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Seasonal changes in energetics and torpor patterns in the subtropical blossom-bat *Syconycteris australis* (Megachiroptera)

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Abstract Little is known about how animals from tropical and subtropical climates adjust their energy expenditure to cope with seasonal changes of climate and food availability. To provide such information, we studied the thermal physiology, torpor patterns and energetics of the nocturnal blossom-bat (*Syconycteris australis* 18 g) from a subtropical habitat in both summer and winter. In both seasons, *S. australis* frequently entered daily torpor at ambient temperatures between 12 and 25°C when food and water were withheld. Unlike patterns observed in temperate animals, mean minimum metabolic rates during torpor were lower in summer (0.47 ± 0.07 ml O_2 g^{-1} h^{-1}) than in winter (0.75 ± 0.11 ml O_2 g^{-1} h^{-1}). Body temperatures during torpor were regulated at 19.3 ± 1.0°C in summer and at 23.4 ± 2.0°C in winter. Torpor bout duration was significantly longer in summer (7.3 ± 0.6 h) than in winter (5.5 ± 0.3 h), but in both seasons, bout duration was not affected by ambient temperature. Consequently, average daily metabolic rates were also significantly lower in summer than in winter. Body temperatures and metabolic rates in normothermic bats did not change with season. Our findings on seasonal changes of torpor in this bat from the subtropics are opposite to those made for many species from cold climates which generally show deeper and longer torpor in winter and are often entirely homeothermic in summer. More pronounced torpor in subtropical *S. australis* in summer may be due to low or unpredictable nectar availability, short nights which limit the time available for foraging, and long days without access to food. Thus, the reversed seasonal response of this subtropical bat in comparison to temperate species may be an appropriate response to ecological constraints.

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Introduction

Hibernation and daily torpor are characterised by controlled reductions of metabolic rate (MR) and body temperature (T_b) and are widely used by small mammals and birds to overcome adverse environmental conditions (Hudson 1978; Wang 1989). Seasonal changes in torpor patterns occur in many mammals that inhabit areas with cold climates. Torpor is generally much more pronounced in winter and in many species does not occur at all during summer. Because both hibernation and daily torpor can substantially reduce energy expenditure, it is widely believed that they are adaptations of endothermic species from cold climates and are employed to overcome periods of cold exposure and low food availability during winter.

Nevertheless, a number of species from tropical and subtropical regions that never experience very low ambient temperature (T_a) also may enter torpor (Bartholomew et al. 1970; McNab 1989; Genoud et al. 1990; Stephenson and Racey 1994; McNab and Bonaccorso 1995; Ortmann et al. 1996; Schmid 1996; Audet and Thomas 1997). These observations suggest that torpor may be used widely for energy conservation by many species that experience periodic food shortages even in warm climates. Unfortunately, little is known about seasonal changes of torpor patterns and energetics in species from the tropics and subtropics. A priori, one might predict that if seasonal changes in thermal biology occur in warm climates they follow the same pattern as those observed in temperate regions, but are less pronounced. Conversely, since cold exposure in the subtropics in winter is relatively modest, and seasonal changes in food availability often differ from those in cold climates, seasonal changes of torpor, if they do occur, may differ from those for temperate species.

To provide information on how physiological variables are affected by seasonal changes of ecological constraints in the subtropics, we investigated seasonal variation in torpor patterns of the common blossom-bat, *Syconycteris australis*. This species regularly displays daily torpor in the laboratory when food is withheld overnight and T_a is below about 26°C, and at lower T_as may even enter spontaneous torpor (food and water available) occasionally (Coburn and Geiser 1996; Geiser et al. 1996). To test the hypothesis that seasonal changes differ from those in temperate species, we measured physiological variables of bats that were collected from the same subtropical site in both summer and winter.

Materials and Methods

Bats were captured with mist nets near Iluka on the north coast of New South Wales, Australia (29°13′S, 153°21′E). Nine adult male bats (body mass 18.0 ± 1.1 SD g) were caught on 20–24 February 1995 (summer) and nine adult male bats (body mass 17.5 ± 1.0 g) were caught on 24–29 June 1995 (winter).

