

# Natural Use of Heterothermy by a Small, Tree-Roosting Bat during Summer

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## ABSTRACT

Little is known about the use of heterothermy by wild bats during summer, especially for tree-roosting species. Because thermal conditions within tree roosts can fluctuate widely with ambient temperature, which affects thermoregulatory energy expenditure during diurnal roosting, we measured skin temperatures of free-ranging male *Nyctophilus geoffroyi* (8 g) to quantify the relation between summer torpor use and roost thermal conditions. Bats roosted under bark on the northern (sunny) side of trees and entered torpor every day, usually near sunrise. Bats exhibited two bouts of torpor on most days: the first occurred in the morning, was terminated by partially passive rewarming, and was followed by a period of normothermy during the warmest part of the day; a second torpor bout occurred in the late afternoon, with arousal near sunset. On the warmest days, bats had only a single, short morning bout. On the coolest days, bats remained torpid throughout the day, and one 2-d bout was observed. Thus, presumably owing to their poorly insulated roosts and the high energetic cost of normothermy at temperatures below 30°C, the extent and timing of heterothermy was closely related to the cycle of diurnal temperatures. Our study indicates that torpor use is important for energy maintenance during summer diurnal roosting of *N. geoffroyi* and likely of other small, tree-roosting bats.

## Introduction

Physiological function and behaviour of small endotherms such as bats are strongly affected by thermal and other environmental

conditions. While resting, the energetic cost of maintaining a constant, high (normothermic) body temperature ( $T_b$ ) in small bats rises steeply when ambient temperature ( $T_a$ ) decreases below about 30°C (Herreid and Schmidt-Nielsen 1966; Kulzer et al. 1970; Genoud 1993; Geiser and Brigham 2000). Hence, thermoregulation throughout the diurnal rest phase can be energetically expensive, even at relatively high roost  $T_a$ . Furthermore, during cool weather, insect activity and therefore foraging success and energy intake of insectivorous bats typically declines dramatically (Paige 1995; Hickey and Fenton 1996). Torpor is likely an important factor in allowing insectivorous bats to manage their energy expenditure and survive in temperate climates (Hock 1951; Stones and Wiebers 1967; Kulzer et al. 1970; Lyman 1970; Studier 1981; Geiser and Brigham 2000). During torpor, metabolic rates are reduced substantially and can be as low as 2%–3% of basal rates at  $T_a$  below 10°C (Hock 1951; Studier 1981; Geiser and Brigham 2000).

At least some Temperate Zone species enter torpor regularly while day roosting during summer (Audet and Fenton 1988; Hamilton and Barclay 1994; Grinevitch et al. 1995; Hickey and Fenton 1996; Chruszcz and Barclay 2002). Previous studies have focused on the effect of reproductive condition on extent of torpor use, whereas relatively little attention has been given to the timing of thermoregulatory behaviours, particularly in relation to daily rhythms in roost temperature (Chruszcz and Barclay 2002). This information is needed to understand daily energy use (McLean and Speakman 1999) and refine predictions of thermal criteria important for roost selection (Law 1996; Brigham et al. 1997b; Vonhof and Barclay 1997; Law and Anderson 2000). Furthermore, research has been limited chiefly to species roosting in buildings (Audet and Fenton 1988; Hamilton and Barclay 1994; Grinevitch et al. 1995; Hickey and Fenton 1996), with only one study of natural roosts within rock crevices (Chruszcz and Barclay 2002). Currently, very little is known about the use of heterothermy by tree-roosting bats, despite their prevalence in temperate climates.

Potential roost sites in trees vary considerably in thermal microclimate because of differences in thermal buffering qualities, height, and exposure to solar radiation (Humphrey et al. 1977; Calder et al. 1983; Kurta 1985; Nicolai 1986; Vonhof and Barclay 1997; Sedgely 2001). Bats using shallow, poorly insulated tree roosts, such as under exfoliating bark, presumably experience wide diurnal fluctuations in temperature. Furthermore, diurnal roost  $T_a$  may be heated above external  $T_a$  by solar radiation, depending upon aspect, exposure, and bark colouration (Calder et al. 1983; Nicolai 1986; Kerth et al. 2001; C.

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Turbill, unpublished data). Since  $T_a$  strongly affects the cost of thermoregulation, diurnal patterns of heterothermy should correspond closely to the dynamics of roost temperature fluctuations. Hence, although thermal physiology of tree-roosting and cave-roosting bats appears similar under constant  $T_a$  in the laboratory (Genoud 1993; Geiser and Brigham 2000), natural patterns of thermoregulatory behaviour are likely to differ substantially (Geiser et al. 2000).

