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Daily torpor and energetics in a tropical mammal, the northern blossom-bat *Macroglossus minimus* (Megachiroptera)

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Abstract Little is known about torpor in the tropics or torpor in megachiropteran species. We investigated thermoregulation, energetics and patterns of torpor in the northern blossom-bat *Macroglossus minimus* (16 g) to test whether physiological variables may explain why its range is limited to tropical regions. Normothermic bats showed a large variation in body temperature (T_b) (33 to 37 °C) over a wide range of ambient temperatures (T_as) and a relatively low basal metabolic rate (1.29 ml O_2 g^{-1} h^{-1}). Bats entered torpor frequently in the laboratory at T_as between 14 and 25 °C. Entry into torpor always occurred when lights were switched on in the morning, independent of T_a. MRs during torpor were reduced to about 20–40% of normothermic bats and T_bs were regulated at a minimum of 23.1 ± 1.4 °C. The duration of torpor bouts increased with decreasing T_a in non-thermoregulating bats, but generally terminated after 8 h in thermoregulating torpid bats. Both the mean minimum T_b and MR of torpid *M. minimus* were higher than that predicted for a 16-g daily heterotherm and the T_b was also about 5 °C higher than that of the common blossom-bat *Syconycteris australis*, which has a more subtropical distribution. These observations suggest that variables associated with torpor are affected by T_a and that the restriction to tropical areas in *M. minimus* to some extent may be due to their ability to enter only very shallow daily torpor.

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Abbreviations $ADMR$ average daily metabolic rate · BMR basal metabolic rate · MR metabolic rate · RMR resting metabolic rate · TMR metabolic rate during torpor · T_a air temperature · T_b body temperature · TNZ thermal neutral zone · $\dot{V}O_2$ rate of oxygen consumption

Introduction

Many small insectivorous bats of the suborder Microchiroptera from temperate and cool climates use torpor to conserve energy (Lyman 1982). When exposed to low ambient temperatures (T_a), bats lose heat rapidly due to their relatively large surface area. When these conditions are coupled with periods of food scarcity they cannot meet the energy requirements of sustaining a constant high body temperature (T_b) and energy-expensive flight because of very limited internal energy stores. The ability to enter torpor allows bats to survive adverse conditions, because daily energy expenditure can be reduced substantially by lowering their T_b and metabolic rate (MR) (Hock 1951; Thomas 1995; Geiser and Ruf 1995).

In contrast, bats of the suborder Megachiroptera were in the past believed to be strictly homeothermic (Ransome 1990). Because most of them are large and are restricted to tropical and sub-tropical areas where seasonal changes of food availability are less pronounced than in temperate climates, it was surmised that there was no need to employ torpor. However, more recent studies on small (< 20 g) fruit and blossom-bats (Bartholomew et al. 1970; Kulzer and Storf 1980; McNab and Bonaccorso 1995; Coburn and Geiser 1996; Geiser et al. 1996) have shown that some small megachiropteran species are indeed heterothermic.

The most detailed measurements of physiological variables in a heterothermic megachiropteran are available for the common blossom-bat *Syconycteris australis* (17 g) of Australia (Geiser et al. 1996). This species entered daily torpor readily, allowed T_b to fall below 20 °C and showed a substantial reduction of MR. The distribution range of *S. australis* extends much further south than that of other small Australian megachiropterans bordering on areas with a temperate climate (Law 1994). One of the reasons for this southerly distribution may be due to their effective use of torpor (Geiser et al. 1996). In contrast, the northern blossom-bat *Macroglossus minimus* (syn. *M. lagochilus*) (14–18 g), which is the only other blossom-bat species found in Australia, is restricted to the tropics (McKean et al. 1995). There is some evidence that *M. minimus* from New Guinea is also heterothermic (McNab and Bonaccorso 1995), but limited quantitative data on physiological variables have been reported.

The purpose of the present study was to quantify physiological variables of both torpid and normothermic *M. minimus*. We tested whether the different distributions of the two Australian blossom-bats can be explained by differences in the frequency of torpor or differences in physiological variables associated with torpor.

