

Hibernation by tree-roosting bats

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Abstract In summer, long-eared bats (*Nyctophilus* spp.) roost under bark and in tree cavities, where they appear to benefit from diurnal heating of roosts. In contrast, hibernation is thought to require a cool stable temperature, suggesting they should prefer thermally insulated tree cavities during winter. To test this prediction, we quantified the winter thermoregulatory physiology and ecology of hibernating tree-roosting bats, *Nyctophilus geoffroyi* and *N. gouldi* in the field. Surprisingly, bats in winter continued to roost under exfoliating bark (65%) on the northern, sunny side of trees and in shallow tree cavities (35%). Despite passive re-warming of torpid bats by 10–20°C per day, torpor bouts lasted up to 15 days, although shorter bouts were also common. Arousals occurred more frequently and subsequent activity lasted longer on warmer nights, suggesting occasional winter foraging. We show that, because periodic arousals coincide with maximum roost temperatures, when costs of rewarming and normothermic thermoregulation are minimal, exposure to a daily temperature cycle could largely reduce energy expenditure during hibernation. Our study provides further evidence that models of torpor patterns and energy expenditure from hibernators in cold temperate climates are not directly applicable in milder climates, where prolonged torpor can be interspersed with more frequent arousals and occasional foraging.

Keywords Arousal · Bat · Hibernation · *Nyctophilus* · Torpor

Abbreviations

MR	Metabolic rate
T_a	Ambient temperature
T_b	Body temperature
T_{skin}	Skin temperature

Introduction

Winter presents a critical energy bottleneck for small bats in temperate climates. Energy requirements are high for thermoregulation at a low ambient temperature (T_a), yet foraging is often unproductive because their insect food supply is reduced or seasonally unavailable (Williams 1961; Taylor 1963). In addition, bats cannot store food for long periods, nor can they carry the relatively large amount of fat needed to sustain high rates of energy expenditure at low T_a . It is well known, however, that temperate bats overcome this energy crisis by entering a period of hibernation over the temperate winter season.

Hibernation consists of a series of prolonged torpor bouts lasting days or weeks, during which body temperature (T_b) and metabolic rate (MR) are substantially reduced, interrupted by arousals and brief periods of normothermic thermoregulation and perhaps activity (French 1985; Geiser and Kenagy 1988; Körtner and Geiser 2000). Over a wide range of T_a , torpid T_b is within 1–2°C of T_a and allowed to fluctuate passively; however, at T_a below a torpor T_b set point often around 2°C, thermoregulatory heat production resumes to maintain T_b above this lower level (Heller and Hammel 1972; Geiser and Ruf 1995; Geiser 2004). Hibernators have MR as low as 3–4% of basal levels during torpor (Hock 1951; van Breukelen and Martin 2002; Geiser 2004) and hibernation, despite periodic arousals, can reduce energy expenditure by >80% compared to continuous

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normothermic thermoregulation (Wang 1978; Thomas et al. 1990; Geiser 2007).

The physiology of torpor in captive bats has been studied for well over a century (Hall 1832; Lyman 1970). However, quantitative studies on the thermoregulatory behaviour and ecology of wild bats during winter are scant and primarily restricted to bats roosting in caves (Thomas 1995; Park et al. 2000) or rock crevices (Arlettaz et al. 2000), whereas bats hibernating in trees, although common in temperate regions, have not been investigated in detail (McNab 1982; Kunz and Lumsden 2003; Speakman and Thomas 2003; O'Donnell and Sedgely 2006; Turbill 2006a). Whereas caves provide a stable thermal microclimate for hibernating bats (Thomas 1995; Park et al. 2000), tree roosts provide much less insulation from the external daily T_a cycle (Sluiter et al. 1973; Turbill 2006a).

During summer, poor insulation of tree roosts from the daily T_a cycle and exposure to solar radiation causes a diurnal increase in roost T_a . This results in partial passive re-warming of torpid bats during arousal and a period of high roost T_a that minimises thermoregulatory costs during a coinciding period of normothermia while resting (Geiser et al. 2004; Turbill et al. 2003; Turbill 2006b). During winter, we predict that bats will use tree roosts that provide much greater thermal insulation than during summer. A cool, stable T_a is considered optimal during hibernation because it maximises the duration of torpor bouts at minimal T_b and MR and therefore provides the greatest energy savings.

To test this prediction in tree-roosting bats, we document the winter roosting and thermal ecology of two species of Australian long-eared bats, *Nyctophilus geoffroyi* (7.5 g) and *N. gouldi* (8.5 g), which roost under bark and in shallow tree crevices in summer (Turbill et al. 2003; Turbill 2006b). Seasonal trapping and body mass data suggest these bats hibernate over winter in southern Australia (Phillips and Inwards 1985; Brigham and Geiser 1998). We used temperature telemetry to test the prediction that *Nyctophilus* spp. select tree cavities in winter that, unlike summer roosts, provide a large degree of thermal insulation, and to examine how thermal conditions in winter tree roosts affect torpor, arousals and energy savings during hibernation.