The lesser long-eared bat (*Nyctophilus geoffroyi* Leach, 1821; 8 g, family Vespertilionidae) typically roosts solitarily under bark and in shallow tree crevices (Lumsden et al. 2002) and, like many other Australian bats of the suborder Microchiroptera, readily enters torpor in the laboratory (Kulzer et al. 1970; Geiser and Brigham 2000; Geiser, in press). To investigate the bats' natural use of heterothermy during summer, we used temperature telemetry to locate and record skin temperature ( $T_{\text{skin}}$ ) of male *N. geoffroyi* in their diurnal roosts.

## Material and Methods

The study was conducted in Eastwood State Forest (now Imbota Nature Reserve; 30°35'S, 151°44'E), at an altitude of 1,000 m and located approximately 10 km southeast of Armidale on the Northern Tablelands of New South Wales, Australia. Eastwood contains 215 ha of open forest dominated by *Eucalyptus* and *Acacia* trees, with a grassy ground cover and a sparse, patchy midlayer of shrubs and small trees. The Northern Tablelands have cool winters and mild summers: average maximum and minimum midsummer (January) temperatures for Armidale are 26.7° and 13.8°C, respectively. Temperatures recorded at Eastwood ranged from 7° to 34°C over the study periods. The annual rainfall for the study area is approximately 800 mm.

Bats were captured using mist nets and harp traps and then fitted with a temperature-sensitive radio transmitter (Titley Electronics, model LTM) and released on the night of capture. The transmitters were glued to the skin in the middorsal region after a small patch of fur was clipped to expose the skin. Transmitters weighed 0.55 g (6.8% of average body mass) and had a battery life of approximately 12 d. This additional load did not appear to influence flight performance upon release. Furthermore, pregnant *Nyctophilus geoffroyi* often carry twins with a mass of about 1.4 g each at birth (in total, 32% of the mother's body mass; Lumsden and Bennett 1995). Before use, each transmitter was calibrated to the nearest 0.1°C against a precision thermometer in a water bath between 5° and 40°C, where pulse rate was regressed against transmitter temperature. We used external transmitters to measure  $T_{\text{skin}}$  because they transmit farther, do not involve surgery, and the error between core  $T_b$  and  $T_{\text{skin}}$  in small mammals is negligible when they are at rest (Audet and Thomas 1996; Barclay et al. 1996; Körtner and Geiser 2000b).

Telemetry was used to locate bats within roosts and to monitor the  $T_{\text{skin}}$  of seven individual male *N. geoffroyi* in 25 different

roost locations over 39 complete days during summer (November/December 1998, February/March 1999, and November 2002). Bats were radio tracked for 4–9 d before transmitters became detached or the batteries failed. The distance range of transmitter reception was approximately 1 km, although this varied from 300 m to 1.5 km with terrain and the location of the roosting bat/transmitter. Roost locations were recorded ( $\pm 10$  m) and interroost distances calculated using a handheld global positioning system unit (GARMIN 12). The precise location of roosting bats was determined either by observing the transmitter aerial, using the receiver at close range without an aerial, or by watching the roost at dusk. The precise location of two roosts could not be determined, and roost height was estimated ( $\pm 1$  m) by the direction of greatest signal strength.

Remote receiver/data-logging stations (Körtner and Geiser 1998) placed in the vicinity of roosting bats recorded  $T_{\text{skin}}$  measurements every 10 min. These stations were checked every morning to determine whether they were in the reception range of the bat transmitter(s), and  $T_{\text{skin}}$  data were downloaded to a portable computer every 2–5 d.  $T_a$  was recorded every 10 min (T-Tec data logger; type E, resolution  $\pm 0.2^\circ\text{C}$ ) in the shade approximately 1 m from the ground at the study site.

Bats were considered to be in torpor when  $T_{\text{skin}}$  was below 28°C for longer than 30 min because  $T_b$  below 31°C is commonly used to define torpor in mammals (Hudson and Scott 1979) and the maximum  $T_b - T_{\text{skin}}$  differential in small resting bats is 3°C (Audet and Thomas 1996; Barclay et al. 1996). Most importantly, this threshold  $T_{\text{skin}}$  was found to clearly demarcate the beginning and end of periods where normothermic thermoregulation was abandoned. Torpor bout length was calculated as the time interval when  $T_{\text{skin}}$  was below 28°C (>30 min). The term "daytime" and calculation of daytime  $T_a$  refer to the time from sunrise to sunset, whereas "daily" refers more generally to any 24-h period.

Minitab Statistical Software (version 13.1) was used to analyse data. Proportional data were arcsine square root transformed. Because repeated measurements were made on the same individual, standard errors given with overall means were calculated from the sum of the individual variances/square root of the number of individuals. Numerical values are presented as means  $\pm 1$  SE for  $N =$  number of observations from  $n =$  number of individuals. Repeated-measures ANOVA was used to compare between category means, with bat individuals as the independent factor. Tukey pairwise comparison of means was used to identify which categories differed. ANCOVA was used when examining least-square linear regressions to test for equality of regression slopes and intercepts between bat individuals.

