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ORIGINAL PAPER

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# Torpor and thermal energetics in a tiny Australian vespertilionid, the little forest bat (*Vespadelus vulturnus*)

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**Abstract** Data on thermal energetics for vespertilionid bats are under-represented in the literature relative to their abundance, as are data for bats of very small body mass. Therefore, we studied torpor use and thermal energetics in one of the smallest (4 g) Australian vespertilionids, *Vespadelus vulturnus*. We used open-flow respirometry to quantify temporal patterns of torpor use, upper and lower critical temperatures ($T_{uc}$ and $T_{lc}$) of the thermoneutral zone (TNZ), basal metabolic rate (BMR), resting metabolic rate (RMR), torpid metabolic rate (TMR), and wet thermal conductance ($C_{wet}$) over a range of ambient temperatures ($T_a$). We also measured body temperature ($T_b$) during torpor and normothermia. Bats showed a high proclivity for torpor and typically aroused only for brief periods. The TNZ ranged from 27.6°C to 33.3°C. Within the TNZ $T_b$ was 33.3 ± 0.4°C and BMR was 1.02 ± 0.29 $mlO_2$ $g^{-1}$ $h^{-1}$ (5.60 ± 1.65 mW $g^{-1}$) at a mean body mass of 4.0 ± 0.69 g, which is 55 % of that predicted for a 4 g bat. Minimum TMR of torpid bats was 0.014 ± 0.006 $mlO_2$ $g^{-1}$ $h^{-1}$ (0.079 ± 0.032 mW $g^{-1}$) at $T_a$ = 4.6 ± 0.4°C and $T_b$ = 7.5 ± 1.9. $T_{lc}$ and $C_{wet}$ of normothermic bats were both lower than that predicted for a 4 g bat, which indicates that *V. vulturnus* is adapted to minimising heat loss at low $T_a$. Our findings support the hypothesis that vespertilionid bats have evolved energy-conserving physiological traits, such as low BMR and proclivity for torpor.

**Keywords** Australian bats · Body size · BMR · Thermal biology · Vespertilionidae

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**Abbreviations** BMR: Basal metabolic rate · $C_{wet}$: Wet thermal conductance · MR: Metabolic rate · RMR: Resting metabolic rate · $T_a$: Ambient temperature · $T_b$: Body temperature · $T_{lc}$: Lower critical temperature · TMR: Torpid metabolic rate · TNZ: Thermoneutral zone · $T_{uc}$: Upper critical temperature · $\dot{V}O_2$: Rate of oxygen consumption

## Introduction

Body size exerts influence on most aspects of animal physiology (Schmidt-Nielsen 1984). In endotherm physiological traits like basal metabolic rate (BMR), minimum thermal conductance and propensity for heterothermy are all strongly influenced by body size (e.g., Bradley and Deavers 1980; Geiser 1998; Speakman and Thomas 2003). Thus, it is important to obtain data on physiological traits from animals across the entire range of body mass. In mammals, obtaining these data from species at the lower end of the size distribution is likely the most logistically difficult because individuals of these species are often secretive and difficult to capture. Therefore, data for small species are under-represented relative to their abundance. Arguably, however, the smallest species provide the greatest insight into factors governing scaling relationships and energetics because they represent animals living at the boundary of restrictions imposed on body size by natural selection.

Bats are one taxonomic group that ranges widely in body mass, from 2 g to over 1,000 g, but which is largely composed of very small species. Smith et al. (2003) compiled body mass data for 839 bat species, of which 348 (41%) were smaller than 10 g. This likely underestimates the proportion of very small bats because data are unavailable for about 200 species, many of which are certainly smaller than 10 g. The point is illustrated even more strongly in Australia where, of roughly 75 bat species, at least 44 (almost 60%) include adult individuals smaller than 10 g, and 15 species (20%) include individuals smaller than 5 g (Menkhorst and Knight

2001). However, none of the species smaller than 5 g has been studied in terms of its thermal energetics. In their analysis of the influence of body mass and other factors on BMR in 84 bat species, Speakman and Thomas (2003) made use of all available data but were only able to include 18 species smaller than 10 g, which represents about 21% of the species in their analysis, a much smaller proportion than that for bats on the whole. Thus, it is clear that energetic data for bat species at the lower end of the body mass distribution are under-represented in the physiology literature relative to their abundance.

Just as it is vital to obtain good data from species spanning the full range of body size, it is important to obtain representative data across taxonomic groups. Again, the Speakman and Thomas (2003) analysis of BMR illustrates this point for bats. For the family of Vespertilionidae , BMR data were only available for 13 species, about 15% of the total in their analysis. However, vespertilionids are the most diverse family of bats with about 350 species worldwide, or roughly 35% of total species (Nowak 1991). Therefore, as for small bats, thermal energetic data from this family are under-represented in the literature, so it is important to obtain data for a greater number of vespertilionids. This is especially important because sufficient phylogenetic information is not yet available to allow for meaningful phylogenetically corrected analyses of physiological traits in bats. Therefore, under-representing certain taxonomic groups in review analyses of physiological traits may skew scaling relationships.

