Thermal energetics of *Nyctophilus geoffroyi* (Chiroptera: Vespertilionidae) at the southern limits of its distribution

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**Abstract**

The energetics of the lesser long-eared bat, *Nyctophilus geoffroyi*, at the southern limits of its distribution was examined to determine whether this species shows any latitudinal variation in this aspect of its physiological ecology. Estimates of metabolic rate were obtained from the oxygen consumption of adult bats in a non-reproductive condition. Values for the thermoneutral zone were similar but thermal conductance was lower than for bats from mainland of Australia. Euthermic body temperature was higher (37.4 ± 0.2°C) and the ambient temperature at which *N. geoffroyi* entered torpor has a downward shift of 10°C at the southern limits of its distribution. The basal metabolic rate (1.12 ± 0.14 mL O$_2$ g$^{-1}$ h$^{-1}$) also was lower than in lower latitudes. Thermal conductance of the bats in Tasmania was lower than that found in New South Wales or Western Australia (0.29 v. 0.38–0.39 mL O$_2$ g$^{-1}$ h$^{-1}$°C$^{-1}$). All of these differences are apparently adaptations to a cooler environment.

**Introduction**

An insight into the natural history of a species may be gained through measurement of metabolic parameters, with special adaptations or physiological abilities indicated by deviations from a general pattern (Tomasi 1985). It is also important to understand the energetics of a species in order to assess the influence of abiotic factors (e.g. climate) in limiting distribution (Barclay 1991). World-wide, bats are the second most diverse mammalian order (after rodents) in terms of number of species, and this group has the greatest diversity in morphology, diet and behaviour (Mills *et al.* 1996; Churchill 1998). Bat distributions cover a wide range of climatic conditions, but the most rigorous thermal conditions exist in the temperate regions with climatic extremes and seasonal limitations in prey abundance (Hosken 1997).

Many studies have been conducted on the energetics of temperate-zone microchiropteran bat species, but very little work has been undertaken on the energetics of any bat species at the limits of its distribution. Recently, Arlettaz *et al.* (2000) studied *Tadarida teiotus* at a latitude of 45–46°N, the northernmost outpost of any molossid bat in the world. Climatic factors are generally the major determinant of these limits and therefore climatic extremes experienced at the latitudinal limits of a species’ distribution should influence the thermal energetics of that species. In Australia this could result in demonstrable differences between conspecifics at the higher latitudes of mainland Australia. For example, one might expect that bats from southern Tasmania (43°S) would have a lower thermoneutral zone, lower thermal conductance, higher $T_b$ and should enter torpor at a lower $T_a$.

To test this hypothesis the energetics of the lesser long-eared bat, *Nyctophilus geoffroyi*, from southern Tasmania (representing the southern distributional limits for this species)
were investigated. *Nyctophilus geoffroyi* is a small (7–10 g) insectivorous bat that uses aerial foraging and gleaning from foliage to capture prey. It is reported to roost solitarily, primarily in crevices and tree hollows. It is endemic to Australia and has a widespread distribution across many habitat types (Hall 1984; Maddock and Tidemann 1995).

The results from this study are to be compared with results obtained from the thermoregulation of *N. geoffroyi* in New South Wales (Geiser and Brigham 2000) and Western Australia (Hosken and Withers 1999).

