

Hibernation by a free-ranging subtropical bat (*Nyctophilus bifax*)

Clare Stawski · Christopher Turbill · Fritz Geiser

Received: 10 October 2008 / Revised: 2 December 2008 / Accepted: 8 December 2008 / Published online: 27 December 2008
© Springer-Verlag 2008

Abstract Knowledge about torpor in free-ranging subtropical bats is scarce and it is widely believed that low and stable ambient temperatures are necessary for prolonged torpor. We present temperature-telemetry data from free-ranging male ($n = 4$) and female ($n = 4$) subtropical vespertilionid bats, *Nyctophilus bifax* (~10 g), exposed to pronounced daily fluctuations of ambient temperature. All bats used torpor on every day in winter and both males and females exhibited multi-day torpor bouts of up to 5.4 days. Although females were larger than males, patterns of torpor were similar in both sexes. Torpor use was correlated with prevailing weather conditions and, on days when bats remained torpid, maximum ambient temperature was significantly lower than on days when bats aroused. Moreover, the duration of interbout normothermic periods at night increased with increasing average nightly ambient temperature. Skin temperature of torpid bats varied by $10.2 \pm 3.6^\circ\text{C day}^{-1}$ ($n = 8$, $N = 47$) and daily minimum skin temperature was positively correlated with the daily minimum ambient temperature. Our study shows that prolonged torpor is an important component of the winter

ecology of a subtropical bat and that torpor and activity patterns of *N. bifax* predominantly reflect prevailing weather conditions.

Keywords Arousal · Austral winter · Insectivorous · Multi-day torpor · Temperature

Abbreviations

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

Introduction

Torpor is characterised by pronounced reductions in body temperature (T_b), metabolic rate (MR) and water loss (Hock 1951). Torpor is a key strategy employed by many mammals to conserve energy and water and to overcome adverse environmental conditions. Low ambient temperature (T_a) or a decrease in food availability are often prerequisites for use of torpor (Wang 1989). However, individuals of some species regularly enter torpor even when food is available and weather conditions are mild (Turbill et al. 2003). In these individuals, torpor appears to be part of a normal daily routine that is used to manage energy and/or water requirements.

Torpor is predominantly employed by small mammals, which, because of their large surface area to volume ratio, require large amounts of energy relative to their size to maintain an elevated warm T_b (normothermia). Microchiropterans (microbats) are among the smallest mammals (most of them weigh <25 g) and because many species feed on insects, their energy supply and requirements are

Communicated by I. D. Hume.

C. Stawski (✉) · C. Turbill · F. Geiser
Department of Zoology,
Centre for Behavioural and Physiological Ecology,
University of New England, Armidale, NSW 2351, Australia
e-mail: cstawski@une.edu.au

F. Geiser
e-mail: fgeiser@une.edu.au

Present Address:

C. Turbill
Research Institute of Wildlife Ecology,
University of Veterinary Medicine Vienna,
Savoyenstrasse 1, 1160 Vienna, Austria

strongly affected by T_a (Fenton 1983). The use of torpor to cope with low food availability is widespread among microbat species belonging to several families and inhabiting a range of climates (Henshaw 1970; McManus and Nellis 1971; Genoud et al. 1990; Arlettaz et al. 2000; Geiser and Brigham 2000; Turbill and Geiser 2006; Willis et al. 2006; Wojciechowski et al. 2007).

Most work on thermal biology has been conducted on temperate-zone bats, which generally employ short bouts of torpor lasting less than a day during the warmer months and prolonged multi-day torpor during winter hibernation (Speakman and Thomas 2003; Geiser 2004). In contrast, knowledge about the thermal biology of free-ranging bats in subtropical or tropical habitats, with vastly different environmental conditions and energetic constraints, is scarce. However, even in tropical regions insect abundance can be greatly reduced during winter (Fenton 1983), limiting the amount of food available to insectivorous microbats. A reduction in winter activity of bats in tropical regions also has been observed (Richards 1989) and several subtropical microbats frequently employ short torpor bouts coinciding with times of low T_a , even during summer (Turbill et al. 2003; Jacobs et al. 2007; Vivier and van der Merwe 2007). As torpor use by insectivorous bats is rather flexible, and torpor bout duration generally increases with decreasing T_a in thermo-conforming torpid individuals (Twente and Twente 1965; Avery 1985; Geiser and Kenagy 1988; Arlettaz et al. 2000; Turbill and Geiser 2008), it is possible that free-ranging tropical or subtropical microbats also use prolonged torpor during cold periods in winter.

Appropriate selection of hibernacula is important for microbats as they spend a large portion of their life within roosts and roost microclimates influence survival and other important life processes (Bronner et al. 1999; Kerth et al. 2001; Lourenço and Palmeirim 2004). However, roost selection is of critical importance particularly for tree-roosting bats because they are more exposed to external environmental conditions and T_a fluctuations than cave-dwelling bats (Genoud 1993). As T_a affects torpor bout length and arousal frequency, roost choice will in turn influence torpor patterns and likely will also determine to some extent the use of prolonged torpor by microbats. Thus, differences in selected roost microclimate may explain differences in torpor patterns between individuals and even sexes (Ransome 1971; Humphries et al. 2002; Turbill and Geiser 2006; Jacobs et al. 2007).

The purpose of our study was to quantify the thermal biology, thermoregulatory behaviour and use of torpor of tree-roosting subtropical microbats under natural conditions during winter. We test the hypothesis that microbats use prolonged torpor even in a mild subtropical climate, especially at times when T_a is low and foraging may be unproductive. Moreover, we predict that weather patterns and selection of

roost microclimate will influence winter torpor patterns within and among individuals. To address these aims, we use temperature telemetry to locate roosts and continuously record the skin temperature (T_{skin}) of free-ranging male and female *Nyctophilus bifax* (Vespertilionidae) living in a coastal, subtropical rainforest habitat of eastern Australia.

Methods

Our study was conducted in Iluka Nature Reserve (29°24'S, 153°22'E) on the north coast of New South Wales, Australia, during July and August 2007 (austral winter). This site is near the southern limit of the geographic distribution of *N. bifax*. Iluka Nature Reserve is subtropical according to the Köppen Climate Classification, as the mean T_a of the warmest month is >22°C and the mean T_a of the coldest month is between -3 and 18°C. The reserve contains an area of littoral rainforest and eucalypt forest, receives an average of 1,450 mm of rainfall annually, and the long-term (130 years) mean daily T_a for July ranges from 9.7 to 19°C (Bureau of Meteorology, Australia). During our study period, T_a , measured with temperature dataloggers ($\pm 0.5^\circ\text{C}$, iButton thermochron, Maxim Integrated Products, Inc., Sunnyvale, California, USA) under the canopy in the shade 2 m above the ground, ranged from 4 to 25°C.