Material and methods

The study was conducted in Imbota Nature Reserve (30°35'S, 151°44'E), approximately 10 km southeast of Armidale, on the Northern Tablelands of New South Wales, Australia. Imbota Nature Reserve contains a ~215 ha remnant of open forest and is surrounded by grazing farms. The vegetation has a relatively open canopy of eucalypt trees and a sparse, patchy mid-layer of small trees

and shrubs. At an elevation of 1,000 m ASL, the study site has a cool-temperate climate, but winter days are often sunny. On average, daily T_a in mid-winter (July) at nearby Armidale range from 0.2 to 12.3°C (Australian Bureau of Meteorology).

Temperature telemetry was used to locate roosting bats and measure their skin temperature (T_{skin}) in the field. We monitored a total of 13 *Nyctophilus geoffroyi* and seven *N. gouldi* for periods of 6–45 days each during winter (June 1–August 31) of 2002 and 2003. Bats were captured using mist nets and harp traps. To increase trapping success, nets and traps were set most often on evenings predicted by weather forecasts to have warmer than average nightly T_a . We used external transmitters to measure T_{skin} because they do not require surgery and transmit further than implanted transmitters, and T_{skin} provides a close estimate of T_b for small bats, particularly during torpor (Audet and Thomas 1996; Barclay et al. 1996; Willis and Brigham 2003). Each transmitter (model LB-2NT, Holohil, Canada) was calibrated prior to use against a precision thermometer ($\pm 0.1^\circ\text{C}$) between 2 and 40°C in a water bath. Transmitters were attached to the skin with latex-based glue (Skinbond, Smith and Nephew, Australia) after first trimming a small patch of fur in the mid-dorsal region of bats. Transmitters and glue added 0.45–0.62 g to the mass of bats and remained attached for up to 45 days until the batteries failed or the transmitters fell off.

Bats carrying transmitters were released at their capture site on the night after capture. On the following days, bats were radio-tracked to locate their diurnal roosts. After locating the roost tree, the exact position of roosting bats was found either by observing the wire aerial of the transmitter emerging from the roosting position, scanning the surface of the tree at close range using the receiver without an aerial or the end of a cable from the receiver attached to a long stick, or by observing emerging bats at dusk, sometimes with the aid of a night scope (Moonlight Products, USA). While locating bats, care was taken to minimise disturbance and there was no evidence that our presence at roosts disturbed torpid bats. We placed receiver/datalogger stations (Körtner and Geiser 1998) near roosting bats to continuously record their T_{skin} (via the inter-pulse interval) every 10 min. These dataloggers were downloaded in the field to a laptop computer every few days. We recorded T_a using another datalogger (T-Tec type E datalogger, resolution $\pm 0.2^\circ\text{C}$) placed in the shade 1 m from the ground at mid-slope in the study site. We used ThermoChron iButtons (Maxim, USA) to measure T_a inside unoccupied tree roosts and, for comparison, in other tree cavities.

Roost trees were marked using flagging tape and their positions recorded using a handheld GPS unit (Garmin 12, USA). Roosts were categorised as either under bark or in a tree cavity. Roost height was measured using a tape or a

clinometer. We determined the orientation of roosts under bark around the tree trunk using a compass.

Torpor entries were clearly delineated by a sharp decrease in T_{skin} , whereas active arousals from torpor (as distinct from passive fluctuations in the T_{skin} of torpid bats) were distinguished by a rapid increase in T_{skin} to normothermic levels ($T_{skin} > 28^{\circ}\text{C}$). Owing to the difficulty of capturing bats, and the relatively short duration of measurements for some individuals, data for males and females were not spread evenly throughout winter and this prevented comparisons between the sexes. Minitab Statistical Software (V13.1) was used to analyse the data. Because repeated measurements were made on the same individuals, means \pm 1SD were calculated using the average of values for each individual. General linear modeling (GLM) was used to analyse linear relationships, with “individual” as a random factor. The Rayleigh test was used to examine whether the distribution of circular data, such as time of arousal from torpor and orientation of roosts around tree trunks, differed significantly from random (Zar 1999). Null hypotheses were rejected at a significance level of $P < 0.05$ for $N =$ observations from $n =$ individuals.

Results

Ambient temperature

At the field site over the two winter periods of the study, T_a ranged between daily minima of $2.8 \pm 2.4^{\circ}\text{C}$ and daily maxima of $13.2 \pm 2.4^{\circ}\text{C}$.