Materials and methods

Six *M. minimus* (three males, three females) were captured using mist nets set among flowering mangroves (*Sonneratia alba*) near the Cairns Port on 8 September 1996. After capture bats were fed and flown on the same day to the University of New England, Armidale. Upon arrival the bats weighed 14.0 ± 0.8 g, and were housed in a room (2.2 m × 3.3 m × 3.0 m) containing leaves and branches, and plastic mesh for roosting, and ample room for flight. Bats were maintained throughout the experiment at a T_a of 22 ± 1 °C with a photoperiod of LD 12:12, similar to the natural photoperiod at the time of capture. Lights were on from 0600 to 1800 hours.

The bats were fed a blended mixture of 500 ml apple juice, two bananas, 150 g raw sugar, 150 g 'Glucodin', and 120 g 'Infasoy'. The mixture was frozen and each day one 75-ml portion was defrosted and diluted with an equal volume of water. The food was then placed into six 24-ml plastic feeders situated in positions accessible to the bats. Each day before feeding, the feeders were removed, washed and soaked in Milton antibacterial solution to prevent the growth of microorganisms. Water was available ad libitum in bird feeders. The animals were hand fed for 2 days after arrival in Armidale until their body mass increased and they learned to feed for themselves.

T_b was measured with implanted transmitters. Before implantation, wax-coated, temperature-sensitive transmitters (Minimitter Model X-M, accuracy ±0.1 °C) were calibrated to the nearest 0.1 °C against a precision mercury thermometer in a water bath between 5 and 40 °C. The transmitters weighed approximately 1.2 g and were implanted intraperitoneally under Forthane anaesthesia. The animals were allowed 10 days to recover from the surgery before experiments were conducted.

MR was measured as the rate of oxygen consumption ($\dot{V}O_2$). Bats were placed individually into 0.75-l respirometry chambers, fitted with plastic mesh for roosting, situated within a temperature-controlled cabinet (±0.5 °C). Three animal channels and one reference channel were scanned with solenoid valves. Each channel was read for 3 min in sequence (i.e. the MR of each animal was measured every 12 min). The flow rate was controlled with rotameters at about 300 ml min^{-1} and flow rates were measured with Omega FMA-5606 mass flowmeters. The O_2 content leaving the animal chambers was measured in sequence with an Ametek Applied Electrochemistry S-3A O_2 analyser fitted with a high resolution output board (80335SE).

The T_a inside the respirometer was measured to the nearest 0.1 °C using a digital thermocouple thermometer (Omega DP116). The transmitter signal for T_b measurements was received by a ferrite rod antenna, transformed to a square-wave signal after subtraction of background noise and multiplexed to an AM receiver.

Analog outputs from the flowmeter, O_2 analyser, digital thermometer, and receiver were interfaced to a personal computer via a 14-bit A/D card. The software for data acquisition was written by B. Lovegrove, T. Ruf, and G. Körtner.

The T_b and MR of bats were measured for approximately 22 h beginning in late afternoon. An initial measurement of MR was taken on bats without transmitters to determine whether or not they entered torpor. Food or water were not available to the animals while in the respirometry chamber. Each animal was weighed before and after being measured and a linear decrease in body mass was assumed for calculations of mass-specific MR according to Eq. 3a of Withers (1977).

The resting metabolic rate (RMR) of normothermic bats and MR during torpor (TMR) were measured at T_as of 14–25 °C. RMR values were determined by calculating the mean of the three lowest consecutive $\dot{V}O_2$ values of normothermic animals (over 36 min) after the animals had been in the chambers for 1–2 h. The mean of the corresponding T_a and T_b values were also recorded. For torpid bats the TMR was calculated using the mean of the three lowest consecutive $\dot{V}O_2$ values and the corresponding T_b and T_a values were also calculated. Torpor was defined as having occurred when T_b fell below 30.0 °C or when MR was less than that of bats with a T_b below 30.0 °C at the same T_a. The average daily MR (ADMR) was determined by integrating all measurements over a day. The daytime MR was calculated by integrating all measurements during the light phase.