Bats were caught in mist nets placed across pathways or in openings within the rainforest. Mist nets were opened just prior to sunset and kept open for several hours and checked every 15 min. Adult female ($n = 4$) and adult male ($n = 4$) *N. bifax* (mean body mass 10.1 ± 1.3 g, $n = 8$) were fitted with temperature-sensitive radio transmitters (~ 0.5 g, LB-2NT, Holohil Systems Inc., Carp, Ontario, Canada) providing data for each individual over periods of 10–27 days (preliminary data have been published in Stawski et al. 2008). After trimming a small patch of fur in the mid-dorsal region, we glued transmitters to the skin using a latex adhesive (SkinBond, Smith and Nephew United, Mount Waverley, NSW, Australia). Before attachment, transmitters were calibrated between 5 and 40°C in a water bath against a precision thermometer. One transmitter that was shed 28 days after attachment was re-calibrated and had drifted by $<0.5^\circ\text{C}$ over the entire temperature range from the original calibration. We used external transmitters owing to the difficulties of implanting transmitters into small bats and to maximise transmitter range. In small mammals, the difference between core T_b and T_{skin} is typically $<2^\circ\text{C}$, particularly while the animal is resting or torpid (Audet and Thomas 1996; Barclay et al. 1996; Körtner and Geiser 2000a; Dausmann 2005). Further, T_{skin} measurements are not simply measurements of T_a , as during normothermic thermoregulation the $T_{\text{skin}} - T_a$ differential increases substantially (Fig. 1a).

Bats were released at the site of capture after being held for approximately 2 h. The following morning we tracked bats to their roost locations and did so on all days when they carried transmitters. A receiver/logger (Körtner and Geiser 1998) that recorded transmitter pulse rate and thus T_{skin} every 10 min was set within range of each roosting bat. Receiver/loggers were checked each day to ensure they remained in signal range. We also took manual readings of pulse intervals several times each day to obtain additional data when bats were out of receiver/logger range and to ensure accuracy of logger readings. Data from loggers were downloaded every 2 to 5 days to a laptop computer. The exact location of several roosts was identified by observing bats leaving at dusk, but this was often not possible 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).

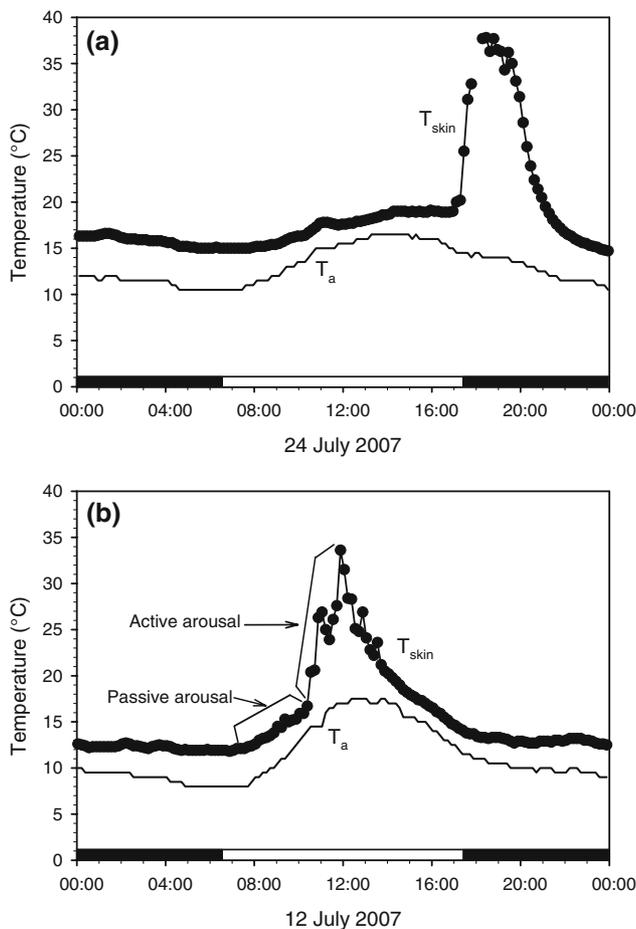


Fig. 1 **a** T_{skin} of a free-ranging female *N. bifax* (upper trace, dotted line) and T_a (lower trace, smooth line) over 1 day showing that in normothermic bats T_{skin} differs from T_a . **b** T_{skin} of a free-ranging male *N. bifax* (upper trace, dotted line) and T_a (lower trace, smooth line) over 1 day showing differences between passive and active arousals. The black and white bars on each graph represent night and day, respectively

Torpor entry was defined as a rapid decrease (mean $0.1 \pm 0.03^\circ\text{C min}^{-1}$) in T_{skin} to temperatures below 28°C . Active arousals were described by relatively fast increases (mean $0.5 \pm 0.1^\circ\text{C min}^{-1}$) in T_{skin} to temperatures above 28°C , whereas passive increases in T_{skin} to a maximum of 32°C were distinguished by slow rewarming rates that followed the general rewarming trend of T_a (mean $0.1 \pm 0.1^\circ\text{C min}^{-1}$; Fig. 1b). Therefore, we calculated torpor bout duration from the time T_{skin} fell below and rose above 28°C , with the exception of times when T_{skin} briefly (<30 min) increased passively to temperatures up to 32°C without active rewarming. These passive arousals were included into torpor bouts.

Statistical analyses were conducted using Minitab Statistical Software (V 13.1). To determine whether the distribution of circular data, i.e. the timing of arousals, differed significantly from random we used the Rayleigh test (Zar 1999). Linear regressions were fitted using the method of least squares and compared using ANCOVA. Individuals were analysed separately and if slopes were the same they were pooled and regressed together. We report data as means \pm SD for n is the number of individuals; N is the number of observations. To account for repeated measures in individuals we used the mean of the values for each individual when calculating means \pm SD. We rejected the null hypothesis if the significance level was $P < 0.05$.