## Results

### Roosting Behaviour

Bats moved a mean distance of  $583 \pm 214$  m (range, 220–1,500 m) from where they were initially trapped to the following

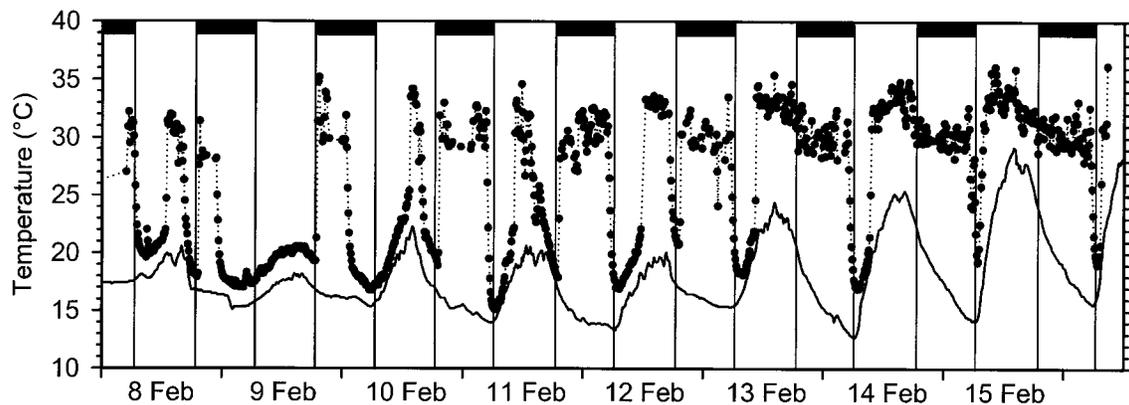


Figure 1. Fluctuations in the skin temperature of a free-ranging male *Nyctophilus geoffroyi* (upper trace) and external ambient temperature (lower trace) over 8.5 d in February (summer) 1999. The horizontal dark bars indicate the nocturnal period (sunset to sunrise).

diurnal roost. Most (65%) roosts were occupied for only 1 d (range, 1–6 d; mean,  $1.7 \pm 1.1$  d;  $N = 23$ ,  $n = 6$ ). On two occasions, bats returned to roost in the exact location used several days previously. The mean distance between consecutive roosts was  $93 \pm 74$  m ( $N = 16$ ,  $n = 6$ ). Although frequently changing roosts, bats roosted within a particular area that ranged in size from approximately 0.5 to 6.25 ha.

Male *Nyctophilus geoffroyi* roosted solitarily at a low height in apparently exposed locations, under exfoliating bark or in shallow crevices in dead wood. Most (78%) roosts were less than 3 m from the ground (range, 0.3–8.0 m; mean height,  $2.2 \pm 0.3$  m;  $N = 25$ ,  $n = 7$ ). Bats roosted under thin bark (~3 mm thick) exfoliating from the trunk of dead *Acacia* sp. trees ( $N = 10$ ,  $n = 4$ ), and live *Eucalyptus viminalis* (ribbon gum) trees ( $N = 5$ ,  $n = 2$ ). Other roosts were within narrow crevices (~ bat's body width) in standing dead timber ( $N = 5$ ,  $n = 2$ ), under lifted sections of the thick bark (~20 mm thick) on live *Eucalyptus caliginosa* (broad-leaved stringybark) trees ( $N = 4$ ,  $n = 2$ ), and 15 cm inside a hollow (10-cm internal diameter) in the top of a small tree stump ( $N = 1$ ,  $n = 1$ ). The aspects of roost locations under bark were not distributed randomly (Rayleigh test;  $P < 0.001$ ) but were concentrated on the northwestern (sunny) side of the tree (mean  $314^\circ$ , 95% CI [ $285^\circ$ – $342^\circ$ ];  $N = 13$ ,  $n = 5$ ).

#### Timing of Heterothermy

Male *N. geoffroyi* exhibited frequent pronounced fluctuations in  $T_{\text{skin}}$  while roosting (Fig. 1), and all seven bats exhibited at least one torpor bout each day. Bats typically remained normothermic throughout the night and entered torpor near sunrise (Fig. 2). However, on four occasions, torpor entry occurred during the night as early as 2142 hours, when minimum nightly  $T_a$ 's were below  $11^\circ\text{C}$ .

