

Seasonality of torpor patterns and physiological variables of a free-ranging subtropical bat

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Accepted 25 October 2009

SUMMARY

Seasonal changes in weather and food availability differ vastly between temperate and subtropical climates, yet knowledge on how free-ranging subtropical insectivorous bats cope with such changes is limited. We quantified ambient temperatures, torpor patterns and thermal physiology of subtropical insectivorous northern long-eared bats, *Nyctophilus bifax*, during summer ($n=13$) and winter ($n=8$) by temperature telemetry. As predicted, ambient conditions varied significantly between seasons, with warmer weather during summer. All bats used torpor on 85% of observation days during summer in comparison to 100% during winter. During summer, patterns of torpor varied and the duration of torpor bouts was not significantly affected by ambient temperature, whereas during winter torpor bout duration was negatively correlated with mean ambient temperature. Mean torpor bout duration in summer was 3.2 ± 1.3 h and in winter was 26.8 ± 11.3 h. Mean arousal time during summer was in the early afternoon and during winter in the late afternoon, and throughout both seasons arousals for possible foraging periods occurred near sunset. Skin temperature was positively correlated with ambient temperatures in both seasons, but the relationship differed between seasons. We show that torpor is used regularly throughout the year in a free-ranging subtropical bat and provide the first evidence demonstrating that torpor patterns and thermal physiology change with season.

Key words: bat, torpor, season, subtropical, summer, winter.

INTRODUCTION

Seasonal variations in climate occur in all habitats, with the most extreme seasonal changes generally occurring in temperate or arctic regions. However, weather conditions in tropical and subtropical regions do vary seasonally and these changes can also be substantial. Changes in ambient temperature (T_a) and rainfall patterns in subtropical regions from summer to winter can be pronounced, resulting in different primary productivity and consequently different physiological demands on animals. Insectivorous bats are small (most weigh <25 g) and have a disproportionately large surface area to volume ratio. Consequently, they need large amounts of energy in comparison to larger animals to remain at normothermic body temperatures (T_b) at T_a lower than their thermal neutral zone (TNZ) and as a result may also be more affected by seasonal changes in weather than other mammals (Brown, 1999; Turbill et al., 2003; Vivier and Van Der Merwe, 2007). Thermoregulatory energy demands would require that insectivorous bats consume enormous amounts of food on cool nights to remain normothermic. However, many moth species and other insects are unable to remain active at low T_a , which greatly reduces the amount of food available to insectivorous bats on cool nights (Taylor, 1963; Richards, 1989; Turbill et al., 2003). Consequently, insect abundance can significantly change daily and also seasonally (Hickey and Fenton, 1996; Jacobs et al., 2007; Stawski and Geiser, 2010). To deal with such energetic constraints and to conserve energy, many insectivorous bats employ torpor, which is characterised by pronounced reductions in T_b , metabolic rate (MR) and water loss (Hock, 1951). Moreover, the use of torpor is often initiated by a decrease in food availability and/or T_a (Wang, 1989), suggesting that it would be beneficial for insectivorous bats to be flexible in

their use of torpor to suit current seasonal and daily weather conditions and therefore insect abundance.

Studies undertaken on the seasonal activity of insectivorous bats from a variety of habitats have found that activity is generally highest during summer and lowest during winter (Richards, 1989; Brigham and Geiser, 1998). However, laboratory studies on torpor use in cool-temperate insectivorous bats established that season *per se* did not have a pronounced effect on torpor use and physiological variables in comparison to environmental conditions and food availability (Geiser and Brigham, 2000; Wojciechowski et al., 2007). Surprisingly, in the subtropical nectarivorous blossom bat (*Syconycteris australis*) seasonal functional changes were observed, but these were the opposite of those commonly observed in other mammals because torpor bouts were longer and T_b lower during summer than in winter (Coburn and Geiser, 1998). However, *S. australis* primarily feed on nectar that is more abundant during winter than during summer, again suggesting that torpor use in this species is predominantly determined by food availability. Importantly, all seasonal functional studies on torpor patterns were undertaken in the laboratory. Seasonal data in free-ranging subtropical insectivorous bats are currently restricted to descriptive information on the seasonal differences in torpor use (Vivier and Van Der Merwe, 2007), whereas information on seasonal changes in physiological variables of torpor patterns and their systematic analysis are entirely lacking.

Therefore, the aim of our study was to obtain detailed quantitative data on the thermal biology of the insectivorous northern long-eared bat, *Nyctophilus bifax* Thomas 1915, during summer and winter from subtropical Australia by using temperature telemetry. Little biological and ecological information is available about *N. bifax*. However, it is known that they are a tree-roosting species, give birth

to young during October, lactate from November to December, and feed on moths, ants and click beetles (Churchill, 1998). We predicted that *N. bifax* will use torpor regularly throughout the year in a subtropical habitat, especially during adverse weather conditions and low food availability. Furthermore, considering the substantial seasonal changes in weather and food availability (Stawski and Geiser, 2010) we hypothesised that thermal biology and torpor patterns of free-ranging *N. bifax* differ seasonally.

MATERIALS AND METHODS

Data on the seasonal patterns and physiological variables of torpor use in free-ranging subtropical insectivorous bats, *Nyctophilus bifax*, were collected at Iluka Nature Reserve (29°24'S, 153°22'E) in Australia, during the Austral winter (July to August 2007) and summer (February to March 2008). Iluka Nature Reserve is a subtropical area of littoral rainforest and eucalypt forest. Some data from our winter study have been published in a descriptive study (Stawski et al., 2009) and some data from our summer study have been published to test the cost-benefit hypothesis of torpor use (Stawski and Geiser, 2010), but all data were re-analysed and new data were included for this seasonal comparison.