Results

Torpor and arousal patterns

All bats used torpor on each day of the field study. Patterns of torpor varied between warm periods when bats aroused each evening at dusk and cool periods when bats remained in prolonged torpor lasting up to 128.5 h (5.4 days; Fig. 2). All bats employed at least one torpor bout lasting >24 h. The mean duration of torpor bouts was 26.8 ± 11.3 h ($n = 8$, $N = 114$), although individuals showed considerable variation in mean torpor bout duration (Table 1). The mean duration of the longest bout recorded for each individual was 82.6 ± 28.2 h ($n = 8$). Overall, bats exhibited a total of 22 torpor bouts that lasted >24 h and 92 torpor bouts that lasted <24 h.

The \log_{10} of the duration of torpor bouts was negatively correlated to mean T_{skin} and T_a of bats during each bout ($P < 0.001$, $R^2 = 52.2\%$; $P < 0.001$, $R^2 = 47.5\%$; Fig. 3a, b; respectively). The mean torpor bout duration ($P = 0.61$, $T = -0.5$, $df = 5$), the mean T_{skin} during each torpor bout ($P = 0.58$, $T = -0.6$, $df = 3$), and the correlation between mean T_{skin}/T_a and torpor bout duration (ANCOVA, $P > 0.05$) did not differ between sexes.

Times of arousal of torpid bats were strongly clumped (Rayleigh test, $P < 0.001$) with a main peak at around

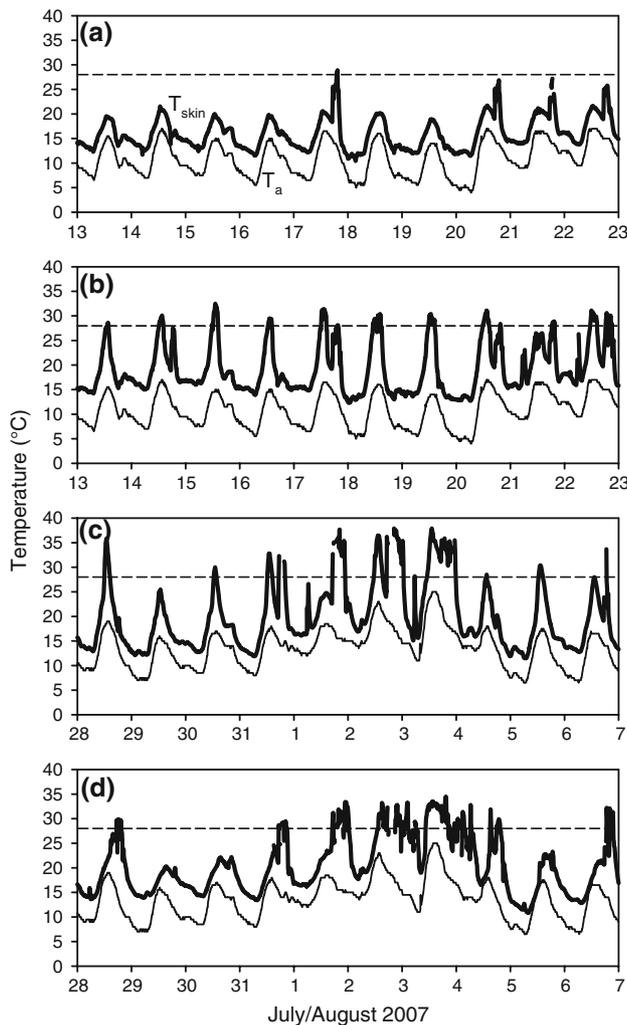


Fig. 2 T_{skin} of two free-ranging male (a, b) and two free-ranging female (c, d) *N. bifax* (upper trace, thick line) and T_a (lower trace, thin line) over 10 days during July (males) and July/August (females) 2007. The dashed line at 28°C indicates the T_{skin} torpor threshold

sunset (0.05 ± 0.1 h after sunset, $n = 8$, $N = 92$) and two smaller peaks, one shortly before dawn and another during the middle of the day (Fig. 4). Times of arousal did not

differ between males and females ($P = 0.44$, $T = -0.9$, $df = 3$). When individuals aroused in the second half of the night, they had always first aroused at around sunset and re-entered torpor before arousing again near sunrise. Maximum daily T_a affected a bat's propensity to arouse in the evening and therefore the duration of torpor bouts (Fig. 5). On days when bats aroused, maximum T_a was significantly higher ($18.5 \pm 0.8^\circ\text{C}$, $n = 8$, $N = 100$) than on days when bats remained torpid ($16.3 \pm 0.7^\circ\text{C}$, $n = 8$, $N = 47$, $P < 0.001$, $T = 5.9$, $df = 13$).

Interbout normothermic periods lasted for a mean of 3.0 ± 0.8 h ($n = 8$, $N = 96$), with some variance among individuals (Table 1). The duration of these normothermic periods was positively correlated with mean nightly T_a ($P < 0.001$, $R^2 = 59.8\%$; Fig. 6a), but did not differ between the sexes (ANCOVA: slope $P = 0.584$, intercept $P = 0.383$). No correlation was observed between the duration of interbout normothermic periods and the duration of the preceding torpor bout ($P = 0.292$, $R^2 = 1.2\%$; Fig. 6b).

Skin temperature

Daily passive fluctuations of T_{skin} during prolonged torpor bouts (>24 h) varied between a minimum of $14.0 \pm 2.5^\circ\text{C}$ ($n = 8$, $N = 47$) and a maximum of $24.2 \pm 2.6^\circ\text{C}$ ($n = 8$, $N = 47$; mean daily range $10.2 \pm 3.6^\circ\text{C}$, $n = 8$, $N = 47$; Table 1). The mean of the lowest minimum T_{skin} recorded for each individual was $12.1 \pm 2.5^\circ\text{C}$ ($n = 8$), while the lowest individual minimum T_{skin} recorded was 9.4°C ($T_a = 6.5^\circ\text{C}$) for a male and 10.8°C ($T_a = 7.5^\circ\text{C}$) for a female. The mean daily minimum T_{skin} for all days, including torpor bouts of <24 h, was $14.7 \pm 2.4^\circ\text{C}$ ($n = 8$, $N = 147$) and varied among individuals (Table 1), but did not differ between sexes ($P = 0.692$, $T = -0.4$, $df = 4$).

