

## Daily torpor and energy savings in a subtropical blossom-bat, *Syconycteris australis* (Megachiroptera)

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### Introduction

Torpor is characterised by a substantial reduction of metabolic rate (MR), body temperature ( $T_b$ ) and other physiological functions. In hibernating species,  $T_b$  may drop close to or even below 0°C (Barnes 1989; Lyman 1982) and MR may fall as low as 1% of the basal metabolic rate (BMR) (Geiser & Ruf 1995). However, torpor does not always involve such a dramatic change in metabolism and  $T_b$ . Shallow daily torpor lasts only for several hours and the drop of MR and  $T_b$  during this form of torpor is less pronounced than during hibernation. The  $T_b$  is usually between 11 and 28°C and MR is reduced to about 30% of BMR, although this is quite variable (Hudson 1973; Geiser & Ruf 1995).

Both hibernation and daily torpor have been well studied in insectivorous bats of the suborder Microchiroptera. In contrast, very little is known about heterothermy in bats of the suborder Megachiroptera ('fruit bats'). In the past it was widely believed that megachiropterans were strictly homeothermic (Ransome 1990). However, there is some evidence that some small species of the Megachiroptera are heterothermic (Bartholomew *et al.* 1970) and torpor patterns of the common or Queensland blossom-bat, *Syconycteris australis*, have been described (Geiser *et al.* 1996). This species enters torpor when food is withheld, and remains torpid for one to over ten hours. The  $T_b$  during torpor is regulated at around 18°C and the MR during torpor falls to approximately 10% of that observed during resting (Coburn 1995; Geiser *et al.* 1996). While the torpor patterns of *Syconycteris australis* are well known, the extent of energy that is saved by the use of daily torpor has not been determined. Such information can provide some insight into energy restrictions on this species within its natural range and the relative importance of these restrictions in controlling the distribution of *Syconycteris australis* in Australia.

### Material and Methods

Nine adult male *Syconycteris australis* were captured with mist nets near Iluka on the NSW north coast, at the mouth of the Clarence River (29°13'S, 153°21'E) in both summer (February) and winter (June). Body mass of bats upon capture was 18.0±1.1 g (SD) in summer, and 17.5±1.0 g (SD) in winter. Upon arrival at the University of New England, bats were released into a large holding room which provided ample room for the bats to fly. The room was fitted with branches and wide plastic mesh for roosting and for providing access to feeders. Air temperature ( $T_a$ ) was maintained at 20±1°C and relative humidity

above 40%. Photoperiod was set at the natural photoperiod of the time of capture which was 13L:11D (lights on 0530h, lights off 1830h) in summer and 10L:14D (lights on 0700h, lights off 1700h) in winter. These settings were maintained for the duration of the experiment.

Bats were fed daily on a blended mixture of 200mL apple juice, 2 bananas, 150g raw sugar, 150g 'Glucodin' and 120g 'Infasoy' provided in ten 30mL feeders. Single portions were defrosted daily and diluted by half with water. Water was provided *ad libitum* in bird feeders and shallow dishes.

The MR was measured as rate of oxygen consumption. Daily fluctuation of MR was measured over a minimum of 22 hours each, usually beginning around 1500 to 1600h, set to  $T_a$  12°C, 18°C and 25°C for both summer and winter samples. Food and water were not available during these measurements. Photoperiod during all measurements was as experienced in the holding room. Measurements were conducted in 1L respirometer chambers fitted with wide plastic mesh for roosting. Flow rates (approx. 300mL min<sup>-1</sup>) were adjusted by rotameters and measured by Omega FMA 5606 mass flowmeters. Chambers were placed inside a temperature-controlled cabinet ( $\pm 0.5^\circ\text{C}$ ). The  $T_a$  within each of the chambers was monitored with calibrated thermocouples, and read by an Omega digital thermometer (to nearest 0.1°C).  $T_b$  was measured with implanted temperature-sensitive transmitters (Mini-mitter Model X-M,  $\pm 0.1^\circ\text{C}$  accuracy) (for details, see Geiser *et al.* 1996). External noise was kept to a minimum during all measurements. Bats were weighed before and after all measurements and a linear decrease in body mass was assumed for calculation of mass-specific metabolic rates. Oxygen consumption was measured with Ametek Applied Electrochemistry S-3A oxygen analysers as described (Geiser *et al.* 1996).