We report data from eight non-reproductive individual *N. bifax* from winter (measured for 10–27 days) and thirteen non-reproductive individual *N. bifax* from summer (measured for 1–12 days). Bats were captured with mist nets and were weighed using a pro-Fit™ pocket/travel scale (0.1g resolution, InterTAN Australia PTY Limited; Cat. No. 63-9534). Although *N. bifax* were non-reproductive during the times of our study, females were checked to confirm that they were not lactating or pregnant. After removal of a small patch of fur, temperature-sensitive radio transmitters (~0.5g, LB-2NT, Holohil Systems Inc., Carp, ON, Canada) were attached to the mid-dorsal skin region using latex adhesive (SkinBond; Smith and Nephew United; Mount Waverley, NSW, Australia) to obtain data on the skin temperature (T_{skin}) of *N. bifax*. Owing to the difficulty of implanting transmitters into small microbats and because the difference between T_{b} and T_{skin} for small mammals while torpid is $<2.0^{\circ}\text{C}$ (Audet and Thomas, 1996; Barclay et al., 1996), we felt that the use of external transmitters was appropriate for our study. To ensure the accuracy of T_{skin} data, transmitter pulse rate was regressed against transmitter temperature, by calibrating transmitters before use at temperatures between 5.0 and 40.0°C in a water bath against a precision thermometer (0.1°C resolution). We found that transmitters drifted by $<1.0^{\circ}\text{C}$ over the entire temperature range as we were able to re-calibrate three transmitters 7 to 28 days after initial calibration, which were worn by bats and shed.

Bats were located on every day they carried transmitters and the T_{skin} of each bat was monitored every day *via* telemetry during both study periods. We determined the exact location of several roosts, when possible, during summer and winter, however, this was often not feasible because of the thick vegetation and large number of possible roost sites in a small area. Approximate roost locations were marked with tape and recorded with a handheld global positioning system unit (GARMIN eTrex). A remote receiver/logger (Körtner and Geiser, 2000a) was used to continuously record the T_{skin} of each bat once every 10 min when bats were in transmission range. Every 2–4 days we downloaded the data from the receiver/loggers to a laptop computer. T_{a} in both summer and winter was measured with temperature data loggers ($\pm 0.5^{\circ}\text{C}$, iButton Thermochron DS1921G, Maxim Integrated Products Inc., Sunnyvale, CA, USA) that were placed in the same location during both seasons under the canopy of the rainforest in the shade 2 m above the ground.

During the summer study when T_{skin} was $<28.0^{\circ}\text{C}$ for >30 min bats were considered to be torpid. We felt that the use of this definition for torpor was appropriate, as the $T_{\text{b}}-T_{\text{skin}}$ differential of torpid small mammals is typically $<2.0^{\circ}\text{C}$ and many studies use $T_{\text{b}}<30.0^{\circ}\text{C}$ to define torpor (Barclay et al., 2001). For our winter study, torpor bouts were similarly defined, with the exception of passive fluctuations where T_{skin} occasionally increased to temperatures $>28.0^{\circ}\text{C}$ (max 32.0°C) for <30 min without an obvious active arousal and such passive fluctuations were included into torpor bouts.

Statistical analyses

Data are reported as means \pm s.d. for the number of individuals (n) and the number of observations (N). Statistix (V 1.8, 2007) was used to conduct most statistical analyses. A Rayleigh test was used to determine whether circular data (timing of arousals and torpor entries) differed significantly from random. To account for repeated measures in individuals when calculating means \pm s.d. for torpor bouts and T_{skin} , the mean of the values for each individual were used. For regressions and timing of events, such as arousals and torpor entries, multiple data points for each individual were included in analyses. If the significance level was $P<0.05$, the null hypothesis was rejected. To determine the random effect of individuals we compared linear regressions in Statistix to check for differences in slopes by using ANOVA. No differences were found in the slopes of individuals for any of the regressions and therefore individuals were pooled and regressed together. Minitab (V 13.1, 2000) was used to determine the effect of body mass on all statistical analyses. Body mass and season were used as covariates in a general linear model for mean torpor bout duration, mean maximum torpor bout duration, mean minimum T_{skin} and minimum $T_{\text{skin}}-T_{\text{a}}$ and it was found that body mass had no effect on any of these variables, whereas season did have a significant effect on all variables. For all regressions for both seasons body mass was included as a predictor to determine the effect it had on the given variable (torpor bout duration, T_{skin} , and $T_{\text{skin}}-T_{\text{a}}$). Body mass had no effect on any of the variables for both seasons, except for T_{skin} during summer and this is included in the results.

RESULTS

T_{a} during winter varied between a minimum of $8.2\pm 2.2^{\circ}\text{C}$ ($n=29$) and maximum of $17.4\pm 2.3^{\circ}\text{C}$ ($n=29$), with a mean daily range of $9.2\pm 1.9^{\circ}\text{C}$ ($n=29$). During summer, T_{a} varied between a minimum of $18.3\pm 1.2^{\circ}\text{C}$ ($n=26$) and a maximum of $25.0\pm 2.3^{\circ}\text{C}$ ($n=26$), with a mean daily range of $6.7\pm 2.2^{\circ}\text{C}$ ($n=26$). As predicted, both minimum and maximum T_{a} during winter were significantly lower than during summer ($P<0.001$, $t=21.3$, d.f.=44.8; $P<0.001$, $t=12.3$, d.f.=53; respectively), however, the daily range of T_{a} was significantly larger during winter than in summer ($P<0.001$, $t=4.6$, d.f.=53; Fig. 1). Mean daily T_{a} was higher during summer ($21.2\pm 1.3^{\circ}\text{C}$, $n=26$) than in winter ($12.4\pm 2.2^{\circ}\text{C}$, $n=29$; $P<0.001$, $t=18.7$, d.f.=46.3; Fig. 1). During winter, mean night T_{a} was significantly lower ($10.9\pm 2.4^{\circ}\text{C}$, $n=28$) than during summer ($20.1\pm 1.2^{\circ}\text{C}$, $n=25$; $P<0.001$, $t=17.6$, d.f.=40.4; Fig. 1).