Bats were maintained at the University of New England in a holding room (3.5 × 2.1 × 3.0 m) that provided enough space for flight. The room was fitted with branches and wide plastic mesh for roosting and for providing access to feeders. T_a was maintained at 20 ± 1°C and relative humidity above 40%. Throughout the experiments, photoperiod was maintained at the natural photoperiod of the time of capture which was 13L:11D (lights on 0530 hours, lights off 1830 hours) in summer and 10L:14D (lights on 0700 hours, lights off 1700 hours) in winter.

Bats were fed daily using a blended food mixture (Geiser et al. 1996). Food (about 33 ml/bat) was provided to bats in ten plastic feeders. Feeders were washed and soaked in Milton antibacterial solution each day. Water was provided ad libitum in bird feeders and shallow dishes.

The MR was measured as rate of oxygen consumption ($\dot{V}O_2$). The daily fluctuation of MR was measured at constant T_a ranging from 12 to 25°C over a minimum of 22 h. Measurements began around 1600 hours and the same procedures were followed for both summer- and winter-acclimatised animals.

Basal metabolic rates (BMRs) were measured separately in post-absorptive animals during daylight hours beginning at around 0900 hours. For BMR measurements, T_a was increased from 28°C by about 2°C increments to a maximum of about 36°C. Each temperature increment lasted for 1–2 h and determination of BMR usually took about 7–8 h. MR was considered to be basal when three consecutive minimal readings over 36 min were observed in normothermic bats. The thermoneutral zone (TNZ) was estimated from the T_a range in which BMR values of individual bats were observed.

Food and water were not available to bats during measurements of MR. Photoperiod during all measurements was the same as in the holding room.

MR measurements were conducted in 1-l respirometer chambers fitted with wide plastic mesh for roosting. Flow rates (approx. 300 ml min^{-1}) were controlled with rotameters and measured by mass flowmeters (Omega FMA 5606). Chambers were placed inside a quiet, temperature-controlled cabinet (±0.5°C). The T_a within each chamber was monitored with a calibrated thermocouple and read to the nearest 0.1°C by a digital thermometer (Omega DP116). Body mass was recorded before and after all measurements and a linear decrease in body mass was assumed for calculation of mass-specific metabolic rates.

Percent oxygen was measured by Ametek Applied Electrochemistry S-3A oxygen analysers. Two systems were used for MR measurements. Usually, a single-channel S-3AI, fitted with a high-resolution output board (80335SE) was used. Four channels, three animal and one reference channel (outside air), were measured in sequence for 3 min each (i.e. each channel and reference were measured once every 12 min). Solenoid valves controlled the sampling. Outputs from the flowmeters, oxygen analyser and thermocouples were recorded on a personal computer via an A/D 14-bit converter card. On occasion, a dual-channel S-3AII system was used; two bats were measured simultaneously every 3 min and solenoid valves switched to outside air for 3 min out of every 30 min. Output from oxygen analyser, flow meters and thermocouples was transferred to a personal computer using a Datataker DT100 data logger.

Data from MR measurements were used to calculate MR of torpid animals (TMR), resting metabolic rate (RMR), BMR, torpor frequency and torpor bout length. BMR was calculated using the lowest steady-state metabolic rate values of normothermic bats within the TNZ (see above). RMR was calculated from the lowest steady-state oxygen consumption values in resting, normothermic bats below the TNZ. TMR was determined by selecting the lowest steady-state MR of torpid bats. Average values for RMR, BMR and TMR for each individual were calculated from measurements over a minimum of 36 min. The average daily metabolic rate (ADMR) was calculated as the mean of all MR measurements of each individual over a 22- to 24-h 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.