The basal metabolic rate (BMR) was measured on separate occasions. Animals were placed in the chambers in the morning at a T_a of about 28 °C. The T_a was then slowly increased through the day by 2 °C increments lasting for approximately 2 h each to a maximum T_a of 33 °C. The BMR was calculated from the mean of the three lowest consecutive $\dot{V}O_2$ readings of each individual. The thermal neutral zone (TNZ) was defined as the T_a range over which BMR of the individual bats was measured.

Length of a torpor bout was determined from the time when T_b fell below 30 °C during torpor entry until it increased again to 30 °C during arousal.

Thermal conductance for normothermic and torpid individuals was calculated using the equation $C = MR/T_b - T_a$).

We tested whether the "set point" for T_b during torpor (at which animals increase their TMR to prevent a further drop in T_b) is related to the lowest T_b at which they can fly. For this experiment, torpor was induced at T_a 17 ± 1 °C. Torpid bats were transferred to T_a 22 ± 1 °C and T_b was continuously measured via the transmitter signal. Bats were observed until they were able to fly.

Upon completion of the experiments and removal of transmitters, bats were released at their site of capture on 13 December 1996.

All data are presented as means ± one standard deviation. Regressions were fitted by the least-squares method. In those instances in which a single regression line did not fully explain the interrelation between two variables, two regression lines were fitted through the split data set. Best-fit linear regressions were assumed when the sum of the residual sum of squares for the two regressions were minimised. Data illustrated in the figures usually represent means of two measurements from the same individual at the same T_a; occasionally only a single determination for one individual is shown. "N" represents the number of individuals and "n" the total number of measurements.

Results

M. minimus entered torpor between T_as of 14 and 25 °C (Figs. 1, 2). Torpor entry always occurred in the morning, immediately after the light switched on and was characterised by a decrease in MR and T_b. After several hours, bats aroused and MR and T_b returned to resting values. All bats showed only a single bout of torpor on a given day. During the dark phase bats were usually active with MR about twice that during rest.

Although the general pattern of torpor at different T_as was similar, T_b and MR of torpid bats were lower at T_a 20 °C than at T_a 24 °C (Fig. 1). The lowest T_bs were measured at T_a 15 °C; however, TMR was increased in comparison to that at T_a 20 °C (Fig. 1), an indication of the onset of thermoregulation by torpid bats since the T_b had reached the set-point.

The T_b of torpid individuals was strongly affected by T_a, while that of normothermic individuals was little affected by T_a. However, T_b of normothermic bats did vary between about 33 and 37 °C at all T_as measured (Fig. 2). The mean T_b of normothermic bats below the TNZ was 35.6 ± 1.5 °C ($N = 5$, $n = 24$). Torpid bats lowered T_b with decreasing T_a. The relationship between T_a and T_b of torpid bats was best described by two linear regressions with a transition at 20.4 °C. Above T_a 20 °C, T_b approached T_a ($P < 0.02$; $r^2 = 0.86$), below 19 °C the T_b fell only slightly and showed no significant relationship with T_a ($P < 0.29$; $r^2 = 0.16$). This suggests that thermoregulation of bats in steady-state torpor commences near T_a 20 °C. The average T_b for torpid bats was 23.1 ± 1.4 °C at T_a 14.8 ± 0.2 °C ($N = 4$), 24.1 ± 1.8 °C at T_a 16.9 ± 0.2 °C ($N = 5$), 25.3 ± 1.6 °C at T_a 19.9 ± 1.0 °C ($N = 5$), and 28.5 ± 0.9 °C at T_a 24.4 ± 0.3 °C ($N = 3$). The lowest individual T_b recorded for a torpid bat was 21.6 °C.

The MR of both normothermic and torpid bats was also affected by T_a (Fig. 3). The BMR was 1.29 ± 0.20 ml O_2 g^{-1} h^{-1} (T_b 35.5 ± 1.1 °C; body mass 16.3 ± 1.3 g; $N = 5$). This was observed within the TNZ which ranged between T_a 30.9 and 33.0 °C. For normothermic, resting individuals below the TNZ, RMR increased linearly with decreasing T_a ($P < 0.0001$, $r^2 = 0.86$). In contrast, the TMR fell from 0.96 ± 0.27 ml O_2 g^{-1} h^{-1} ($N = 3$) at T_a 24.4 ± 0.3 °C to the mean minimum of 0.70 ± 0.19 ml O_2 g^{-1} h^{-1} (T_b 25.3 ± 1.6 °C; body mass 15.5 ± 1.5 g ; $N = 5$) at T_a 19.9 ± 0.1 °C. The minimum TMR of an individual bat was 0.52 ml O_2 g^{-1} h^{-1} (T_b 23.6 °C, T_a 19.9 °C). At lower T_as, TMR

