can be expected that patterns of torpor use will differ between the two reproductive conditions. Given that the energy intake during foraging is the source of energy for maintenance and growth and that space constrains fat storage, the combination of foraging duration (proxy for energy intake) and reproductive condition should also influence thermoregulation. For energy intake, ambient conditions that affect insect availability (Anthony et al. 1981; Beasley and Adams 1994; Benton et al. 2002; Bryant 1975) are likely to influence the amount of time bats forage at night. Since energetic requirements and flight ability vary with reproductive condition, they should also affect foraging duration. Whether or not bats entered torpor the day before should also influence how they forage at night given their limited ability to store energy. Finally, if torpor is used to compensate for times when foraging was not successful, there should be an inverse relationship between the two factors.

Materials and methods

Study area

Our study took place 10 km south of Maple Creek, Saskatchewan, Canada (49°54'23"N, 109°28'48"W) at two different sites (West site in 2011 and East site in 2012)

approximately 4 km apart. Both sites were within 1 km of a reservoir and a small creek. The study area was characterised by rolling hills mostly covered in native grasslands grazed by livestock. There were a few patches of land cultivated for crops or sown with grasses for hay. At the West site, the primary roost was located in a valley between two ridges. The bats typically occupied a garage with an open attic at this site. They were also observed in several areas of the attic and the roofline. The creek at West site was surrounded by short shrubs and occasional trembling aspen (*Populus tremuloides*). Similar to the West site, the East site roost was located between two ridges. The bats roosted in the rafters and behind fascia of a house without an open attic space as well as in several mature balsam poplar (*Populus balsamifera*) trees. The creek at East site was surrounded by *P. balsamifera* and *P. tremuloides*, as well as hawthorn (*Crataegus* spp.).

Capture and handling of animals

From mid-May to August 2011–2012, we caught *E. fuscus* in mist nets placed outside roosts. Upon capture, we assessed reproductive condition and measured body mass (using a digital balance) for each individual. Females were classified as pregnant based on abdominal shape or the detection of a foetus when the abdomen was gently palpated (Racey 1988), or lactating if they expressed milk and had bare patches around the nipples (Racey and Swift 1981). Thirty-two females were equipped with a temperature-sensitive radio-transmitter (BD-2T, Holohil Systems Limited, Carp, ON, Canada) affixed to the interscapular region using surgical adhesive (Ostobond, Montreal Ostomy Inc., Vaudreuil-Dorion, QC, Canada) after first clipping fur in the region. We calibrated transmitters before attachment in a water bath at 10 °C intervals from 0 to 40 °C and compared pulse rate and temperatures to the manufacturer's calibration curves to ensure accuracy. All protocols were performed in accordance with guidelines of the Canadian Council on Animal Care and were approved by the University of Regina President's Committee on Animal Care (AUP#12-03).

T_{sk} measurements

We located day roosts of all bats the morning following transmitter attachment until transmitters fell off. At each roost site, temperature data loggers (± 0.5 °C, iButton, DS1921, San Jose, CA, USA) were hung in the shade 1 m from the ground within 3 m of the roost tree in the cardinal directions. Ambient temperature was logged every 10 min and values from all four loggers were averaged. We deployed a data logger (SRX-400, Lotek Wireless Inc., Newmarket, ON, Canada) near the day roost to record

transmitter signals beginning the morning following attachment. The datalogger calculated and stored T_{sk} data every 10 min using manufacturer calibration curves of inter pulse intervals. From the T_{sk} data, we used Willis' (2007) torpor onset threshold (T_{onset}) to calculate a number of descriptive torpor variables for each bat day (one bat day = one transmitter active on one individual for one day) from the time that bats returned from foraging to emergence the next night. T_{onset} was calculated for each bat day following the equation Willis (2007) developed based on data collected from simultaneous measures of metabolic rate through respirometry and T_b through implanted transmitters. This threshold identifies the T_b that is associated with initial metabolic depression during torpor:

$$T_{onset} - 1SE = (0.041) \times \text{Body mass} + (0.040) \times T_a + 31.083.$$

A bat was considered to be in torpor if T_{sk} dropped ≥ 0.1 °C below T_{onset} for ≥ 2 consecutive readings (i.e., > 20 min). Torpor depth was defined as the maximum number of degrees that T_{sk} fell below T_{onset} . Torpor duration was the total amount of time a bat spent in torpor per day. An integrative term, torpor degree-minutes, was calculated as the area under the curve which takes into account the combination of torpor depth and duration (Lausen and Barclay 2003). The heterothermy index (HI; Boyles et al. 2011) was also calculated to describe the degree of T_{sk} fluctuation for each bat day.

Foraging measurements

We actively tracked bats on all nights following transmitter attachment until the transmitter fell off the bat or the battery died. Using triangulation, we located the bats every 15 min from dusk until dawn using telemetry receivers (R-1000, Communication Specialists, Inc., Orange, CA, USA) and 5-element yagi antennae. Two or three people, each with a receiver and antenna, were situated at predetermined high points on the landscape. All observers independently classified bats as moving or stationary based on signal modulation. A bat was assumed to be flying if the signal strength was variable (i.e., alternating between loud and quiet signals) and stationary if the signal was of constant strength (Brigham et al. 2000; Henderson and Broders 2008). Ambient temperature and wind speed were measured every 30 min as the mean value over 5 min using a handheld anemometer (Kestrel 2000, Birmingham, MI, USA).