Like many bat species from the northern hemisphere, Australian bats exhibit traits that allow them to cope with low and unpredictable energy availability (Hosken 1997; Hosken and Withers 1999; Geiser and Brigham 2000; Geiser 2004). Geiser and Brigham (2000) and Geiser (2005) hypothesised that, like other Australian mammals, Australian bats may be typified by relatively low BMR. Coupled with a strong proclivity for torpor use, low BMR could allow Australian bats to use energy even more frugally than northern hemisphere species, facilitating their survival during periods of drought and food shortage which are common in many Australian ecosystems (Geiser and Brigham 2000; Geiser 2005). Willis et al. (2005) suggested that vespertilionids in general, not just Australian species, may be characterised by a relatively low BMR and frugal energy use, which could reflect a phylogenetic effect or a consequence of the largely insectivorous diet of this family (McNab 1989, 1992; Speakman and Thomas 2003). These hypotheses remain largely untested, however, as there are few data on torpor use and energetics for Australian bats.

To address these hypotheses about energy use in bats and to add to available energetic data for very small vespertilionids, we studied the thermal energetics of one of the smallest Australian species, the little forest bat (*V. vulturnus*). Only four species of Australian bats are smaller than *V. vulturnus* (Menkhorst and Knight 2001) and, at about 4 g, it is the smallest bat studied to date in terms of its thermal physiology and energetics, and the only member of its genus.

## Materials and methods

We captured male and female *V. vulturnus* using harp traps set in Imbota Nature Reserve (30°35′S, 151°44′E) in the northern tablelands of New South Wales, Australia. Captured bats were transported 10 km to the University of New England in Armidale, where they were housed in cloth bags for 2 to 10 h until being measured. We checked female bats for evidence of reproduction by gentle palpation of the abdomen to discern pregnancy and the presence of bare patches around the nipples or expression of milk to identify lactation. We checked if bats were adult or sub-adult based on the degree of ossification of the finger joints (Anthony 1988). Measurements were conducted on 16 *V. vulturnus* (7 female, 9 male) during autumn and winter. We trapped outside the breeding period and no reproductive females were captured during any of our trapping sessions. Bats were provided with water in the morning prior to metabolic recording but were not fed prior to metabolic trials to ensure they were postabsorptive during recording.

We used open flow respirometry to record the metabolic rate (MR) of bats measured as the rate of oxygen consumption ($\dot{V}O_2$). Measurements were conducted in a temperature-controlled cabinet. Each bat's body mass was recorded immediately before and after the recording trial and we assumed a linear decrease in mass during recording for calculations of mass-specific MRs. Bats were placed in airtight 50 ml transparent plastic metabolic chambers, lined with plastic mesh for roosting. Chambers were small to minimise washout time and allow for accurate measurement of $\dot{V}O_2$ at low levels during torpor but still allowed space for bats to hang freely and move around inside the chambers. Outside air was pumped into the chamber at a rate of 135 ml/min. This flow rate was high enough to maintain $O_2$ concentration in the excurrent air stream above 20% during normothermia and low enough to allow for accurate measurement of a differential between incurrent and excurrent $O_2$ concentration at low MR during torpor. Incurrent air was dried with silica gel and flow rate was controlled with rotameters (Aarlborg 7908, New York, USA) and measured with mass flowmeters (Omega FMA-5606, Stamford USA, accuracy ±2% of full scale). Mass flowmeters were calibrated using a soap film bubble meter (Levy 1964). Excurrent air was also dried with silica gel and percentage oxygen was then measured with a single channel oxygen analyser sensitive to a resolution of better than 0.001% (FOX, Sable Systems International Inc., Las Vegas USA). The oxygen analyser was calibrated using outside air and a certified gas mix consisting of 0.885% $CO_2$ and 19.30% $O_2$ in nitrogen (BOC Gases, North Ryde, Australia). To ensure long-

term stable readings, we maintained the analyser in a constant temperature room and further insulated it from temperature variation using styrofoam. Four channels (3 animals and 1 outside-air reference) were scanned sequentially with solenoid valves for 3 min each (i.e., the MR of each animal and the reference were scanned once in every 12 min). Outputs from the flowmeters and thermocouples (Omega DP116, Stamford, USA) measuring $T_a$ inside the metabolic chambers to $\pm 0.1$°C were transferred to computer via a 14-bit A/D converter card and oxygen analyser output was transferred via a digital serial connection. As the analyser was also equipped with an analog output, we calibrated the A/D converter by comparing the serial and analog outputs of the analyser. All equipment was calibrated prior to use.