Torpor was used by all individuals on all days (100%) during winter and on 85% of observation days during summer. Torpor bout durations ranged from 0.8 to 128.5 h in winter and from 0.7 to 21.2 h in summer. Mean torpor bout duration was significantly longer during winter (26.8 ± 11.3 h, $n=8$, $N=114$) than in summer (3.2 ± 1.3 h, $n=13$, $N=122$; $P<0.001$, $t=6.0$, d.f.=7.1; Table 1) and so were mean maximum torpor bout durations recorded for each individual (winter: 83.7 ± 27.6 h, $n=8$; summer: 8.2 ± 6.2 h, $n=13$;

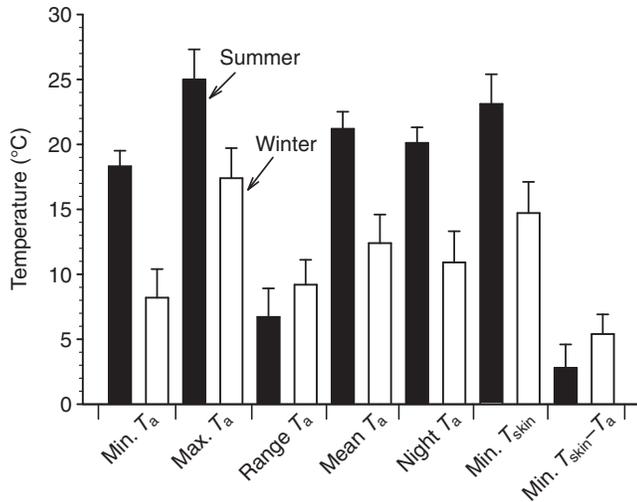


Fig. 1. Differences in temperature between summer (black bars) and winter (white bars; means and standard deviations). Min. T_a is the mean of all daily minimum T_a ; Max. T_a is the mean of all daily maximum T_a ; Range T_a is the mean of all daily range of T_a (max. T_a -min. T_a); Mean T_a is the mean of all daily mean T_a ; Night T_a is the mean of all night T_a (sunset to sunrise); Min. T_{skin} is the mean of all individuals' mean torpid minimum T_{skin} ; Min. $T_{skin}-T_a$ is the mean of all individuals' mean differentials.

$P < 0.001$, $t = 7.6$, d.f. = 7.4). Daily patterns of torpor during summer varied (Fig. 2A) and the most common pattern of torpor was two or more torpor bouts during the day (55%); less common were one morning or one afternoon torpor bout (21.7%), remaining torpid during the day (8.7%), and lastly, no torpor (14.6%). Winter torpor patterns generally involved short normothermic periods in the evening or no normothermic periods over several days (Fig. 2B). Torpor bout duration (\log_{10}) decreased with increasing T_a during winter ($F_{1,107} = 96.0$, $P < 0.001$, $R^2 = 0.5$), however, this relationship was not significant during summer ($P = 0.2$; Fig. 3). Nevertheless, when torpor bout duration (\log_{10}) and T_a from summer and winter were pooled and regressed together this relationship was significant ($F_{1,226} = 410.3$, $P < 0.001$, $R^2 = 0.6$) and increased R^2 in comparison to winter-only data. The percentage of bats that used torpor on a given day during summer increased with decreasing daily minimum T_a ($F_{1,22} = 4.9$, $P = 0.04$, $R^2 = 0.2$), average T_a ($F_{1,22} = 6.9$, $P = 0.02$, $R^2 = 0.3$) and evening (sunset to midnight) T_a ($F_{1,21} = 16.5$, $P < 0.001$, $R^2 = 0.5$).

Daily entries into torpor during summer reached an absolute peak at 36.0 ± 26.6 min ($n = 12$, $N = 42$) after sunrise, but this pattern was not statistically significant (Rayleigh $Z = 2.0$, $P = 0.132$; Fig. 4A). Timing of arousals during summer was non-randomly distributed (Rayleigh $Z = 7.1$, $P = 0.001$; Fig. 4A) with a mean time (angle) of $13:05 \pm 4:44$ h ($n = 13$, $N = 128$) and arousals for possible foraging

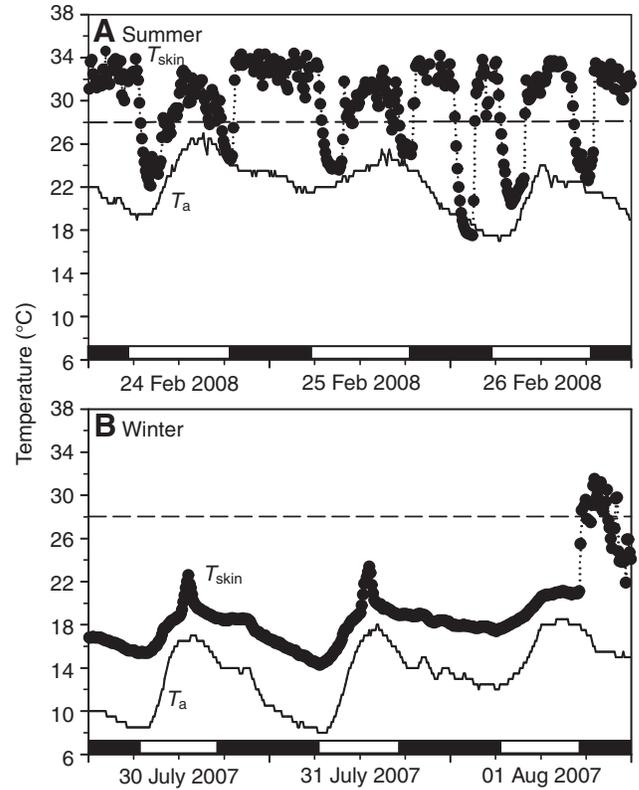


Fig. 2. T_{skin} (upper trace, dotted line) and T_a (lower trace, smooth line) of two different *N. bifax* individuals over 3 days during summer (A) and winter (B). The dashed line indicates the torpor threshold, 28°C, and the horizontal black and white bars at the bottom of the graphs denote night and day, respectively.

periods occurred 14.5 ± 21.4 min ($n = 13$, $N = 41$) before sunset. During winter, both entries into torpor and arousals from torpor were non-randomly distributed (Rayleigh $Z = 24.6$ and 72.0 , $P < 0.001$; Fig. 4B) at a mean time (angle) of $19:56 \pm 4:00$ h ($n = 8$, $N = 122$) and $16:26 \pm 2:29$ h ($n = 8$, $N = 116$), respectively. Arousals for probable foraging periods during winter occurred 4.5 ± 11.4 min after sunset ($n = 8$, $N = 92$).