Analysis

For each of the torpor and foraging characteristics, we generated an a priori candidate set of models based on

our hypotheses and incorporating factors that have been reported to influence either characteristic (e.g., T_a , roost type, food availability, time of day, food availability; Doucette et al. 2012; Munn et al. 2010; Willis et al. 2006; Wojciechowski et al. 2007; Jacobs et al. 2007; Lausen and Barclay 2006; Körtner and Geiser 2000; Oelkrug et al. 2011). The candidate models were formulated to identify which variables on their own influenced the torpor or foraging characteristic (additional information on model generation can be found in Online Resources 1). In addition to the univariate models, we formulated hypotheses for which combinations of variables would be important in describing torpor or foraging patterns. For the torpor models (torpor depth, duration, degree-minutes, torpor/no torpor, HI), we included reproductive condition (pregnant or lactating), minimum daily T_a , roost type (tree or building), and previous night's foraging duration as potential explanatory parameters. For the foraging models, number of foraging bouts (Barclay 1989; Lučan and Radil 2010), reproductive condition (e.g., Brigham 1991; Dietz and Kalko 2007; Encarnação and Dietz 2006), day torpor duration, minimum nightly T_a and average nightly wind speed (Arbuthnott and Brigham 2007; Barclay 1991; Kusch et al. 2004) were included. In all models, individual bat and date were included as random effects because multiple bats were often tracked simultaneously and each bat was followed over several days. Our modelling procedure accounts for both the pseudoreplication and dependence in these data since repeated measurements were taken from each individual and day.

We ran the global models which included all explanatory parameters for each response variable as linear mixed-effects models or as generalised linear mixed-effects models (Package lme4; Bates et al. 2012) depending on the response variable in question. Once the fit of the global model was sufficient (e.g., no pattern in residuals, qq norm plots not deviating from line, Hosmer–Lemeshow test was not significant) and assumptions were met, we ran all models in the candidate set, then calculated log likelihood and AIC_c to rank models. We also calculated Akaike weights (w_i) for each model within the set, which indicates the probability of correctly identifying the top model (Burnham and Anderson 2002). The cumulative Akaike weight (Σw_i) was calculated to identify the confidence set of models ($\Sigma w_i \geq 0.95$). When model selection uncertainty occurred ($w_i < 0.9$), we used a model averaging approach with the confidence set of models to generate a composite model (the averaged model; Burnham and Anderson 2002). To determine the relative importance for each variable, we summed the values of w_i for the models in which each variable was included. Finally, we calculated the new parameter estimates (β), unconditional standard error (\widehat{se}) and 85 % confidence intervals; if 85 % confidence intervals

encompassed 0 they were considered to be uninformative parameters (Arnold 2010).

In the torpor depth, duration, and degree-minute models, we used a subset of the data with only bat days that had at least one bout of torpor included (Klüg and Barclay 2013). Using this subset avoids zero inflation because torpor was not used on approximately one-third of the bat days. In addition, when identifying torpor patterns it is uninformative to model days during which torpor was not employed. The full data set was used in the heterothermy index and torpor or no torpor models.

We also performed a Pearson correlation to evaluate the relationship between torpor and foraging duration. Significance was assumed based on an alpha value of 0.05. All values are presented as the mean (\bar{x}) \pm standard deviation (SD) or parameter estimates (β) \pm unconditional standard error (\widehat{se}). All analyses were completed in program R (version 2.15.2; R Core Team 2012).

Results

Thermoregulation

We collected thermoregulatory and foraging data for 32 female (13 pregnant, 19 lactating) *E. fuscus* over 97 bat days (44 and 53 bat days, respectively). Twenty bats occupied only building roosts, six used only tree roosts, and six used both roost types during the tracking period. There were three general thermoregulatory patterns used by bats (Fig. 1). In the first pattern, the bats maintained normothermic temperatures with minimal T_{sk} fluctuation (Fig. 1a). In the second pattern, bats would have slight T_{sk} depressions below T_{onset} (typically <7 °C; Fig. 1b). In the final pattern, T_{sk} would be depressed >10 °C below T_{onset} , and often >13 °C (Fig. 1c). Individuals entered at least one torpor bout on 65 % of bat days with an average of 2.4 torpor bouts per day (Table 1). There was a significant relationship between torpor depth and duration in both pregnant and lactating bats (Fig. 2; parameter estimate \pm SE, pregnant: 47.3 ± 4.0 , $p < 0.001$; lactating 66.4 ± 6.2 , $p < 0.001$). Overall, no combination of parameters described whether or not torpor was used on a given day (top model = intercept model, Akaike weight (w_i) = 0.2; Table 2).

