The metabolic rate and thermal conductance of the eastern barred bandicoot (Perameles gunnii) at different ambient temperatures

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Abstract

We investigated the metabolic rate, thermoneutral zone and thermal conductance of the eastern barred bandicoot in Tasmania. Five adult eastern barred bandicoots (two males, three non-reproductive females) were tested at temperatures of 3, 10, 15, 20, 25, 30, 35 and 40°C. The thermoneutral zone was calculated from oxygen consumption and body temperature, measured during the daytime: their normal resting phase. It was found that the thermoneutral zone lies between 25°C and 30°C, with a minimum metabolic rate of 0.51 mL g⁻¹ h⁻¹ and body temperature of 35.8°C. At cooler ambient temperatures (3–20°C) the body temperature decreased to approximately 34.0°C while the metabolic rate increased from 0.7 to 1.3 mL g⁻¹ h⁻¹. At high temperatures (35–40°C) both body temperature (36.9–38.7°C) and metabolic rate (1.0–1.5 mL g⁻¹ h⁻¹) rose. Thermal conductance was low below an ambient temperature of 30°C but increased significantly at higher temperatures. The low thermal conductance (due, in part, to good insulation, a reduced body temperature at lower ambient temperatures, combined with a relatively high metabolic rate) suggests that this species is well adapted to cooler environments but it could not thermoregulate easily at temperatures above 30°C.

Introduction

Many studies have shown that the energy metabolism of marsupials is 30–35% less than that of equivalent-sized placental mammals (MacMillen and Nelson 1969; Dawson and Hulbert 1970; Withers 1992). However, marsupials are able to regulate their body temperatures in a similar way to most placental mammals (Robinson and Morrison 1957; Dawson 1969; Withers 1992). Animals exposed to high ambient temperatures attempt to maintain their body temperature (T_b) either with behavioural responses (postural changes or avoidance) or with some form of physiological regulation (alterations in circulatory function and evaporative cooling).

To cope with low temperatures, small mammals rely primarily on metabolic adjustments, while larger species are also able to adjust through changes in insulation (Pohl 1976). The main metabolic adjustment is an increase of their metabolic rate, either with muscular activity and exercise, or with involuntary muscle contractions (shivering), or by non-shivering thermogenesis (increased metabolic rate without noticeable muscle contractions) (Schmidt-Nielsen 1983).

Thermal conductance (C_wet) is a measure of the ease by which heat enters or leaves an animal. It is also a way of determining the lower critical body temperature of an animal at different lower ambient temperatures (Fournier and Thomas 1999). This can be accomplished by calculation of a value for the lower critical ambient temperature from the equation

\[ M = C_{\text{wet}}(T_b - T_a), \]

where M is the metabolic heat production and T_a is the ambient temperature.
This study investigates the thermoneutral zone of the eastern barred bandicoot (Perameles gunnii) and its thermal conductance at different temperatures. The thermoneutral zone is the temperature range within which the metabolic heat production is unaffected by a temperature change (Schmidt-Nielsen 1983). Hulbert and Dawson (1974a, 1974b, 1974c) studied the thermoregulating abilities of the perameloid marsupials on mainland Australia and found that at high ambient temperatures (40°C) some animals could not thermoregulate easily (i.e. T_b did not stabilise) while their thermoneutral zone (TNZ) was between 25°C and 30°C. We aimed to examine the thermoregulating abilities of the eastern barred bandicoot from Tasmania, Australia’s southernmost and coolest State.

Materials and Methods

Animals

Five adult eastern barred bandicoots, two males and three females (non-lactating and non-reproductive), were caught in the wild during August–October 2001. The animals were fed apples, peanut butter and bread, sunflower seed and cooked mince. They were housed individually in cages with dimensions 2.3 × 1.9 × 1 m at the University of Tasmania. All animals were weighed (to ±10 g) on a Salter balance and fasted for at least 7 h prior to any measurements. The average body mass of the animals was ~803 g. The Ethics committee of the University of Tasmania, acting in accord with the Australian Code of Practice, approved all experiments (A6212), and the Tasmanian Parks and Wildlife Service provided the permit for the trapping of the bandicoots (FA 01133).