The lowest individual T_{skin} recorded was 9.4°C during winter and 16.0°C during summer. Mean minimum torpid T_{skin} was significantly lower during winter ($14.7 \pm 2.4^\circ\text{C}$, $n = 8$, $N = 147$) than during summer ($23.1 \pm 2.3^\circ\text{C}$, $n = 13$, $N = 63$; $P < 0.001$, $t = 7.8$, d.f. = 19.0; Fig. 1, Table 1). During summer, daily minimum torpid T_{skin} occurred 196 ± 191 min ($n = 13$, $N = 57$) and during winter 197 ± 99 min ($n = 8$, $N = 144$) after the daily minimum T_a . Minimum torpid T_{skin} was positively correlated with the corresponding T_a during winter ($F_{1,143} = 71.8$, $P < 0.001$, $R^2 = 0.3$) and also during summer ($F_{1,56} = 41.9$, $P < 0.001$, $R^2 = 0.4$;

Table 1. Data for variables examined for all free-ranging *N. bifax* during summer and winter

Season	No. days of data	Body mass* (g)	Torpor bout duration (h)	Daily minimum T_{skin} ($^\circ\text{C}$)
Summer	5.7 ± 3.2 (13)	9.5 ± 1.0 (13)	3.2 ± 1.3 (13, 122)	23.1 ± 2.3 (13, 63)
Winter	19.4 ± 5.8 (8)	10.1 ± 1.3 (8)	26.8 ± 11.3 (8, 114)	14.7 ± 2.4 (8, 147)
<i>P</i> -value	<0.001	0.2	<0.001	<0.001
<i>t</i> -value	6.1	1.3	5.9	7.8

Values are mean \pm s.d.

Significance of difference from two sample *t*-tests from the means of individuals (d.f. = 19).

*Body mass at capture.

Values in brackets are the number of individuals (*n*) and the number of observations (*N*), respectively.

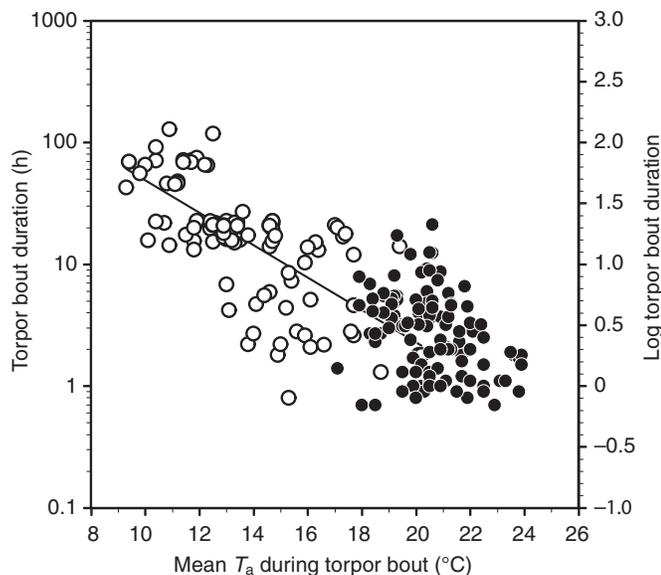


Fig. 3. Duration of torpor bouts as a function of mean T_a during a torpor bout in summer (black circles; $P=0.2$) and winter [white circles, solid line; torpor bout duration (\log_{10})= $3.0-0.1 \times (\text{mean } T_a; \text{ in } ^\circ\text{C})$; $F_{1,107}=96.0$, $P<0.001$, $R^2=0.5$].

Fig. 5A). However, the slope of this relationship differed significantly between seasons (summer=1.3; winter=0.6; $F_{1,198}=10.7$, $P<0.001$). Furthermore, it was found that body mass had a significant effect on T_{skin} during summer ($P=0.005$) and changed the slope of the relationship between minimum torpid T_{skin} and T_a (new slope=1.2). Partial regression plots for the adjusted relationship between minimum torpid T_{skin} and T_a have been included for both summer and winter (Fig. 5B). The differential between minimum T_{skin} and the corresponding T_a was larger during winter ($5.4 \pm 1.5^\circ\text{C}$, $n=8$, $N=140$) than during summer ($2.8 \pm 1.8^\circ\text{C}$, $n=13$, $N=57$; $P=0.003$, $t=3.4$, d.f.=19.0). Further, the relationship between this differential and T_a was significant during winter ($F_{1,143}=39.3$, $P<0.001$, $R^2=0.2$), but not during summer ($P=0.2$; Fig. 6).

DISCUSSION

We provide the first evidence of seasonal changes in torpor patterns and thermal physiology of a free-ranging insectivorous bat from a subtropical region. Our study shows that torpor in winter is more frequent, deeper and longer than in summer. Although short bouts of torpor were observed during both seasons, the range of the duration of torpor bouts during winter (0.8 to 128.5 h) was much greater than during summer (0.7 to 21.2 h). Consequently, the longer torpor bouts during winter suggest that *N. bifax* are more energetically constrained during winter than in summer. Interestingly, in addition to the predicted lower T_a in winter, it was found that the daily range of T_a experienced by bats studied here during winter was significantly greater than during summer. These seasonal differences in T_a will affect insect abundance and it was found that insect abundance at Iluka Nature Reserve during summer is 14-fold of that during winter (Stawski and Geiser, 2010). Therefore, T_a and insect abundance are likely responsible for much of the seasonal changes in torpor patterns of *N. bifax* in this subtropical climate.