Roosts

Both bat species roosted solitarily under exfoliating bark on the trunk of trees (33/51 roosts) and in tree cavities (18/51) during winter (Table 1). Trees occupied by roosting bats ranged in size from 13 to 73 cm in diameter at breast height (DBH). Roost trees were typically in a decayed condition, with 57% (29/51) of roosts in dead trees, five of which were stumps less than 2 m in height. Bats roosted at a height of 2.4 ± 1.7 m above the ground (range: 0.35–8.0 m; tree canopy height: 18–26 m), with 15% of roosts <1 m above the ground. The orientation of roosting bats under bark was strongly biased towards the northern side of the tree trunk (mean aspect: $351^{\circ} \pm 23^{\circ}$ 95% CI; Fig. 1; Rayleigh test: $Z = 10.8, P < 0.001$). This was not related to any bias in the orientation of potential roost sites because exfoliating bark was randomly distributed at the four cardinal orientations around the trunk of roost trees ($F_{3,84} = 0.11, P > 0.05$).

Duration of roost occupancy varied widely and to some extent depended on torpor bout durations. Nevertheless, while some bats always moved to another roost following

Table 1 Type of roost and tree species occupied by *Nyctophilus geoffroyi* ($n = 13$) and *N. gouldi* ($n = 7$) during winter

Type of roost	<i>N. geoffroyi</i>	<i>N. gouldi</i>	Total
Exfoliating bark			
<i>Eucalyptus caliginosa</i>	2	0	2
<i>E. viminalis</i>	17	4	21
<i>E. blakelyi</i>	3	1	4
<i>Acacia filicifolia</i>	4	2	6
Total exfoliating bark	26	7	33 (65%)
Tree cavity			
<i>E. caliginosa</i>	8	4	12
<i>E. viminalis</i>	3	2	5
<i>E. blakelyi</i>	1	0	1
Total cavity	12	6	18 (35%)

Values are numbers of roosts located

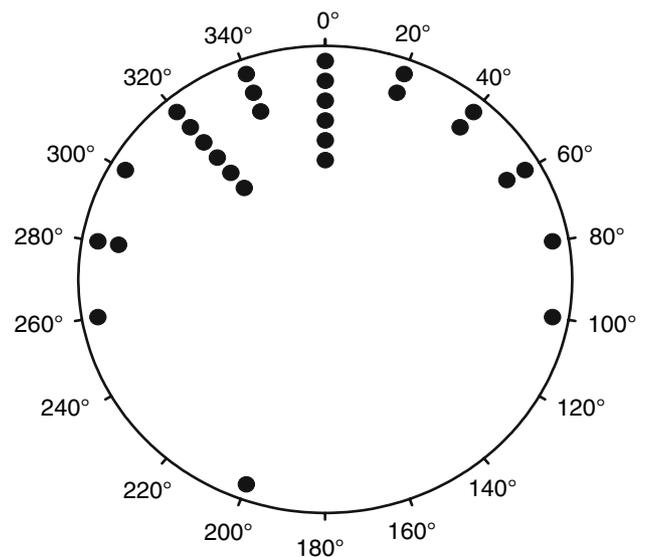


Fig. 1 Orientation of roosts ($\pm 10^{\circ}$; $N = 28$; dots) under exfoliating bark of trees occupied by *Nyctophilus geoffroyi* ($n = 11$) and *N. gouldi* ($n = 3$) during winter. Mean orientation: $351^{\circ} \pm 23^{\circ}$ (95% CI) (Rayleigh test: $z = 10.8, P < 0.001$)

arousal from torpor, others remained in the one roost over several torpor-arousal cycles lasting up to 48 days (including visual observations). Bats moved an average distance of 214 ± 189 m between consecutive roosts ($N = 49$). On ten occasions, after using other roosts, individuals returned to the exact roosting position occupied previously.

Torpor

During winter both bat species spent a large proportion of time in torpor and activity was restricted to brief periods (Fig. 2). The duration of torpor bouts was variable throughout winter, with continuous torpor bouts lasting up to 15.1 days in *N. geoffroyi* and 10.8 days in *N. gouldi*

