38 Prolonged torpor use during winter by a free-ranging bat in subtropical Australia

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Abstract

Prolonged torpor or hibernation is commonly employed by bats found in temperate regions. In contrast, data on the use of prolonged torpor in bats from tropical or subtropical regions is entirely lacking. We used radio-telemetry to measure skin temperatures (T_{skin}) of free-ranging *Nyctophilus bifax* (~11 g) during winter in a coastal subtropical habitat in north-eastern New South Wales. All bats employed torpor bouts that lasted for > 48 hours on at least one occasion during the study period. The minimum T_{skin} we recorded was 10.8°C. Torpor patterns were affected by ambient temperature (T_a); during cooler periods bats remained torpid throughout the whole day, whereas on warmer days they aroused near sunset, likely to forage for several hours before becoming torpid again. The T_{skin} of torpid bats was influenced by their choice of tree roost, such that their daily T_{skin} fluctuations were greater in exposed roosts compared to more insulated ones. We provide the first evidence for the use of prolonged torpor in a free-ranging bat that is restricted to tropical and subtropical habitats. This illustrates the energetic constraints facing small endotherms even in subtropical climates and their flexibility to vary the duration of torpor and activity to suit prevailing conditions.

Introduction

Henshaw (1970) suggested that tropical and subtropical bats, unlike their temperate-zone relatives, are unable to use prolonged torpor owing to the high prevailing T_a. This led to the hypothesis that temperate-zone bats are therefore unable to occupy tropical regions because they depend on hibernation as an integral part of the yearly cycle (McNab 1974). Empirical evidence, however, does not support these ideas. Hibernacula temperatures of temperate-zone vespertilionid and rhinolophid bats range from -10–21°C (Webb *et al.* 1996). Moreover, *Miniopterus schreibersii* hibernates successfully at T_a ranging from 9.9–19°C (Brown 1999), well above the T_a previously suggested to permit hibernation in temperate bats (Humphries

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et al. 2002). Given that many subtropical regions frequently experience T_a below 20°C during winter, prolonged torpor by bats in these regions seems likely.

Most studies of thermoregulation by microbats focus on temperate-zone species, whereas information from tropical and subtropical regions, especially for free-ranging bats, is scarce. Most of Australia is subject to a generally warm climate, yet factors such as unpredictable weather, wide daily fluctuations in T_a and limited food resources do select for energy conservation strategies (Geiser 2006). Even in summer, *Vespadelus pumilus* (4 g) uses short bouts of torpor in a subtropical region where T_a is mild and food abundant (Turbill *et al.* 2003b). Taken together, this evidence leads to the prediction that prolonged torpor bouts will be used by subtropical species during cooler weather in winter. Several temperate-zone Australian bat species, including *Nyctophilus* spp. and *Chalinolobus morio*, enter prolonged torpor lasting up to two weeks and *N. geoffroyi* uses prolonged torpor (~40 hr) even in summer during unusually cool weather (Turbill *et al.* 2003a; Turbill 2006).

We quantified the thermal biology of Northern Long-eared Bats (*Nyctophilus bifax*, Vespertilionidae) to test whether a species restricted to subtropical and tropical regions employs prolonged torpor during winter. We also evaluated the influence of variability in weather patterns and selection of diurnal roosts on torpor use and foraging activity during winter.

Materials and methods

Our study was conducted during July and August 2007 in Iluka Nature Reserve (29° 24' S 153° 22' E) on the north coast of New South Wales (NSW), Australia, which is near the southern limit of *N. bifax*. The Reserve is an area of littoral rainforest and eucalypt forest. It receives approximately 1,450 mm of rainfall annually and long-term (130 years) average daily T_a for July ranges from 9.7 (min.) to 19°C (max.) (Bureau of Meteorology, Australia). During our study period T_a, measured with temperature thermochrons (± 0.5°C, iButton, Maxim Integrated Products, Inc., Sunnyvale, California, USA), ranged from 4–25°C.

For this preliminary study, we report data from four adult females (body mass 11.2 ± 0.6 g) captured with mist nets and measured over 21 (n = 2) or 17 days (n = 2). Bats were fitted with temperature-sensitive radio transmitters (0.6 g, LB-2NT, Holohil Systems Inc., Carp, Ontario, Canada; ~5% of the bat's body mass), attached to their back. We clipped a small patch of fur in the mid-dorsal region and glued transmitters to the skin using a latex adhesive (SkinBond, Smith and Nephew United, Mount Waverley, NSW, Australia). Bats were held for a maximum of 2 hr before being released at the site of capture. Transmitters were calibrated before use against a precision thermometer in a water bath at temperatures of 5–40°C. Owing to the difficulties of implanting transmitters in small bats, we used external transmitters. The difference between internal body temperature (T_b) and T_{skin} in small mammals during rest and torpor is generally small (Barclay *et al.* 1996; Dausmann 2005; Willis & Brigham 2003).