As in other species of insectivorous bats (Ransome, 1971; Park et al., 2000; Rambaldini and Brigham, 2008), torpor bout duration in *N. bifax* decreased with increasing T_a during winter, but this

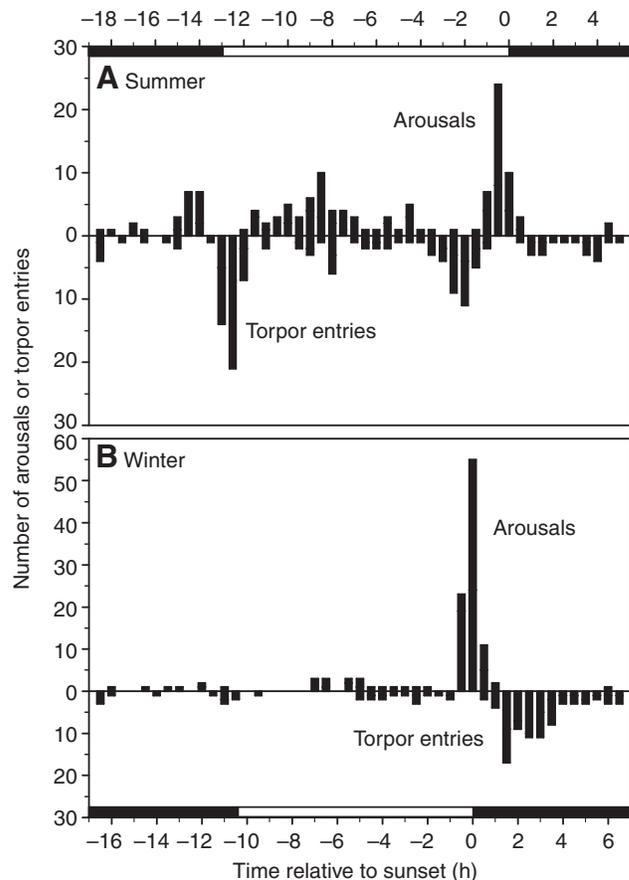


Fig. 4. Distribution of times of arousals from torpor (top half of graphs) and entries into torpor (bottom half of graphs) of *N. bifax* during summer (A) and winter (B) relative to the time of sunset (0h). Each individual contributed several points to these graphs, ranging from 4 to 48 data points. Each bar represents a 30 min period. The horizontal black and white bars at the top and bottom of the graphs denote night and day, respectively.

relationship was not significant during summer. However, the weak effect of T_a on torpor bout duration during summer was most probably due to the narrow range of T_a experienced, but when this range was increased by adding all data from winter, the relationship became statistically significant. This suggests that there is no clear seasonal change on the influence of T_a on torpor bout duration. Even though T_a showed no effect on torpor bout duration during summer it was found that T_a does affect the percentage of bats that enter torpor on a given day. Therefore, although the weather was most probably mild enough during summer to forage and insect abundance was high, torpor was still used more often on cooler days during summer for energy conservation.

Preliminary data for MR of *N. bifax* (C.S., unpublished data) suggest that they are similar to those of *N. geoffroyi*. Therefore, by using resting and torpid MR of *N. geoffroyi* (Geiser and Brigham, 2000), we were able to calculate approximate energy expenditure for *N. bifax* during summer and winter. Normothermic thermoregulation of *N. bifax* for 1 h during the day in summer at T_a 25°C (near mean daily max T_a) requires 532 J/h , whereas in winter at T_a 15°C (near mean daily max T_a) they require 1165 Jh^{-1} , more than twice as much. However, torpor at T_a 15°C during winter reduces energy expenditure to approximately 16 Jh^{-1} , which is a mere 1% of the resting MR for the same time period. The torpid

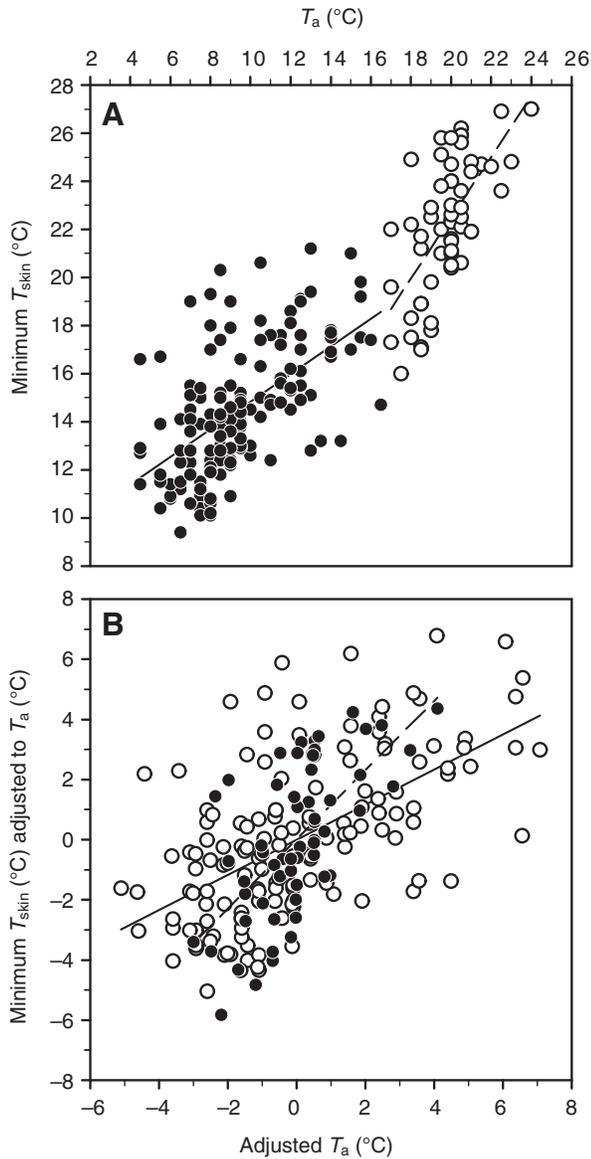


Fig. 5. (A) Daily torpid minimum T_{skin} as a function of T_a during summer [black circles, dashed line; minimum T_{skin} ($^{\circ}\text{C}$) = $-2.8 + 1.3 \times T_a$ ($^{\circ}\text{C}$); $F_{1,56} = 41.9$, $P < 0.001$, $R^2 = 0.4$] and winter [white circles, solid line; minimum T_{skin} ($^{\circ}\text{C}$) = $9.1 + 0.6 \times T_a$ ($^{\circ}\text{C}$); $F_{1,143} = 71.8$, $P < 0.001$, $R^2 = 0.3$]. (B) Partial regression plot of daily torpid minimum T_{skin} adjusted for T_a as a function of adjusted T_a during summer (black circles, dashed line) and winter (white circles, solid line).