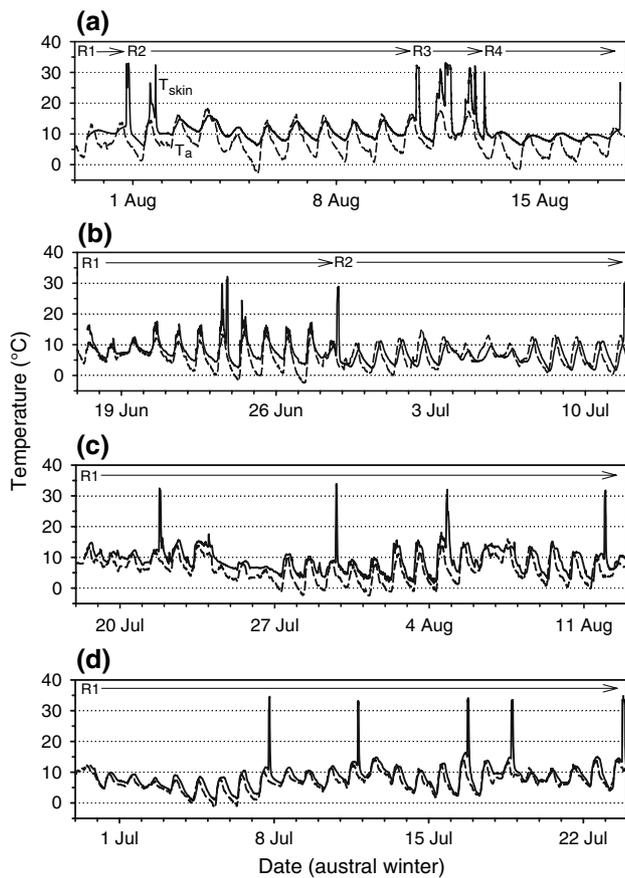


Fig. 2 Skin temperature (solid lines) of a (a) female (#119) and (b) male *Nyctophilus geoffroyi* (#460) and a (c) female (#920) and (d) male *N. gouldi* (#700) and external ambient temperature (dashed lines) during winter. Roost occupancy is shown at top of each frame (R1 = roost 1, R2 = roost 2, etc)

(Fig. 3). In early winter, males employed short torpor bouts often lasting <1 day. Short torpor bouts were also employed by both sexes throughout winter during brief periods of relatively mild weather. For example, a female *N. geoffroyi* (#119 in Fig. 2) aroused on three consecutive nights (10–12 August) when T_a during the night were $>5^\circ\text{C}$ warmer than average. On days when bats aroused, maximum T_a were significantly higher (by 2.0°C) than on days when bats remained in torpor ($F_{1,300} = 25.5$, $P < 0.001$). The duration of torpor bouts was negatively related to average T_{skin} over the torpor bout (Fig. 4; $F_{1,107} = 41.4$; $P < 0.001$; \log_{10} bout duration (d) = $1.23 - 0.99 \times$ average torpid T_{skin} ($^\circ\text{C}$), $R^2 = 0.28$); however, considerable variation in the duration of torpor bouts was not explained by torpid T_{skin} ($\sim T_b$).

Arousals

Bats most often aroused shortly after sunset (Fig. 5). Time of arousals ($N > 2$ for all individuals) differed significantly from random in 10 out of 12 *N. geoffroyi* and 7 out of 7 *N. gouldi* (Rayleigh tests, $P < 0.05$). In the one male

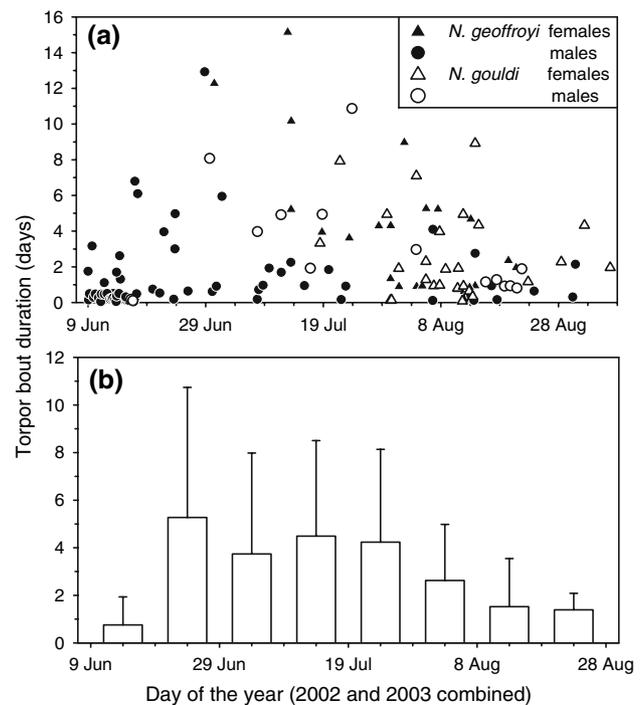


Fig. 3 Torpor bout durations of (a) individual bats and (b) average ($\pm 1\text{SD}$) duration of torpor bouts for all bats combined ($n = 3-9$) as a function of the date of entry into torpor (in 10-day bins) during winter