When torpor was employed, the mean duration was 289.5 ± 328.3 min per day (Table 1) and mean depth was 5.1 ± 4.9 °C with a mean minimum T_{sk} of 27.6 ± 4.9 °C. Integrating torpor depth and duration resulted in bats employing torpor for $1,452.3 \pm 3,039.3$ °C min and the HI ranged from 0.8 °C (near perfect normothermy) to 13.7 °C (long and deep torpor bouts, see Fig. 1 for example) with a mean HI of 3.1 ± 3.0 °C. Bats roosting in trees used torpor for more than twice as long as those roosting in buildings (559 ± 426.6

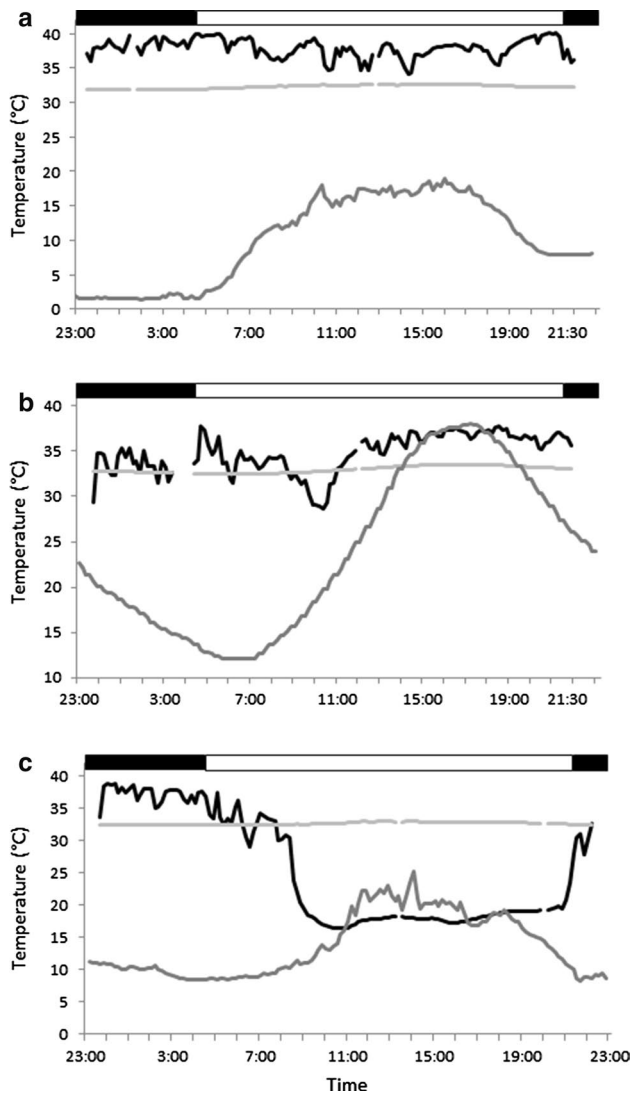


Fig. 1 Examples of **a** normothermy (HI = 1.39), **b** “shallow” torpor (HI = 2.92), and **c** “deep” torpor (HI = 13.33) thermoregulatory patterns exhibited by pregnant and lactating *Eptesicus fuscus*. Light grey lines represents torpor onset temperature (T_{onset}) calculated following Willis (2007), dark grey line represents ambient temperature and black line represents skin temperature (T_{sk}). Black bars along the x-axis indicate night

vs. 200.8 ± 219.2 min, respectively) and at greater depths (7.8 ± 6.2 and 4.1 ± 4 °C, respectively; Fig. 3).

The torpor response variables, torpor depth, duration and degree-minutes were modelled using data from 25 bats over 55 bat days, and HI was modelled using data from 29 bats over 79 bat days (Tables 2, 3). The top model for torpor depth included roost type and reproductive condition ($w_i = 0.27$). When model averaged, torpor depth model included reproductive condition ($\beta = 1.31 \pm \hat{s}\hat{e} = 1.11$), roost type ($\beta = 2.72 \pm \hat{s}\hat{e} = 1.79$), foraging ($\beta = -0.84 \pm \hat{s}\hat{e} = 0.63$) and minimum T_a ($\beta = 0.02 \pm \hat{s}\hat{e} = 0.22$). In this model, the only informative

Table 1 Summary of daily thermoregulatory characteristics of pregnant and lactating *Eptesicus fuscus*