Results of these measurements were used to calculate MR of torpid animals (TMR) and resting metabolic rate (RMR) over 36 minutes. RMR was calculated from the lowest steady-state oxygen consumption values in resting, normothermic bats below the thermoneutral zone (TNZ). TMR was determined by selecting the lowest steady-state MR of torpid bats. The energetic cost of torpor was calculated as the average energetic cost of a torpor bout including cost of arousal. This was calculated from the time when MR fell below RMR during entry, to the end of the arousal overshoot. The equivalent cost of resting was calculated as the mean RMR of the same individual during the same measurement. The average cost of torpor was expressed as a percentage of the average cost of RMR over the same time period. Torpor bout length was defined as the time period between MR falling below 75% RMR during torpor entry, and MR returning to 75% RMR during arousal. Average daily metabolic rate (ADMR) was calculated as the mean of all measurements recorded for any one individual over a 22 to 24 hour period.

Linear regressions were performed using the method of least squares. Similarities or differences between seasons were tested by comparing regression lines using analysis of covariance (ANCOVA). Comparison of means between both season and  $T_a$  were analysed using two-way analysis of variance (General Linear Model — method designed for unbalanced data), referred to in the text as ANOVA. Tests were performed using 'Minitab 9.0'. Levels of significance were set at  $p \leq 0.05$  for all tests. All means are presented plus or minus the standard error of the mean (SEM). Sample sizes are denoted as  $n =$  number of individuals.

## Results

The MR and  $T_b$  of *Syconycteris australis* showed pronounced daily fluctuations (Fig. 1). In all cases activity began after lights out and continued throughout the dark phase. This active phase was characterised by considerable fluctuations in metabolic rate and a relatively steady  $T_b$  of around 35°C. Immediately after lights on, three patterns of MR and  $T_b$  fluctuations were observed. The most frequent of these is shown in Fig. 1A, in which the bat showed a single, uninterrupted torpor bout. The TMR dropped to approximately 10% of RMR, and  $T_b$  during torpor approached  $T_a$ . Arousal usually occurred in the early afternoon (1300h to 1500h).

In 18% of observations bats did not enter torpor at all, but maintained their MR at a low resting level during daylight hours (Fig. 1B). A third pattern (Fig. 1C) was observed on only four occasions and only in animals collected during summer, where the bat entered torpor and showed several partial arousals throughout the day.

When the metabolic cost of resting at each  $T_a$  and season was compared with the cost of torpor, the use of uninterrupted torpor reaped some energetic benefit in all instances. Average reduction of energy expenditure during torpor in comparison to rest in summer were  $44.8 \pm 2.8\%$  ( $n=4$ ) at  $T_a$  12°C,  $64.3 \pm 2.8\%$  ( $n=7$ ) at  $T_a$  18°C and  $45.3 \pm 4.2\%$  ( $n=3$ ) at  $T_a$  25°C. In winter, average reduction of energy expenditure during torpor was  $42.4 \pm 3.1\%$  ( $n=5$ ) at  $T_a$  12°C,  $54.3 \pm 2.4\%$  ( $n=7$ ) at  $T_a$  18°C and  $45.7 \pm 7.0\%$  ( $n=2$ ) at  $T_a$  25°C. The average reduction of energy expenditure during torpor (in comparison to resting) differed significantly between  $T_a$ s (ANOVA,  $p < 0.001$ ) with energy reductions being most pronounced at  $T_a$  18°C. However, no differences between season were detected (ANOVA,  $p > 0.05$ ) (Fig. 2).