Measurements were taken over approximately 24 h to ensure that we recorded the entire daily thermal cycle (Geiser and Brigham 2000). All measurements of MR represent the minimum 30-min average obtained during a period when MR was stable at a constant $T_a$ for at least 1 h. We used 2 $T_a$ protocols to record resting metabolic rate (RMR), torpid metabolic rate (TMR) and BMR of bats over a range of temperatures. In the first protocol, bats ($N = 6$) were placed in the chambers in the afternoon (13:00–15:00), $T_a$ was held constant overnight, and measurements of TMR were obtained the following morning. This allowed for entry into torpor in the early morning hours, when other Australian vespertilionids use torpor in the wild (Turbill et al. 2003a, 2003b), and ensured that TMR and $T_b$ reached steady-state minima before TMR values were recorded (Geiser and Brigham 2000). During these trials, typically bats entered torpor in the afternoon, as well, immediately after being placed in the chambers but they often aroused from these torpor bouts at dusk. If their normothermic $\dot{V}O_2$ remained stable for at least an hour during these dusk arousals, we also recorded a RMR measurement at that $T_a$. The following morning, after recording a stable TMR measurement, we raised the temperature to between about 26°C and 36°C for measurement of BMR. After $\dot{V}O_2$ and chamber $T_a$ were stable for at least 1 h, we began recording and after a second hour at the initial $T_a$, we slowly increased chamber $T_a$ in approximately 2°C increments. We ensured that $T_a$ and MR were stable at each increment for at least an hour before recording the 30-min minimum average MR for that hour. In this way we recorded $\dot{V}O_2$ over a $T_a$ range between about 26°C and 40°C, which allowed us to quantify the boundaries of the TNZ. A maximum of three measurements per animal were taken within this $T_a$ range for any individual. For our second recording protocol, bats ($N = 10$) were placed in the chambers during the late morning (11:00–12:00) and recording continued overnight, again for about 24 h. The timing of TMR and RMR measurements was the same as for the first protocol but, this time, we measured MR between 26°C and 40°C as described above, before measuring TMR (i.e., prior to turning $T_a$ down in the late afternoon).

We measured $T_b$ to the nearest 0.1° with a digital thermometer (Omega, Stamford, USA) by inserting a fine, calibrated thermocouple probe 0.5 cm into the rectum. $T_b$ was measured at the end of each 24-h recording session, and occasionally during mid-session in the afternoon, before turning $T_a$ down, or morning, after recording TMR. We only report $T_b$ values if we were able to obtain a measurement within 15 s of removing a bat from the chamber. We did not record $T_b$ for metabolic measurements corresponding with all $T_a$s to avoid disturbing the bats during recording. Torpor bouts and arousals were obvious in time course plots of metabolic trials because MR fell rapidly to a reduced steady-state level. We defined the onset of torpor bouts as the beginning of these rapid reductions of MR (Willis et al. 2005).

We obtained repeated measurements of the same individuals at different $T_a$, because of the inherent difficulty associated with catching large numbers of this species. However, we took steps to minimise pseudoreplication bias by obtaining roughly the same numbers of measurements from each individual ($3.4 \pm 1.5$, McNab 2003), and by reporting both the number of measurements ($n$) and number of individuals ($N$) for each variable. Furthermore, to avoid underestimating coefficients of variation and intraspecific variability, we calculated SD for each variable based on number of individuals rather than number of measurements. Means are expressed ± SD. We used Equation 3a of Withers (1977) for the calculation of the metabolic rate and the standard equation, $C_{wet} = MR/(T_b\text{-}T_a)$, to calculate wet thermal conductance. $Q_{10}$ was calculated using the equation $Q_{10} = (MR_1/MR_2)^{10/(Tb1\text{-}Tb2)}$. We assumed a conversion factor of 0.179 ml $O_2$ $h^{-1} = 1$ mW for conversion from oxygen consumption to SI units of metabolic rate. We used the iterative two phase regression approach advocated by Nickerson et al. (1989) to quantify $T_{lc}$ and $T_{uc}$. The significance level for all null hypothesis tests was assessed at $P < 0.05$.

## Results

*Vespadelus vulturnus* showed a strong tendency to use torpor in the laboratory (Fig. 1a, b). All bats entered torpor soon after being placed in the metabolic chamber or when we reduced $T_a$ below thermoneutrality, and remained torpid for most of the recording trial (Fig. 1a, b). We recorded 23 arousals by 15 bats during all trials. Sixty-one percent of arousals (14/23, $N = 8$ bats) were spontaneous at stable $T_a$ and these lasted for $96 \pm 180$ min on average (Fig. 1b). There was a loose circadian pattern to spontaneous arousals. Forty-three percent (6/14) occurred in the evening, $15 \pm 93$ min before lights off and these bats remained normothermic for $136 \pm 118$ min ($N = 6$ bats). The remaining 57% (8/14) occurred $65 \pm 213$ min before lights were on the following morning with normothermia lasting for $67 \pm 38$ min ($N = 6$ bats). Five bats