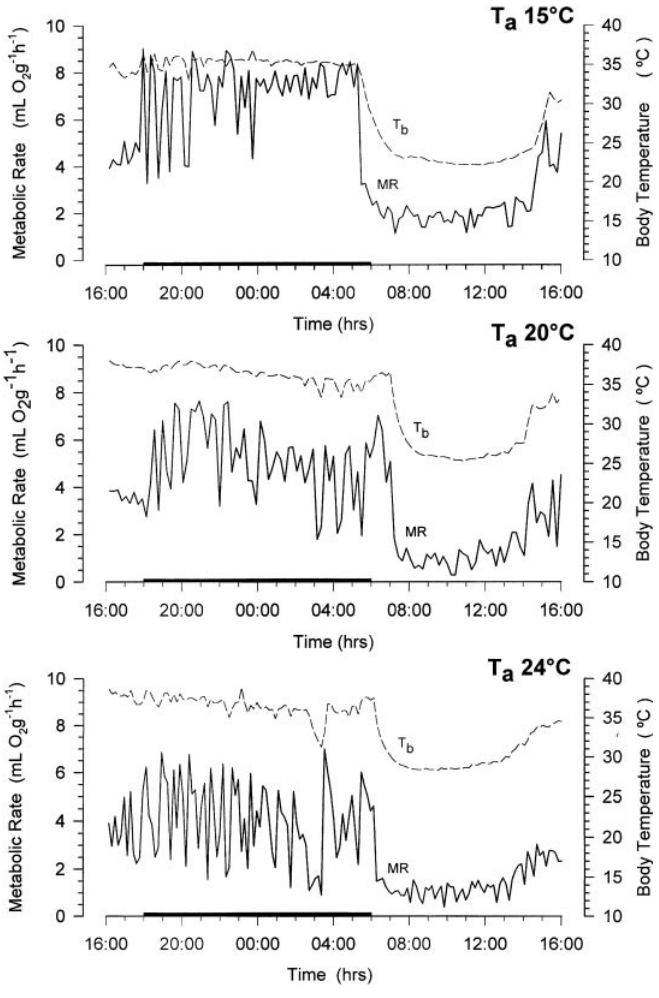

Fig. 1 Daily fluctuations of body temperature (T_b) and metabolic rate (MR) of *Macroglossus minimus* at three different ambient temperatures (T_a 15 °C; T_a 20 °C;T_a 24 °C). The solid bar represents the dark phase

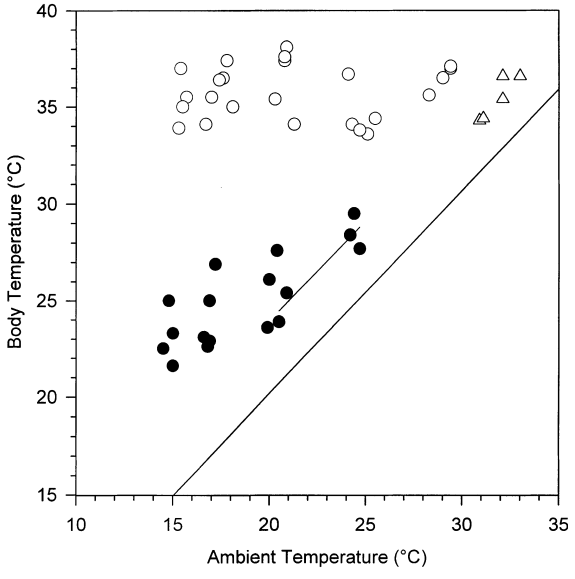

Fig. 2 T_b of normothermic (*open symbols*) and torpid (*closed symbols*) *M. minimus* as a function of T_a. The T_b in the TNZ is shown as *open triangles*. The T_b of normothermic bats was not affected by T_a. The T_b of torpid bats fell with T_a. This relationship was best described by two regressions intersecting at T_a 20.4 °C. Above a T_a of 20 °C the regression was significant ($T_b = 3.31 + 1.03T_a$, $P < 0.02$, $r^2 = 0.86$) showing that T_b decreased with decreasing T_a (shown). Below the set point, T_b was not significantly related to T_a ($T_b = 14.20 + 0.59T_a$; $P < 0.291$) (not shown), suggesting that animals were regulating their T_b