Daily minimum T_{skin} was positively correlated with the corresponding T_a (i.e. measured at the same time as T_{skin}) and also with the daily minimum T_a ($P < 0.001$,

Table 1 Mean \pm SD for the given variables for individual free-ranging *N. bifax* during winter

Bat	# Days of data	Body mass (g)	Torpor bout duration (h)	Duration of interbout normothermia (h)	Passive T_{skin} fluctuations ($^\circ\text{C}$)	Daily minimum T_{skin} ($^\circ\text{C}$)
A ♂	10	8.7	25.5 \pm 22.0 (8)	1.8 \pm 0.5 (7)	13.3 \pm 0.9 (5)	11.5 \pm 1.1 (10)
B ♂	27	9.2	36.1 \pm 31.3 (16)	3.4 \pm 2.5 (15)	9.8 \pm 2.9 (11)	12.5 \pm 1.9 (27)
C ♂	27	9.3	24.2 \pm 20.4 (17)	2.9 \pm 1.1 (16)	15.4 \pm 2.4 (7)	14.2 \pm 2.1 (23)
G ♂	16	8.7	12.3 \pm 12.3 (17)	2.9 \pm 1.7 (11)	10.9 \pm 3.0 (7)	19.0 \pm 1.5 (14)
D ♀	21	10.7	46.2 \pm 30.9 (7)	1.9 \pm 1.9 (3)	12.0 \pm 6.6 (6)	17.1 \pm 2.1 (20)
F ♀	21	10.7	24.2 \pm 21.1 (17)	3.4 \pm 3.3 (14)	3.8 (1)	13.6 \pm 1.6 (20)
I ♀	17	11.9	13.6 \pm 16.1 (22)	3.6 \pm 2.7 (21)	8.9 \pm 3.2 (3)	14.3 \pm 2.2 (17)
J ♀	16	11.7	32.4 \pm 34.9 (10)	4.2 \pm 3.0 (9)	7.5 \pm 4.0 (7)	15.4 \pm 1.4 (16)
Mean	19.4 \pm 5.8 (8)	10.1 \pm 1.3 (8)	26.8 \pm 11.3 (114)	3.0 \pm 0.8 (96)	10.2 \pm 3.6 (47)	14.7 \pm 2.4 (147)

Body mass at capture. The number of observations is shown in brackets

Fig. 3 Torpor bout duration (log 10) as a function of mean T_{skin} during a torpor bout (a; $P < 0.001$, $R^2 = 52.5\%$) and mean T_a during a torpor bout (b; $P < 0.001$, $R^2 = 47.5\%$) for four male (filled circles) and four female (open circles) *N. bifax*. When calculating mean T_{skin} we included passive arousals above 28°C

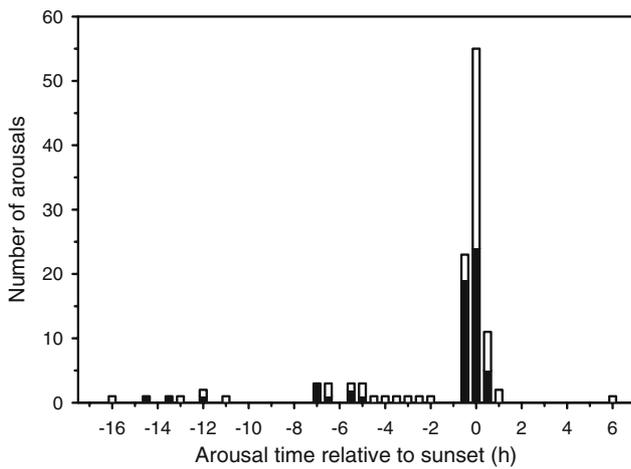
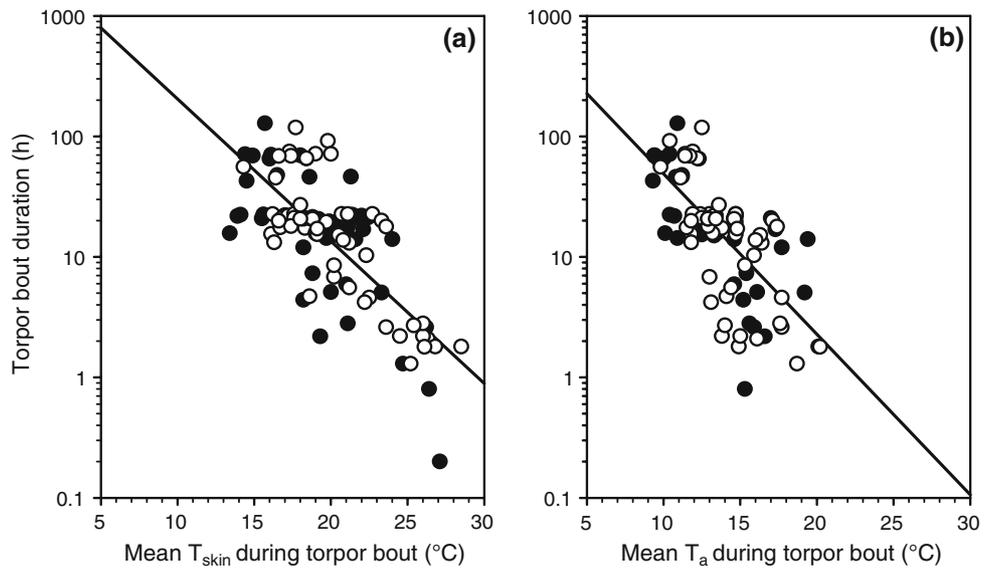


Fig. 4 Times of arousals by *N. bifax* relative to the time of sunset (0 h). Filled bars represent males and open bars represent females. Each bar represents a 30-min period

$R^2 = 33.6\%$; $P < 0.001$, $R^2 = 40.2\%$; Fig. 7a, b; respectively). The relationship between daily minimum T_{skin} and daily minimum T_a did not differ between males and females (ANCOVA: slope $P = 0.186$; intercept $P = 0.767$). However, while the slope of this relationship was the same for all individuals, the intercept differed significantly among individuals (ANCOVA: slope $P = 0.904$; intercept $P < 0.001$), with minimum T_{skin} ranging from 1.4 to 12.1°C above T_a . During torpor bouts the time of daily maximum torpid T_{skin} ($25.2 \pm 2.3^\circ\text{C}$, $n = 8$, $N = 106$) occurred 0.5 ± 0.4 h ($n = 8$, $N = 106$) after the daily maximum T_a ($17.4 \pm 2.3^\circ\text{C}$, $N = 29$) and the time of daily maximum torpid T_{skin} did not vary significantly between males and females ($P = 0.249$, $T = -1.3$, $df = 5$).