Six bats in each season were surgically implanted with temperature-sensitive transmitters (Mini-Mitter Model X-M, ±0.1°C accuracy). Before implantation, wax-coated transmitters were calibrated in a waterbath to the nearest 0.1°C using a precision mercury thermometer. The transmitter package weighing about 1.3 g was implanted intraperitoneally under Forthane (isoflurane) anaesthesia. Antibiotics (mixed into food) were provided and bats were allowed to recover for at least 7 days before any measurements were made. Core T_bs were monitored using an AM receiver and recorded together with measurements of T_a and O_2 consumption.

Measurements of T_b were used to calculate mean T_b of each individual during RMR, TMR and BMR over a minimum of 36 min. Bats with a T_b below 30°C or an MR that was below that of bats with a T_b of < 30°C at the same T_a were considered torpid.

Comparisons of means between both season and T_a were made by two-way analysis of variance (General Linear Model – method designed for unbalanced data), referred to in the text as ANOVA. χ^2 analysis was used to test for differences in the frequency of torpor. Comparisons of two means were conducted using a *t*-test after testing for homogeneity. Linear regressions were performed using the method of least squares. Differences between seasons were tested by comparing regression lines using analysis of covariance (ANCOVA). Tests were performed using 'Minitab'. Levels of significance were set at $P < 0.05$ for all tests. All means in the results are presented as ±1 standard error of the mean (SEM) for the number of individuals (n) that were measured.

Results

Both MR and T_b of *S. australis* showed pronounced daily fluctuations (Fig. 1a,b). Initial fluctuations of MR occurred immediately after measurements began, when bats were exploring their surroundings and settling down after handling. The initial exploratory phase was usually followed by a period of rest, characterised by low normothermic MR. Activity began after lights went off and continued throughout the dark phase. During this active phase, the MR fluctuated substantially and T_b was around 35–37°C. Torpor entry, characterised by a pronounced drop of MR and T_b, always occurred immediately after lights on. Spontaneous arousals,

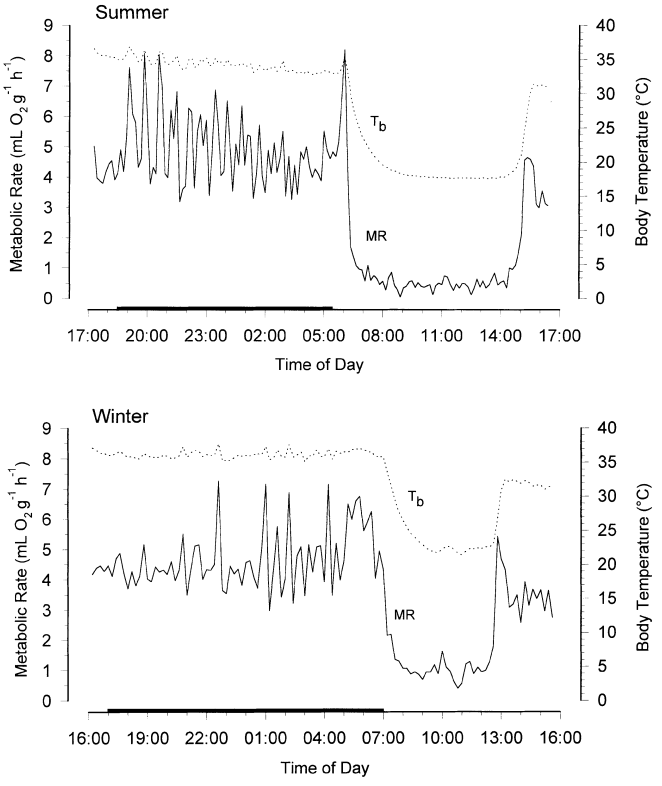

Fig. 1 Daily fluctuations in metabolic rate (*MR*) and body temperature (T_b) for two individual *Syconycteris australis* using torpor in winter and summer at ambient temperature (T_a) 18°C. The *solid bar* represents the period of darkness