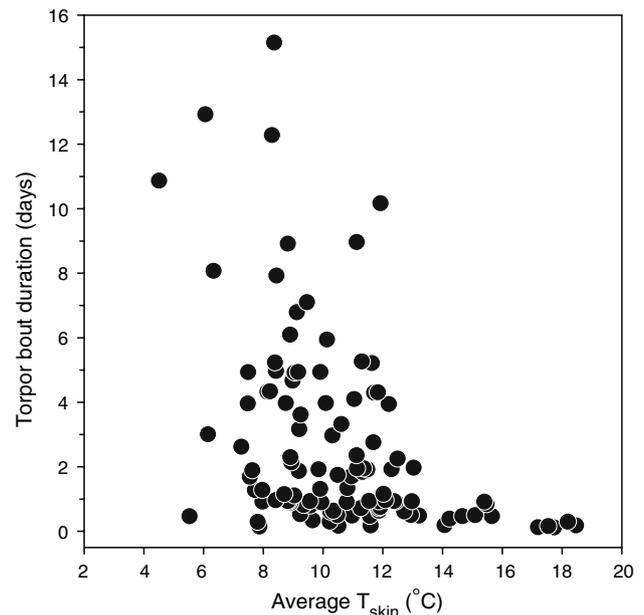


Fig. 4 Duration of torpor bouts by *Nyctophilus geoffroyi* and *N. gouldi* (combined) as a function of average skin temperature during each torpor bout ($F_{1,107} = 41.4$, $P < 0.001$; \log_{10} bout duration (d) = $1.23 - 0.099$ average torpid T_{skin} ($^\circ\text{C}$), $R^2 = 0.28$)

N. geoffroyi arousing often in early winter, times of arousal were diametrically bimodal over 24 h (adjusted Rayleigh test, $P < 0.05$), with one mode at dusk and another mode shortly before dawn. In the remaining individual *N. geoffroyi*,

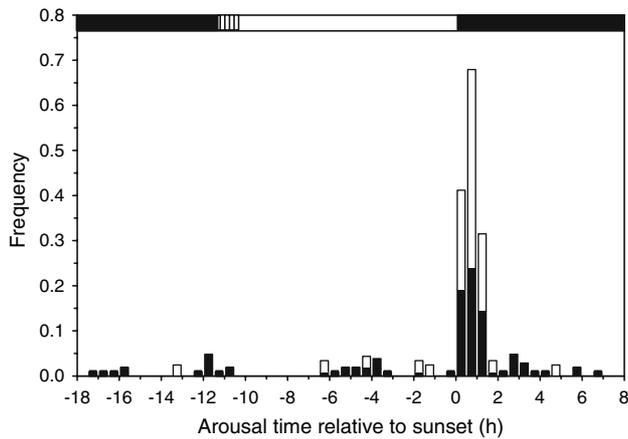


Fig. 5 Times of arousal relative to the time of sunset (0 h) for *Nyctophilus geoffroyi* (filled bars) and *N. gouldi* (open bars) during winter. Vertical bars represent data placed in 30-min bins. Dark/light bars at top show the photophase and stippling indicates variation in times of sunrise relative to sunset over the study period

times of arousal were distributed in a principal cluster at dusk, with several arousals also occurring during the middle of the day (as observed in a few individuals). Substantial passive re-warming of T_b , which appeared to be enhanced by roosts receiving direct solar radiation, preceded these diurnal arousals. Some arousals also occurred during the latter half of the night, although 88% (15/17) of these arousals were by bats that had previously aroused at dusk and subsequently re-entered torpor during the night.

Activity

Following arousal, bats remained normothermic for <3 h on 73% (69/94) of observations. The duration of normothermic bouts was independent of the duration of the preceding torpor bout ($F_{1,92} = 0.2, P = 0.68$), but was positively correlated with average nightly T_a (Fig. 6; all bats combined: $F_{1,87} = 21.8, P < 0.001, R^2 = 20.1\%$). Since rainfall may curtail activity (Erkert 1982) we excluded nights with greater than 3 mm of rainfall, which improved the predictive power of average nightly T_a on normothermic periods (all bats combined: $F_{1,76} = 30.4, P > 0.001, R^2 = 28.6$), (*N. geoffroyi*: $F_{1,48} = 32.0, P < 0.001, R^2 = 40.0\%$), but the relationship was not significant for *N. gouldi* ($F_{1,26} = 1.7, P = 0.2$).

Skin (body) temperature

Torpid bats experienced wide passive daily fluctuations in T_{skin} . In torpid *N. geoffroyi*, T_{skin} fluctuated by $8.3 \pm 2.7^\circ\text{C day}^{-1}$ (range: $1.4\text{--}23.2^\circ\text{C day}^{-1}$; $N = 187, n = 13$) between a daily minimum of $6.9 \pm 1.7^\circ\text{C}$ and maximum of $15.8 \pm 3.3^\circ\text{C}$. In torpid *N. gouldi*, T_{skin} fluctuated by $9.6 \pm 2.5^\circ\text{C day}^{-1}$ (range: $1.2\text{--}18.1^\circ\text{C day}^{-1}$; $N = 99,$