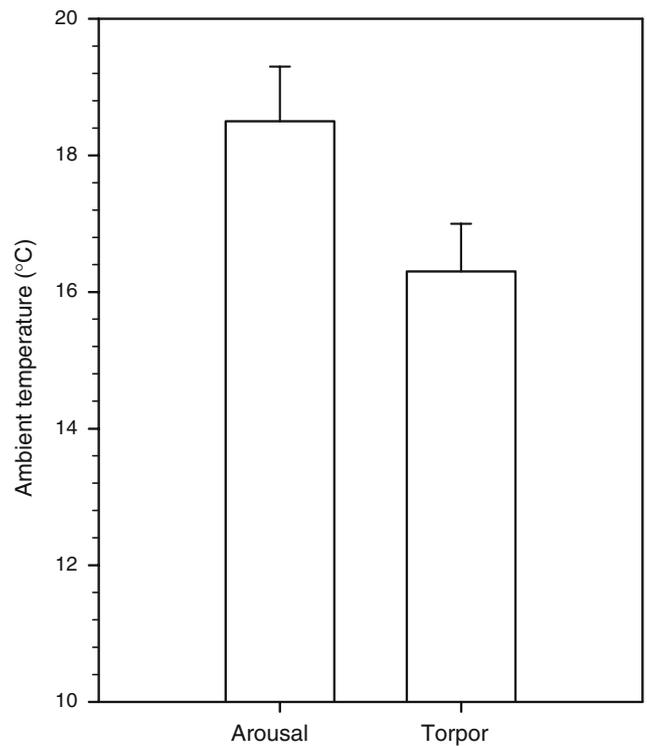


Fig. 5 Mean maximum T_a on days when bats aroused and on days when bats remained torpid

Discussion

Our study shows that subtropical bats can employ prolonged torpor in winter. We observed multi-day torpor in all *N. bifax* with torpor bouts lasting up to 5.4 days, which is similar to, for example, torpor bouts of hibernating hamsters (*Mesocricetus auratus*) or chipmunks (*Tamias amoenus*)

Fig. 6 Duration of interbout normothermia of male (*filled circles*) and female (*open circles*) *N. bifax* as a function of mean nightly T_a (**a**; $P < 0.001$, $R^2 = 59.8\%$) and the duration of the preceding torpor bout (**b**; $P = 0.292$, $R^2 = 1.2\%$)

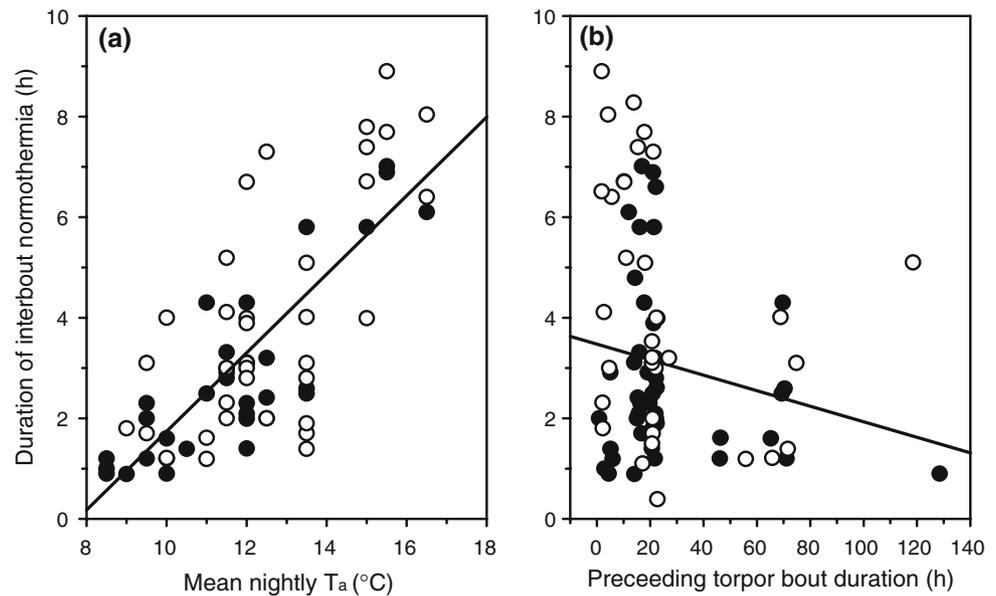
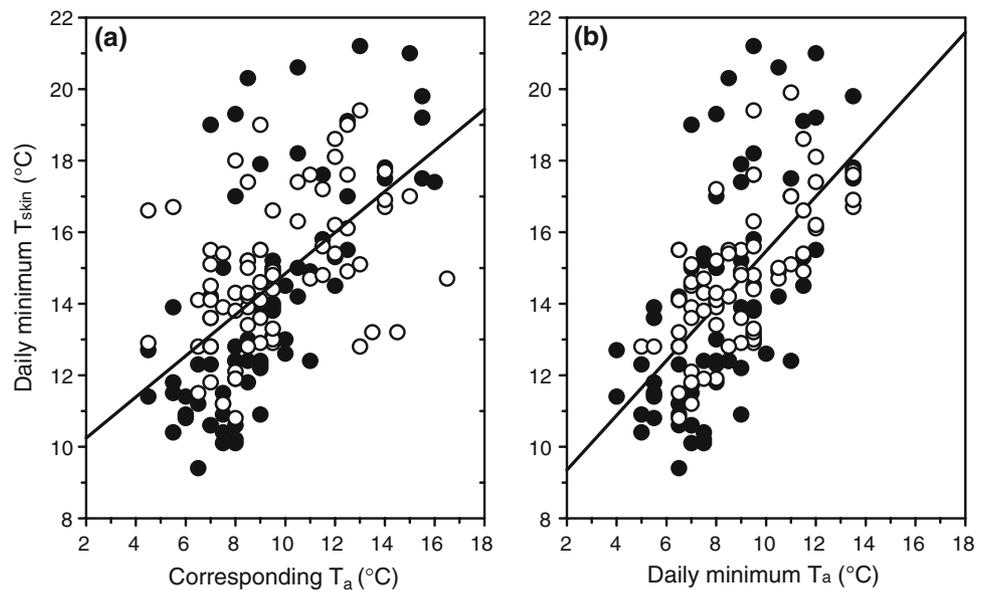


Fig. 7 Daily minimum T_{skin} of male (*filled circles*) and female (*open circles*) *N. bifax* as a function of corresponding T_a (**a**; $P < 0.001$, $R^2 = 33.6\%$) and daily minimum T_a (**b**; $P < 0.001$, $R^2 = 40.2\%$)



exposed to $T_a < 10^\circ\text{C}$ (Pohl 1961; Geiser and Kenagy 1987). Our data refute previous claims that hibernation is restricted to temperate zone bats (McNab 1974) and that prolonged torpor in the subtropics is not possible because of the high prevailing T_a (Henshaw 1970). We show that hibernation in bats is geographically widespread and that low and stable T_a is not a prerequisite for prolonged torpor, although in subtropical regions hibernation patterns obviously differ from that in temperate climates because of the much milder conditions.