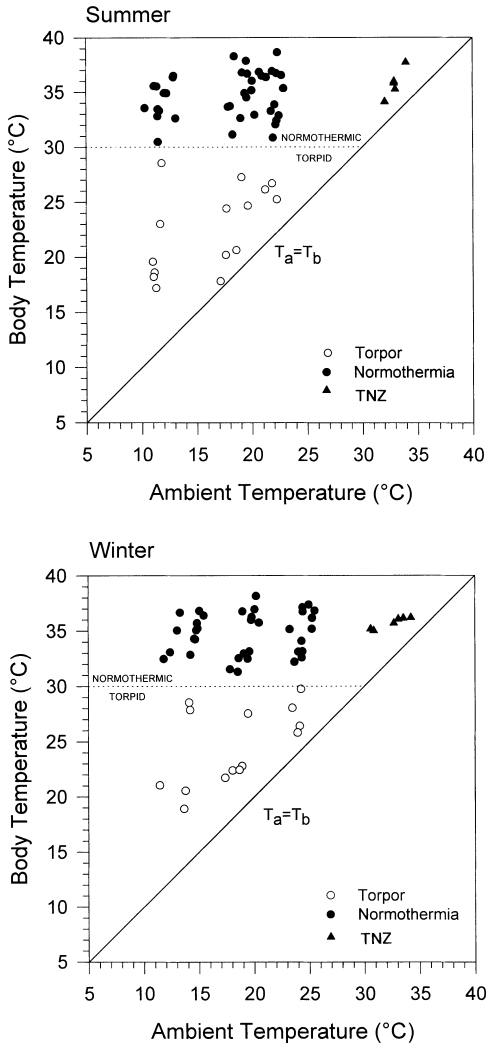

Fig. 2 Body temperature (T_b) as a function of air temperature (T_a) during summer and winter in *S. australis*. The T_b of torpid and resting bats below and within the thermoneutral zone (BMR) are shown. Each data point represents a measurement of an individual bat at a particular T_a. Each individual was measured over the entire range of T_a and values at a particular T_a represent different individuals for which data could be obtained. The *diagonal line* represents $T_a = T_b$, the *broken horizontal line* represents the threshold between normothermia ($T_b > 30$°C) and torpor ($T_b < 30$°C)

characterised by a rise in MR to near-active levels and the consequential rise in T_b, usually occurred between late morning and early afternoon. After arousal, bats were resting and had a low normothermic T_b and MR. The general torpor pattern was similar in both summer and winter and at all T_a, but in summer, torpor was longer and appeared to be deeper than in winter.

Torpor was frequently observed in all summer ($n = 9$) and winter ($n = 9$) bats over the entire range of T_a investigated. Torpor occurred in 80% of observations during summer and in 83% of observations during winter. Torpor frequency was unaffected by T_a or season (χ^2, $P > 0.25$).

T_b during torpor fell with T_a to a minimum of 19.3 ± 1.0°C ($n = 5$) in summer and 23.4 ± 2.0°C ($n = 5$) in winter at a T_a of about 12°C. The minimum individual T_b was 17.2°C in summer and 18.9°C in winter (Fig. 2). The mean minimum T_b during torpor did not differ significantly between seasons, because of the large variance.

In both summer and winter, TMR was lowest around T_a 18°C, but increased both above and below this T_a (Figs. 3, 4). At T_as above 18°C, no differences between seasons in the response of TMR to T_a were detected (ANCOVA, P > 0.10). However, below T_a 18°C, at which bats defended their T_b by proportional thermoregulation, the elevation of the regression for TMR versus T_a was significantly higher in winter than in summer (ANCOVA, $P < 0.001$), while the slopes were indistinguishable (ANCOVA, $P > 0.10$). The mean minimum TMR occurred around T_a 18°C in both seasons and was 0.47 ± 0.07 ml g^{-1} h^{-1} ($n = 9$) in summer which was significantly lower ($P < 0.05$) than the 0.75 ± 0.11 ml g^{-1} h^{-1} ($n = 8$) measured in winter.