We tracked bats to their roost on all days when they carried transmitters. A remote receiver/data logger (Körtner & Geiser 1998) was set within range of each bat to record transmitter pulse rate and thus T_{skin} once every ten minutes. Exact roost locations were often difficult to determine because of the thick vegetation and large number of potential roosts in a small area. However, several roosts were located by observing bats leaving at dusk. Approximate roost locations were recorded with a handheld global positioning system unit (GARMIN eTrex).

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 range of the receiver/loggers and to ensure accuracy of logger readings.

We used a T_{skin} threshold of 28°C to delineate torpor bouts – a conservative approach we feel is appropriate for external transmitters. However, on a few occasions, T_{skin} increased above 28°C (to a maximum of 32°C) at a similar rate to the increase in T_a, indicating passive rewarming without obvious active arousal. Therefore, we assumed that rewarming was passive if the rate of increase of T_{skin} was < 0.3°C/min (maximum active rewarming rate over 10 min was 0.8 ± 0.3°C/min, n = 4, N = 3,801) and included these periods into torpor bouts. This is consistent with findings that prolonged torpor is possible despite passive rewarming to near normothermic levels (Dausmann *et al.* 2005).

All statistical analyses were conducted using Minitab Statistical Software. We report data as means ± SD for n = the number of individuals and N = the number of observations.

Results

Torpor pattern

All four bats employed torpor each day with bouts commencing between 18:43 and 06:54. The duration of torpor bouts ranged from 1.3 hr to 118.5 hr (4.9 days; Figure 1) and each bat remained in torpor for > 48 hr at least once. Arousals occurred 8 ± 14 min after sunset (n = 4, N = 47) after which bats left the roost location for 60 ± 16 min, presumably to forage. The maximum T_a on days when bats aroused (19.0 ± 0.2°C, n = 4, N = 53) was significantly greater than on days when bats remained torpid (16.8 ± 0.4°C, n = 4, N = 23; T = 9.29, DF = 4, $p < 0.05$).

The daily minimum T_{skin} that we recorded throughout the study period ranged from 10.8°C (T_a = 7.5°C) to 19.9°C (T_a = 11°C) and was positively correlated with daily minimum T_a for all bats (Figure 2). The T_{skin} of torpid bats followed the daily T_a cycle, although T_{skin} was always several degrees higher.

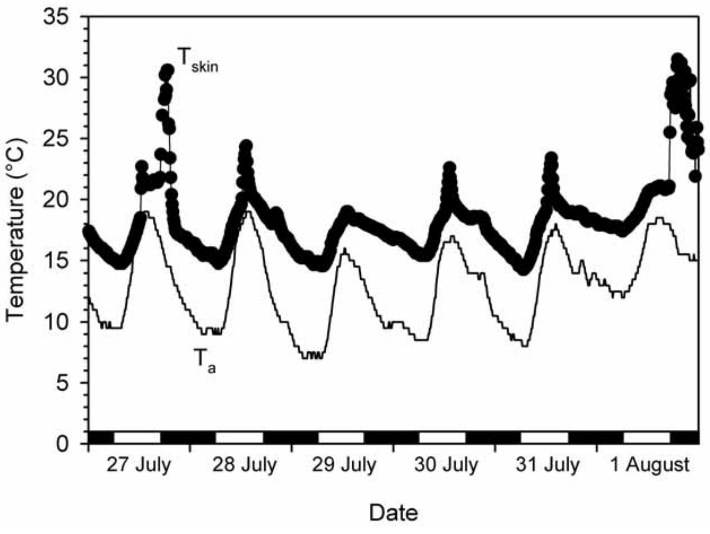

Figure 1.

T_{skin} of a free-ranging female *N. bifax* (upper trace) and T_a (lower trace) during a prolonged torpor bout (4.9 days) in winter. Dark horizontal bars indicate night and light horizontal bars indicate daytime.