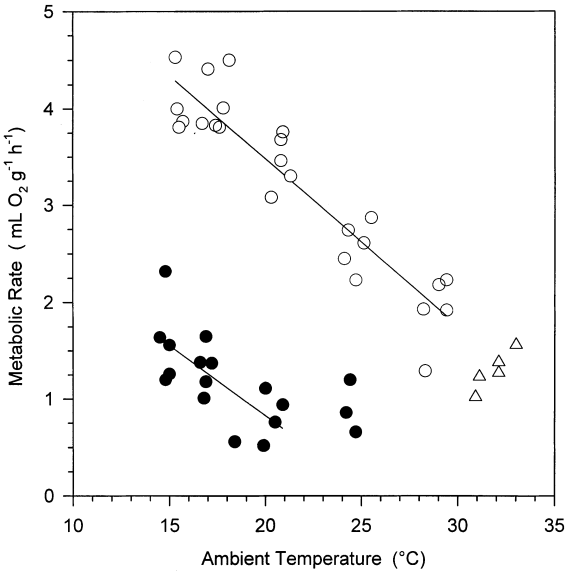

Fig. 3 The MR of *M. minimus* as a function of T_a. The *open circles* represent the MR of normothermic individuals at rest (RMR; RMR = 6.93–0.17T_a ($P < 0.000$, $r^2 = 0.86$). *Open triangles* show the basal MR of each individual and *closed circles* represent torpid individuals. A linear regression was fitted to MRs during torpor (TMRs) below a T_a of 20.4 °C (i.e. the T_a below which animals began to thermoregulate, see Fig. 2). TMR of thermoregulating, torpid bats increased significantly with decreasing T_a (TMR = 3.74–0.15T_a, $P < 0.003$, $r^2 = 0.50$)

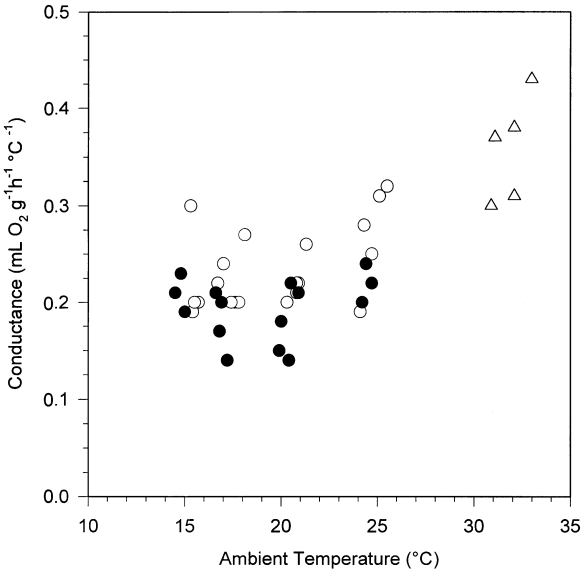

Fig. 4 Thermal conductance of normothermic (*open symbols*, *circles below TNZ*, *triangles within TNZ*) and torpid (*closed symbols*) *M. minimus* as a function of T_a. The minimum conductance of torpid bats was significantly lower than that of normothermic bats (paired *t*-test, $P < 0.01$)

increased parallel to the RMR ($P < 0.003$, $r^2 = 0.50$). The mean TMR at T_a 16.9 ± 0.2 °C was 1.32 ± 0.24 ml O_2 g^{-1} h^{-1} ($N = 5$) and 1.60 ± 0.45 ml O_2 g^{-1} h^{-1} ($N = 5$) at T_a 14.8 ± 0.2 °C.