During diurnal roosting, *N. geoffroyi* used three general pat-

terns of heterothermy (Fig. 3). On 59% of roost days ( $n = 6$ ), bats displayed two torpor bouts per day, in the morning and late afternoon, so that  $T_{\text{skin}}$  followed a W-shaped pattern (Fig. 3A). On these days, bats actively rewarmed between 0800 and 1331 hours (mean, 1102 hours  $\pm$  0201 hours; Fig. 4), maintained normothermy approximately over the period of warmest  $T_a$ , and reentered torpor between 1230 and 1756 hours (mean, 1545 hours  $\pm$  0145 hours). Bats aroused from afternoon torpor bouts shortly after sunset (Fig. 4). On 28% of roost days ( $n = 5$ ), bats only entered one torpor bout during the morning (Fig. 3B). On these days, bats aroused earlier, between 0758 and 1057 hours (mean, 0917 hours  $\pm$  0114 hours), after which normothermy was maintained. On 13% of roost days ( $n = 3$ ), bats remained torpid throughout the day (Fig. 3C) and aroused

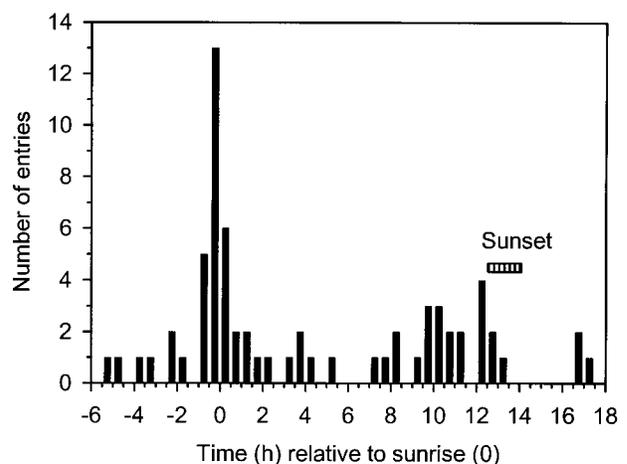


Figure 2. Distribution of times of entry into torpor relative to time of sunrise (0). Each vertical bar represents the total number of torpor entries that occurred within a half-hour period. The horizontal striped bar represents relative times of sunset over the study period.