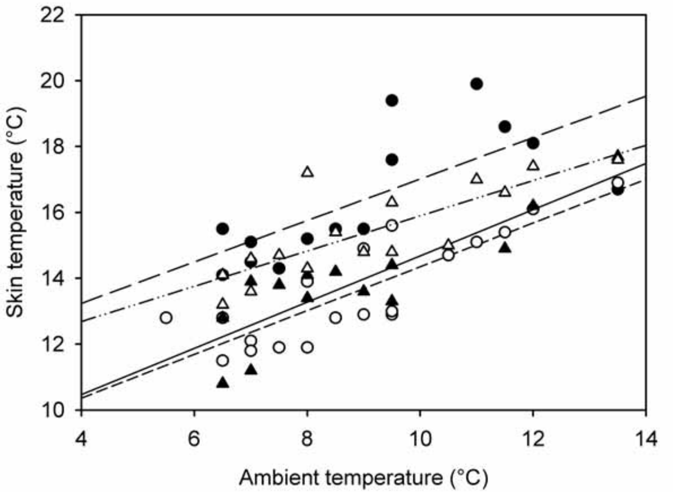

Figure 2. Daily minimum T_{skin} as a function of daily minimum T_a for four female *N. bifax*. Different individuals are shown by different symbols/lines (•/– – –, ○/- - -, ▴/——, △/—··—··—··) and all regressions were significant ($p < 0.05$; $r^2 = 0.51$ to 0.75).

Roost locations and thermal biology

All bats used several roosts but usually within a restricted area with a radius of ~30 m. Three bats remained within the rainforest throughout the observation period, whereas one female repeatedly switched locations between the rainforest and the roof of a house outside the Reserve. The use of different roosts had a pronounced effect on daily T_{skin} patterns, with a greater amplitude of daily fluctuations in the house (14.7 ± 1.6°C, N = 9) compared to the rainforest (9.6 ± 2.6°C, N = 5, T = -3.95, DF = 5, $p < 0.05$; Figure 3). The duration of torpor

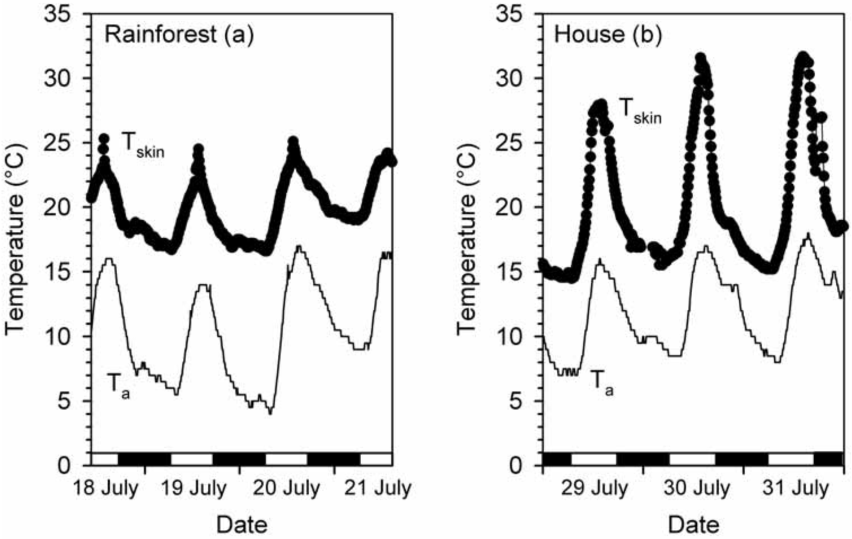

Figure 3. T_{skin} of a free-ranging female *N. bifax* (upper trace) and T_a (lower trace) while roosting in the rainforest (a) vs the roof of a house (b). Dark horizontal bars indicate night and light horizontal bars indicate daytime.

bouts was also significantly greater when the bat roosted in the rainforest (81.8 ± 14.3 hr, N = 2) vs the house (31.9 ± 22.2 hr, N = 5, T = 3.52, DF = 3, $p < 0.05$). The daily maximum T_a while this bat roosted in the rainforest (16.3 ± 1.4°C, N = 5) was significantly lower than when she roosted in the house (18.6 ± 1.9°C, N = 9, T = -2.59, DF = 10, $p < 0.05$).

Discussion

Our study is the first to document prolonged torpor use by a bat in a subtropical climate. All female *N. bifax* employed torpor for > 48 hr and bouts lasted up to 4.9 days during our winter study. This behaviour meets most definitions of hibernation (Willis *et al.* 2006). Occasional bouts of activity were usually restricted to brief periods after dusk. In contrast, bats from a subtropical environment in South Africa displayed only short bouts of torpor lasting < 24 hr in the cold season (Jacobs *et al.* 2007; Vivier & van der Merwe 2007). For small bats, the energy required to maintain a high and stable T_b increases greatly when T_a is below 30°C (Speakman & Thomas 2003), and therefore torpor should be energetically beneficial even at relatively warm T_a. At the minimum T_a of 4°C experienced by *N. bifax* at Iluka Nature Reserve, the metabolic rate required for normothermy would be predicted to be ~7 times basal levels, whereas during torpor at low T_b it could be < 5% of basal levels, i.e. a 160-fold difference (Geiser & Brigham 2000). In temperate regions, small bats must hibernate to escape cold conditions and shortage of food. However, the use of prolonged torpor for energy or water conservation may also be beneficial to bats in subtropical and tropical climates, as they also experience a decrease in T_a as well as restricted food and water availability during winter (Dausmann *et al.* 2005; Schmid *et al.* 2000).