Multiple torpor bouts also resulted in a significant energetic benefit (ranging between 41 and 56%) in comparison to rest. These values were very close to the summer means at  $T_a$  12°C and 25°C, suggesting that there is little energetic penalty for the use of multiple torpor bouts in a day.

When bats remained normothermic, MR was maintained at about 75% of RMR measured after arousal and  $T_b$  was regulated at around 32°C.

At low  $T_a$ s, ADMR was influenced by the length of torpor bouts. Increasing torpor bout duration led to an overall decrease in ADMR (Fig. 3). At  $T_a$  12°C a torpor bout of 10 hours resulted in an ADMR reduction to 74% of that extrapolated to zero hours (absence of torpor). A similar pattern was observed at  $T_a$  18°C; however, at  $T_a$  25°C, ADMR appeared to be little affected by torpor bout length.

## Discussion

Daily torpor is extremely effective in reducing energy expenditure in *Syconycteris australis*. All torpor bouts at all  $T_a$ s resulted in a reduction in energy expenditure. For both summer and winter samples, torpor resulted in maximal average reduction in energy expenditure of 54–64% at  $T_a$  18°C, and although lower values of 42–45% and 45–46% were achieved at  $T_a$  12°C and  $T_a$  25°C respectively, the reduction was still substantial. The more pronounced reduction of energy expenditure at  $T_a$  18°C may be expected, as no extra cost is required for thermoregulation (as at  $T_a$  12°C) and MR is not limited by a high  $T_b$  at high  $T_a$ s (as at  $T_a$  25°C). A similar pattern was found for the rufous hummingbird (*Selasphorus rufus*), where energy expenditure decreased with a decreasing  $T_a$  above the set point for  $T_b$ , below which the pattern was reversed as the bird began to defend its  $T_b$  (Kenagy 1989).