All six bats studied entered torpor at T_as below 24 °C, but only three individuals used torpor at T_as above 24 °C. Pooling data for individuals, the frequency of torpor was 90% when bats were exposed to T_as below 24 °C and 50% above 24 °C. If an individual did not enter torpor in the morning it still lowered MR on average to 66% of the RMR measured in the afternoon and T_b dropped to approximately 32 °C.

Thermal conductance of normothermic bats decreased with T_a from 0.36 ± 0.05 ml O_2 g^{-1} h^{-1} °C^{-1} in the TNZ to a minimum of 0.22 ± 0.02 ml O_2 g^{-1} h^{-1} °C^{-1} at T_a 20–15 °C (Fig. 4). Torpid bats also showed a decline in conductance from values that were similar to those of normothermic bats at T_a 24 °C. At approximately T_a 20 °C, the point at which TMR was minimal, the conductance of torpid bats was significantly ($P < 0.01$) lower (0.19 ± 0.03 ml O_2 g^{-1} h^{-1} °C^{-1}) than that of normothermic bats, but increased again to normothermic values in thermoregulating, torpid bats at T_a 15 °C.

The duration of torpor bouts were inversely related to T_a (Fig. 5). Length of torpor bouts ranged from 36 min to just over 9 h. The mean duration of torpor bouts was 4:32 ± 3:54 h at a T_a of approximately 24 °C, 6:00 ± 2:27 h at T_a 20 °C, 8:01 ± 1:43 h at T_a 17 °C, and 8:21 ± 1:43 h at T_a 15 °C. When fitted with two linear regressions, a transition occurred at T_a 20 °C, similar to the transition observed for the other variables. This suggests that at the T_as at which T_b was regulated by an increase of TMR, torpor bout duration showed no further prolongation with a decrease in T_a.

The minimum T_b of torpid bats was well below the T_b at which bats could fly. Four torpid bats at T_a 17 °C with a T_b of 23.5 ± 1.0 °C could not fly. The bats re-

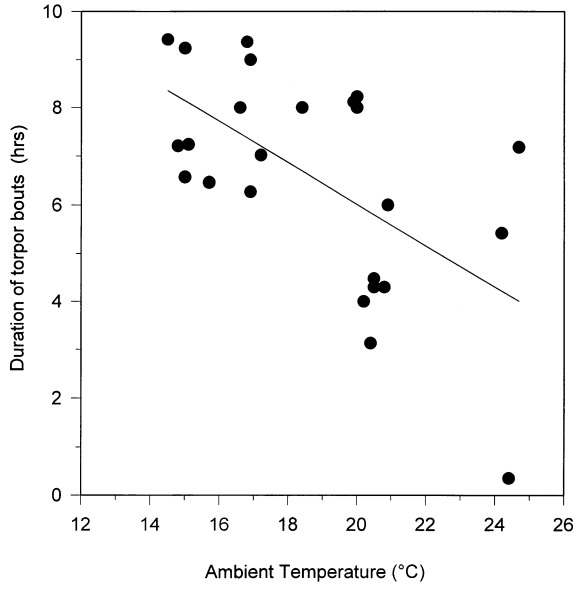

Fig. 5 Duration of torpor bouts in *M. minimus* as a function of T_a. Length of torpor bouts increased with decreasing T_a (length of torpor bout = 14.60–0.43T_a, $P < 0.002$, $r^2 = 0.35$). However, below T_a 20 °C torpor bout length was maintained for approximately 8 h

mained motionless and were transferred to T_a 22 °C to facilitate rewarming. At T_b 26 °C they were able to crawl, but they could not fly until their T_b reached approximately 29 °C. Two individuals rewarmed at a rate of 0.85 °C min^{-1} when rewarming from T_b 23.5 – 29.0 °C.