Mean torpor bout length of undisturbed, single bouts during summer ranged from 7.1 to 8.2 h in summer and from 4.9 to 6.5 h in winter (Fig. 5). Torpor bout length differed between seasons at all T_as (ANOVA, $P < 0.001$), but was not affected by T_a (ANOVA, $P > 0.10$). On average, summer individuals remained torpid for around 1.7–2.7 h longer than those tested during winter (Fig. 5).

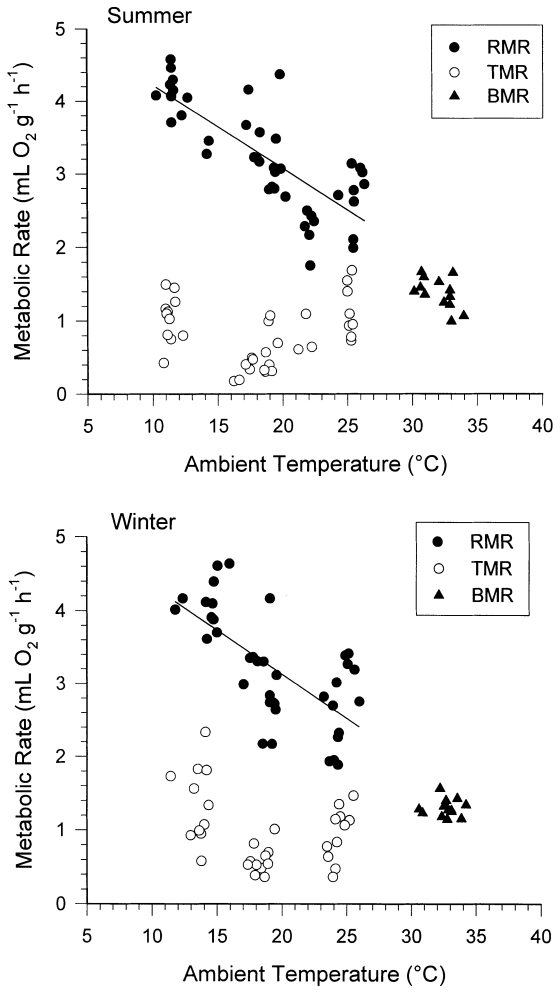

Fig. 3 Metabolic rates as a function of ambient temperature (T_a) for summer and winter, in *S. australis* showing metabolic rates below and within the thermoneutral zone (*BMR*), during torpor (*TMR*) and rest (*RMR*). Each data point represents a measurement of an individual bat at a particular T_a. Each individual was measured over the entire range of T_a and values at a particular T_a represent different individuals for which data could be obtained. Regression equations for metabolic rates at rest are: summer RMR (ml O_2 g^{-1} h^{-1}) = $5.36 - 0.114T_a$ (°C) ($P < 0.001$, $r^2 = 0.63$); winter RMR (ml O_2 g^{-1} h^{-1}) = $5.55 - 0.121T_a$ (°C) ($P < 0.001$, $r^2 = 0.45$)