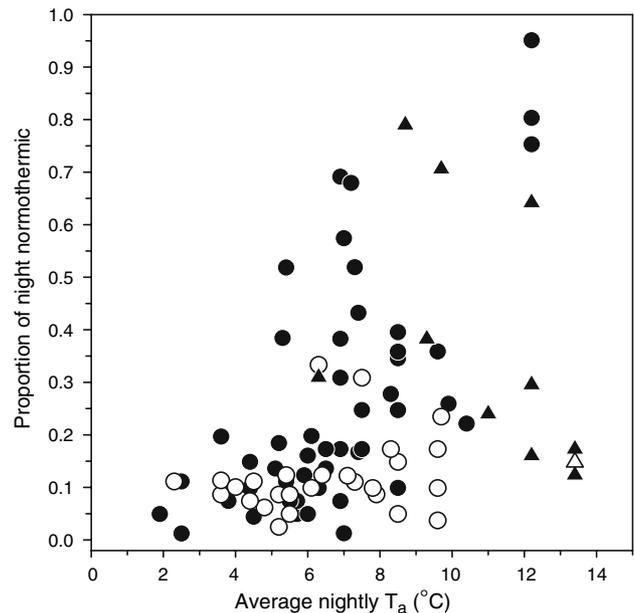


Fig. 6 Proportion of the night spent normothermic by *Nyctophilus geoffroyi* (filled symbols) and *N. gouldi* (open symbols) following arousal from torpor as a function of the average nightly ambient temperature (T_a). The duration of nocturnal normothermic periods was significantly related to average nightly T_a for all bats combined ($F_{1,87} = 21.8, P < 0.001, R^2 = 20.1\%$). Nights when rain (>3 mm/night) may have prevented some activity are shown by triangle symbols. Excluding rain affected nights, the relationship was stronger for all bats combined ($F_{1,76} = 30.4, P > 0.001, R^2 = 28.6\%$) and for *N. geoffroyi* separately ($F_{1,48} = 32.0, P < 0.001, R^2 = 40.0\%$) but data for *N. gouldi* alone were not significant ($F_{1,26} = 1.7, P = 0.2$)

$n = 7$) between a daily minimum of $4.3 \pm 0.5^\circ\text{C}$ and maximum of $14.3 \pm 2.0^\circ\text{C}$. The daily amplitude of torpid T_{skin} did not differ significantly between the two species ($T = 1.05, P = 0.32$).

The time of daily maximum torpid T_{skin} was $15:51 \pm 2:29$ h in *N. geoffroyi* ($2:47 \pm 2:26$ h later than daily maximum T_a) and $15:32 \pm 2:34$ h in *N. gouldi* ($2:21 \pm 2:22$ h later than daily maximum T_a). The amplitude and timing of daily torpid T_{skin} fluctuations was a function of the external daily T_a cycle and variability in thermal insulation afforded by selected tree roosts. Inspection of traces of torpid T_{skin} indicates that bats in roosts under bark were often passively warmed above external daily T_a maxima by solar heating of roosts. “iButton” dataloggers placed in unoccupied roosts confirmed the effects of solar heating on T_a within roosts under-bark on the northern side of trees and the thermal buffering of cavity roosts (Fig. 7).

Discussion

Our study provides the first quantitative investigation of the hibernation ecology of tree-roosting bats. Contrary to

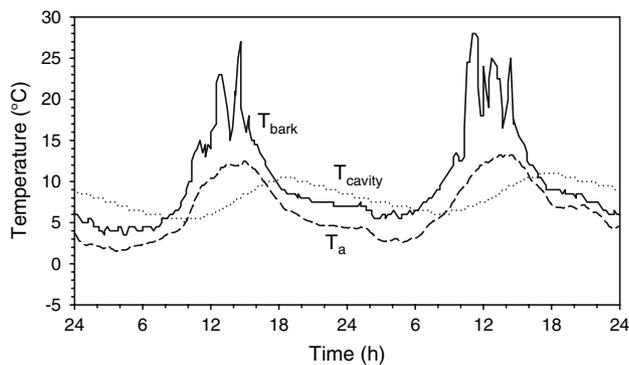


Fig. 7 Daily temperature fluctuation in unoccupied roosts of a male *Nyctophilus geoffroyi* (#460) over 2 days in June 2002. Roosts were under bark on the northern side of the trunk of a tree (T_{bark} solid line), in a cavity in a tree stump (T_{cavity} dotted line) and external ambient temperature (T_{a} dashed line)

expectations, *Nyctophilus geoffroyi* and *N. gouldi* roosted under exfoliating bark and in poorly insulated tree cavities during winter, where they employed torpor bouts lasting up to 15 days. Because they roosted on the northern, sun-exposed side of trees, torpid bats were passively warmed from a T_{skin} as low as 2°C up to 15 or 20°C on a daily basis, even during prolonged torpor bouts. Such large daily passive fluctuations in T_{b} have not been previously recorded in hibernating bats and span the total range of previously recorded hibernacula T_{a} (Nagel and Nagel 1991; Webb et al. 1995). Arousals were synchronised with dusk and normothermic periods lasted longer on warmer nights, suggesting bats occasionally foraged during winter. This may also be important for solitary tree-roosting bats to carry out other activities, such as drinking or mating. Exposure to a wide daily T_{a} cycle in winter roosts may invoke arousals on warmer evenings, when foraging is possible and some energy intake can sustain greater levels of winter activity. Furthermore, passive re-warming of torpid bats prior to arousals, and warm roost T_{a} during interbout normothermia, minimise the energetic cost of periodic arousals, which, under constant cold conditions, constitute the most energetically expensive aspect of hibernation.