Thermoregulatory characteristic	Overall		Pregnant		Lactating		House		Tree	
	$\bar{x} \pm SD$ (range)	n, N	$\bar{x} \pm SD$ (range)	n, N	$\bar{x} \pm SD$ (range)	n, N	$\bar{x} \pm SD$ (range)	n, N	$\bar{x} \pm SD$ (range)	n, N
HI (°C)	3.1 ± 3 (0.8–13.7)	30, 79	3.4 ± 3.5 (0.7–17.0)	13, 45	3.6 ± 3.3 (0.8–14.3)	18, 52	2.8 ± 2.4 (1.1–13.3)	22, 55	4 ± 4 (0.8–13.7)	11, 24
Time after return to first torpor bout (min)	301.2 ± 316.6 (0–1,256)	25, 55	427 ± 306 (10–1,256)	11, 34	248 ± 334 (0–1,023)	16, 36	356.6 ± 342.2 (0–1,256)	16, 40	153.6 ± 168 (0–570)	9, 15
Total duration of torpor (min)	298.5 ± 328.3 (20–1,160)	25, 55	234 ± 267 (20–890)	11, 34	386 ± 392 (20–1,160)	16, 36	200.8 ± 219.2 (20–890)	16, 40	559 ± 426.6 (20–1,160)	9, 15
Depth of torpor ($T_{\text{onset}} - T_{\text{sk}}$) (°C)	5.1 ± 4.9 (0.3–20.7)	25, 55	4.2 ± 5 (0.4–18)	11, 34	5.5 ± 4.9 (0.2–20.7)	16, 36	4.1 ± 4 (0.3–17)	16, 40	7.8 ± 6.2 (0.9–20.7)	9, 15
Minimum torpid T_{sk} (°C)	27.6 ± 4.9 (12–32.4)	25, 55	28.1 ± 5.3 (14.5–32.4)	11, 34	27.1 ± 4.9 (12–32.2)	16, 36	28.6 ± 4 (15.6–32.4)	16, 40	24.9 ± 6.2 (12–32)	9, 15
T_a at minimum torpid T_{sk} (°C)	17.4 ± 5.8 (2.6–37.6)	25, 55	15.3 ± 5.4 (2.6–24.1)	11, 34	19 ± 4.2 (11.3–28.1)	16, 36	16.9 ± 6 (2.6–37.6)	16, 40	18.9 ± 4.9 (7.6–25.5)	9, 15
Torpor degree-minutes (°C min)	$1,452.3 \pm 3,039.3$ (4.6–13,319.6)	25, 55	$1,128.7 \pm 2,789.7$ (4.6–11,103.8)	11, 34	$1,742 \pm 3,268.3$ (11.6–13,319.6)	16, 36	$823.5 \pm 2,269$ (4.6–11,103.6)	16, 40	$3,128.9 \pm 4,140.3$ (15.6–13,319.6)	9, 15
Number of torpor bouts	2.4 ± 1.5 (1–7)	25, 55	2.4 ± 1.5 (1.0–7.0)	11, 34	2.3 ± 1.5 (1.0–6.0)	16, 36	2.2 ± 1.2 (1–5)	16, 40	3 ± 2.1 (1–7)	9, 15

T_{onset} was calculated following Willis (2007) N bat days, n individual bats

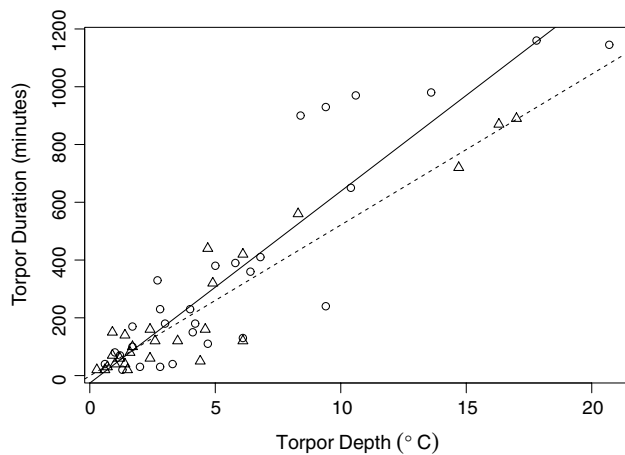


Fig. 2 Relationship between torpor duration and torpor depth in pregnant (triangles, dotted line) and lactating (circles and solid line) *Eptesicus fuscus*. Both relationships are significant (parameter estimate \pm SE, pregnant: 47.3 ± 4.0 , $p < 0.001$; lactating 66.4 ± 6.2 , $p < 0.001$)

parameter (85 % confidence intervals do not encompass 0) was roost type with a relative parameter weight of 0.8. The top model included for torpor duration was roost type ($w_i = 0.55$). The composite model included roost type ($\beta = 0.92 \pm \hat{se} = 0.3$) and reproductive condition ($\beta = 0.4 \pm \hat{se} = 0.4$). Roost type was the only informative parameter with a relative weight of 0.77. For torpor degree-minutes, intercept model ($w_i = 0.59$) was the top model. The heterothermy index model included reproductive condition ($w_i = 0.40$). No parameters were informative in describing torpor degree-minutes or HI.

Foraging

Bats spent 185.1 ± 87.7 min foraging per night, usually making at least two trips (Table 4). On average, lactating bats foraged for 100 min longer per night than pregnant bats (Table 5; $t = 3.164$, $p = 0.003$). The mean number of foraging trips was 2.4 and 1.6 for lactating and pregnant bats, respectively.

Foraging duration was modelled using data collected from 29 individual bats over 83 bat days. Parameters included in the top model were number of trips and reproductive condition (Table 5, $w_i = 0.54$), with relative parameter weights of 0.73 and 0.78, respectively. The composite model included foraging trips ($\beta = 0.29 \pm \hat{se} = 0.10$) and reproductive condition ($\beta = 0.66 \pm \hat{se} = 0.24$). Both foraging trips and reproductive condition were informative parameters.