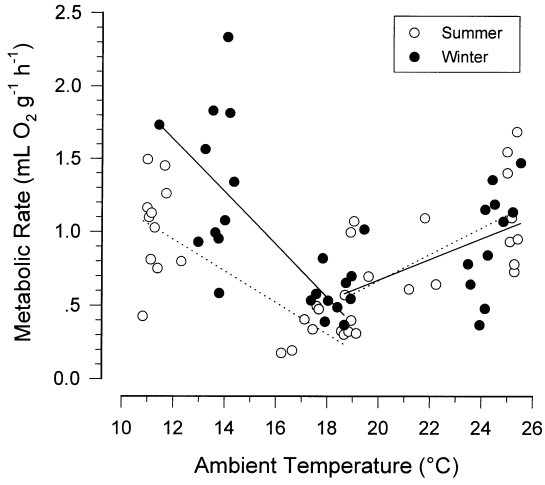

Fig. 4 Response of metabolic rates during torpor (TMR) of *S. australis* in summer (*broken lines*, *open symbols*) and winter (*solid lines and symbols*). Each data point represents a measurement of an individual bat at a particular T_a. Each individual was measured over the entire range of T_a and values at a particular T_a represent different individuals for which data could be obtained. Regression equations for summer are: TMR (ml O_2 g^{-1} h^{-1}) = $2.23 - 0.107T_a$ (°C) ($P < 0.001$, $r^2 = 0.62$) for T_a 12–18°C, and TMR (ml O_2 g^{-1} h^{-1}) = $-1.12 + 0.089T_a$ (°C) ($P = 0.003$, $r^2 = 0.42$) for T_a 18–25°C. Regression equations for winter are: TMR (ml O_2 g^{-1} h^{-1}) = $3.79 - 0.180T_a$ (°C) ($P = 0.001$, $r^2 = 0.50$) for T_a 12–18°C, and TMR (ml O_2 g^{-1} h^{-1}) = $-0.725 + 0.070T_a$ (°C) ($P = 0.033$, $r^2 = 0.29$) for T_a 18–25°C

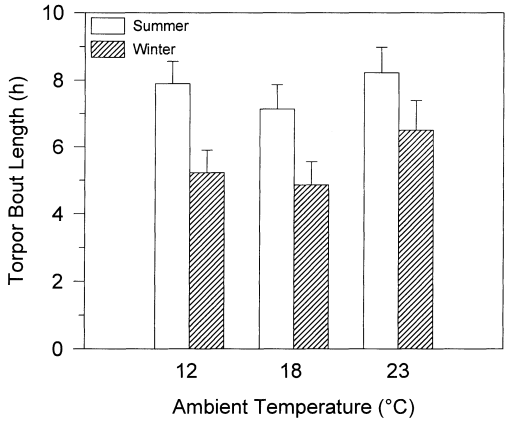

Fig. 5 Average torpor bout length in hours in *S. australis* at three ambient temperatures for both summer and winter. Values represent means ±SE for $n = 6$ (T_a 12 ± 2°C), $n = 9$ (T_a 18 ± 2°C) and $n = 8$ (T_a 23 ± 2°C) in summer and $n = 5$ (T_a 12 ± 2°C), $n = 7$ (T_a 18 ± 2°C) and $n = 7$ (T_a 23 ± 2°C) during winter. Torpor bouts at all T_as differed between seasons ($P = 0.001$)

The MR of normothermic, resting bats was minimal between T_as of 30.2–34.2°C, but increased significantly below and above this range. We thus assumed that the TNZ ranged from 30.2 to 34.2°C. The BMR within this TNZ was 1.38 ± 0.21 ml g^{-1} h^{-1} (summer, $n = 9$) and 1.30 ± 0.11 ml g^{-1} h^{-1} (winter, $n = 9$) (Fig. 3) and the corresponding T_b was 35.8 ± 1.3°C ($n = 5$) during summer and 35.7 ± 0.5°C ($n = 6$) in winter (Figs. 2, 3). Variables did not differ between seasons.

The range for resting T_b below the TNZ in summer fell between 30.5°C and 34.9°C, and between 31.3°C and 35.1°C in winter. Resting T_b in both seasons was not affected by T_a ($P > 0.10$) and the T_b during rest did not differ between seasons (ANCOVA, $P > 0.10$).

In summer and winter, RMR was inversely related to T_a (summer: $P < 0.001$, $r^2 = 0.63$; winter: $P < 0.001$, $r^2 = 0.45$) (Fig. 3). When regression lines for RMR between summer and winter were compared, no differences were detected for either slope or elevation (ANCOVA, $P > 0.10$).

The ADMR was inversely related to T_a in both summer and winter (Fig. 6). The ADMR in summer was lower than in winter particularly at low T_a and elevations of the two linear regressions differed significantly between seasons (ANCOVA, $P < 0.001$), whereas the slopes were indistinguishable ($P > 0.05$).