Torpor and arousals

Male bats aroused on most evenings during early winter. A male bias in the capture of vespertilionid bats during early winter has also been found in seasonal trapping studies (McNab 1982; Tidemann 1982; Phillips and Inwards 1985; Brigham and Geiser 1998). Moreover, limited field data on two individuals of another tree-roosting bat *Chalinolobus morio* also suggest a difference in frequency of arousals between the sexes during early winter (Turbill 2006a). Increased activity of males is probably related to the timing of mating during late autumn and throughout winter in

temperate vespertilionid bats (Racey 1982; Phillips and Inwards 1985; Hosken 1997; Hosken et al. 1998). Captive male *N. gouldi* have been observed to copulate with torpid females during early winter (Phillips and Inwards 1985). Importantly, unlike gregarious cave-roosting bats, *Nyctophilus* and possibly other tree-roosting species that hibernate solitarily must leave their roost to carry out these activities during arousals. Thus, the frequent arousals of male bats may serve to find and mate with females, and therefore increase their chances of siring offspring.

Nyctophilus appear to forage during some arousals from hibernation. Arousals occurred at dusk when nightly T_{a} is warmest and insects are most likely to be active (Taylor 1963). Arousals were more frequent and activity lasted longer during infrequent periods of relatively mild T_{a} , which typically lasted one or two nights. Insect activity was greater on these warmer nights (pers. obs.) and captured bats often voided faeces in the capture bag, suggesting feeding. It is possible that *Nyctophilus* respond to some threshold level of passive re-warming during torpor that indicates foraging opportunities. In comparison, to predict nightly insect abundance, cave-roosting bats must rely on small changes in T_{a} delayed over several days (Ransome 1971), detect changes in barometric pressure, or sample external conditions by randomly arousing from torpor. Mild winter nights were often related to the approach of low-pressure “cold front” weather systems, which travel from west to east across the southern half of the Australian continent during winter. On nights preceding cold fronts, high cloud cover and mild north-westerly winds contribute to above average T_{a} , which is then replaced by colder T_{a} and often rainfall. On some mild winter nights, it seemed that foraging was curtailed by the arrival of cooler, rainy weather, as observed for other bats in summer (Kunz 1974).

Its unlikely, however, that foraging for food was the only reason for many arousals. Bats also aroused on cold nights, when our data suggest they were absent from their roosts for <20 min or remained in their roost. Another possible reason for periodic arousals is to drink (Speakman and Racey 1989; Hays et al. 1992; Thomas and Cloutier 1992; Thomas and Geiser 1997). On one occasion a bat was recorded at a nearby dam during the 20-min interval when it was absent from its roost, suggesting it may have been drinking. Evaporative water loss during prolonged torpor exceeds metabolic water production in some hibernating cave-roosting bats (Speakman and Racey 1989; Thomas and Cloutier 1992) and is likely greater in tree- than cave-roosting bats because of the variable T_{a} and lower humidity in tree roosts (Thomas and Cloutier 1992; Thomas and Geiser 1997).

If arousals are triggered by a threshold imbalance in body homeostasis, such as a deficiency in water or blood glucose, or a build-up of metabolic wastes, then the

duration of torpor bouts should reflect total metabolic activity during each bout (Willis 1982). In a variety of studies, the duration of a torpor bout increases with decreasing T_a above the torpor T_b setpoint (Twente and Twente 1965; Twente et al. 1985; Ransome 1971; French 1982; Geiser and Kenagy 1988; Buck and Barnes 2000; Park et al. 2000) and the supposedly recuperative interbout normothermic periods also increase in duration (French 1985). We also found that the duration of torpor bouts by *Nyctophilus* was greater at lower T_{skin} during torpor. However, several prolonged torpor bouts at relatively high average T_{skin} (Fig. 7: 15.1 days at 8°C, 10.2 days at 12°C and 1.9 days at 20°C) indicate that most torpor bouts were curtailed before reaching any physiological limit as a function of T_a , T_b or MR, as observed previously (e.g. Park et al. 2000). For hibernators in mild temperate climates, the variation in torpor duration and persistence of a circadian activity rhythm suggest that exogenous factors, including foraging opportunities, are important in triggering arousals. With regard to the duration of interbout normothermic periods, these were not a function of torpor bout duration and mostly <3 h in our study, unlike for laboratory studies, suggesting that restorative functions occur rapidly or even immediately following arousal.