MR during summer (T_a 25°C) at 39Jh^{-1} is also low, only 7% of the energy used during normothermia. Therefore, it seems worthwhile for individuals of *N. bifax* to use torpor as observed here regularly throughout the rest period in both summer and winter. However, in comparison to winter, arousal from torpor and remaining normothermic during summer requires much less energy because of the relatively high T_b , so they can be more flexible with torpor use as shown by the frequent arousals.

Although entries into torpor during summer in the current study occurred statistically randomly throughout the day, many bats entered torpor shortly before or after sunrise similar to temperate insectivorous bats (Turbill et al., 2003; Rambaldini and Brigham, 2008). By contrast, during winter *N. bifax* entered torpor much earlier

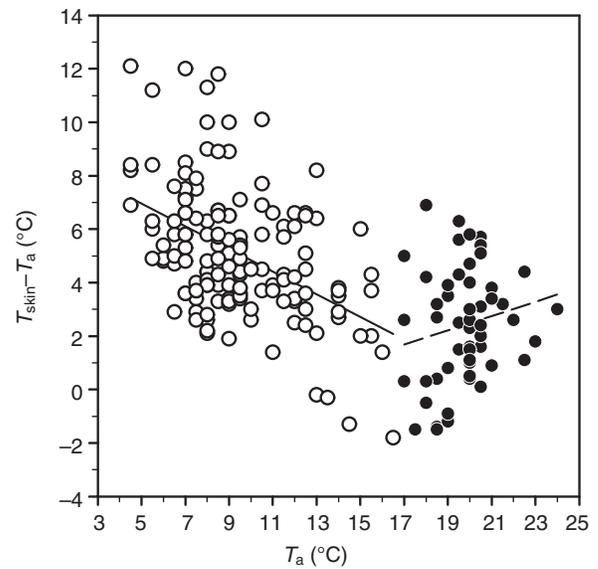


Fig. 6. The differential between daily torpid minimum T_{skin} and T_a as a function of T_a during summer (black circles; $P = 0.2$) and winter [white circles, solid line; $T_{\text{skin}} - T_a$ ($^{\circ}\text{C}$) = $9.1 - 0.4 \times T_a$ ($^{\circ}\text{C}$); $F_{1,143} = 39.3$, $P < 0.001$, $R^2 = 0.2$].

during the night if they had aroused in the evening, probably due to the cold night T_a . Arousals from torpor for possible foraging trips during both summer and winter occurred near sunset, as for other insectivorous bats (Park et al., 2000; Turbill et al., 2003; Turbill, 2006). However, whereas most arousals for possible foraging trips during summer occurred 15–30 min before sunset, during winter most occurred just shortly after sunset. Frequent daily arousals (two to three times per day) from torpor during summer, as observed here, have been described in another subtropical microbat species (Vivier and Van Der Merwe, 2007) and are probably because costs of arousals are low for small mammals as they have only little tissue to heat, they often passively arouse to a certain T_b and because of the above mentioned relatively high T_b during summer (Geiser and Baudinette, 1990; Turbill et al., 2008; Warnecke et al., 2008).

During both seasons T_{skin} in *N. bifax* was generally a few degrees above T_a and time of daily minimum torpid T_{skin} was around 3 h after the time of daily minimum T_a , which is most likely a reflection of ambient conditions within roosts. Also, during summer, the delay in minimum torpid T_{skin} in comparison to minimum T_a may be a result of bats foraging or being normothermic during the part of the night when T_a is at its lowest, as they often entered torpor after sunrise. Daily minimum torpid T_{skin} during winter was significantly lower in comparison to summer, and was positively correlated with T_a during both winter and summer, similar to other *Nyctophilus* species (Morris et al., 1994; Geiser and Brigham, 2000). However, this relationship differed between seasons and the slope was greater during summer (1.3) than in winter (0.6). Furthermore, it was found that body mass influenced daily minimum torpid T_{skin} during summer but not during winter, which may contribute to the seasonal variation in the relationship between daily minimum torpid T_{skin} and T_a . It is important to note, however, that the influence of body mass on the relationship between daily minimum torpid T_{skin} and T_a was weak. The difference in slopes between seasons may also be explained by $T_{\text{skin}} - T_a$, which was significantly higher during winter than in summer. Additionally, the relationship between the $T_{\text{skin}} - T_a$ differential and T_a was significant during winter, but not

during summer. Throughout winter $T_{\text{skin}}-T_a$ decreased as T_a increased, suggesting that as T_a becomes lower the bats either begin to thermoregulate or are residing in roosts that remain above a certain T_a . During summer the $T_{\text{skin}}-T_a$ differential remained relatively constant over the range of T_a experienced and the smaller differential may be a reflection of the higher T_a during summer, which would allow the bats to continuously thermo-conform and lower their T_{skin} to near T_a . This in turn may explain why the relationship between daily minimum torpid T_{skin} and T_a is stronger during summer than in winter.

The seasonal differences in the relationship between T_{skin} and T_a may also be explained by roost choice, such that *N. bifax* may be choosing more thermally insulated roosts during winter. As T_a was measured in only one location during both studies we do not know how different roost T_a was to external T_a . However, it is known that *N. bifax* uses a wide variety of roosts, such as foliage and tree hollows (Lunney et al., 1995). Previous studies have shown that roost choice influences torpor bout durations, T_{skin} and also the amount of energy expended while roosting (Willis and Brigham, 2005; Stawski et al., 2008). It is therefore likely that individuals select specific roosts depending on their energy requirements, the current weather conditions and also the season (Boyles et al., 2007).

