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Summer torpor in a free-ranging bat from subtropical Australia

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Abstract

It is widely believed that torpor is mainly an adaptation of endotherms for cold stress and food limitation. We studied torpor use in the wild by a small tree-roosting microbat from a sub-tropical area during summer when food was abundant. Surprisingly, two torpor bouts per day were employed on each roost-day observed. The first bout occurred in the early morning and the second bout in the late afternoon, whilst a period of normothermia was maintained over the warmest part of the day. Torpor likely reduced energy expenditure substantially, and may be common in small microbats whose day-roosts are poorly insulated, even in sub-tropical climates.

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1. Introduction

Small microchiropterans (microbats) have high energy requirements for maintenance, thermoregulation and locomotion. Due to their relatively large body surface area, the thermal neutral zone (TNZ) of small (<10 g) microbats is restricted to ambient temperatures (T_a) of around or greater than 30°C (Hock, 1951; Kulzer et al., 1970; Geiser and Brigham, 2000). Energy required for thermoregulation increases steeply at T_a below 30°C, and small temperate-zone microbats show a high proclivity to enter torpor in the laboratory (Lyman, 1970; Geiser, 2003; Speakman and Thomas, 2003). As insect prey availability is much reduced at low T_a (Hickey and Fenton, 1996), temperate-zone microbats enter extended bouts of torpor and hibernate throughout winter (e.g. Park et al., 2000). Some species also enter short torpor bouts usually lasting less than a day in summer, particularly during cool weather (Audet and

Fenton, 1988; Hickey and Fenton, 1996; Turbill et al., 2001; Chruszcz and Barclay, 2002).

Most studies of torpor in microbats have concentrated on temperate species. Studies of torpor use by sub-tropical and tropical microbats are limited and almost entirely restricted to the laboratory. These studies indicate that insectivorous tropical species, especially from the families Rhinolophidae and Vespertilionidae, also readily enter torpor in captivity (Kulzer, 1965; McNab, 1969; Genoud, 1993). Food availability can be much reduced during the dry winters typical of the tropics, and minimum daily T_a can, in some parts, be relatively low. Some small tropical mammals have been found to even hibernate for prolonged periods during the dry season (Dausmann et al., 2000). However, during the wet summer season insect activity is high and T_a generally warm to hot in the tropics and sub-tropics. Hence, it may seem unlikely that tropical and sub-tropical free-ranging microbats are energetically stressed enough to necessitate regular use of torpor during spring/summer.

We used temperature-telemetry to examine the thermoregulatory patterns of free-ranging male eastern

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forest bats (*Vespadelus pumilus*, Vespertilionidae; 4–5 g). This species is restricted to the sub-tropical eastcoast of Australia between latitudes 18° and 33°S (Churchill, 1998). Our study was conducted in late spring/early summer when T_a were mild. At this time plant productivity was high and insects were abundant and active throughout the night (pers. obs.). At the study site, male *V. pumilus* roost frequently in dead trees, but also in large eucalypt trees, and in understorey species such as *Acacia melanoxylon* (Law and Anderson, 2000). During late spring, male *V. pumilus* are excluded from female maternity roosts and therefore typically roost solitarily (Law and Anderson, 2000).

2. Materials and methods

2.1. Study area

The study was conducted in November/December (late spring/early summer) at Lorne State Forest (31° 88'S 152° 37'E), on the mid-north coast of NSW, Australia. The area experiences a warm, sub-tropical climate, and the mean maximum and minimum temperatures in December at the nearby town of Wauchope are 28.2°C and 15.8°C, respectively (Bureau of Meteorology, Australia). The study site contains wet sclerophyll forest dominated by Blackbutt (*Eucalyptus pilularis*), Flooded Gum (*Eucalyptus grandis*) and other eucalypt trees, with a dense mesic understorey (Law and Anderson, 2000).

2.2. Temperature telemetry

Temperature-sensitive radio transmitters (Titley Electronics, model LTM) were fixed onto the skin of the back between the shoulder blades using quick-setting glue. The transmitters weighed 0.4 g (approximately 8.3% of mean body mass: 4.8 g) and were calibrated to the nearest 0.1°C prior to use between 5°C and 40°C, where pulse rate was regressed against transmitter temperature. The error between skin temperature (T_{skin}) and core T_b in small microbats is less than 3°C when they are at rest, and negligible during torpor (Audet and Thomas, 1996; Barclay et al., 1996). Bats were considered to be in torpor when T_{skin} dropped below the lowest T_{skin} observed in that individual immediately prior to foraging activity (Barclay et al., 2001) (i.e. below about 28°C).

Remote receiver/data-logging stations (details in Körtner and Geiser, 1998) were used to record T_{skin} measurements of roosting bats every 10 min, and T_a were recorded by a datalogger (T-Tec; type E, resolution $\pm 0.2^\circ\text{C}$) placed in the shade approximately 1 m from the ground. During the study period T_a ranged from 14.4°C to 27.2°C.

Skin temperatures of four male *V. pumilus* were measured over a total of 4.5 roost-days: two roost-days for one individual, one roost-day for another two individuals, and one afternoon/morning for a further individual. Means are shown ± 1 standard deviation for 'n' the number of individuals measured; 'N' is the number of observations.

3. Results

Bats entered torpor during the morning and afternoon of each roost day, with a period of normothermy maintained during the middle of the day, resulting in a characteristic W-shape (e.g. Figs. 1A and B). Initial torpor entries and final arousals for each roost day matched the light/dark cycle, and the period of normothermic T_b coincided closely with the time of warmest daily T_a .