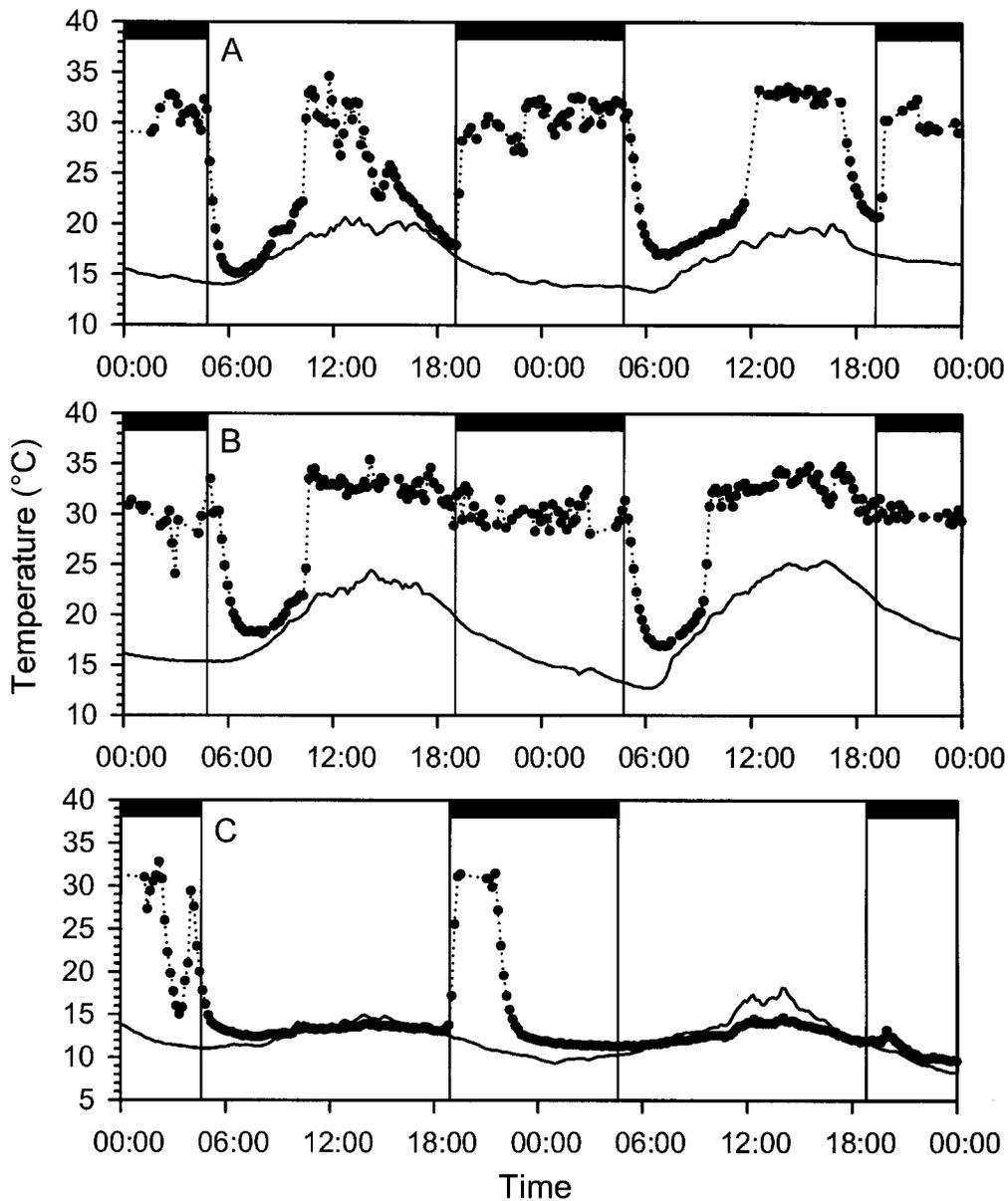


Figure 3. Three examples of skin temperature (*upper traces*) and external ambient temperature (*lower traces*) over 2 d that demonstrate the three general daily patterns of heterothermy used by free-ranging male *Nyctophilus geoffroyi* during summer. On most days, a W-shaped pattern (A) of two bouts per day was observed, where a period of normothermy coincided with high ambient temperatures; on the warmest days, torpor was used only during the morning (B); on the coolest days, bats remained torpid throughout the day (C), and on one occasion, torpor lasted for 40 h 30 min.

near sunset, although on one occasion a bat remained in torpor for 40 h 30 min.

When the relationship between the amplitude of daytime  $T_a$  and pattern of heterothermy was analysed by considering patterns as treatments within bat subjects, mean maximum daytime  $T_a$  differed significantly between each of the three patterns ( $F_{2,30} = 8$ ;  $P < 0.005$ ; Tukey test,  $P < 0.05$ ). Single torpor bouts

in the morning were used on days with the highest maximum daytime  $T_a$  ( $28.4^\circ \pm 1.1^\circ\text{C}$ ), two bouts per day occurred on days with a moderate maximum daytime  $T_a$  ( $23.7^\circ \pm 0.8^\circ\text{C}$ ), and bats remained torpid throughout days with the coolest maximum daytime  $T_a$  ( $18.6^\circ \pm 1.4^\circ\text{C}$ ).

The duration of torpor bouts and the logarithm of minimum  $T_{\text{skin}}$  reached during that bout were linearly related ( $F_{1,60} =$

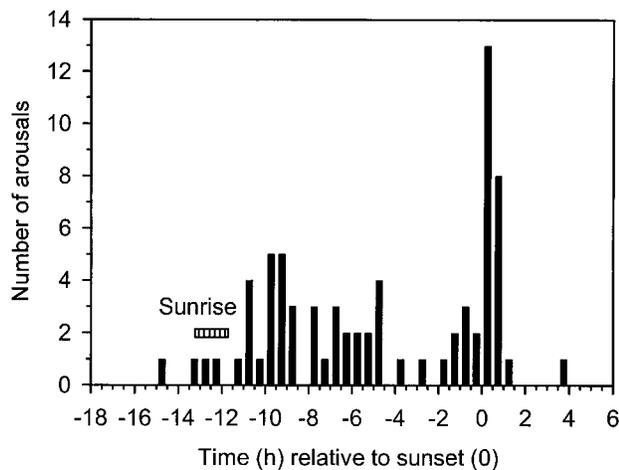


Figure 4. Distribution of times of arousal from torpor relative to time of sunset (0). Each vertical bar represents the number of torpor arousals that occurred within a half-hour period. The horizontal striped bar represents relative times of sunrise over the study period.

88,  $P < 0.001$ ,  $r^2 = 0.59$ ; Fig. 5), independent of bat individuals ( $F_{5,49} = 0.9$ ,  $P > 0.5$ ). In general, short bouts at high minimum  $T_{\text{skin}}$  occurred during the afternoon, whereas longer bouts were entered before dawn. Owing to the influence of temperature upon length of torpor bouts and number of bouts per day, mean daytime  $T_a$  had a significant negative effect on the proportion of the daytime spent in torpor ( $F_{1,32} = 24$ ,  $P < 0.001$ ,  $r^2 = 0.69$ ; Fig. 6). The slope of this relationship did not differ significantly among individuals ( $F_{5,27} = 0.68$ ,  $P > 0.5$ ); however, as the intercepts of each regression differed significantly ( $F_{5,32} = 5.4$ ,  $P < 0.001$ ), the overall average proportion/daytime spent in torpor differed among individuals.