Measurements

Oxygen consumption was measured for the five adult bandicoots using open-circuit respirometry. Each animal was placed individually into a sealed test chamber (25 × 26 × 28 cm) equipped with air-intake tube, air-egress tube, and air-temperature thermometer. The animals were tested between 1100 and 1500 hours (the hours of normal sleep and quiescent phase) at 3, 10, 15, 20, 25, 30, 35 and 40°C. Each temperature was tested on a separate day. The test chamber was fully immersed in a water bath in a darkened room. Atmospheric air was pumped into the chamber at a rate of 3 L min⁻¹ regulated via a rotameter with direct scale reading, produced and calibrated by Halu Glass (Tasmania). The air passed through a 1-m-long coiled copper pipe inside the water bath, thus ensuring that air entering the chamber was at a temperature similar to that of the water bath. A sample of egress-air was scrubbed of water and CO₂ and the difference in O₂ concentration between the ambient air and the excurrent air (which was leaving the chamber) passed through drying tubes (containing silica gel) and indicating soda lime before entering the oxygen analyser (AMETEK S-3A/11, two channels and N-37M oxygen sensor). The difference between the percentage of oxygen of the air entering and air leaving the chamber could be read directly on the analyser. After a 30-min settling period, each animal was left in the apparatus until the difference in O₂ concentration per minute had stabilised for a minimum of 3 min; this occurred after ~15 min and was recorded as the change in O₂ concentration between the ambient air and the egress air. The analyser was then left at zero.

The animal’s body temperature was taken by inserting a thermocouple approximately 2 cm into the rectum, immediately after each experimental period. Oxygen consumption, $\dot{V}_{O_2}$, was calculated using Withers’ (2001) formula and C_wet was calculated according to Herreid and Kessel (1967) and Rose et al. (1998).

As evaporative water loss was not measured, our results are ‘wet’ conductance (C_wet). The constant of 20.1 was then used to convert millilitres of O₂ to joules (assuming RQ = 1.0: Kleiber 1961) to allow comparison with other studies (Table 1).

Statistical analysis

Data are presented as means ± standard error of the mean (s.e.m.) unless stated otherwise. The effect of ambient temperature on the rate of oxygen consumption, thermal conductance and body temperature was analysed using SPSS 10.0 for Windows. The analysis compared means with a one-way ANOVA (with temperature as the independent variable); P < 0.05 was regarded as statistically significant. Homogeneity of variances was tested and subsequently a number of a priori contrast tests were applied.
Results

The change in $\dot{V}_O_2$ with temperature is presented in Fig. 1. Metabolic rates at different ambient temperatures were significantly different (ANOVA, $F_{7,32} = 5.8$, $P < 0.001$). There are no significant differences between $T = 25^\circ C$ and $T = 30^\circ C$, where the metabolic rate of the eastern barred bandicoot lies between $0.51 \pm 0.02$ mL $O_2$ g$^{-1}$ h$^{-1}$ and $0.62 \pm 0.05$ mL $O_2$ g$^{-1}$ h$^{-1}$ (ANOVA contrast, $F_{1,8} = 0.015$, $P = 0.97$). These values are lower than those found at all other ambient temperatures (ANOVA contrast, $F_{1,32} = 46.9$, $P < 0.001$). Thus the thermoneutral zone is 25–30°C.

At the high temperature of 40°C, after removal of the chamber lid the subjects were observed breathing in a rapid and shallow manner, i.e. they were panting. At 35°C and 40°C ambient temperatures, bandicoots were observed licking their fur when removed from the chamber. At low temperatures, shivering of the rump was the most obvious behaviour and the metabolic rate was raised.

Fig. 2 shows that the $C_wet$ changed significantly at the higher ambient temperatures (ANOVA, $F_{7,32} = 9.030$, $P < 0.001$). At ambient temperatures between 3°C and 25°C $C_wet$ varied little: all the values were low. There was a significant difference between $C_wet$ at these lower temperatures and at 30°C (ANOVA contrast, $F_{1,28} = 14.6$, $P = 0.017$). At the highest temperatures (35°C and 40°C) the values of $C_wet$ were significantly higher than at
all other ambient temperatures (ANOVA contrast, $F_{1,32} = 16.9$, $P = 0.008$). At these temperatures, some of the bandicoots could not thermoregulate: when their body temperature was measured after removal from the chamber it had increased to 43°C.