Foraging vs. torpor

We assessed the relationship between torpor and foraging in two ways. First, we assessed torpor use on the day after foraging the previous night; the relationship between the previous night's foraging time and total torpor varied between pregnant and lactating bats (Fig. 4a). In pregnant bats, there was no relationship between foraging and torpor duration. There was a weak negative correlation for lactating bats ($r = -0.3$, $p = 0.04$). A similar pattern was found for all thermoregulation parameters (HI, torpor depth, degree-minutes). The second way we assessed the relationship was foraging at night after torpor during the day; there was no relationship between torpor and foraging for either reproductive condition (Fig. 4b).

Table 2 Torpor expression and degree-minutes model selection with no model averaging

Model	K^*	Torpor/no torpor				Degree minutes			
		L	ΔAIC_c	w_i	ER	L	ΔAIC_c	w_i	ER
Null	3	-48.2	0.00	0.27		-64.9	0.00	0.59	
mdt + pnf + RC + RT	7	-47.5	7.66	0.01	46.00	-72.3	25.23	0.00	>1,000
fRT	4	-47.8	1.22	0.15	1.84	-65.0	2.62	0.16	3.7
fRC	4	-48.1	2.02	0.10	2.75	-64.9	2.32	0.18	3.20
pnf	4	-47.7	1.12	0.16	1.75	-70.8	14.32	0.00	>1,000
mdt	4	-48.1	1.82	0.11	2.48	-67.2	6.92	0.02	31.89
RC + RT	5	-47.8	3.50	0.05	5.76	-65.0	5.25	0.04	13.80
pnf + RT	5	-47.5	3.00	0.06	4.49	-70.3	15.65	0.00	>1,000
pnf + RC	5	-47.7	3.40	0.05	5.48	-70.6	16.35	0.00	>1,000
mdt + RT	5	-47.7	3.50	0.05	5.76	-67.3	9.75	0.00	130.97

K is the number of parameters in each model, L (log Likelihood) is the goodness of fit of the model, and ΔAIC_c is the difference in AIC_c from the top model to each subsequent model. w_i (Akaike weight) is strength of evidence for each model and ER (evidence ratio) is the number of times more likely the top model is better than each model. Models include minimum daily temperature (mdt), previous night's foraging duration (pnf), reproductive condition (RC) and roost type (RT)

* plus one parameter for degree-minutes models excluding the null model

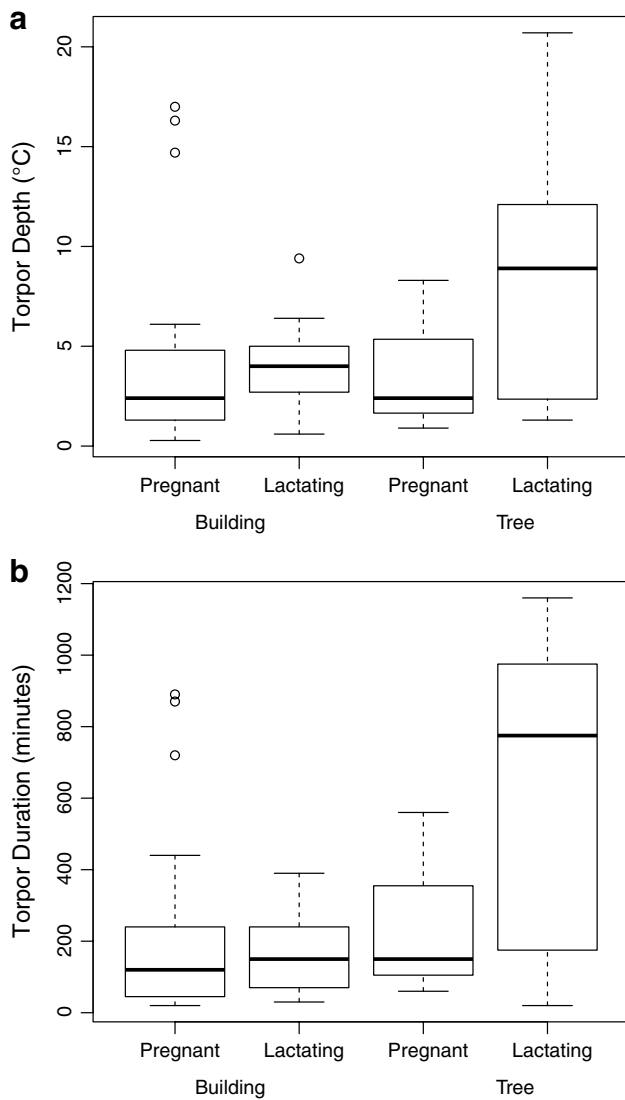


Fig. 3 Parameters of torpor use by pregnant and lactating *Eptesicus fuscus* during the inactive period (from return to roost until emergence). **a** Torpor duration is the sum of time spent in torpor per day and **b** torpor depth ($T_{\text{onset}} - \text{minimum } T_{\text{sk}}$), 0 on y-axis represents the torpor threshold. Boxplots have five sections: thick lines indicate the median value, the upper and lower bound of the box are the 25th and 75th quartiles (the height of box is the interquartile range), the upper and lower whiskers are the minimum and maximum values, or 95 % confidence intervals and circles indicate outliers ($1.5 \times \text{IQR}$)