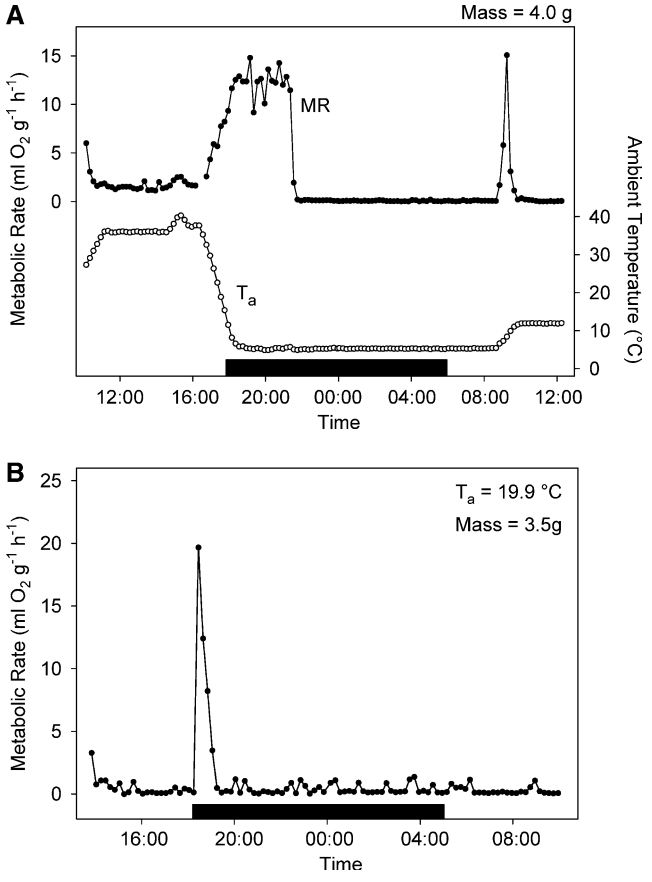


**Fig. 1** Time courses of metabolic rate (MR) recording trials for individual *V. vulturnus* at different levels of ambient temperature ($T_a$, **a**) and at a constant temperature (**b**). *Filled circles* indicate MR and *circles* represent $T_a$. *Dark bars* indicate the dark phase

aroused spontaneously in both the evening and morning. Thirty-nine percent of all arousals (9/23, $N=8$ bats) did not occur spontaneously at stable $T_a$ but occurred in response to a change in chamber $T_a$ (Fig. 1a). In these cases, typically, bats aroused to normothermia for only a short time (40 ± 25 min) and then re-entered torpor almost immediately. The maximum MR we observed during arousal was 19.67 $mlO_2$ $g^{-1}$ $h^{-1}$. The longest torpor bout we observed was 16 h 42 min but it is likely that torpor could have lasted much longer because this individual and others were disturbed either when we adjusted chamber $T_a$ or removed bats to record $T_b$.

The thermoneutral zone of *V. vulturnus* ranged from $T_a = 27.6°$ to 33.3°C (Fig. 2a). Within the TNZ, average BMR was 1.02 ± 0.29 $mlO_2$ $g^{-1}$ $h^{-1}$ ($n=10$, $N=5$) at a mass of 4.0 ± 0.69 g which equates to 5.60 ± 1.65 mW $g^{-1}$. Body temperature within the TNZ was 33.3 ± 0.4°C ($n=3$, $N=3$) and increased sharply to as high as 36.7°C when $T_a$ was raised above $T_{uc}$. Below $T_{lc}$ the RMR of normothermic bats increased linearly with falling $T_a$ according to the relationship RMR ($mlO_2$ $g^{-1}$ $h^{-1}$) = 15.35–0.518 $T_a$ (°C, $P<0.001$, $r^2=0.99$, $n=9$, $N=8$, Fig. 2a).

Below thermoneutrality, bats were most often thermoconforming and substantially reduced MR during torpor to a minimum TMR of 0.014 ± 0.006 $mlO_2$ $g^{-1}$ $h^{-1}$, which equates to 0.079 ± 0.032 mW $g^{-1}$, at $T_a = 4.6 \pm 0.4$°C ($n=5$, $N=5$), $T_b = 7.5 \pm 1.9$ ($n=4$, $N=4$), and mean mass = 4.1 ± 0.14 g ($n=5$, $N=5$, Fig. 2a, b). One bat reached a minimum $T_b$ of 5°C and two others allowed $T_b$ to fall to 6.5°C. Above $T_a = 2.5$°C, $T_a$ and TMR were exponentially related by the equation TMR ($mlO_2$ $g^{-1}$ $h^{-1}$) = 0.0172 + 0.0006×1.264$^{Ta}$ ($P<0.0001$, $r^2=0.94$, $n=21$, $N=15$, Fig. 2B). TMR increased greater than 10-fold between the steady-state minimum of about