**Materials and Methods**

Bats were captured using harp traps at the base of Mt Wellington, near Hobart, Tasmania (42°53’S, 147°19’E) in wet sclerophyll forest at approximately 400 m altitude. Captured animals were transported to the University of Tasmania and housed in an outdoor flight cage (3 × 1.5 × 2 m) under conditions of natural light and temperature. Bats were fed mealworms (*Tenebrio molitor*) with occasional supplementation of wild-caught moths. Mealworms were kept in a substrate of wheat bran, Wombaroo™ small insectivore mix and Heinz™ high-protein baby cereal. Inca™ Ornithon, a vitamin and mineral supplement, was added to the drinking water, which was supplied *ad libitum*. Metabolic investigations into thermal energetics were conducted in autumn 2000 after the bats had been in captivity for several months. All bats appeared healthy and maintained a stable body mass averaging 9.8 ± 0.3 g before each experiment. The bats were deprived of food for at least 6 h, which was sufficient for them to be post-absorptive (Genoud 1993; Morris et al. 1994). Measurements were taken between 10:00 and 16:30 hours. Each bat was placed into a respirometry chamber (250 mL) equipped with a conical hessian structure to allow the bats to roost. The chambers were placed into a controlled-temperature water bath (±1.0°C) at ambient temperatures (T<sub>a</sub>) of 5–40°C in intervals of 5°C. VO<sub>2</sub> was measured using an Ametek™ 3A/D oxygen analyser with an N.37M oxygen sensor and an Ametek R2 flow-control meter. The analyser was calibrated such that the incoming air had an O<sub>2</sub> content of 20.92%. VO<sub>2</sub> measurements were taken using an Ametek carbon dioxide analyser with a P.61B carbon dioxide sensor and an R1 flow-control meter. Airflow into the chamber was controlled at 100–150 mL min<sup>–1</sup> using the flow-control meter. VO<sub>2</sub> and VCO<sub>2</sub> were calculated following Withers (1977) and results expressed as means ± s.e. These values allowed the calculation of the respiratory quotient (RQ) (respiratory exchange ratio, RER), the ratio of oxygen consumed to carbon dioxide produced.

Oxygen consumption rates (VO<sub>2</sub>, mL O<sub>2</sub> g<sup>–1</sup> h<sup>–1</sup>) and carbon dioxide production rates (VCO<sub>2</sub>, mL CO<sub>2</sub> g<sup>–1</sup> h<sup>–1</sup>) were measured continuously using flow-through respirometry. Bats were weighed to the nearest 0.1 g before each experiment. The bats were deprived of food for at least 6 h, which was sufficient for them to be post-absorptive (Genoud 1993; Morris et al. 1994). Measurements were taken between 10:00 and 16:30 hours. Each bat was placed into a respirometry chamber (250 mL) equipped with a conical hessian structure to allow the bats to roost. The chambers were placed into a controlled-temperature water bath (±1.0°C) at ambient temperatures (T<sub>a</sub>) of 5–40°C in intervals of 5°C. VO<sub>2</sub> was measured using an Ametek™ 3A/D oxygen analyser with an N.37M oxygen sensor and an Ametek R2 flow-control meter. The analyser was calibrated such that the incoming air had an O<sub>2</sub> content of 20.92%. VO<sub>2</sub> and VCO<sub>2</sub> measurements were taken using an Ametek carbon dioxide analyser with a P.61B carbon dioxide sensor and an R1 flow-control meter. Airflow into the chamber was controlled at 100–150 mL min<sup>–1</sup> using the flow-control meter. VO<sub>2</sub> and VCO<sub>2</sub> were calculated following Withers (1977) and results expressed as means ± s.e. These values allowed the calculation of the respiratory quotient (RQ) (respiratory exchange ratio, RER), the ratio of oxygen consumed to carbon dioxide produced.

Wet thermal conductance (C, mL O<sub>2</sub> g<sup>–1</sup> h<sup>–1</sup> °C<sup>–1</sup>) was calculated from the formula C = VO<sub>2</sub> (T<sub>b</sub> – T<sub>a</sub>)<sup>–1</sup>. Values were calculated only for ambient temperatures below 35°C; as above this, the temperature differential becomes very small and unreliable and makes accurate determination difficult (Hosken 1997). Body temperature (T<sub>b</sub>) was measured to the nearest 0.1°C by inserting a fine calibrated thermocouple probe 1 cm into the rectum within 60 s of removal of the bat from the chamber. Bats were considered torpid when Tb fell below 28.5°C.

Five bats (3 non-reproductive females and 2 males) were used throughout this study. The metabolic rate of each bat was measured at each ambient temperature, once when the bat was euthermic and once when it was torpid. Bats were held in the respirometry chambers until a steady state of VO<sub>2</sub> was reached (≥15 min euthermic, ≥2 h torpid). Sampling in a steady state for ≥10 min was used to calculate VO<sub>2</sub> and VCO<sub>2</sub>. Data were analysed using repeated-measures ANOVA with Tukey’s *post hoc* tests. Significance levels of 0.05 were used and results are expressed as means ± s.e. unless otherwise indicated.