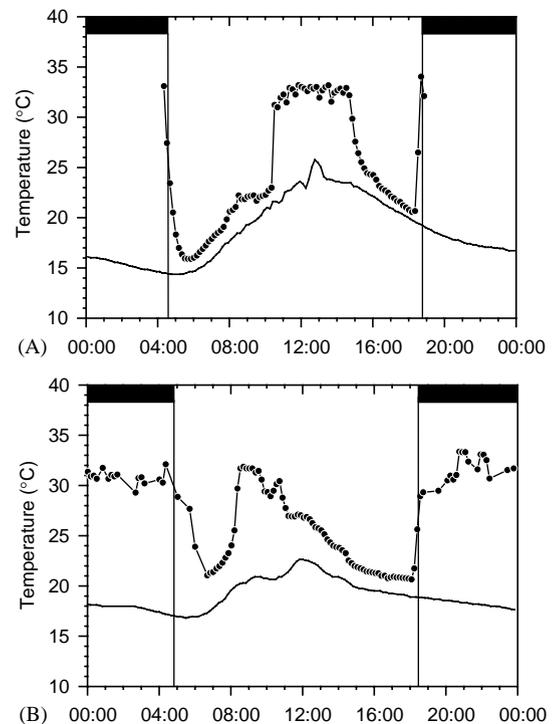


Fig. 1. Skin temperature of *Vespadelus pumilus* (upper trace with symbols) in tree roosts and external ambient temperature (lower trace) on 1st December 1999 (A) and (in a different individual) on 8th November 1998 (B). Dark bars indicate the scotophase between sunset and sunrise. This W-shaped temporal pattern of thermoregulatory behaviour was observed on each complete roost-day. Note that roost temperatures, as approximately indicated by torpid T_{skin} , were similar to T_a , but up to 5.6°C warmer in the early afternoon in some roosts (B).

On each roost-day, torpor was entered around dawn, at 3 ± 11 min before sunrise ($n = 4$, $N = 5$). Morning torpor bouts lasted an average of $234 \text{ min} \pm 116 \text{ min}$ ($n = 3$, $N = 4$), and bats aroused before midday. After a variable time (range: 151–512 min) of midday normothermia, bats entered a second bout of torpor. These afternoon bouts lasted an average of $251 \pm 108 \text{ min}$ ($n = 4$, $N = 5$), and active arousals occurred near dusk, at 6 ± 12 min before sunset ($n = 4$, $N = 6$).

Body temperatures of roosting bats cooled rapidly upon entry into torpor at dawn until a minimum T_{skin} as low as 16°C (at a T_{a} of 14.5°C) was reached. During the morning, T_{skin} of torpid bats rose slowly, apparently due to passive heating from rising T_{a} (and presumably rising roost temperatures). Initiation of active heat production and arousal, as indicated by a distinctive rapid rise in T_{skin} to normothermic values, occurred after T_{skin} warmed by up to 7°C above the minimum T_{skin} . During afternoon torpor bouts, T_{skin} initially cooled rapidly, after which T_{skin} continued to slowly cool reflecting decreasing T_{a} (and presumably decreasing roost temperatures). Minimum T_{skin} during afternoon bouts occurred immediately prior to active arousal at sunset, and reached as low as 20.5°C (at a T_{a} of 20°C).

The T_{b} of torpid bats did not appear to be defended by metabolic heat production because T_{skin} were nearly stable during torpor, rising or falling only slowly reflecting fluctuations in T_{a} . Body temperatures during torpor were therefore likely to be indicative of roost T_{a} . If so, roost T_{a} appeared to be similar to external T_{a} in one roost (Fig. 1A), as $T_{\text{skin}} - T_{\text{a}}$ were mostly less than 2°C during torpor. Whereas within a different roost (Fig. 1B), roost T_{a} appeared to be several degrees warmer than external T_{a} , particularly in the early afternoon when T_{skin} during torpor were as much as 5.6°C above T_{a} . Nevertheless, in both roosts there was only a small time delay between fluctuations in external and roost T_{a} (as indicated by T_{skin}).

4. Discussion

Our study provides the first quantitative data on torpor use in a free-ranging sub-tropical microbat. What is especially interesting is that torpor was used at a time of warm T_{a} and an abundance of food. This contradicts previous assumptions that torpor is only entered by sub-tropical bats in response to a shortage of food (McNab, 1969). Whilst food intake was presumably high at this time of the year, roost temperatures (as approximately indicated by T_{b} during torpor) of *V. pumilus*, although relatively warm, were up to 15°C below their TNZ in the early morning and late afternoon. Hence, considerable energetic savings could be gained by entering torpor at these times. For example, even at T_{a} of 25°C the

metabolic rate of small vespertilionids can be reduced to about 10% of resting normothermic values upon entering torpor (Geiser and Brigham, 2000). Further energy was conserved due to partial re-warming by passive heating during the morning prior to active arousals (Lovegrove et al., 1999; Geiser and Drury, 2002), and by coinciding normothermic T_{b} with maximum T_{a} during the middle of the day.

A similar W-shaped temporal pattern of T_{b} has been previously observed during summer in free-ranging *Nyctophilus geoffroyi* (7.5 g) roosting under bark and in tree crevices (Turbill et al., 2001). Unlike species in well-insulated roosts, such as caves, tree-roosting bats are often exposed to T_{a} below the TNZ in the morning and late afternoon and high T_{a} around midday. Consequently, even in sub-tropical climates, two bouts of torpor per day are probably common during summer in small, tree-roosting microbats.

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