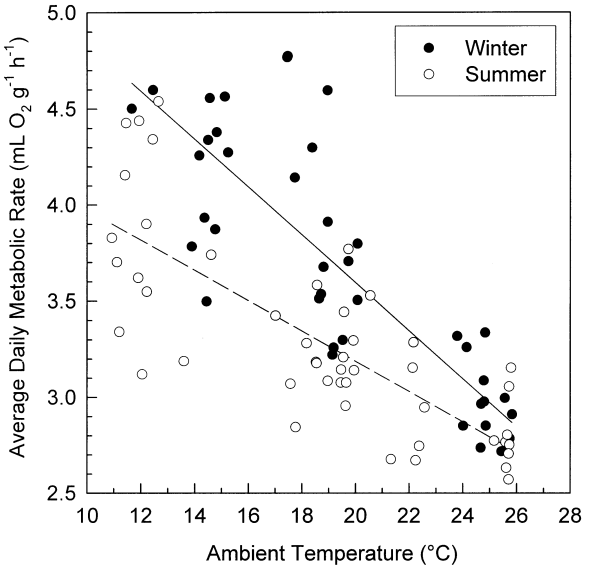

Fig. 6 Average daily metabolic rate (ADMR) as a function of ambient temperature in *S. australis* during summer (*broken line*, *open symbols*) and winter (*solid line and symbols*). Each data point represents a measurement of an individual bat at a particular T_a. Each individual was measured over the entire range of T_a and values at a particular T_a represent different individuals for which data could be obtained. Elevations of the regressions differed between seasons ($P < 0.001$) and regression equations were: summer: ADMR (ml O_2 g^{-1} h^{-1}) $= 4.76 - 0.079T_a$ (°C) ($P < 0.001$, $r^2 = 0.60$); winter: ADMR (ml O_2 g^{-1} h^{-1}) $= 6.09 - 0.125T_a$ (°C) ($P < 0.001$, $r^2 = 0.68$)

Discussion

Our study provides the first detailed results on seasonal changes of torpor patterns in a mammal from a subtropical climate. Torpor in the blossom-bat *S. australis* occurred over a range of T_a in both summer and winter. The prediction that seasonal changes in torpor patterns are less pronounced than in species from temperate climates was not supported. On the contrary, torpor in *S. australis* was more pronounced in summer than in winter, which is opposite to seasonal changes of torpor in species from cold climates.

Physiological variables measured here for *S. australis* were very similar to those of other daily heterotherms (Geiser and Ruf 1995). Metabolic rates were reduced by about 30–60% of BMR as in other species, T_b was regulated around 20°C, and bouts lasted for several hours. Seasonal changes were most pronounced for TMR, which in summer was about 63% of the winter value, and for torpor bouts, which were about 40% longer in summer than in winter. As a consequence of the low TMR and long bouts, ADMR was significantly lower in summer than in winter. This reduction in ADMR suggests that the use of torpor provides potential for a significant reduction in daily energy expenditure especially during summer. The T_b in summer also appeared to be lower than in winter, but means were indistinguishable because of large variation.

In contrast to several physiological variables of bats in torpor, values for normothermic blossom-bats did not show any detectable seasonal changes. This differs from many other, particularly cold-climate endotherms, which may show a change in BMR and thermal conductance in winter (Feist and White 1989). However, a number of other mammals show no seasonal change in BMR as in the present study (Geiser and Baudinette 1987; Feist and White 1989). The BMR measured in both seasons was relatively low (Dawson 1989), which may be attributed to this species' diet of nectar and pollen (MacMillen 1985).

Most studies investigating seasonal changes in torpor patterns have been conducted on hibernators, many of which are strictly homeothermic in summer and show periods of torpor only during winter (Hudson 1973; Wang 1989). Species exhibiting exclusively daily torpor, like *S. australis*, are not as well studied, but most of these appear to display more pronounced torpor in winter than in summer. Studies on North American mice (*Peromyscus* spp.), and small insectivorous marsupials from Australian arid zones with unpredictable rainfall and low winter T_a (*Sminthopsis* spp.) revealed that torpor is usually more frequent and deeper in winter; however, it may occur occasionally during most times of the year (Gaertner et al. 1973; Geiser and Baudinette 1987; Tannenbaum and Pivorun 1988). The hamster *Phodopus sungorus* from Siberia shows no spontaneous torpor in summer, but like other species displays torpor in winter (Heldmaier and Steinlechner 1981; Geiser and Heldmaier 1995). In contrast to these species, but similar to *S. australis*, the coastal small insectivorous Australian marsupials, *Antechinus stuartii* and *A. flavipes*, from temperate areas with predictable rainfall, show more pronounced torpor in summer, when they are about half grown, than in winter, when they have reached adult body mass (Geiser 1988). However, in contrast to *S. australis*, this response in *Antechinus* spp. appears to be explained largely by the pronounced change in body mass.