**Results**

There were significant differences in metabolic rates measured at the different ambient temperatures (F<sub>4,35</sub> = 8.013, P < 0.001) (Fig. 1). Basal metabolic rate (BMR) for *Nyctophilus geoffroyi* was 1.119 ± 0.186 mL O<sub>2</sub> g<sup>–1</sup> h<sup>–1</sup> (T<sub>b</sub> = 37.4 ± 0.6°C, N = 5) and occurred at T<sub>a</sub> of 35°C. As T<sub>a</sub> decreased the metabolic rate (MR) of the bats increased linearly (Fig. 1). There was no significant difference between MR measured at T<sub>a</sub> above 30°C; below 30°C, however, significant differences emerged, e.g. metabolic rates at 5°C and 10°C were different to all others (0.001 < P < 0.028). When bats entered torpor they...
maintained a temperature differential of approximately 12°C between $T_a$ and $T_b$ and so were considered to be torpid but thermoregulating. Torpid bats displayed no significant change in MR with $T_a$ from 5°C to 15°C ($F_{2,12} = 0.567, P = 0.582$).

There were significant changes in euthermic $T_b$ over the different $T_a$ ($F_{4,35} = 9.324, P > 0.001$) (Fig. 2). Post hoc Tukey’s tests showed that $T_b$ was significantly lower at $T_a$ between 15°C and 20°C ($0.001 < P < 0.05$).

Examination of the raw data showed that the lowest $T_b$ for a euthermic bat was 28.1°C and the highest $T_b$ for a torpid bat was 26.1°C, so we have assumed that the Tasmanian bats enter torpor with a $T_b$ of approximately 27–28°C. Three of the five bats became torpid at $T_a = 15°C$ ($F_{2,12} = 6.884, P = 0.01$); all bats could become torpid at lower ambient temperatures. At $T_a$ of 5°C most bats had a $T_b$ of 16–17°C.
There was no significant difference in thermal conductance over the range of temperature during torpor ($F_{2,12} = 1.192, P = 0.337$) (Fig. 3). A significant difference was obtained between mean thermal conductance measured at different $T_a$ during euthermy ($F_{5,35} = 9.85, P < 0.001$) (Fig. 4). However, this was only due to the high thermal conductance at $T_a = 40^\circ$C; all other values were not significantly different ($0.769 < P < 0.999$). During torpor, $C$ was reduced by 40% to 63% of euthermic values.

No significant difference in RQ was found during euthermy ($F_{5,35} = 2.102, P = 0.069$), nor in torpid bats ($F_{2,12} = 0.807, P = 0.469$) (Fig. 4). There was, however, a significant difference between the values obtained for torpid and euthermic bats ($F_{1,16} = 2.71, P = 0.037$)
Thermal energetics of Nyctophilus geoffroyi

Aust. J. Zoology 47

Discussion

The minimum rate of metabolism for euthermic N. geoffroyi occurred between 30°C and 40°C; there was no significant change in body temperature between ambient temperatures of 25°C and 35°C. The thermoneutral zone for N. geoffroyi therefore probably falls within the range of 30°C and 35°C. This is similar to results for N. geoffroyi obtained by Hosken and Withers (1999) and Geiser and Brigham (2000) (Table 1).

The basal metabolic rate of 1.119 ± 0.064 is lower than the rates found for the same species on mainland Australia (Table 1). However, N. geoffroyi in Tasmania is considerably heavier (10 g; Green 1977; 9.8 g: this study) than the mainland forms (7 g in New South Wales and 8 g in Western Australia) (Table 1). Converting the data to Weight 0.75 reduced these differences in BMR. However, the converted values still show that the Tasmanian form has a lower BMR (Table 1). A related species, N. gouldi from New South Wales, has a similar mass (10 g) to the Tasmanian N. geoffroyi and a similar metabolic rate of 1.22 mL g⁻¹ h⁻¹ (Geiser and Brigham 2000).