Fig. 3 shows changes in body temperature after the experiment at different temperatures. There were significant changes over the range of ambient temperatures (ANOVA, $F_{7,32} = 5.779$, $P < 0.001$) At an ambient temperature of 20°C and below, the body temperature of the bandicoots was ~34.0°C (33.4–34.3°C). Above these ambient temperatures the body temperature increased significantly to 35.8°C (35.78–35.82) in the TNZ (ANOVA contrast, $F_{1,28} = 8.25$, $P = 0.007$) and significantly higher again at ambient temperatures of 35 and 40°C (ANOVA contrast, $F_{1,32} = 28.1$, $P < 0.001$). Body temperature did not vary significantly within the TNZ (ANOVA contrast, $F_{1,8} = 0.015$, $P = 0.97$).

In Fig. 4 we have plotted the mean metabolic rate against mean body temperature. It can be seen that metabolic rate increases as body temperature rises or falls below a $T_b$ of ~36°C.

**Discussion**

Our results, showing that the eastern barred bandicoot has a TNZ between 25°C and 30°C, are in agreement with Hulbert and Dawson (1974a), who found that different species of
bandicoots from different regions and climatic zones have a similar TNZ. Larcombe (2002) found that *Isoodon obesulus* from near Perth, Western Australia, has a TNZ between 25°C and 35°C. At ambient temperatures of 25–30°C the eastern barred bandicoot’s $C_{\text{wet}}$ remained low (0.956 and 2.382 J g$^{-1}$ h$^{-1}$ °C respectively). Hulbert and Dawson (1974b) stated that *Perameles gunnii* has a ‘deep and dense coat’, which would provide considerable insulation. Kinnear and Shield (1975) showed that *Macrotis lagotis*, a desert-dwelling bandicoot, also has a high and narrow TNZ, extending from 27–30°C to 32.5–35°C. At ambient temperatures below the TNZ, the bandicoot’s $T_b$ was lower.

We found that thermal conductance was correlated with the changes in ambient temperature. Consequently, at ambient temperatures lower than that of the body temperature, the $C_{\text{wet}}$ decreases, maintaining homeothermy (Herreid and Kessel 1967) while at higher ambient temperatures $C_{\text{wet}}$ is increased by evaporative means. This could have been achieved in various ways, e.g. by piloerection and peripheral blood flow changes. Heat production of animals at low temperatures is usually achieved by a rise in oxygen consumption due, in part, to muscular contractions (shivering), which occurred in our experiment. On the contrary, when mammals are ‘at rest’ within their thermoneutral zone they produce a minimal basal amount of heat (Nicol and Maskrey 1977; Richardson et al. 1994).

The fact that $C_{\text{wet}}$ remained low and did not change significantly at ambient temperatures of 3–30°C indicates the high fur insulation (Hulbert and Dawson (1974b) and good thermoregulatory abilities of this species at lower temperatures, as might be expected of an animal living in a cooler environment. Although, conductance was low and metabolic rate increased at ambient temperatures below the TNZ, body temperature did drop by almost 2°C, perhaps indicating an energy-saving strategy.

In Table 1 we compare various thermal parameters of six different bandicoots measured in their TNZ, $T = 25°C$. The wet thermal conductance of the eastern barred bandicoot is much lower than that of the golden bandicoot (*Isoodon auratus*) (Withers 1992) (Table 1). Hulbert and Dawson (1974a, 1974b) give ‘dry’ thermal conductance values for several other species of bandicoot but these are not easily compared with our data for $C_{\text{wet}}$. Larcombe (2002) did not measure thermal conductance but we have made the calculations from metabolic rate and body temperature data at the TNZ given in his paper. If the relationship between wet and dry conductance is as found by Withers (1992) in *I. auratus*, thermal conductance of the eastern barred bandicoot would be lower than that of all other bandicoots for which we have measurements. This would be expected, as it has better insulation.