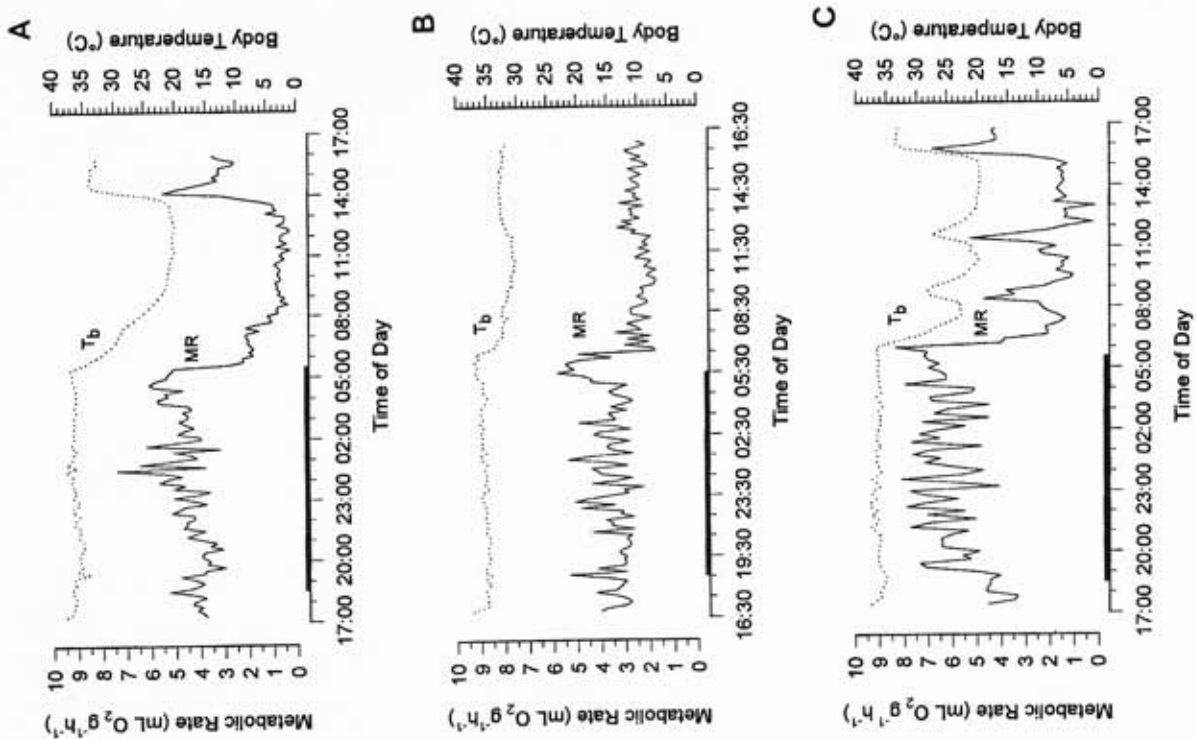


Fig. 1. Three patterns of daily fluctuations in  $T_b$  and MR at  $T_a$  18°C observed in *S. australis*. Uninterrupted daily torpor (A) was observed most frequently, while low RMR without torpor (B) and multiple torpor bouts (C) were observed occasionally. Dark bars represent period of darkness.

A reduction of energy expenditure was also observed in bats that remained normothermic throughout the day, but with a low  $T_b$  of about 32°C and a MR reduced to approximately 75% of the "normal" RMR. However, a significantly greater amount of energy was saved by employing daily torpor. The reasons as to why individuals may choose to remain at rest rather than entering torpor are unclear.

By looking at the energy that can be saved by entering torpor, even if only on a daily basis, it becomes obvious why torpor is a very successful strategy in overcoming food shortages and/or the energetic demands of increased thermoregulation during exposure to cold. Reduction of ADMR by the use of torpor in *Syconycteris australis* were similar to that in Djungarian hamsters, *Phodopus sungorus*, the deer mouse, *Peromyscus maniculatus* (Ruf & Heldmaier 1993) and the fat-tailed dunnart, *Smithopsis crassicaudata* (Holloway & Geiser 1995). However, it is possible that part of the reduction in energy expenditure may be from the reduced level of activity during the night, a scenario which may be applicable to many species, including *S. australis* (Ruf & Heldmaier 1993).

ADMR was found to decrease with increasing torpor bout length (Fig. 3). A longer period of time where the metabolic rate is minimal, as during torpor, would be expected to decrease the overall metabolic rate over a 24 hour period. This effect of torpor on ADMR shows how important the use of torpor can be in helping to reduce overall daily energy expenditure, especially when food resources are scarce or low temperatures require greater heat production for thermoregulation.

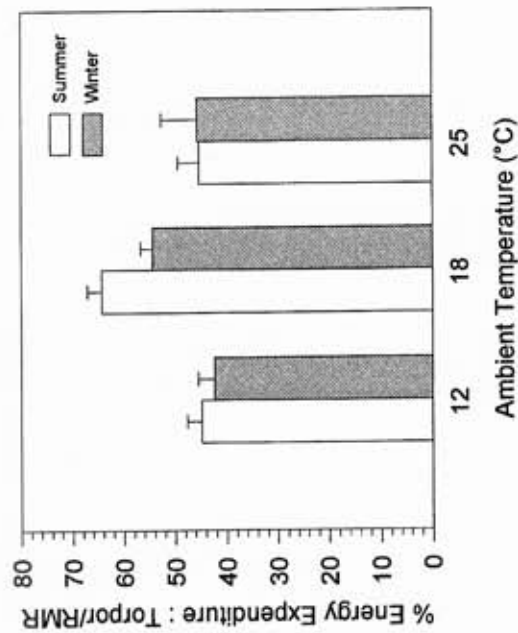


Fig. 2. Percentage reduction of energy expenditure during torpor in comparison to rest in *S. australis* at three ambient temperatures during summer and winter. Values represent means  $\pm$  SE for  $n=4$  ( $T_a$  12°C),  $n=7$  ( $T_a$  18°C) and  $n=3$  ( $T_a$  25°C) in summer and  $n=5$  ( $T_a$  12°C),  $n=7$  ( $T_a$  18°C) and  $n=2$  ( $T_a$  25°C) during winter.