Below the thermoneutral zone euthermic bats exhibit a typical mammalian pattern of thermal adjustment, with metabolic rate increasing as ambient temperature decreases. In N. geoffroyi, this results in a substantial increase in metabolic cost. At 5°C, metabolic rate has increased almost 500% over the minimum rate experienced at 35°C. Bats are able to use torpor to offset this metabolic cost. N. geoffroyi entered torpor at a Ta of 15°C and below. Torpid bats at all Tₐs were still thermoregulating, maintaining a temperature differential of approximately 12°C between Tₑ and Tₐ. The use of torpor resulted in metabolic savings of 28–85% of endothermic values at ambient temperatures below 20°C. As the data in Table 1 indicate, there are minor variations in metabolic parameters between geographical locations but there are differences in the ambient temperature at which bats will enter torpor. N. geoffroyi in Tasmania has a downward shift of 10°C in the Tₑ at which it enters torpor. This may be an adaptation to the more extreme conditions experienced at the limits of its distribution.

To gain a better understanding of differences in thermoregulatory strategies it is necessary to examine the degree to which body temperature is regulated relative to ambient temperature (Henshaw and Folk 1966). The entrance into torpor is usually based on Tₑ but

Table 1. Comparative energetics of Nyctophilus geoffroyi

Data for New South Wales (NSW) are from Geiser and Brigham (2000), those for Western Australia (WA) are from Hosken and Withers (1999), and those for Tasmania are from this study. Masses are for captive individuals. TNZ, thermoneutral zone; BMR, basal metabolic rate; Tₑ(T), body temperature in the thermoneutral zone; Tₑ(T), ambient temperature at which bats entered torpor; Tₑ(T), body temperature at which bats entered torpor; C, conductance

<table>
<thead>
<tr>
<th></th>
<th>NSW</th>
<th>WA</th>
<th>Tasmania</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>6</td>
<td>8</td>
<td>5</td>
</tr>
<tr>
<td>Mass (g)</td>
<td>7</td>
<td>8.0 ± 0.1 (s.e.)</td>
<td>9.8 ± 0.03 (s.e.)</td>
</tr>
<tr>
<td>TNZ (°C)</td>
<td>29–33</td>
<td>35–40</td>
<td>30–35</td>
</tr>
<tr>
<td>BMR (mL O₂ g⁻¹ h⁻¹)</td>
<td>1.36 ± 0.17 (s.d.)</td>
<td>1.42 ± 0.1 (s.e.)</td>
<td>1.12 ± 0.03 (s.e.)</td>
</tr>
<tr>
<td>BMR (W₀.⁷⁵)</td>
<td>2.24</td>
<td>2.35</td>
<td>1.98</td>
</tr>
<tr>
<td>Tₑ(E) (°C)</td>
<td>35.7 ± 0.7 (s.d.)</td>
<td>31.6 ± 0.2 (s.e.)</td>
<td>37.4 ± 0.2 (s.e.)</td>
</tr>
<tr>
<td>Tₑ(T) (°C)</td>
<td>30</td>
<td>26</td>
<td>26</td>
</tr>
<tr>
<td>Tₑ(T) (°C)</td>
<td>25</td>
<td>24.2</td>
<td>15</td>
</tr>
<tr>
<td>C (mL O₂ g⁻¹ h⁻¹ C⁻¹)</td>
<td>0.38</td>
<td>0.39</td>
<td>0.29 ± 0.16 (s.e.)</td>
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as bats are thermolabile, $T_b$ should be used in conjunction with some other measurement to
determine the onset of torpor. Geiser and Ruf (1995) suggest that minimum oxygen
consumption may be a better indicator of torpor.

Porter et al. (1994) state that posture is an important variable in regulating heat loss.
Exposed surface area may be significantly influenced by behaviour and posture, and at
lower $T_a$ bats predominantly assume a curled-up posture. Observation of the posture of bats
in this study was not possible due to the design of the respirometry chambers and shelters
in which the bats hung, but upon removal from the chambers bats were commonly found
hunched up in the top of the hessian structure. It is assumed, in view of the thermal
ductance data, that the bats were reducing their surface area to regulate their level of
thermal conductance, as observed by Porter et al. (1994).