Torpor bout durations of *N. bifax* were influenced by the prevailing weather. Periods of cool T_a when bats remained in prolonged torpor alternated with relatively mild periods during which bats aroused at dusk, left the roost and presumably foraged for several hours. This variable pattern of prolonged versus shorter torpor bouts suggests the thermoregulatory behaviour of *N. bifax* is strongly influenced by environmental cues, and that bats use torpor in a flexible way to match changes in energy reserves and availability. On relatively cool winter nights, insect activity likely declines enough to make arousal and foraging not energetically worthwhile, whereas on warmer nights foraging is advantageous. Microbats forage sometimes during winter in temperate climates on warmer nights or during periods when insects are active (Arlettaz *et al.* 2000; Avery 1985). Food availability is known to affect the use of torpor by small heterotherms, including bats. Blossom Bats, *Syconycteris australis*, did not enter torpor if food was available at T_a = 18°C, but when food was withheld they displayed torpor even at 25°C (Coburn & Geiser 1996). Torpor bouts were prolonged in captive fasted *Myotis myotis* relative to individuals provided with food *ad libitum* (Wojciechowski *et al.* 2007). A temperature-determined food supply also affected the use of torpor and activity by *N. geoffroyi* (Ellis *et al.* 1991). Our results indicate that weather patterns, which determine nightly temperatures and insect activity, are an important predictor of the thermoregulatory behaviour and activity patterns for hibernating subtropical bats.

The type of roost also influenced the amplitude of daily T_{skin} fluctuations during torpor. A previous study on roost selection by *N. bifax* at Iluka Nature Reserve found they often use foliage and less frequently tree hollows (Lunney *et al.* 1995). Whereas foliage provides little insulation against external conditions, tree hollows provide a thermal buffer. Bats may move among roosts with different thermal characteristics as a consequence of prevailing weather conditions (Ransome 1968, 1971). Our data suggest that bats chose roost locations based on external T_a and whether or not it might be profitable to arouse in the evening to feed. One bat moved from a natural roost in the rainforest during cool weather to a roost under the roof of a house during warmer weather. This selection of roost type had a pronounced effect on the magnitude of torpid T_{skin} fluctuations, which were much less in the rainforest than in the house. The bat aroused more regularly to feed when roosting in the house, which suggests that exposure to a higher daytime T_a may be beneficial for arousal.

When *N. bifax* did arouse, they always did so within 30 min before or after sunset, comparable to other hibernating bats (Park *et al.* 2000). However, the time of entry into torpor after normothermic periods was not nearly as predictable. During summer when T_a is much higher, free-ranging *Vespadelus pumilus* in a subtropical area are active throughout the night and enter torpor around sunrise (Turbill *et al.* 2003b). Similarly, *N. geoffroyi* usually enter torpor around sunrise in summer, with the exception of particularly cold nights when they stop foraging and enter torpor earlier (Turbill *et al.* 2003a). Although Turbill *et al.* (2003a) collected data during summer in a temperate region, it may prove to be a similar outcome to our study. We found that time of entry into torpor probably also reflects lower T_a and reduced insect activity at night.

Our study contributes to the emerging body of data on torpor use by bats in subtropical and tropical climates (Bartels *et al.* 1998; Coburn & Geiser 1996; Genoud 1993; Jacobs *et al.* 2007; Kelm & von Helversen 2007; Turbill *et al.* 2003b; Vivier & van der Merwe 2007). Moreover, we provide further evidence against the hypothesis that prolonged torpor (a.k.a. hibernation) cannot occur at high T_a and is restricted to temperate regions. In contrast to temperate regions, animals in the tropics and subtropics use prolonged torpor despite experiencing warm T_a during winter, and therefore metabolic inhibition during torpor may play an important role (Dausmann *et al.* 2005; Geiser & Brigham 2000; McManus & Nellis 1972). Our results, albeit preliminary, support the contention that hibernation by bats is likely to be widespread in subtropical and perhaps tropical regions. Unlike hibernation in cold climates, however, prolonged torpor coinciding with periods of unfavourable weather conditions is interspersed with nights during which bats are active. This illustrates the energetic constraints facing small insectivorous bats, even those living in regions with mild climates. It appears that dynamic use of prolonged or short bouts of torpor by microbats is important for adjusting energy balance relative to prevailing conditions.

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