Discussion

We found that of all the parameters incorporated into our models to describe torpor characteristics, roost type was the most important, followed by reproductive condition. Overall, bats roosting in trees expressed torpor more often and deeper than bats roosting in buildings. However, there were no differences in torpor expression between *E. fuscus* in different reproductive states. Foraging duration was explained most by foraging trips and reproductive condition

but not by torpor use. The results show that this population of *E. fuscus* adjusts activity in response to increased energy demands through increasing foraging time, not by altering thermoregulatory patterns.

Thermoregulation

Contrary to our predictions, we found that reproductive condition did not describe the frequency of torpor use. Overall, at least one torpor bout was used on the majority of bat days by individuals in both reproductive conditions, but the specific characteristics of torpor bouts differed. We found that lactating bats had a tendency to use deeper and longer torpor bouts than pregnant bats, although this difference was not significant. Also, contrary to the expected inverse relationship between foraging duration and torpor duration for all reproductive stages, we found a slightly negative relationship existed between these two activities for lactating bats only. These results suggest that reproduction and torpor are not mutually exclusive and the relationship between energy consumption and conservation is not a direct one in reproductive female *E. fuscus*.

Based on the assumption that both physiological state and environmental conditions influence torpor use, we expected a collection of environmental factors (e.g., T_a or wind) and physiological factors (e.g., foraging effort and reproductive condition) would be important for predicting its use. Similar to other studies (Christian and Geiser 2007; Brigham et al. 2000), none of the factors we included in our models described whether or not torpor was used. This suggests that parameters other than those we measured affect whether or not reproductive female *E. fuscus* employ torpor.

When taken together, reproductive condition and roost type described the nature of torpor expression better than by themselves. Lactating bats roosting in trees used deeper and longer torpor bouts than those in buildings. Interestingly, HI was not explained by roost type, only reproductive condition, which suggests the difference in torpor expression between roost types does not result in differences in overall T_{sk} fluctuation. This indicates that even though not using deep or long bouts of torpor, bats roosting in buildings were entering torpor frequently but not deeply. Although deep and long torpor bouts accrue greater energy savings at the cost of slower biological processes (such as immune response, slowed growth and development; Lovegrove et al. 1999), frequent shallow torpor bouts also have benefits both energetically (Webb et al. 1993) and possibly developmentally (i.e., fewer negative effects on foetal development or milk production). Therefore, the torpor patterns employed by reproductive bats in this study likely made the trade-off between minimising the potential costs of torpor while maximising energy savings.

Table 3 Results of thermoregulatory model selection with model averaging

Model	K	Depth				ln(Torpor Duration + 1)				HI			
		L	$\Delta AICc$	w_i	ER	L	$\Delta AICc$	w_i	ER	L	$\Delta AICc$	w_i	ER
Null	3	-159.3	3.22	0.05	5.0	-84.3	3.2	0.11	4.89	-183.1	1.12	0.23	1.75
mdt + pnf + RC + RT	8	-153.9	3.08	0.06	4.7	-88.3	21.4	0.00	>1,000	-186.1	16.64	0.00	>1,000
RT	5	-156.7	0.67	0.19	1.4	-81.6	0.0	0.55		-182.5	2.20	0.13	3.00
RC	5	-157.4	2.27	0.09	3.1	-83.4	3.7	0.09	6.36	-181.4	0.00	0.40	
pnf	5	-158.8	4.97	0.02	12.0	-89.5	15.9	0.00	>1,000	-187.8	12.70	0.00	572.50
mdt	5	-159.9	7.27	0.01	38.0	-86.5	10.0	0.00	148.41	-184.2	5.40	0.03	14.88
RC + RT	6	-155.1	0.00	0.27		-81.2	1.8	0.22	2.49	-181.0	1.44	0.19	2.06
pnf + RT	6	-155.2	0.40	0.22	1.2	-87.1	13.6	0.00	909.37	-186.9	13.24	0.00	751.73
pnf + RC	6	-156.6	3.20	0.05	5.0	-88.8	17.0	0.00	>1,000	-185.6	10.74	0.00	215.38
mdt + RT	6	-157.4	4.70	0.03	10.5	-83.8	6.9	0.02	31.90	-183.6	6.74	0.01	29.15

Model averaging												
Parameter	β	\hat{se}	Upper CI	Lower CI	β	\hat{se}	Upper CI	Lower CI	\hat{se}	Upper CI	Lower CI	
Intercept	4.31	1.11	5.91	2.71	4.78	0.2	5.07	4.49	2.81	0.58	3.65	1.97
RC	1.31	1.79	3.89	-1.27	0.40	0.4	0.98	-0.17	1.15	0.87	2.40	-0.10
RT	2.72	1.47	4.84	0.60	0.92	0.3	1.35	0.49	0.28	0.61	1.16	-0.60
pnf	-0.84	0.63	0.07	-1.75								
mdt	0.02	0.22	0.34	-0.30								