The greater the insulation an animal exhibits, the lower the values of thermal
ductance. In N. geoffroyi, $C$ was not related to $T_a$ and was indicative of active
metabolism with increasing thermogenesis as $T_a$ declined. The use of torpor results in a
reduction in $C$ of 40–63% of endothermic values. The mean rate of $C$ is lower than that
found in this species on mainland Australia (Table 1). This reduction would assist, no doubt,
the species in reducing heat loss by lowering the thermal gradient between $T_b$ and $T_a$.
Conduction varies due, in part, to changes in insulation, peripheral vasoconstriction
(Hosken and Withers 1999) and surface area.

Clustering is widely reported in the literature to be another method of reducing thermal
ductance. Roverud and Chappell (1991) found that Noctilio albiventris sheltering in
clusters reduced their exposed body surface by about 60%, which provided large energy
savings. As bats in this study were measured individually, clustering is not proposed to have
a major effect on our measurements of MR. N. geoffroyi is reported to normally be a solitary
tree-roosting species (Maddock and Tidemann 1995; Churchill 1998), yet all the bats in this
study roosted in clusters for most of the time they were in captivity, irrespective of the
number of different roosting opportunities they were given. It therefore seems likely that,
in Tasmania, N. geoffroyi uses clustering as one of a suite of behavioural thermoregulatory
mechanisms for maximising energetic savings.

Respiratory quotients approaching 1.0 are indicative of carbohydrate oxidation to
provide metabolic fuel, while RQs approaching 0.7 are indicative of fat oxidation (Morris
et al. 1994). The results obtained in this study indicate that for endothermic bats at higher
$T_a$ when MR is relatively low, carbohydrate oxidation alone is able to fuel metabolic
activity. At lower $T_a$ when MR is relatively high, bats switch to oxidation of fat as a more
efficient fuel source for metabolic activity.

The low RQ of torpid bats is also indicative of fat oxidation. Morris et al. (1994) found
that torpid N. gouldi exhibited intermittent respiration bouts alternating with periods of
apnoea. This resulted in discontinuous and disproportional gas exchange. The monitored
traces of $V_{O_2}$ and $V_{CO_2}$ for the bats in this study showed no evidence of intermittent
breathing or period of apnoea, but this could influence the downward trend in RQ during
torpor. During torpor, the acid/base balance may be shifted, subsequently resulting in
changes in the respiratory quotient. Speakman and Racey (1987) found that in brown
long-eared bats (Plecotus auritus) the RQ varied between 0.7 and 0.95 when the bats were
fed mealworms. Similar results have been recorded for Nyctophilus major (Hosken 1997),
N. geoffroyi (Hosken and Withers 1999) and Chalinolobus gouldii (Hosken and Withers
1997).

Some care must be taken when interpreting the results of studies on captive animals as
conditions in captivity may have a significant effect. In Artibeus jamaicensis, $T_a$ and time
Thermal energetics of Nyctophilus geoffroyi

in captivity had a significant effect on both Tb and oxygen consumption: data gained from bats soon after capture were representative of natural thermoregulatory patterns, whereas data on captive bats were indicative of maximum homeothermic capabilities (Studier and Wilson 1979). However, in Western Australia, Hosken (1997) found that in N. major there was no evidence of any effect of duration in captivity on the energetic responses of bats. Bats deprived of food for over 12 h to ensure they are ‘post-absorptive’ may not reflect normal thermoregulatory patterns as mild food deprivation may lead to significant differences in body temperature and metabolic rate (Kurta and Fujita 1988). Careful examination of both the experimental conditions and the housing and maintenance conditions must be considered to determine the likelihood of any effects of captivity.

In conclusion, the Tb at which N. geoffroyi enters torpor is similar throughout its range but the corresponding Ta is significantly lower at the southern limits of its distribution. Tasmania receives much lower levels of solar radiation throughout the year (Davies 1965) than do either of the other two sites at which N. geoffroyi has been studied (in New South Wales and Western Australia). This is, in turn, expected to reduce the effect of passive re-warming due to solar radiation. The fact that torpor is induced at a lower Ta than on mainland Australia may be in compensation for the reduction in passive re-warming. This may be seen as an adaptation to more rigorous climatic conditions.

Acknowledgments

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References


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