Evidence from some studies on bats suggests that torpor use may be more dependent on food availability and environmental variables rather than season *per se* (Coburn and Geiser, 1998; Wojciechowski et al., 2007). The seasonality of torpor use seen in many species is therefore most probably a response to changes in food availability as food abundance is often seasonal and is affected by ambient conditions. For example, activity by insects is dependent on T_a and many insects are unable to fly or move at low T_a , resulting in a decline in insect abundance from summer to winter (Richards, 1989; Stawski and Geiser, 2010). Also, many plant species flower seasonally because of rainfall patterns and other weather conditions, which explains why some nectarivorous mammal species use torpor more often during summer than winter (Coburn and Geiser, 1998; Boyer and Barnes, 1999). Therefore, the effect of T_a in some circumstances may be indirect, as it is more likely for an individual to become torpid when energetically compromised by lack of food. Our data support this because torpor use is more prevalent during winter, when insect abundance was lowest (Stawski and Geiser, 2010). However, from an energetic point of view it is still beneficial for a small animal to remain torpid while not active during any time of the year to conserve energy, regardless of food abundance.

In the past it was assumed that low and stable T_a is necessary for an animal to hibernate (Henshaw, 1970). In the subtropical winter even when T_a was variable and much warmer than in temperate winters, *N. bifax* entered prolonged torpor bouts (up to 128.5h) regularly which clearly classify them as 'hibernators' (Geiser and Ruf, 1995; Schmid and Ganzhorn, 2009). Consequently, the short bouts of torpor observed in our study during summer, as found for dormice, most likely are short bouts of hibernation, which simply are shortened because of high and fluctuating T_a , rather than daily torpor (Geiser, 2004; Bieber and Ruf, 2009). This suggests that *N. bifax*, like *N. geoffroyi*, is reducing MR and T_b significantly more during these short bouts of hibernation in comparison to the shallow torpor bouts seen in daily heterotherms, thus maximising energy savings (Geiser and Brigham, 2000; Geiser, 2004). Our current study and preliminary data that show MR are similar in both seasons (C. S., unpublished data) provide further support for the argument that, apart from the observed temperature effects, there is no apparent functional difference between the physiology of prolonged and short

bouts of torpor of hibernators, which are capable of showing both (Hock, 1951; Geiser and Brigham, 2000; Bieber and Ruf, 2009). *N. bifax*, like many other species of bats and other mammals, appear to be 'opportunistic hibernators' and make use of increased food availability during occasional increases in T_a during winter and enter prolonged bouts of torpor when conditions are unfavourable (Körtner and Geiser, 2000b).

To conclude, it seems that the seasonal differences seen in torpor use is to a large extent a result of seasonal changes in food abundance as caused by changes in T_a and an individual's energy needs. This further suggests that species that use prolonged torpor during winter and also short bouts of torpor during summer are functionally using the same type of torpor, and that differences in torpor patterns and thermal physiology are mainly ecological rather than physiological. Lastly, it seems clear that *N. bifax* is a hibernating tropical/subtropical species that use torpor regularly throughout the year during times of energetic stress and even during times when they are in good body condition and food is abundant, probably to minimise exposure to predators (Stawski and Geiser, 2010).

ACKNOWLEDGEMENTS

We would like to thank Stuart Cairns, Gerhard Körtner, Brad Law, Anaïs LeBot, Alexander Riek, Margaret and Michal Stawski, Christopher Turbill, Courtney Waugh and Philip Withers for their contributions to this study. Permits to undertake this research were issued by New South Wales National Parks and Wildlife Service and the Animal Ethics Committee of the University of New England. Grants that supported this research were obtained from the University of New England and Bat Conservation International to C.S. and the Australian Research Council to F.G.

REFERENCES

- Audet, D. and Thomas, D. W. (1996). Evaluation of the accuracy of body temperature measurement using external radio transmitters. *Can. J. Zool.* **74**, 1778-1781.
- Barclay, R. M. R., Kalcounis, M. C., Crampton, L. H., Stefan, C., Vonhof, M. J., Wilkinson, L. and Brigham, R. M. (1996). Can external radiotransmitters be used to assess body temperature and torpor in bats? *J. Mammal.* **77**, 1102-1106.
- Barclay, R. M. R., Lausen, C. L. and Hollis, L. (2001). What's hot and what's not: defining torpor in free-ranging birds and mammals. *Can. J. Zool.* **79**, 1885-1890.
- Bieber, C. and Ruf, T. (2009). Summer dormancy in edible dormice (*Glis glis*) without energetic constraints. *Naturwissenschaften* **96**, 165-171.
- Boyer, B. B. and Barnes, B. M. (1999). Molecular and metabolic aspects of mammalian hibernation. *BioScience* **49**, 713-724.
- Boyles, J. G., Dunbar, M. B., Storm, J. J. and Brack, V. J. (2007). Energy availability influences microclimate selection of hibernating bats. *J. Exp. Biol.* **210**, 4345-4350.
- Brigham, R. M. and Geiser, F. (1998). Seasonal activity patterns of two species of *Nyctophilus* bats based on mist-net captures. *Aust. Mammal.* **20**, 349-352.
- Brown, C. R. (1999). Metabolism and thermoregulation of individual and clustered long-fingered bats, *Miniopterus schreibersii*, and the implications for roosting. *S. Afr. J. Zool.* **34**, 166-172.
- Churchill, S. (1998). *Australian Bats*. Sydney: New Holland Publishers (Australia) Pty Ltd.
- Coburn, D. K. and Geiser, F. (1998). Seasonal changes in energetics and torpor patterns in the subtropical blossom-bat *Syconycteris australis* (Megachiroptera). *Oecologia* **113**, 467-473.
- Geiser, F. (2004). Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annu. Rev. Physiol.* **66**, 239-274.
- Geiser, F. and Baudinette, R. V. (1990). The relationship between body mass and rate of rewarming from hibernation and daily torpor in mammals. *J. Exp. Biol.* **151**, 349-359.
- Geiser, F. and Brigham, R. M. (2000). Torpor, thermal biology, and energetics in Australian long-eared bats (*Nyctophilus*). *J. Comp. Physiol. B* **170**, 153-162.
- Geiser, F. and Ruf, T. (1995). Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. *Physiol. Zool.* **68**, 935-966.
- Henshaw, R. E. (1970). Thermoregulation in bats. In *About Bats* (eds B. H. Slaughter and D. W. Walton), pp. 188-232. Dallas: Southern Methodist University Press.
- Hickey, M. B. C. and Fenton, M. B. (1996). Behavioural and thermoregulatory responses of female hoary bats, *Lasiurus cinereus* (Chiroptera: Vespertilionidae), to variations in prey availability. *Ecoscience* **3**, 414-422.
- Hock, R. J. (1951). The metabolic rates and body temperatures of bats. *Biol. Bull.* **101**, 289-299.
- Jacobs, D. S., Kelly, E. J., Mason, M. and Stoffberg, S. (2007). Thermoregulation in two free-ranging subtropical insectivorous bat species: *Scotophilus* species (Vespertilionidae). *Can. J. Zool.* **85**, 883-890.
- Körtner, G. and Geiser, F. (2000a). Torpor and activity patterns in free-ranging sugar gliders *Petaurus breviceps* (Marsupialia). *Oecologia* **123**, 350-357.
- Körtner, G. and Geiser, F. (2000b). The temporal organization of daily torpor and hibernation: Circadian and circannual rhythms. *Chronobiol. Int.* **17**, 103-128.