To investigate whether torpor lowered daily energy expenditure, we determined the effect of torpor bout length on ADMR and the daytime MR. The ADMR and torpor bout length were negatively related at a T_a of 20 °C (ADMR = 4.45–0.17 torpor bout length; $P < 0.007$, $r^2 = 0.42$). The ADMR of bats exhibiting torpor bouts of 8 h at T_a 20 °C was 3.32 ± 0.78 ml O_2 g^{-1} h^{-1}, while that of bats remaining normothermic was 4.82 ± 0.57 ml O_2 g^{-1} h^{-1}. At other T_as the relationship between ADMR and the duration of torpor bouts was not significant due to low sample sizes and narrow bout ranges. Moreover, at low T_as bats always became torpid, therefore we could not compare measurements for bats that entered torpor with those that remained normothermic. The average daytime MR (0600 hours onward) also decreased significantly with an increased duration of torpor at a T_a 20 °C and 24 °C (T_a 20 °C: daytime MR = 3.41–0.23 torpor bout length, $P < 0.000$, $r^2 = 0.70$; T_a 24 °C: daytime MR = 2.40–0.15 torpor bout length, $P < 0.049$, $r^2 = 0.66$). Regressions at the others T_as also had negative slopes between the two variables, but were not significant.

Discussion

Our study shows that the northern blossom-bat *M. minimus*, which in Australia has a distribution restricted to tropical regions, enters daily torpor over a wide range of T_as. However, torpid bats showed a thermoregulatory increase of TMR below about T_a 20 °C and did not allow their T_b to fall below about 23 °C. Although torpor by these bats was relatively shallow, it did result in a reduction in energy expenditure.

Normothermic bats regulated T_b over a wide range of T_as between about 33 and 37 °C when at rest, but increased their T_b significantly ($P < 0.01$) during activity. This T_b is similar to many small mammals; however, the regulation of T_b in *M. minimus* was less precise than has been reported for many other species (Withers 1992). The BMR of *M. minimus* measured in the present study was about 90% of that reported by McNab and Bonaccorso (1995) and about 80% of that predicted for a 16-g bat (Hayssen and Lacy 1985). The flexible T_b and the low BMR allows bats to reduce energy expenditure during the resting phase even when they are normothermic, and may be a reflection of their diet which consists largely of nectar, an energy-rich but unpredictable resource (MacMillen 1985).

The use of torpor by *M. minimus* significantly reduced MR. The MR of torpid bats was 60–80% of that in normothermic, resting bats at the same T_a. The most energy-efficient T_a for torpor was at about 20 °C, below which torpid bats began to thermoregulate. At this T_a, TMR was 20% of RMR and 54% of the BMR. The Q_{10} between the BMR and the mean TMR at T_a 20 °C was 1.82 suggesting that the reduction of the TMR below BMR was due to temperature effects (Geiser 1988) and there was no evidence for metabolic inhibition.

Torpor also affected daily energy expenditure. Both the ADMR and the daytime MR were negatively related to torpor bout length at some T_as suggesting that torpor is important for energy conservation. However, at other T_as ADMR was not affected by torpor bout length, although the TMR was significantly reduced in comparison to the RMR. This shows that as in other heterothermic mammals ADMR is not only affected by the energy expenditure during torpor, but also the energy expenditure during the active phase at night (Song and Geiser 1997).

The minimal thermal conductance of normothermic *M. minimus* was approximately 15% lower than predicted for a 16-g mammal (Herreid and Kessel 1967). During torpor, conductance fell even further to a minimum value that was about 30% below that predicted. However, conductance during torpor was not correlated with TMR, suggesting that MR during torpor can not be explained by low conductance. It is likely that the very low conductance during torpor is a consequence of low MR and thus low peripheral circulation (Hosken and Withers 1997).

M. minimus entered torpor strictly on a daily basis; bats always became torpid when lights came on in the morning and they aroused spontaneously after several hours. This timing of entry into torpor differs from many other heterothermic mammals which begin torpor during the night well before daylight, particularly when T_a and food availability are low. In some species there is strong evidence that the onset of torpor is affected by energy expenditure with earlier entries into torpor when MR is high (Geiser 1986; Hiebert 1992). However, like *M. minimus*, the related common blossom-bat *S. australis* also entered torpor at the beginning of the light phase (Geiser et al. 1996) independent of T_a and thus the amount of energy used during the night. In the field, *S. australis* does not return to its roost until dawn (Law 1993) suggesting that termination of activity and the onset of rest or torpor phase in blossom-bats occurs at the beginning of the light phase. This suggests that the onset of torpor in these species is not determined by the amount of energy they used before torpor entry, but rather by photoperiod or a strong circadian rhythm.