Although most work on torpor has been conducted in temperate regions, and it is widely believed that torpor is not required in warm climates, there is substantial evidence from field and laboratory work demonstrating that both

mega- and microbats from the tropics and subtropics employ torpor (McManus and Nellis 1971; Genoud et al. 1990; Genoud 1993; Turbill et al. 2003; Jacobs et al. 2007; Kelm and von Helversen 2007; Vivier and van der Merwe 2007). Nevertheless, bats in all of these studies displayed short bouts of torpor lasting less than 1 day that are often described as “daily torpor”, in contrast to multi-day torpor in the hibernators. However, torpor bout duration is inversely related to temperature in thermo-conforming, torpid mammals and even in hibernators bouts of torpor lasting less than 1 day are common at $T_a > 20^\circ\text{C}$, especially when these animals are exposed to strong daily T_a cycles (Twente and Twente 1965; Song et al. 1997; Körtner and Geiser 2000b; Geiser 2004). Although torpor bout duration

may be similar at high T_a in hibernators and daily heterotherms, torpor metabolic rates in hibernators are much lower than those of daily heterotherms (Song et al. 1997; Geiser and Brigham 2000; Geiser 2004) suggesting that torpor in hibernators and daily heterotherms differs functionally. In contrast to our study, torpor use in other tropical and subtropical bat species was examined for periods of <2 weeks. Our long-term study over 5 weeks, including variation in weather patterns, shows that *N. bifax*, like other subtropical bats, arouse from torpor daily during a period of warm weather in winter. However, this did not preclude entering prolonged torpor during cold spells. Thus, the use of short bouts of torpor by subtropical or tropical bats does not necessarily indicate the use of daily torpor exclusively (i.e. by a daily heterotherm), but perhaps more correctly represents short torpor bouts by a species capable of hibernation. It is likely that further work will identify prolonged torpor bouts in at least some other tropical and subtropical bats.

Torpor bout duration in *N. bifax* was strongly affected by T_a as in previous studies on hibernating bats and rodents (Twente and Twente 1965; Ransome 1971; French 1982; Geiser and Kenagy 1987, 1988; Park et al. 2000; Rambaldini and Brigham 2008). Most torpor bouts observed here lasted for <1 day and likely occurred between nocturnal feeding periods made possible during mild nights in the subtropics when insects remain active. Even microbats from temperate climates are more active and may forage during warm weather in winter (Avery 1985; Hays et al. 1992; Arlettaz et al. 2000; Turbill 2008; Turbill and Geiser 2008). Nevertheless, the occurrence of prolonged torpor in our bats suggests that during cold periods it is not worthwhile for the bats to arouse and forage, likely because of the reduced abundance of flying insects on these nights (Richards 1989). We found that the average duration of prolonged torpor bouts was about three days and coincided with cold weather when average daily T_a was cooler than $\sim 12^\circ\text{C}$. Our results suggest that weather patterns, which determine thermoregulatory costs and insect activity, are an important predictor of torpor expression and activity patterns for subtropical bats during winter. Further, it seems possible that bats are able to sense changes in weather patterns via changes in barometric pressure (Turbill 2008; Turbill and Geiser 2008) and use this to decide whether to arouse or to remain torpid.

The T_{skin} of torpid bats during most of our study was generally several degrees higher than T_a and T_{skin} passively followed the general trend of daily T_a changes, suggesting that usually they were thermo-conforming as for many hibernating species (Lyman 1970). The large $T_{\text{skin}} - T_a$ differential measured here is likely because T_a was measured only 2 m above the ground, whereas bats generally roosted at heights above ~ 10 m. The lowest T_{skin} recorded

in our study for a male was 9.4°C ($T_a = 6.5^\circ\text{C}$) and for a female was 10.8°C ($T_a = 7.5^\circ\text{C}$) and daily minimum T_{skin} matched day-to-day variation in external T_a , hence the winter roosts of *N. bifax* typically provided little buffering against short-term fluctuations in external T_a . However, different T_{skin} during steady-state torpor suggest that roost microclimates differed among individuals and over time.

Unlike cave-roosting bats, tree-roosting *N. bifax* are exposed to large daily fluctuations in T_a and consequently large T_{skin} fluctuations during torpor. On some occasions, bats passively re-warmed to near normothermic levels without obvious active arousal. Experiencing such large daily fluctuations in T_{skin} and hence T_b may reduce the necessity for full periodic arousals from prolonged torpor bouts (Dausmann et al. 2005), but could also facilitate passive arousals with low energetic investment on relatively warm days when bats may attempt to forage (Ruczyński 2006; Turbill and Geiser 2008). In our study, maximum T_{skin} during torpor bouts generally occurred shortly after maximum T_a and on some days would remain high until around sunset when bats typically aroused. A passive increase of T_b because of increasing ambient and roost T_a reduces costs of rewarming substantially in comparison to active endothermic re-warming of T_b (Lovegrove et al. 1999; Geiser et al. 2004; Turbill et al. 2008). Moreover, by experiencing daily fluctuations in T_a , *N. bifax* can arouse in response to short term changes in winter weather patterns that are correlated with increased insect activity (Turbill 2008), but remain torpid on nights when the energy return would be insufficient.

Bats were normothermic for longer on warm than cool nights likely because of reduced thermoregulatory costs and increased insect food abundance (French 1982; Avery 1985; Hays et al. 1992; Park et al. 2000; Christie and Simpson 2006; Turbill and Geiser 2008). However, interbout normothermic periods lasted on average only about 3 h and were not influenced by the duration of the preceding torpor bout (Fig. 6b). This suggests that prolonged torpor in *N. bifax*, perhaps because of their small size (French 1982), does not require long recovery periods, at least for torpor bouts shorter than a week. Our findings raise the question of whether interbout normothermia is more than simply a post-torpor recovery event.