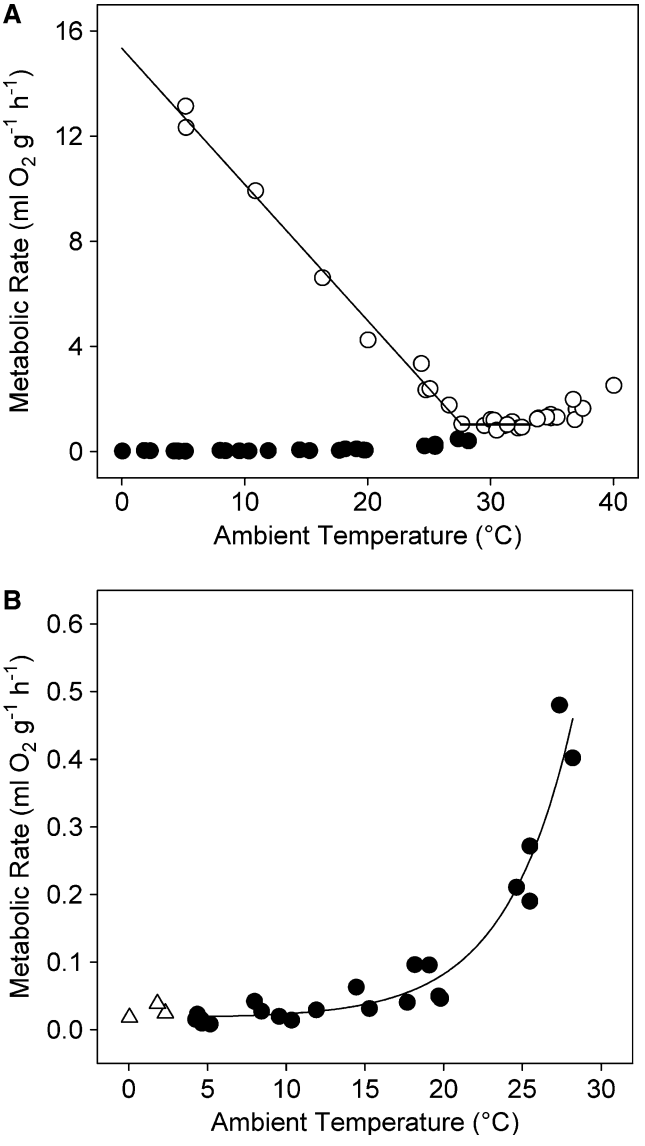


**Fig. 2** **a** Relationship between MR and $T_a$ for *V. vulturnus* during normothermia (*circles*) and torpor (*filled circles*). **b** Torpid MR plotted against $T_a$. Values included in the regression analysis are indicated by *dark circles*, and *open triangles* are $T_a$ values below the minimum set-point during which bats increased metabolic rate to maintain body temperature ($T_b$). See Results for regression equations

0.014 $mlO_2$ $g^{-1}$ $h^{-1}$ at 5°C and values of about 0.25 $mlO_2$ $g^{-1}$ $h^{-1}$ at 25°C.

During torpor the relationship between $T_a$ and $T_b$ approximated 1:1 (Fig. 3). Above $T_a$ = 4.5°C, torpid bats maintained a $T_b$-$T_a$ differential of 1.7 ± 1.3°C and there was no significant relationship between $T_a$ and the $T_b$-$T_a$ differential ($r^2 = 0.20$, $P = 0.10$, $n = 15$, $N = 14$). The constant $T_b$-$T_a$ differential during torpor was likely maintained because the $C_{wet}$of torpid bats increased with increasing $T_a$ (see below). Below $T_a = 2.5$°C, bats increased TMR twofold to 0.027 ± 0.01 $mlO_2$ $g^{-1}$ $h^{-1}$ to maintain $T_b$ (Fig. 2a, b). The $T_b$-$T_a$ differential at this point increased to 4.3 ± 1.3°C at an average $T_b$ of 5.8 ± 0.7 ($n = 3$, $N = 3$, Fig. 3). The $Q_{10}$ was 5.3 between BMR and the minimum TMR (i.e., at $T_a = 4.6$°C), 8.8 between BMR and TMR of thermoconforming bats at 20°C, and 3.0 for thermoconforming bats between minimum TMR at 20°C and minimum TMR. This indicates that reductions in metabolic rate during torpor, especially at high $T_b$, exceed those predicted based on temperature effects alone and illustrates the role of metabolic inhibition during torpor.

We were only able to measure $T_b$ for one normothermic bat below thermoneutrality (Fig. 3) to avoid disturbing animals during recording sessions. Therefore, for the other individuals, we calculated $C_{wet}$ using a $T_b$ of 33.3°C, the mean $T_b$ we recorded within the TNZ. This assumption introduces only a small error into the calculation (less than 10% even if the actual $T_b$ varied from 33.3°C by ±3°C). On this basis, wet thermal conductance of normothermic bats below the TNZ was 2.38 ± 0.19 mW $g^{-1}°C^{-1}$ ($n = 5$, $N = 5$) and was significantly higher than $C_{wet}$ for thermoconforming torpid bats between 5°C and 25°C (0.49 ± 0.73 mW $g^{-1}°C$, $t$ test, $t = 5.6$, $P < 0.001$, $n = 10$, $N = 9$, Fig. 4). The $C_{wet}$ of torpid bats increased more than twofold between a $T_a$ of 5°C and $T_a < 5$°C, which was below the set-point for minimum $T_b$.