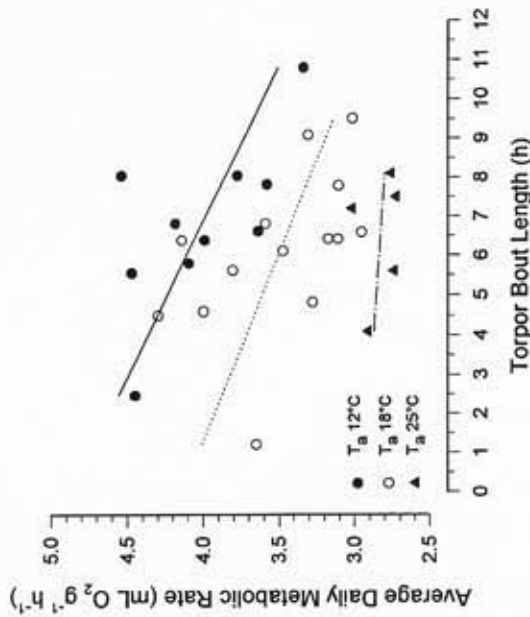


Fig. 3. Regression analysis of average daily metabolic rate (ADMR) as a function of torpor bout length in *S. australis* at three ambient temperatures. Figure shows a general decrease in ADMR with increasing torpor bout length. Regression equations are as follows:

$$(T_a 12^\circ\text{C}) \text{ADM}R(\text{mL O}_2 \text{ g}^{-1} \text{ h}^{-1}) = 4.87 - 0.125 \text{ Bout length (h)} \quad (P=0.04, r^2 = 0.42)$$

$$(T_a 18^\circ\text{C}) \text{ADM}R(\text{mL O}_2 \text{ g}^{-1} \text{ h}^{-1}) = 4.14 - 0.105 \text{ Bout length (h)} \quad (P=0.07, r^2 = 0.25)$$

$$(T_a 25^\circ\text{C}) \text{ADM}R(\text{mL O}_2 \text{ g}^{-1} \text{ h}^{-1}) = 2.95 - 0.018 \text{ Bout length (h)} \quad (P=0.71, r^2 = 0.05)$$

*Syconycteris australis* is the only small member of the Australian Megachiroptera to be found outside tropical climates. The southerly extreme of this distribution falls in an area that could be considered as transitional between subtropical and temperate climates (Law 1994a). As a result, the southerly distribution of this species is very interesting from an energetic perspective. Is it possible that the use of torpor by this bat enables it to save enough energy to cope with the thermoregulatory demands of its southerly distribution? Of course, this question cannot be resolved here, but requires further comparative studies with other small megachiropteran species from the tropics.

From the results of this study, however, we may speculate that the range of *S. australis* is more likely to be limited by food availability rather than cold exposure. This is supported firstly by the apparent lack of differences in torpor duration between  $T_a$ s, and secondly by the fact that no torpor was observed at a  $T_a$  of 25°C when food was available in excess, while bats readily entered torpor at a  $T_a$  of 25°C when food was absent. This observation supports the argument that bats depending on a diet of nectar, pollen and fruit appear to be restricted more by food availability than by the energy cost of thermoregulation (Fenton 1983). Food availability would appear to be a limiting resource for the *Syconycteris australis* at the southern end of its distribution (Law 1994b). Indeed, the local abundance of *S. australis* showed a positive correlation with the density of food resources, with a noticeable immigration of individuals to an area of abundant food resources occurring within only a week (Law 1995). The changes in food availability for *S. australis* is likely to have a profound effect on their energy budget. When food is scarce, commuting distance

between the roost and feeding sites may be substantially increased, making the use of torpor for energy conservation attractive. The alternative of shifting roost positions to reduce commuting distances may be possible (Law 1993). However, limited areas of coastal rainforest in recent years may have eliminated this behavioural option, making the physiological option of torpor a convenient and effective alternative.

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