#### Skin Temperatures

$T_{\text{skin}}$  ranged from a minimum of  $9.1^\circ\text{C}$  during torpor to a maximum normothermic temperature of  $36.9^\circ\text{C}$ . Mean normothermic  $T_{\text{skin}}$  (i.e., values  $>28^\circ\text{C}$ ) was  $31.6^\circ \pm 0.5^\circ\text{C}$  ( $N = 2,544$ ,  $n = 7$ ). Torpor occurred only when  $T_a$ 's were below  $25^\circ\text{C}$ . Bats cooled rapidly upon entry into torpor, typically taking about 1 h before the rate of cooling of  $T_{\text{skin}}$  slowed substantially, and mean maximum rate of cooling over 10 min was  $0.6^\circ \pm 0.1^\circ\text{C min}^{-1}$  ( $N = 63$ ,  $n = 7$ ). During torpor,  $T_{\text{skin}}$  fluctuated passively more or less in synchrony with external  $T_a$ , and there was no evidence that  $T_b$ 's were metabolically defended against  $T_a$ , as indicated by the lack of an increase in  $T_{\text{skin}} - T_a$  differentials. Minimum  $T_{\text{skin}}$  during each torpor bout was reached shortly after torpor entry near dawn both for morning bouts and full-day bouts and just before arousal near dusk for afternoon bouts. The greatest differentials between minimum  $T_{\text{skin}}$  and  $T_a$  (up to  $9^\circ\text{C}$ ) occurred during bouts lasting less than 2 h, when bats appeared not to have reached steady state torpor.

Excluding these short bouts, mean  $T_{\text{skin}} - T_a$  differential at the time of minimum  $T_{\text{skin}}$  was  $1.6^\circ \pm 1.0^\circ\text{C}$  (range,  $-1.7^\circ$  to  $4.8^\circ\text{C}$ ;  $N = 45$ ,  $n = 7$ ). Hence, roost temperatures were similar to  $T_a$  at times of minimum  $T_{\text{skin}}$ .

Arousals from morning torpor bouts that occurred between 0800 and 1400 hours almost always involved an initial period of passive increase in  $T_{\text{skin}}$  with rising  $T_a$  (Figs. 1, 3). During these arousals, active heat production, as indicated by a substantial increase in warming rates and increased differentials between  $T_{\text{skin}}$  and  $T_a$ , was initiated only after  $T_{\text{skin}}$  had increased passively to between  $16^\circ$  and  $25^\circ\text{C}$  (mean  $T_{\text{skin}}$ ,  $21.9^\circ \pm 0.6^\circ\text{C}$ ;  $N = 34$ ,  $n = 7$ ). Arousals near sunset did not involve a passive warming component. Active arousal typically took less than 20 min, and mean maximum active rate of rewarming from torpor over 10 min was  $1.0^\circ \pm 0.1^\circ\text{C min}^{-1}$  ( $N = 63$ ,  $n = 7$ ).

#### Discussion

Our study is the first to describe in detail the natural thermoregulatory behaviour of a Temperate Zone bat roosting in trees. Male *Nyctophilus geoffroyi* frequently entered torpor during diurnal roosting in summer, and timing of heterothermy appeared to respond closely to both the light/dark cycle and fluctuations in diurnal  $T_a$ .

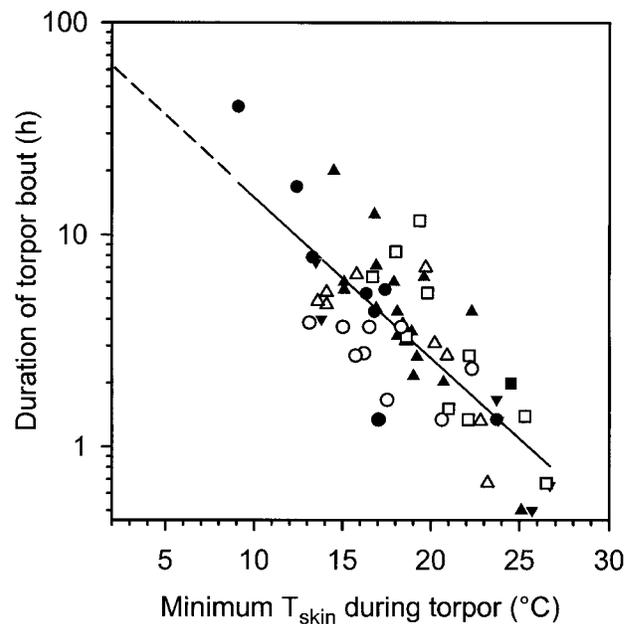


Figure 5. Duration of torpor bouts in *Nyctophilus geoffroyi* as a function of minimum skin temperature reached during each torpor bout ( $F_{1,60} = 88$ ,  $P < 0.001$ ,  $r^2 = 0.59$ ;  $\log_{10}$  bout length [h] =  $-0.08$  minimum  $T_{\text{skin}}$  [ $^\circ\text{C}$ ] + 1.94). Individuals are identified with different symbols. Regression lines for each individual did not differ significantly ( $F_{5,49} = 0.9$ ,  $P > 0.5$ ).