## Discussion

*Vespadelus vulturnus* showed a strong proclivity to use torpor in the laboratory, which is not surprising given previous work on Australian and Northern Hemisphere vespertilionids. Members of this family frequently use torpor in the laboratory (Hosken 1997; Hosken and Withers 1999; Geiser and Brigham 2000; Cryan and Wolf 2003; Willis and Brigham 2003; Willis 2003) and field (Lausen and Barclay 2003; Turbill et al. 2003a, 2003b; Willis 2005). Patterns of torpor in *V. vulturnus* were only loosely correlated to photoperiod, much less so than for other Australian vespertilionids like *Nyctophilus geoffroyi* or *N. gouldi* (Geiser and Brigham 2000). Most spontaneous arousals in our study occurred within only about an hour and a half of lights off or several hours of lights on. In other words, *V. vulturnus* was flexible in terms of its timing of torpor use and arousal. The "physiological decision" to enter or arouse from torpor in this species could be more strongly influenced by endogenous or external cues other than photoperiod. Levels of circulating leptin are known to influence torpor use (Geiser et al. 1998), so this and other hormonal cues associated with hunger, satiety and energy reserves could influence arousal timing in *V. vulturnus*. On the other hand, free-living *V. vulturnus* may depend on diurnal $T_a$ variation as a cue for initiating torpor onset and arousal. This species typically roosts in small colonies of 5–18 individuals in tree hollows or building roofs (Churchill 1998) and, therefore, is likely exposed to

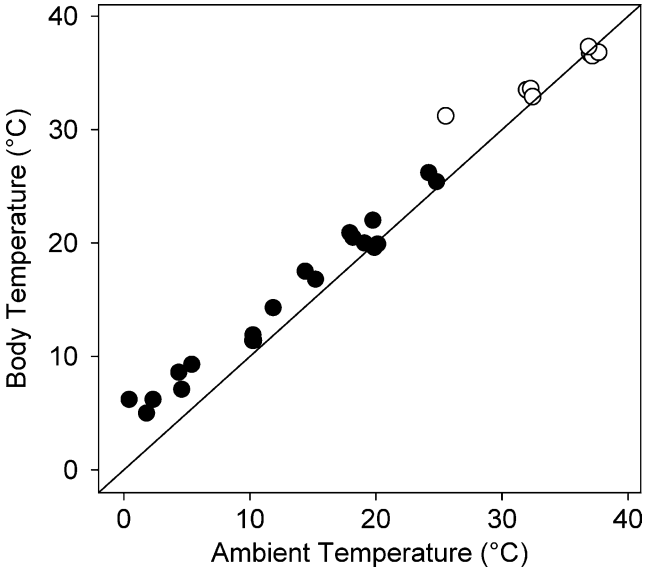


**Fig. 3** Relationship between $T_a$ and $T_b$ during recording trials for torpid (*filled circles*) and normothermic (*circles*) *V. vulturnus*. The *solid line* indicates a 1:1 relationship

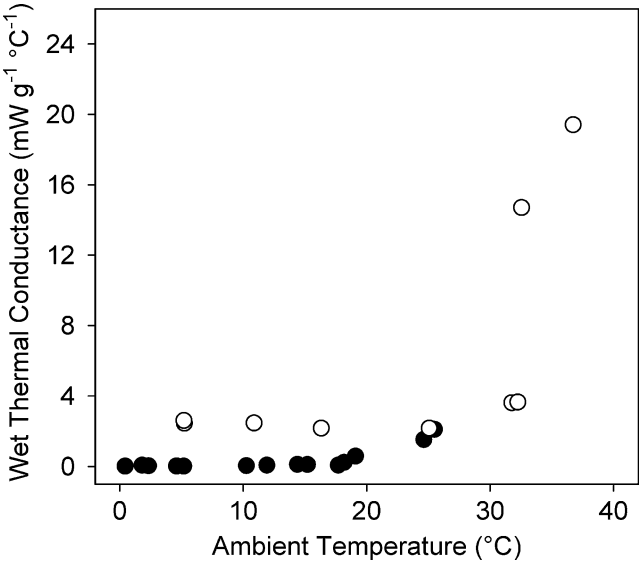


**Fig. 4** Relationship between $T_a$ and wet thermal conductance for torpid (*filled circles*) and normothermic (*circles*) *V. vulturnus*

highly variable $T_a$ during an average day. Passive warming can help endotherms arouse from torpor at dramatically reduced energetic cost (Geiser and Drury 2003), and the diurnal roost $T_a$ profile exerts strong influence on arousal timing in other tree-rooting Australian vespertilionids in the field (Turbill et al. 2003a, 2003b) and laboratory (Turbill et al. 2004). These observations, coupled with our findings suggest that *V. vulturnus* may rely on an exogenous $T_a$ cue to regulate the timing of torpor and arousal, rather than photoperiod. Quantifying torpor use in free-ranging *V. vulturnus* would be useful because torpor patterns often vary widely between field and laboratory studies (Geiser et al. 2000). However, this will not be possible until the development of temperature-sensitive radiotransmitters that are smaller than those currently available.