- Lunney, D., Barker, J., Leary, T., Priddel, D., Wheeler, R., O'Connor, P. and Law, B. (1995). Roost selection by the north Queensland long-eared bat *Nyctophilus bifax* in littoral rainforest in the Iluka World Heritage Area, New South Wales. *Aust. J. Ecol.* **20**, 532-537.
- Morris, S., Curtin, A. L. and Thompson, M. B. (1994). Heterothermy, torpor, respiratory gas exchange, water balance and the effect of feeding in Gould's long-eared bat *Nyctophilus gouldi*. *J. Exp. Biol.* **197**, 309-335.
- Park, K. J., Jones, G. and Ransome, R. D. (2000). Torpor, arousal and activity of hibernating greater horseshoe bats (*Rhinolophus ferrumequinum*). *Funct. Ecol.* **14**, 580-588.
- Rambaldini, D. A. and Brigham, R. M. (2008). Torpor use by free-ranging pallid bats (*Antrozous pallidus*) at the northern extent of their range. *J. Mammal.* **89**, 933-941.
- Ransome, R. D. (1971). The effect of ambient temperature on the arousal frequency of the hibernating greater horseshoe bat, *Rhinolophus ferrumequinum*, in relation to site selection and the hibernation state. *J. Zool. (London)* **164**, 353-371.
- Richards, G. C. (1989). Nocturnal activity of insectivorous bats relative to temperature and prey availability in tropical Queensland. *Aust. Wildl. Res.* **16**, 151-158.
- Schmid, J. and Ganzhorn, J. U. (2009). Optional strategies for reduced metabolism in gray mouse lemurs. *Naturwissenschaften* **96**, 737-741.
- Stawski, C. and Geiser, F. (2010). Fat and fed: frequent use of summer torpor in a subtropical bat. *Naturwissenschaften* **97**, 29-35.
- Stawski, C., Turbill, C. and Geiser, F. (2008). Prolonged torpor use during winter by a free-ranging bat in subtropical Australia. In *Hypometabolism in Animals: Hibernation, Torpor and Cryobiology* (eds B. G. Lovegrove and A. E. McKechnie), pp. 353-360. Pietermaritzburg, South Africa: University of KwaZulu-Natal.
- Stawski, C., Turbill, C. and Geiser, F. (2009). Hibernation by a free-ranging subtropical bat (*Nyctophilus bifax*). *J. Comp. Physiol. B* **179**, 433-441.
- Taylor, L. R. (1963). Analysis of the effect of temperature on insects in flight. *J. Anim. Ecol.* **32**, 99-117.
- Turbill, C. (2006). Thermoregulatory behavior of tree-roosting chocolate wattled bats (*Chalinolobus morio*) during summer and winter. *J. Mammal.* **87**, 318-323.
- Turbill, C., Körtner, G. and Geiser, F. (2003). Natural use of heterothermy by a small, tree-roosting bat during summer. *Physiol. Biochem. Zool.* **76**, 868-876.
- Turbill, C., Körtner, G. and Geiser, F. (2008). Timing of the daily temperature cycle affects the critical arousal temperature and energy expenditure of lesser long-eared bats. *J. Exp. Biol.* **211**, 3871-3878.
- Vivier, L. and Van Der Merwe, M. (2007). The incidence of torpor in winter and summer in the Angolan free-tailed bat, *Mops condylurus* (Microchiroptera: Molossidae), in a subtropical environment, Mpumalanga, South Africa. *Afr. Zool.* **42**, 50-58.
- Wang, L. C. H. (1989). Ecological, physiological, and biochemical aspects of torpor in mammals and birds. In *Advances in Comparative and Environmental Physiology*, vol. 4 (ed. L. C. H. Wang), pp. 361-401. Germany: Springer-Verlag.
- Warnecke, L., Turner, J. M. and Geiser, F. (2008). Torpor and basking in a small arid zone marsupial. *Naturwissenschaften* **95**, 73-78.
- Willis, C. K. R. and Brigham, R. M. (2005). Physiological and ecological aspects of roost selection by reproductive female hoary bats (*Lasiurus cinereus*). *J. Mammal.* **86**, 85-94.
- Wojciechowski, M. S., Jefimow, M. and T gowska, E. (2007). Environmental conditions, rather than season, determine torpor use and temperature selection in large mouse-eared bats (*Myotis myotis*). *Comp. Biochem. Physiol.* **147A**, 828-840.