Bold values make up the confidence set ($w_i = 0.95$) used for model averaging and informative model-averaged parameters. The confidence set was averaged following Burnham and Anderson (2002). Model averaged parameter estimate (β) and unconditional standard error (\hat{se}) with associated upper and lower 85 % confidence intervals. For table and parameter descriptions refer to Table 2

Table 4 Summary of foraging data for pregnant ($n = 12$ bats, $N = 36$ bat days) and lactating ($n = 18$, $N = 47$) *Eptesicus fuscus*

Foraging characteristic	Overall $\bar{x} \pm SD$ (range)	Pregnant $\bar{x} \pm SD$ (range)	Lactating $\bar{x} \pm SD$ (range)
Total foraging time (minutes)	185.1 \pm 87.7 (20–350)	142.5 \pm 78.4 (40–310)	236.7 \pm 71.5 (75–350)
Number of foraging trips	2.1 \pm 1.0 (1–4)	1.6 \pm 0.8 (1–4)	2.4 \pm 0.9 (1–4)
Duration of first foraging trip (minutes)	106.0 \pm 57.7 (20–330)	108.8 \pm 59.8 (40–270)	115.4 \pm 58.7 (30–330)
Emergence (minutes past sunset)	115.3 \pm 39.5 (72–389)	109.6 \pm 20.1 (72–190)	113.6 \pm 34.7 (90–389)
Final return to roost (minutes past sunrise)	-86.4 \pm 119.9 (-301–57)	-155.3 \pm 125.4 (-301–57)	-32.2 \pm 81.1 (-300–37)
T_a at emergence ($^{\circ}C$)	15.0 \pm 4.3 (3.3–23.4)	12 \pm 2.6 (3.3–17.2)	17.5 \pm 2.4 (9.8–23.4)
Minimum night T_a ($^{\circ}C$)	11.4 \pm 4.4 (-0.4–19.1)	8.6 \pm 2.7 (-0.4–14.6)	13.9 \pm 3.0 (6.1–19.1)

Total foraging time refers to the amount of time each individual was moving (determined through telemetry) outside of the roost. A complete foraging trip occurred when a bat emerged from the roost, flew and returned to the same roost after >20 min

Foraging patterns

As expected, lactating bats spent more time foraging and made more foraging trips than pregnant bats. Based on differences in energetic requirements during pregnancy and lactation, lactating bats were expected to forage longer than pregnant bats. Although we could not test it, we assumed that because bats in both conditions remained close to the roost at all times, longer periods of foraging equates to greater prey consumption. Also, because young bats cannot thermoregulate proficiently and require external sources of warming (Sano 2000; Zahn 1999) as well as feeding, it

is not surprising that lactating bats made more, but shorter, foraging trips than pregnant bats. Our findings are consistent with several studies (e.g., Aldridge and Brigham 1991; Brigham 1991; Grinevitch et al. 1995; Lučan and Radil 2010; O'Donnell 2002). However, contrary to our results, others have found no difference between reproductive conditions in foraging duration (e.g., Dzal and Brigham 2013; Wilkinson and Barclay 1997) or that pregnant bats foraged longer than lactating bats (Dietz and Kalko 2007). Sample sizes and methods are similar in all of these studies; therefore, it is likely that species, site, and year influence foraging activity. For example, Grinevitch et al. (1995) and Wilkinson

Table 5 Foraging duration model selection

Model	<i>K</i>	<i>L</i>	Δ AICc	w_i	ER
Null	4	−99.1	5.41	0.04	14.94
Trips + Tamin*Awind + tor_dur + RC	9	−105.3	30.25	0.00	>1,000
RC	5	−96.2	1.77	0.22	2.43
Trips	5	−96.5	2.27	0.17	3.13
Tamin	5	−99.9	9.07	0.01	93.41
Awind	5	−101.0	11.27	0.00	280.61
Tor_dur	5	−106.2	21.77	0.00	>1,000
Tamin*Awind	6	−101.7	15.00	0.00	>1,000
Trips + RC	6	−94.1	0.00	0.54	
Trips + tor_dur + RC	7	−101.3	16.59	0.00	>1,000
Tamin*Awind + RC	7	−99.9	13.99	0.00	>1,000
Model averaging					
Parameter	β	\hat{se}	Upper CI	Lower CI	
Intercept	−0.7	0.34	−0.03	−1.37	
Trips	0.29	0.10	0.49	0.09	
RC	0.66	0.24	1.13	0.19	

Bolded values make up the confidence set ($\Sigma w_i = 0.95$) used for model averaging. Models include the number of foraging trips taken (Trips), minimum nightly temperature (Tamin), average wind speed (Awind), daily torpor duration (tor_dur) and reproductive condition (RC). For table description, see Table 2

and Barclay (1997) studied foraging by *E. fuscus* at the same site but in different years, which suggests that year influences foraging behaviour. We could not assess the effect of year because we studied bats at each site in different years.