The breadth of the TNZ in *V. vulturnus* was 5.7°C, from 27.6°C to 33.3°C, which is surprisingly wide for such a small endotherm. TNZ breadth does tend to scale with body mass in bats such that large pteropodids may have TNZs spanning up to 15°C while smaller species have TNZs as small as 1°C (Speakman and Thomas 2003). There is considerable variation in this relationship, however, and a number of other relatively small bat species have very broad TNZs, including *Eptesicus fuscus* (breadth of 9–10°C, 15 g, Willis 2003), *Lasiurus cinereus* (5–10°C, 25–40 g, Cryan and Wolf 2003), and most notably, *Mops condylurus* (12–15°C, 23 g, Maloney et al. 1999). In part, this likely reflects the fact that $T_b$ is variable for many small bats, including *V. vulturnus* (Fig. 3), within the TNZ. The large naked wing surface of bats may also allow them to exploit relatively minor postural adjustments to dramatically alter thermal conductance within the TNZ, and thereby increase their range of thermoneutral temperatures. Further study addressing the allometry of TNZ breadth in mammals from different taxonomic groups would be useful for addressing this question, as would comparisons of TNZ and minimum thermal conductance among bats species that differ in wing surface area.

BMR of *V. vulturnus* was only about 55% of that predicted for bats on the basis of body mass (Speakman and Thomas 2003). This is consistent with two not necessarily mutually exclusive hypotheses about residual BMR variation in bats: (1) The Vespertilionidae are characterised by relatively low BMR, either as a consequence of phylogeny or due to the largely insectivorous diet of the family (Speakman and Thomas 2003; Willis 2003); and (2) Australian bats have evolved low BMR to reduce energy expenditure in the face of unpredictable resource abundance characteristic of many Australian ecosystems (Geiser and Brigham 2000; Geiser 2005). To test Hypothesis 1, we re-analysed Speakman and Thomas (2003) data. We excluded datapoints for two species included in the original analysis, because bats in these studies did not appear to be under standard conditions, and we added published BMR data from an additional six vespertilionids and our value for *V. vulturnus*, which brought the species count for the family to 18. We plotted values of vespertilionid BMR separately from those for all other species included in the analysis and compared the regression lines, following Zar (1999). The mean of absolute residuals for the BMR–body mass relationship was significantly lower for vespertilionids than for all other bats ($t$ test, $t = 2.1$, $P = 0.04$, df = 85). The vespertilionid line also had a significantly steeper slope than the line for all other species ($t = 4.7$, $P < 0.001$, df = 83) and the regression lines intersected at a body mass of 32.2 g, a value greater than the maximum body size of most vespertilionids (Fig. 5). These results demonstrate that vespertilionids, in general, are characterised by a low BMR relative to other bats. Speakman and Thomas (2003) suggested that their data upheld McNab (1989, 1992) view that diet and feeding habits rather than phylogeny or other variables, account for the bulk of residual BMR variation after effects of body mass are removed. However, this conclusion may be premature as neither their analysis, nor ours, can differentiate between effects of diet or phylogeny for the Vespertilionidae because virtually all members of this family are insectivorous.

To test Hypothesis 2, we compared the mean of residuals for the BMR–body mass relationship in the six species of Australian Vespertilionidae for which data are now available to values for the remaining 12 species from the rest of the world. We found no significant difference between the two groups ($t$ test, $t = 0.98$, $P = 0.34$, df = 16). This suggests that Australian vespertilionids are not necessarily characterised by low BMR

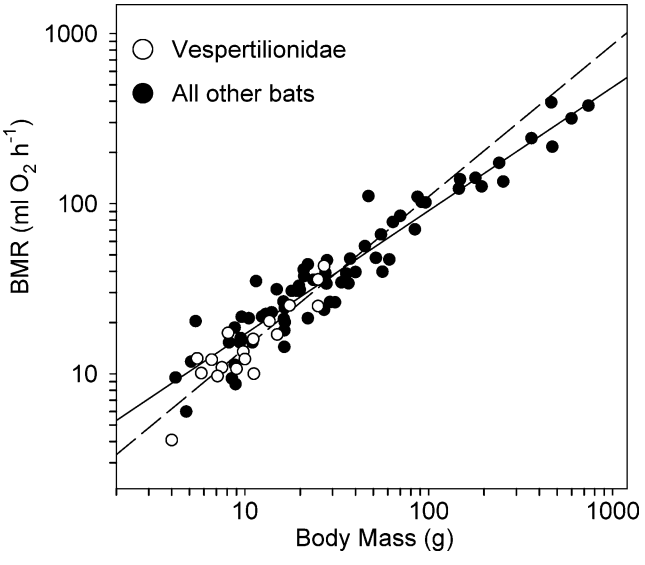


**Fig. 5** Relationship between the base 10 logarithm of body mass and the base 10 logarithm of basal metabolic rate in 18 species of bats, including *V. vulturnus*, from the family Vespertilionidae ($Log_{10}BMR = 0.257 + 0.893 \times Log_{10}BM$, $F_{1,16} = 64.98$, $r^2 = 0.80$, $P < 0.001$), plotted with the same relationship for the remaining 69 species of bats of all other families for which data are available ($Log_{10}BMR = 0.508 + 0.726 \times Log_{10}BM$, $F_{1,67} = 723$, $r^2 = 0.92$, $P < 0.001$)

but that low maintenance metabolism is a generalised trait of this family of bats. However, until a complete phylogeny of bats is available and meaningful phylogenetically corrected analyses are possible, it remains unlikely that questions regarding residual BMR variation will be resolved for bats.