Daily T_b fluctuations

The traditional view is that prolonged hibernation requires constant and low T_a . In contrast, *Nyctophilus* remained in continuous, multi-day torpor despite passive daily fluctuations in T_b of up to 20°C per day. Whereas hibernators in very cold climates must be well insulated from the freezing external conditions, this is not the case in milder climates. At one extreme, fat-tailed dwarf lemurs (*Cheirogaleus medius*) hibernate over the dry tropical winter season, despite experiencing large daily variations in T_b (Dausmann et al. 2005). In the laboratory, bat species vary in their response to short-term changes in T_a during torpor. A change in T_a ($\sim T_b$) between 2 and 10°C does not provoke arousals in a range of torpid bat species (Davis and Reite 1967; Sluiter et al. 1973; Speakman et al. 1991), whereas an increase in T_a above 10°C provokes arousal in several cave-roosting bats, but not in *Lasiurus borealis*, a tree-roosting species, which remained in torpor until T_a reached around 20°C (Davis and Reite 1967). Prolonged torpor up to about 5 days has also been observed in pregnant foliage roosting bats in spring, despite variable T_b (Willis et al. 2006). Bat species may differ in their sensitivity to short-term changes in T_a as an arousal stimulus according to the thermal conditions they typically experience while roosting. Our study shows that some tree-roosting bats are capable of prolonged torpor despite experiencing wide daily T_a fluctuations during winter hibernation.

Energy expenditure during hibernation

In comparison to MR in normothermic bats, a daily cycle in T_a between 2 and $\sim 20^\circ\text{C}$ will cause a relatively small increase in average daily torpid MR because of the large and exponential reduction of MR during torpor in small bats (Hock 1951; Geiser and Brigham 2000). In contrast, T_a has a steep linear affect on energy costs of rewarming and, in particular, thermoregulating during interbout normothermic periods, which constitute the most energetically expensive phase of hibernation (Wang 1978; Thomas et al. 1990). By selecting winter tree roosts that are exposed to the daily T_a cycle and often heated by the sun, *Nyctophilus* may considerably reduce their energy expenditure during arousals, which occur at times of elevated roost T_a , and this may provide a large overall saving to their winter energy budget. To explore this possibility, we compare energy costs during exposure to either a constant T_a of 10°C or a 24 h sinusoidal T_a cycle of 5°C amplitude around 10°C. We assume that arousals co-occur with daily T_a maxima and subsequent normothermic periods last 3 h before bats re-entered torpor. We use values of torpor and resting normothermic MR published by Geiser and Brigham (2000) and a formula describing arousal costs as a function of T_a for *N. geoffroyi* (arousal cost (kJ) = $0.84 - 0.026 \times T_a$ (°C); Turbill 2006c). As predicted, energy expenditure during 24 h in torpor increases only slightly from 0.217 kJ at a constant 10°C to 0.220 kJ at a daily T_a cycle between 5 and 15°C (assuming consumption of 1 ml $\text{O}_2 = 20.1$ J energy). This small increase is far out-weighed by energy savings gained from exposure to a warmer T_a during arousals: energy costs of rewarming and 3 h of normothermia are reduced from 4.28 kJ at 10°C to 3.40 kJ at about 15°C. This represents a net saving of 0.877 kJ or 22.8 mg of fat (assuming 1 J = 0.026 mg fat) over 24 h and 0.865 kJ or 22.5 mg fat over 5 days in torpor. Multiplied over 18 torpor/arousal cycles, each lasting 5 days (=90 day winter), exposure to such a daily T_a cycle would provide an energy saving of 15.6 kJ or 405 mg of fat, representing >10% of a bat's total winter fat stores (Phillips and Inwards 1985; Kunz et al. 1998). These “back of the envelope” calculations reflect the enormous reduction in MR during torpor and the strong influence of T_a on thermoregulatory costs of small bats, and highlight the importance of periodic arousals in estimating their winter energy expenditure. Our analysis shows clearly that, counter to initial expectations, selection of poorly insulated and solar-heated winter roosts could provide a large energy saving to tree-roosting bats, particularly if, like *Nyctophilus*, they arouse more frequently during winter hibernation.

Our field data of hibernation by *Nyctophilus* and studies of other species in relatively mild climates (e.g. Avery 1985; Hays et al. 1992; Arlettaz et al. 2000; Park et al.

2000) cast doubt on predictions that hibernation is only possible at T_a below around 12°C because at warmer T_a energy consumption exceeds energy availability (Humphries et al. 2002). The generality of this model, which is based on unlikely assumptions and data from a single bat species, to all hibernating mammals is questionable because: (1) the correlation between torpor duration and T_a (or torpid T_b) is variable both within and among species, and prolonged torpor is possible even at mild and variable T_a ; (2) daily fluctuating T_a can significantly affect winter energy expenditure; and (3) foraging opportunities occur more often in a warmer climate. The stable, cold T_a usually associated with hibernation may simply reflect the need in very cold climates for thermal insulation against sub-freezing conditions. In warmer climates, the use of torpor, arousal and foraging during winter by small bats form a continuum, reflecting shifting energetic trade-offs in physiological state, T_a and food availability, and their ability to rapidly enter and arouse from torpor.

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