Although the eastern barred bandicoot in Tasmania has the highest basal metabolic rate of all bandicoots so far studied, this value is similar to that of its congener *P. nasuta*. Both *Isoodon* species have values similar to each other but considerably lower than those of *Perameles*.

At an ambient temperature of 40°C the animals responded by increasing $\dot{V}_O_2$ and their body temperature; some to as high as 43°C. Nicol and Maskrey (1977) state that a lethal body temperature in this species is near 43°C. Two animals were removed from the experimental chamber, as they were unable to stabilise their $\dot{V}_O_2$; one of them had a $T_b$ of 43°C. Only a few marsupials have good thermoregulating abilities at high temperatures, e.g. the red kangaroo (*Macropus rufus*) (a desert species) and the eastern grey kangaroo (*Macropus giganteus*) (Dawson et al. 2000).

At high temperatures, some marsupials lick and spread saliva on their fur. Licking does contribute to the evaporative heat loss but it appears to be of only marginal significance
Table 1. Comparison of the metabolic rate, thermal conductance and body temperature of *P. gunnii* with those of other bandicoots

\( T_a = 25^\circ C \)

<table>
<thead>
<tr>
<th>Species</th>
<th>Weight (g)</th>
<th>Metabolic rate (mL g(^{-1}) h(^{-1}))</th>
<th>Conductance ((J g^{-1} h^{-1}^\circ C))</th>
<th>Body temperature ( ^\circ C )</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Perameles gunnii</em></td>
<td>800–1000</td>
<td>0.51</td>
<td>0.818 (wet)</td>
<td>35.1 (35.5)</td>
<td>This paper; Nicol and Maskrey (1977)</td>
</tr>
<tr>
<td><em>Perameles nasuta</em></td>
<td>645</td>
<td>0.49</td>
<td>0.771 (dry)</td>
<td>36.1</td>
<td>Hulbert and Dawson (1974a, 1974b)</td>
</tr>
<tr>
<td><em>Isoodon obesulus</em></td>
<td>1020</td>
<td>0.41</td>
<td>0.981 (wet)</td>
<td>33.4</td>
<td>Larcombe (2002)</td>
</tr>
<tr>
<td><em>Isoodon macrourus</em></td>
<td>1551</td>
<td>0.374</td>
<td>0.614 (dry)</td>
<td>35.9</td>
<td>Hulbert and Dawson (1974a, 1974b)</td>
</tr>
<tr>
<td><em>Isoodon auratus</em></td>
<td>339</td>
<td>0.346</td>
<td>1.53 (wet), 1.05 (dry)</td>
<td>33.8</td>
<td>Withers (1992)</td>
</tr>
<tr>
<td><em>Macrotis lagotis</em></td>
<td>1011</td>
<td>0.355</td>
<td>0.794 (dry)</td>
<td>34.9</td>
<td>Hulbert and Dawson (1974a, 1974b)</td>
</tr>
</tbody>
</table>
(Dawson 1969). Dawson et al. (1969) showed licking to be an inefficient use of water for the dissipation of body heat although there are many blood vessels in the forelimbs. In our study, it was obvious that Perameles gunnii licked its fur at high ambient temperatures (35–40°C). This was observed at the end of \( V_O_2 \) measurements and after lifting the lid from the metabolic box when animals were observed still licking and with fur darkened with saliva. Nicol and Maskrey (1977) demonstrated licking and panting at \( T_b = 38.5°C \) and the eastern barred bandicoot licked its forefeet and abdomen at \( T_b = 39°C \). With the exception of Macrotris lagotis (a desert-dwelling species), all bandicoots studied showed some dependence on saliva spreading as a means of regulating body temperature (Nicol and Maskrey 1977).

To summarise, the eastern barred bandicoot in Tasmania has a higher basal metabolic rate than the other bandicoots (Table 1) from mainland Australia. However, its average body temperature is similar to that of other species of bandicoot. The adaptation of the eastern barred bandicoot to the cooler ambient temperatures in Tasmania probably has resulted in an increased metabolic rate. However, this difference has not resulted in a changed thermoneutral zone, a characteristic that appears to be conservative amongst bandicoots.

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References


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