Our observations about BMR support the view that the Vespertilionidae have evolved characteristics allowing for conservative energy use, but it is not clear whether BMR itself, or traits that correlate with BMR, are subject to selection pressures on energy use. It remains to be demonstrated that BMR, as a physiological trait, is directly relevant to reproductive fitness for bats and other small endotherms that show a high proclivity for torpor. In the wild, many of these species probably rarely experience the standard conditions required for BMR measurement (i.e., normothermic, within TNZ, resting, non-reproductive, and post-absorptive). If free-living bats rarely or never experience standard conditions, then BMR is probably not a trait directly subject to natural selection and it is likely that other traits, correlated with BMR, are influenced by selection pressure. Further work is needed to resolve the relevance of BMR to the reproductive fitness and ecophysiology of free-living bats.

*Vespadelus vulturnus* also appears to have evolved a conservative use of energy during torpor. The minimum $T_b$ during torpor of about 5°C was within 0.3°C of the median value for hibernators (Geiser and Ruf 1995) and the $T_b$-$T_a$ differential of thermoconforming bats during torpor (about 1.5–2°C) was in line with that reported in previous studies of northern and southern hemisphere bats (Geiser and Brigham 2000; Henshaw 1968, 1970; Willis et al. 2005). However, the TMR predicted by our regression equation was very low at only 44% of the predicted minimum value for hibernators at $T_b = 5$°C and 29% of that predicted at $T_b = 20$°C (Geiser 1988). Energy costs at 5°C were only 0.15% of those for a normothermic bat at the same $T_a$, 0.07% of maximum MR during arousal from torpor, and 2% of BMR. Even at a relatively high $T_a$ of 20°C, that free-living *V. vulturnus* would commonly experience in their tree-roosts throughout the year, energy costs during torpor were still very low at only 1.6% of RMR and 8% of BMR. These observations suggest that *V. vulturnus* is adapted to maximise energy savings during torpor, beyond the energy savings predicted based on body mass. It is possible that the low TMR we observed could reflect methodology because we allowed more time for bats to reach a steady-state minimum TMR during torpor than most studies. However, it is unlikely that methodological differences alone could account for all of the difference between TMR values we found, and those predicted based on body mass.

Not only does *V. vulturnus* use energy frugally within the thermoneutral zone and during torpor but it also appears that this species has evolved the ability to reduce heat loss, and thus save energy, while normothermic below thermoneutrality as well. The $T_{lc}$ of 27.6°C was 3.4°C lower than that predicted for a 4 g bat (Speakman and Thomas 2003) and wet thermal conductance of normothermic *V. vulturnus* below thermoneutrality was 62% of the mass-predicted value for bats (Bradley and Deavers 1980). Both of these low values suggest that *V. vulturnus* is adapted for minimising heat loss at low $T_a$. Willis (2003) found evidence for geographic variation in $C_{wet}$ in a North American vepertilionid such that individuals from a cold northern study site had lower $C_{wet}$ than individuals from a warmer site. The northern tablelands of NSW have a cool temperate climate that is much colder than other parts of *V. vulturnus*' range, especially in winter. It would be interesting to compare the thermal physiology of this species in different parts of its range to test the hypothesis that Australian vespertilionid bats exhibit intraspecific geographic variation in thermal physiology.

We found a large difference between $C_{wet}$ of normothermic versus torpid bats, and $C_{wet}$ during torpor was only 20% of that during normothermia. This almost certainly reflects physiological adjustments in peripheral vasoconstriction in conjunction with a very low TMR (Geiser 2004). It could also reflect a small measurement error due to a time lag in our measurement of $T_b$ at the end of recording sessions. If bats began rewarming before our torpid $T_b$ measurements were recorded, then we could have overestimated the $T_b$-$T_a$ differential and, therefore, underestimated $C_{wet}$ during torpor. It is also possible that our estimate of $T_b$ during normothermia introduced an error into our calculations. However, it is unlikely that these factors strongly influenced our results. For one, the error associated with estimating normothermic $T_b$ is likely small (see above) and, more importantly, the difference in $C_{wet}$ between torpor and normothermia was actually slightly higher than that predicted on the basis of body mass. Geiser (2004) calculated the relationships between $C_{wet}$ and body mass for hibernators during normothermia, and steady-state torpor and his equations predict that torpid $C_{wet}$ should be 17% of normothermic $C_{wet}$ for a 4 g thermoconforming hibernator. Thus, our torpor value of 20% of the normothermic $C_{wet}$ is in line with that of hibernators in general.

Our data provide more evidence that the Vespertilionidae possess a suite of characteristics which facilitate conservative energy use, including frequent use of torpor, low BMR, low thermal conductance below thermoneutrality, and a relatively low $T_{lc}$. *V. vulturnus* has a low MR during torpor which would reduce energy expenditure even further, particularly at temperatures which this species would commonly experience in its tree roosts. These traits may help vespertilionids cope with unpredictable and/or variable climate conditions and prey availability. More data on small species near the limit for endothermy, like *V. vulturnus*, are important because they help better quantify scaling relationships and provide insight into the selection pressures acting on endothermic animals at the

boundaries of body size restrictions imposed by natural selection.

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