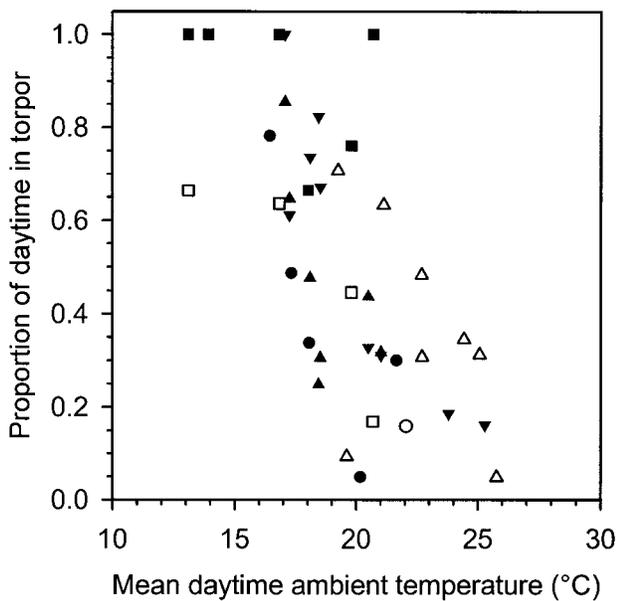


Figure 6. Proportion of the daytime (sunrise to sunset) spent in torpor by *Nyctophilus geoffroyi* as a function of mean ambient temperature over that time ( $F_{1,32} = 24$ ,  $P < 0.001$ ,  $r^2 = 0.69$ ). Individuals are identified with different symbols. The linear relationship was not significantly different between individuals (test of equal slopes:  $F_{5,27} = 0.68$ ,  $P > 0.5$ ); however, the magnitude of the effect differed significantly (test for equal intercepts:  $F_{5,32} = 5.4$ ,  $P < 0.001$ ).

#### Roost Selection

During summer, male *N. geoffroyi* roosted solitarily in a different location almost every day. Frequent roost switching is common in bats using abundant ephemeral roosts such as most tree roosts, but it is rare for bats that use caves or buildings (Lewis 1995). If roost fidelity is deleterious because of increased susceptibility to ectoparasites and/or predation (Lewis 1995), *N. geoffroyi* may switch roosts frequently because of the abundance of alternative roost sites available under exfoliated bark and in tree crevices. Some interroost movements may also be to roosts with thermal characteristics suited to the prevailing weather (Humphrey et al. 1977; Hamilton and Barclay 1994; Lewis 1995). The low height of roosts chosen by *N. geoffroyi* (Tidemann and Flavel 1987; Taylor and Savva 1988; Hosken 1996; Lumsden et al. 2002) may be related to the availability of exfoliated bark (which appeared to be more common at a low height) but may simply reflect the bat's preference for foraging below the canopy (Brigham et al. 1997a).

#### Heterothermy

Free-ranging *N. geoffroyi* altered their thermoregulatory state during the day in accordance with the amplitude and timing of the daily  $T_a$  cycle, frequently maintaining normothermy for

at least part of the day. In captivity, however, under constant  $T_a$ , *N. geoffroyi* remain in torpor throughout the day and actively arouse shortly after lights off (Geiser and Brigham 2000). In contrast to the laboratory and to the stable microclimate within caves and other well-insulated roosts, daily temperatures within tree-cavity roosts may fluctuate widely, depending on the thermal buffering qualities of the tree structure (Humphrey et al. 1977; Körtner and Geiser 2000b). The roosts most often used by solitary male *N. geoffroyi*, under thin bark and in shallow crevices, appeared poorly insulated against  $T_a$  because  $T_{skin}$ 's during torpor were close to and responded passively to changes in external  $T_a$ .

Sunrise was apparently a strong cue for entry into torpor by *N. geoffroyi*. Normothermy is most energetically expensive during diurnal roosting in the early morning when  $T_a$  is normally lowest. Thus, morning torpor bouts appear to be most common during summer in free-ranging bats and other nocturnal heterotherms (Audet and Fenton 1988; Ransome 1990; Kurta 1991; Grinevitch et al. 1995; Geiser et al. 2000). On the coldest nights, *N. geoffroyi* abandoned foraging and entered torpor during the night, as reported for free-ranging *Lasiurus cinereus* (Hickey and Fenton 1996). On these nights, insect abundance was probably low, making foraging unproductive (Taylor and O'Neill 1988; Hickey and Fenton 1996).

Sunset triggered arousals in torpid bats on all but one occasion, and for 3 h after sunset, *N. geoffroyi* never entered torpor. Similarly, the onset of darkness stimulated arousal from torpor in captivity (Geiser and Brigham 2000) and also in *Myotis velifer* (Riedesel and Williams 1976). Even during hibernation, periodic arousals remain synchronized with dusk in some free-ranging cave-dwelling bats (Park et al. 2000). Nightly temperatures and insect abundance are normally highest in the early evenings (Taylor and O'Neill 1988; Hickey and Fenton 1996; C. Turbill, unpublished data), and arousals triggered by sunset therefore precede a time of maximum feeding opportunity.