We found that reproductive condition and number of foraging trips were the most important factors in describing total foraging duration. Surprisingly, the amount of torpor used during the day did not influence the amount of foraging that occurred that night. We expected that if bats used torpor more during the day they would likely need to forage less. However, if bats could not remain active due to insufficient energy reserves during the day, it is possible that foraging duration would remain constant in an effort to increase energy reserves. Small mammals (<25 g) can only store 2–3 days of energy while active (as opposed to hibernating). However, when T_a is reduced, maintaining normothermy would burn through reserves in less time (Bronson 1985; Speakman and Racey 1987; Willis et al. 2005). In comparison with other small mammals, it is likely that bats would have fewer energy reserves than above due to the energetic and costs and reduced manoeuvrability associated with greater wingloading (Norberg and Rayner 1987) as well as the space constraints placed on pregnant bats. Bats that do not have large fat reserves would be more likely to forage regardless of torpor use the previous day because they do not have an energetic “safety net”, something that we could not directly measure.

Torpor vs. foraging

We expected to find an inverse relationship between energy conservation and consumption if torpor use during

reproduction has no physiological costs. We assessed the potential for this relationship in two ways: (1) torpor use following a night of foraging and (2) foraging time following time spent torpid during the day. The inverse relationship was present for torpor following foraging in lactating bats. The different response between reproductive conditions suggests that the detriments of using torpor during reproduction are greater for pregnant bats than lactating bats. Alternatively, because lactation is a more energetically taxing process than pregnancy, if foraging success was low, lactating bats may be required to use torpor. This scenario would also result in an inverse relationship. In temperate regions where the growing season is short, the costs of delaying parturition could outweigh the benefits of saving energy when conditions are not amenable to foraging. The lack of a relationship between foraging at night after torpor during the day is consistent with the hypothesis that torpor is used to maintain a positive energy balance, but bats will forage as much as possible regardless of how or if they use torpor.

Conclusions

Our study provides further evidence that reproduction and torpor are not mutually exclusive. Further work needs to be done to address the T_b at which either gestation ceases and the foetus dies, or milk production ceases or quality declines greatly. We hypothesise that this is the case behind the patterns of torpor we observed in reproductive individuals because lactating females did not enter deep torpor often but regularly used shallow bouts of torpor. It is likely

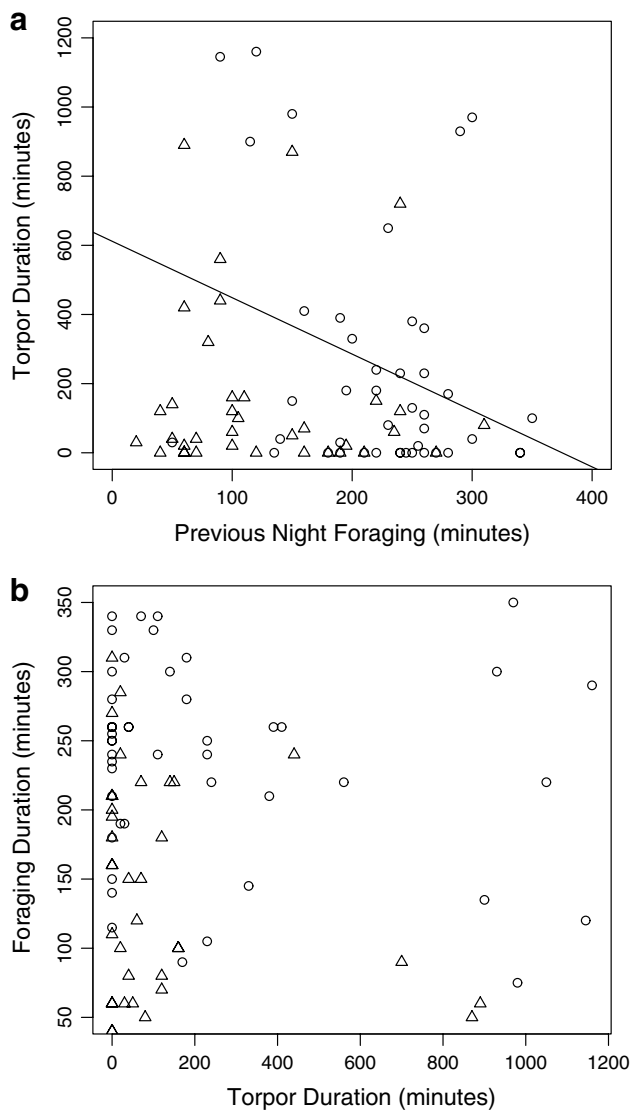


Fig. 4 Relationship between day torpor duration and night foraging duration for pregnant (triangles) and lactating (circles and solid line) *Eptesicus fuscus*. Data are for **a** foraging duration prior to torpor use and **b** torpor duration prior to foraging. Line indicates a significant relationship for lactating bats

that both gestation and lactation are affected to varying degrees along a gradient, but it is essential to understand when torpor is completely detrimental to either the foetus or pup.

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