Most arousals in *N. bifax* occurred shortly after sunset, as in other studies of bats that can be relatively active during the hibernation season (Hays et al. 1992; Park et al. 2000; Turbill and Geiser 2008). However, on especially warm days some bats actively aroused around midday and showed two or more arousals throughout the night, often one just after sunset and another just before sunrise. This pattern of arousal and activity seems common during mild winter conditions, and was also observed, for example in *Scotophilus* microbats inhabiting a subtropical region

(Jacobs et al. 2007). A possible explanation for arousals preceding sunrise is that, despite cool T_a at this time, insect abundance seems to increase just prior to dawn. Presumably, on these nights a second opportunity for foraging just prior to the rest phase outweighs the relatively high costs for thermoregulation at this time.

Bats were more likely to arouse on warm nights than on cool nights throughout winter (Fig. 5). Similar results have been found in mild temperate regions, where hibernating bats are active and forage successfully on some winter nights that are warmer and less windy than usual (Avery 1985; Turbill 2008). The benefits of increased activity during winter, which may include opportunities to feed, mate or change roosts, in some circumstances evidently outweigh the costs of arousing from prolonged torpor (Christie and Simpson 2006). However, with a limited and fluctuating winter food supply, it seems important for microbats to select a roost T_a that provides an accurate signal as to the probable costs and benefits of arousing and foraging during the hibernation season (Ransome 1971; Audet and Fenton 1988; Wojciechowski et al. 2007).

Our study did not reveal functional differences between males and females. However, we observed large individual differences that likely reflected selection of roosts with different microclimates. While our ability to exactly locate roosts was limited by the high roosting sites and dense, complex canopy vegetation, we established that *N. bifax* generally roosted under foliage or in large trees, likely with hollows, which is similar to a previous study (Lunney et al. 1995). These different roosts will have quite different microclimates and, as T_a impacts the thermal biology of microbats, roost microclimate is likely important with regards to the energy reserves that are available to a microbat. Roost choice by some microbat species does appear to be more likely attributed to preferences of T_a rather than of a particular roost (Bronner et al. 1999; Kerth et al. 2001). Further, mass and energy requirements of individual microbats vary, which likely affects the way they use torpor to optimise their energy reserves and therefore their roost T_a requirements. In some microbat species individuals will often roost in different microclimatic conditions even when roosting in the same area (Boyles et al. 2007). Therefore, it seems likely that hibernaculum choice plays an important role in the expression of torpor patterns and may be the reason for some of the differences in torpor use seen among individuals in our study.

In conclusion, we have shown that the use of prolonged torpor in bats is not restricted to regions that experience cold and stable temperatures, but can be used in climates that experience relatively high and variable temperatures. In a subtropical climate during winter *N. bifax* was able to enter torpor for prolonged periods despite experiencing large daily changes in T_a and T_{skin} . However, *N. bifax* were

also able to take advantage of warmer periods during winter to arouse and likely to feed. Not only do patterns and use of torpor vary greatly among species and climates, but they also appear to differ among individuals. These individual differences are largely a result of different roost locations, which could be attributed to varying energy requirements. Therefore, torpor patterns in microbats appear to be highly flexible and many species are likely to be opportunistic in their use of torpor.

Acknowledgments We thank Anaïs Le Bot for help with fieldwork and many great ideas and discussions. For their help in the field and advice we thank Margaret and Mike Stawski, Mark and Anne Brigham and Aaron Trachtenberg. Brad Law provided logistical advice and Gerhard Körtner, Lisa Warnecke and Jamie Turner for helpful discussions. Permits for this study were issued by New South Wales National Parks and Wildlife Service and the Animal Ethics Committee of the University of New England. The work was supported by grants from University of New England and Bat Conservation International to CS and the Australian Research Council to FG.

References

- Arlettaz R, Ruchet C, Aeschmann J, Brun E, Genoud M, Vogel P (2000) Physiological traits affecting the distribution and wintering strategy of the bat *Tadarida teniotis*. *Ecology* 81:1004–1014
- Audet D, Fenton MB (1988) Heterothermy and the use of torpor by the bat *Eptesicus fuscus* (Chiroptera: Vespertilionidae): a field study. *Physiol Zool* 61:197–204
- Audet D, Thomas DW (1996) Evaluation of the accuracy of body temperature measurement using external radio transmitters. *Can J Zool* 74:1778–1781
- Avery MI (1985) Winter activity of pipistrelle bats. *J Anim Ecol* 54:721–738
- Barclay RMR, Kalcounis MC, Crampton LH, Stefan C, Vonhof MJ, Wilkinson L, Brigham RM (1996) Can external radiotransmitters be used to assess body temperature and torpor in bats? *J Mammal* 77:1102–1106
- Boyles JG, Dunbar MB, Storm JJ, Brack V Jr (2007) Energy influences microclimate selection of hibernating bats. *J Exp Biol* 210:4345–4350
- Bronner GN, Maloney SK, Buffenstein R (1999) Survival tactics within thermally-challenging roosts: heat tolerance and cold sensitivity in the Angolan free-tailed bat, *Mops condylurus*. *S Afr J Zool* 34:1–10
- Christie JE, Simpson W (2006) Influence of winter weather conditions on the lesser short-tailed bat (*Mystacina tuberculata*) activity in *Nothofagus* forest, Fiordland, New Zealand *J Zool* 33:133–140
- Dausmann KH (2005) Measuring body temperature in the field—evaluation of external vs implanted transmitters in a small mammal. *J Therm Biol* 30:195–202
- Dausmann KH, Glos J, Ganzhorn JU, Heldmaier G (2005) Hibernation in the tropics: lessons from a primate. *J Comp Physiol B* 175:147–155
- Fenton MB (1983) *Just bats*. University of Toronto Press, Toronto
- French AR (1982) Effects of temperature on the duration of arousal episodes during hibernation. *J Appl Physiol* 52:216–220
- Geiser F (2004) Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annu Rev Physiol* 66:239–274
- Geiser F, Brigham RM (2000) Torpor, thermal physiology, and energetics in Australian long-eared bats (*Nyctophilus*). *J Comp Physiol B* 170:153–162