In contrast to onset of torpor, the duration of torpor in *M. minimus* was temperature-dependent as in many other mammals (French 1982). Overall, bouts of torpor lengthened with decreasing T_a and T_b. However, at T_as below the set point for T_b, bout length was maintained for a maximum of about 8 h. This observation supports the argument that the duration of torpor is linked to levels of energy expenditure and T_b during torpor (Geiser and Kenagy 1988). Above the set point for T_b, the TMR of *M. minimus* decreased with T_a and T_b and

torpor bouts increased. In contrast, at T_as below the set point for T_b, torpor bouts were constant, whereas TMR increased and T_b exhibited only a slight decrease. The correlation between the length of a torpor bout, TMR and T_b provides further support for the hypothesis that in many species the duration of torpor is linked to energy expenditure and T_b both during daily torpor (Geiser 1986) and hibernation (Willis 1982).

The mean minimum T_b observed during torpor in *M. minimus* was about 23 °C. This is 7 °C higher than predicted for a daily heterotherm of that body mass (Geiser and Ruf 1995). The minimum T_b of *M. minimus* was also about 5 °C higher than that of *S. australis* captured in the subtropical part of its range. *S. australis* had minimum T_bs much closer to those predicted for similar-sized heterothermic endotherms. These observations suggest that the minimum T_b of species exhibiting daily torpor is not only strongly affected by body size (Geiser and Ruf 1995), but also by the conditions where they live. The lowest mean monthly T_a that *M. minimus* is exposed to in the wild (near Cairns) is 21 °C, an T_a similar to which the species begins to defend its T_b during torpor. In contrast, the lowest mean monthly T_a that *S. australis* is exposed to in its subtropical range is about 14 °C, which is only slightly below the T_a at which this species defends its T_b during torpor.

While environmental conditions appear to affect the minimum T_b of *M. minimus*, individuals were unable to fly until their T_b was about 29 °C. Similar observations have been made for the insectivorous bat *Miniopterus schreibersii* (Morrison 1959). This suggests that the ability to maintain coordinated movements do not play an important role in the selection of the minimum T_b in heterothermic mammals.

Similar to the minimum T_b, the minimum TMR of *M. minimus* was also higher than predicted (Geiser 1988) and significantly higher than that measured for *S. australis*. This relatively high TMR is further evidence that torpor in the tropical *M. minimus* is relatively shallow.

The fact that *M. minimus* has a less well-developed pattern of torpor than *S. australis* may partly explain its restriction to tropical areas. However, other factors may also restrict the range of *M. minimus* and the exposure to high T_as in the tropics in turn may not provide the selective pressure to lower the T_b beyond the values measured in the present study. These may include the presence of flowering mangroves, particularly *Sonneratia* sp. (Start and Marshall 1976). The lack of mangroves may account for the absence of *M. minimus* on the tropical, but cooler Atherton tablelands in northern Queensland where *S. australis* does occur (B. Law, unpublished data); however, this does not explain the presence of *M. minimus* at altitudes of 1000 m in New Guinea (Flannery 1990). McNab and Bonaccorso (1995) provide some anecdotal evidence that thermoregulation in *M. minimus* at high altitudes in New Guinea may differ from those at low altitudes, but this needs to be verified by detailed physiological investigations.

In the past it was widely believed that torpor is an adaptation restricted to animals inhabiting cold climates. More recent evidence on tropical microchiropteran and megachiropteran bats (Kulzer and Storf 1980; Genoud et al. 1990; McNab and Bonaccorso 1995; Audet and Thomas 1997; present study), and small primates (Schmid 1996) suggests that although cool temperatures may facilitate torpor, it is clearly not an exclusive adaptation to the cold. Torpor appears to be used for energy conservation even in the tropics by species that have a limited ability to store fat and/or have to overcome periods of food shortage. The significant reduction of MR even at moderate T_as certainly demonstrates that torpor is effective in lowering energy expenditure at T_as commonly experienced in the tropics. It is therefore likely that torpor is widely used by small tropical species for conserving their limited energy resources.

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