The tropical origin and tropical-to-subtropical distribution of *S. australis*, and lack of pronounced seasonal changes in climate within its range, might on the surface suggest that there is little environmental pressure for a seasonal change in torpor patterns. Because torpor in *S. australis* was more pronounced in summer than in winter and because this is the opposite to the response of many species from temperate climates (Gaertner et al. 1973; Heldmaier and Steinlechner 1981; Geiser and Baudinette 1987; Tannenbaum and Pivorun 1988; Kenagy 1989; Dark et al. 1994), the question arises as to why they may differ from others and which environmental influences may be responsible for their entirely different response.

Bats depending on a diet of nectar, pollen and fruit appear to be geographically restricted more by food availability than by the energy cost of thermoregulation (Fenton 1983). From the results of our study, we speculate that the distribution of *S. australis* is also more

likely to be limited by food availability than by cold exposure. This is supported firstly by the apparent lack of differences in torpor bout length between T_as, and secondly by the fact that no torpor was observed at T_a 18°C when food was available in excess and that torpor occurred only occasionally in the holding room at T_a 20°C, whereas bats readily entered torpor at T_a 25°C when food was withheld. Since food availability would appear to be a limiting resource for *S. australis* at the southern end of its distribution (Law 1994a,b), a likely explanation for the more pronounced torpor in summer is a response to the relatively low, patchy, or unpredictable nectar availability during this season (Armstrong 1991). Torpor is generally accepted to be a response to energy restrictions, and for *S. australis*, the stress of restricted food availability may be greater than that of low temperatures at colder times of year. Indeed, 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).

Seasonal changes in food availability for *S. australis* are likely to have a profound effect on their energy budget. When food is scarce, commuting distance between roost and feeding sites may be substantially increased, making locomotion more expensive, which may result in a higher torpor frequency. Shifting roost positions to reduce commuting distances may be possible (Law 1993); however, the available area of coastal rainforest which is used for roosting by this bat has been reduced by logging in recent years and may have eliminated or restricted this behavioural option, making the physiological option of torpor a more effective alternative.

The second important and most likely additive factor that has to be considered is the relative length of day and night in summer and winter. In summer, foraging and feeding by bats are restricted by short nights when fuel has to be collected from a limited supply which has to suffice for maintenance and thermoregulation the following long day. In contrast, during winter, bats have ample time to forage and collect food from an abundant resource, and short days without food should not pose as large an energetic problem especially given the moderate daytime temperatures to which they are exposed.

The importance of thermoregulatory energetics in free-ranging *S. australis* is emphasised by their selection of roost sites. Their lowest energy expenditure would be achieved if they roost within the TNZ of T_a 30.2–34.2°C when normothermic and around T_a 20°C when torpid. Roost site selection by *S. australis* according to prevailing T_a does occur (Law 1993). On warm days, bats tend to roost towards the centre of the rainforest patch which is best buffered from high outside temperatures. On cooler days, bats roost closer to the edge of the rainforest. *S. australis* appears to prefer T_as of around 18–24°C, which are optimal for reduction of MR during torpor.

In summary, our study shows that torpor occurs frequently in both summer and winter in the blossom-bat *S. australis* from a subtropical climate. In contrast to most other observations on species from cold climates, torpor was more pronounced in summer than in winter which, although unexpected, appears to be an appropriate physiological adaptation to ecological constraints of their subtropical habitat.

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