- Geiser F, Kenagy GJ (1987) Polyunsaturated lipid diet lengthens torpor and reduces body temperature in a hibernator. *Am J Physiol* 252:R897–R901
- Geiser F, Kenagy GJ (1988) Torpor duration in relation to temperature and metabolism in hibernating ground squirrels. *Physiol Zool* 61:442–449
- Geiser F, Drury RL, Körtner G, Turbill C, Pavey CR, Brigham RM (2004) Passive rewarming from torpor in mammals and birds: energetic, ecological and evolutionary implications. In: Barnes BM, Carey HV (eds) *Life in the cold: evolution, mechanisms, adaptation, and application*. 12th International hibernation symposium. University of Alaska, Fairbanks, pp 51–62
- Genoud M (1993) Temperature regulation in subtropical tree bats. *Comp Biochem Physiol A* 104:321–331
- Genoud M, Bonaccorso FJ, Arends A (1990) Rate of metabolism and temperature regulation in two small tropical insectivorous bats (*Pteropteryx macrotis* and *Natalus tumidirostris*). *Comp Biochem Physiol A* 97:229–234
- Hays GC, Speakman JR, Webb PI (1992) Why do brown long-eared bats (*Plecotus auritus*) fly in winter? *Physiol Zool* 65:554–567
- Henshaw RE (1970) Thermoregulation in bats. In: Slaughter Walton (ed) *About bats*. Southern Methodist University Press, Dallas, pp 188–232
- Hock RJ (1951) The metabolic rates and body temperatures of bats. *Biol Bull* 101:289–299
- Humphries MM, Thomas DW, Speakman JR (2002) Climate-mediated energetic constraints on the distribution of hibernating mammals. *Nature* 418:313–316
- Jacobs DS, Kelly EJ, Stoffberg S (2007) Thermoregulation in two free-ranging subtropical insectivorous bat species: *Scotophilus* species (Vespertilionidae). *Can J Zool* 85:883–890
- Kelm DH, von Helversen O (2007) How to budget metabolic energy: torpor in a small Neotropical mammal. *J Comp Physiol B* 177:667–677
- Kerth G, Weissmann K, König B (2001) Day roost selection in female Bechstein's bats (*Myotis bechsteini*): a field experiment to determine the influence of roost temperature. *Oecologia* 126:1–9
- Körtner G, Geiser F (1998) Ecology of natural hibernation in the marsupial mountain pygmy-possum (*Burramys parvus*). *Oecologia* 113:170–178
- Körtner G, Geiser F (2000a) Torpor and activity patterns in free-ranging sugar gliders *Petaurus breviceps* (Marsupialia). *Oecologia* 123:350–357
- Körtner G, Geiser F (2000b) The temporal organization of daily torpor and hibernation: circadian and circannual rhythms. *Chronobiol Int* 17:103–128
- Lourenço SI, Palmeirim JM (2004) Influence of temperature in roost selection by *Pipistrellus pygmaeus* (Chiroptera): relevance for the design of bat boxes. *Biol Conserv* 119:237–243
- Lovegrove BG, Körtner G, Geiser F (1999) The energetic cost of arousal from torpor in the marsupial *Sminthopsis macroura*: benefits of summer ambient temperature cycles. *J Comp Physiol B* 169:11–18
- Lunney D, Barker J, Leary T, Priddel D, Wheeler R, O'Connor P, 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
- Lyman CP (1970) Thermoregulation and metabolism in bats. In: Wimsatt WA (ed) *Biology of bats*. Academic Press, New York, pp 301–330
- McManus JJ, Nellis DW (1971) Temperature regulation in three species of tropical bats. *J Mammal* 53:226–227
- McNab BK (1974) The behaviour of temperate cave bats in a subtropical environment. *Ecology* 55:943–958
- Park KJ, Jones G, Ransome RD (2000) Torpor, arousal and activity of hibernating greater horseshoe bats (*Rhinolophus ferrumequinum*). *Funct Ecol* 14:580–588
- Pohl H (1961) Temperaturregulation und Tagesperiodik des Stoffwechsels bei Winterschläfern (Untersuchungen an *Myotis myotis* Borkh., *Glis glis* L. und *Mesocricetus auratus* Waterh.). *Z vergl Physiol* 45:109–153
- Rambaldini DA, Brigham RM (2008) Torpor use by free-ranging pallid bats (*Antrozous pallidus*) at the northern part of their range. *J Mammal* 89:933–941
- Ransome RD (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 GC (1989) Nocturnal activity of insectivorous bats relative to temperature and prey availability in tropical Queensland. *Aust Wildl Res* 16:151–158
- Ruczyński I (2006) Influence of temperature on maternity roost selection by noctule bats (*Nyctalus noctula*) and Leisler's bats (*N. leisleri*) in Białowieża Primeval Forest, Poland. *Can J Zool* 84:900–907
- Song X, Körtner G, Geiser F (1997) Thermal relations of metabolic rate reduction in a hibernating marsupial. *Am J Physiol* 273:R2097–R2104
- Speakman JR, Thomas DW (2003) Physiological ecology and energetics of bats. In: Kunz TH, Fenton MB (eds) *Bat ecology*. University of Chicago Press, Chicago, pp 430–492
- Stawski C, Turbill C, Geiser F (2008) Prolonged torpor use during winter by a free-ranging bat in subtropical Australia. In: Lovegrove BG, McKechnie AE (eds) *Hypometabolism in animals: Hibernation, torpor and cryobiology*. 13th International Hibernation Symposium. University of KwaZulu-Natal, Pietermaritzburg, South Africa, pp 353–360
- Turbill C (2008) Winter activity of Australian tree-roosting bats: influence of temperature and climatic patterns. *J Zool (London)* 276:285–290
- Turbill C, Geiser F (2006) Thermal physiology of pregnant and lactating female and male long-eared bats, *Nyctophilus geoffroyi* and *N. gouldi*. *J Comp Physiol B* 176:165–172
- Turbill C, Geiser F (2008) Hibernation by tree-roosting bats. *J Comp Physiol B* 178:597–605
- Turbill C, Law BS, Geiser F (2003) Summer torpor in a free-ranging bat from subtropical Australia. *J Therm Biol* 28:223–226
- Turbill C, Körtner G, 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
- Twente JW, Twente JA (1965) Regulation of hibernating periods by temperature. *Proc Natl Acad Sci USA* 53:1058–1061
- Vivier L, 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 LCH (1989) Ecological, physiological, and biochemical aspects of torpor in mammals and birds. In: Wang LCH (ed) *Advances in comparative and environmental physiology 4—Animal adaption to cold*. Springer-Verlag, Berlin, pp 361–401
- Willis CKR, Brigham RM, Geiser F (2006) Deep, prolonged torpor by pregnant, free-ranging bats. *Naturwissenschaften* 93:80–83
- Wojciechowski MS, Jefimow M, Tęgowska E (2007) Environmental conditions, rather than season, determine torpor use and temperature selection in large mouse-eared bats (*Myotis myotis*). *Comp Biochem Physiol A* 147:828–840
- Zar JH (1999) *Biostatistical analysis*, 4th edn. Prentice Hall International, New Jersey