The W-shaped diurnal pattern of  $T_{skin}$ , with two torpor bouts per day, common for *N. geoffroyi* (Fig. 3A), has been reported previously for a subtropical, tree-roosting bat *Vespadelus pumilus* (Turbill et al. 2003). A similar pattern is also exhibited by free-ranging Australian owl-nightjars (*Aegotheles cristatus*; Brigham et al. 2000) and captive dasyurid marsupials (*Sminthopsis macroura*; Geiser and Drury 2003) exposed to radiant heat during the morning. Poorly insulated diurnal refugia allow passive warming during the day but may provide little thermal buffering from falling  $T_a$  in the afternoon or minimum  $T_a$  overnight. Normothermy at  $T_a$  of 20°C requires resting metabolic rates that are three times basal levels in *N. geoffroyi* (Geiser and Brigham 2000). Hence, although roost temperatures were not cold in the late afternoon, entering torpor would nevertheless have provided considerable energy savings.

Daily energy expenditure could have been reduced further if *N. geoffroyi* had selected roosts that were insulated against

rising  $T_a$ , allowing them to remain torpid throughout the day. Instead, following some passive rewarming, bats showed a proclivity for complete arousal and a period of normothermy. Some individual and daily variation was evident in the initiation of active arousal and normothermy. This may be explained at least partly by differences in energy reserves (Körtner and Geiser 2000a). Normothermy may be desired to provide increased alertness to the risk of predation. However, the limited duration of normothermic periods and the exposed nature of roosts suggest that predation was not a strong threat. Alternatively, normothermia at a time least costly during the diurnal rest phase may have facilitated various physiological processes such as spermatogenesis (Kurta and Kunz 1988; Hosken et al. 1998) and/or behaviours such as grooming.

The extent of passive heating achieved by *N. geoffroyi* was increased by selection of poorly insulated, sun-exposed roosts that appeared to provide temperatures similar to or warmer than external  $T_a$  during the day. Selection of roosts heated by the sun has been reported for other tree-roosting bats (Vanhof and Barclay 1997; Kerth et al. 2001). Partial passive heating considerably reduces the cost of arousal from torpor and therefore results in large overall energy savings (Lovegrove et al. 1999). For example, energy expenditure during active arousals by captive *N. geoffroyi*, as measured by the increase in peak metabolic rate, was reduced by 90% at  $T_a$  of 25°C compared with  $T_a$  of 10°C (Geiser and Brigham 2000). A passive heating component of arousal appears common in free-ranging bats roosting in relatively exposed locations (Vaughan and O'Shea 1976; Chruszcz and Barclay 2002; Turbill et al. 2003) and in other heterotherms that experience wide daily fluctuations in  $T_a$  (Brigham et al. 2000; Körtner et al. 2000; Schmid et al. 2000; Geiser et al. 2002; Mzilikazi et al. 2002).

Passive heating of  $T_b$  to some threshold level, rather than an endogenous rhythm, was apparently used as a cue for active arousal by *N. geoffroyi*. Furthermore, the duration of daytime normothermia closely matched timing of warmest  $T_a$ . The close correlation between roost  $T_a$  and thermoregulatory behaviour apparent for *N. geoffroyi* may be generally applicable among small bats (Turbill et al. 2003) owing to the energetic constraints imposed by their size. Thus, bats in thermally stable diurnal roosts and in captivity under constant  $T_a$  are unlikely to arouse from torpor or maintain normothermy before sunset at  $T_a$  that is 5°C or more below their thermal neutral zone.

During winter, many Temperate Zone bats hibernate for extended periods within roosts with stable, low temperatures. Extrapolation of our summer data on torpor duration relative to minimum  $T_{skin}$  (Fig. 5) predicts that hibernating *N. geoffroyi* with a minimum  $T_{skin}$  ( $\sim T_b$ ) of 2°C (Geiser and Brigham 2000) would stay torpid for 66.3 h. This estimate is short compared with maximum torpor durations of 10–30 d reported for hibernating cave-dwelling bats (French 1985; Ransome 1990). Furthermore, on one occasion, an *N. geoffroyi* remained torpid for 40.5 h at a relatively high minimum  $T_{skin}$  of 9°C (predicted

bout duration, 19.1 h), suggesting that the extrapolation from summer, when torpor was often interrupted by high  $T_a$ , probably underestimates maximum bout duration during winter hibernation (Ellis et al. 1991; Geiser and Brigham 2000).

In conclusion, male *N. geoffroyi* decrease their energy consumption during diurnal roosting in summer by frequent use of torpor and judicious timing of periods of normothermy. Our study emphasizes the interaction between the dynamics of daily temperature cycles within refugia and temporal patterns of thermoregulatory behaviour and hence energy expenditure during the rest phase.

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