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The Development of Endothermy during Pouch Life in the Eastern Barred Bandicoot (*Perameles gunnii*), a Marsupial

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ABSTRACT

Marsupials are born ectothermic and gradually become endothermic during pouch occupancy. In order to study the timing of this transition, we measured the metabolic rates of eight pouch-young eastern barred bandicoots (*Perameles gunnii*) at 25°C (the thermoneutral zone of adults), at 35°C (pouch temperature), and after injection with norepinephrine. From 5 to 7 wk of age, oxygen consumption ($\dot{V}O_2$) was higher at 35°C than at 25°C. At 8 wk, $\dot{V}O_2$ was significantly higher at 25°C than at 35°C. Norepinephrine administration at 5 and 6 wk had no effect on metabolic rate, but at 8 wk, near pouch vacation, it resulted in a significant increase in metabolic rate. Our results indicate that signs of thermoregulation for *P. gunnii* begin at 7 wk, and at 8 wk the species is endothermic, that is, able to increase heat production in response to both cold and norepinephrine. The appearance of fur, first seen at the age of 6 wk and fully developed at 8 wk, coincides with the onset of endothermy.

Introduction

Many studies have focused on the development of thermoregulation in Australian marsupials, for example, *Setonix brachyurus* (Bentley and Shield 1962), *Isoodon macrourus* (Gemmell and Johnston 1985), *Potorous tridactylus* (Gemmell et al. 1987), *Macropus eugenii* (Hulbert 1988), *Trichosurus vulpecula* (Gemmell and Cepon 1993), *Bettongia gaimardi* (Rose et al. 1998), and *Petaurus breviceps* (Holloway and Geiser 2000). These studies have shown that in the early stage of their lives, marsupials have poor thermoregulatory abilities and low heat production, but by final pouch emergence, thermoregulation and heat pro-

duction reach near-adult levels (Setchell 1974; Gemmell and Johnston 1985; Gemmell et al. 1987; Gemmell and Cepon 1993; Rose et al. 1998).

Most research on thermoregulation in marsupials has involved the measurement of either body temperature or oxygen consumption ($\dot{V}O_2$) of pouch young at various ambient temperatures (Hulbert 1988). $\dot{V}O_2$ measured in *Didelphis virginiana*, *S. brachyurus*, and *M. eugenii* suggested that the pouch young acquired much of their fur before acquiring an ability to increase their metabolic rate in response to cold (Hulbert 1988). At this time the pouch young showed a typical adult mammalian response to low ambient temperatures (Hulbert 1988). This occurred at 100 d in *D. virginiana* and at 175 d in *M. eugenii*. Earlier, Shield (1966) observed that *S. brachyurus* were able to thermoregulate during weaning at the age of 153 d. More recently, Holloway and Geiser (2000) showed that sugar gliders (*P. breviceps*) were able to increase their metabolic rate in response to cold at about 90–100 d and that this coincided with a decrease in conductance.

Dawes and Mestyan (1963) injected norepinephrine (NE) into newborn guinea pigs and rabbits and noticed a significant increase in $\dot{V}O_2$ and an increase in body temperature after exposure to ambient temperatures of 20°–25°C. Bockler et al. (1981) noticed that hamsters injected with NE in their thermoneutral zone showed a metabolic effect similar to nonshivering thermogenesis (NST) after cold acclimation. NE is released during sympathetic nervous activity at the sympathetic nerve terminals of thermogenic tissues, particularly brown adipose tissue. Jansky (1973) suggested that one method to detect NST in mammals was by examining the effect of NE on metabolic responses. Loudon et al. (1985) also showed that larger pouch young of the Tasmanian Bennett's wallaby (*Macropus rufogriseus rufogriseus*) increased their $\dot{V}O_2$ after an injection of NE. Rose (1987) recorded the body temperature of pouch bettongs *B. gaimardi*, another Tasmanian marsupial, and reported that bettongs over 13 wk old were able to maintain their resting body temperature at above 30°C. Furthermore, those bettongs showed signs of NST in response to NE (Rose et al. 1998).

Cockburn and Johnson (1988) observed that peramelids (bandicoots) grew more rapidly than other marsupials, possibly because of the sharp increase in their levels of milk fats, which coincides with the deposition of young in nests (Green and Merchant 1988; Ikonomopoulou and Rose 2005). Although *Perameles gunnii* has a very fast growth rate and is weaned at 58–60 d (Heinsohn 1966), bandicoots are similar to other mar-

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supials in that they are born with poor thermoregulatory abilities (Gemmell and Johnston 1985).

Perameles gunnii (Gray 1897), the eastern barred bandicoot, is a marsupial that is an endangered species on the Australian mainland and on the island of Tasmania. Its numbers have steadily declined since 1992 (Mallick et al. 1997). We have shown (Rose and Ikonomopoulou 2005) that adult *P. gunnii* are able to increase their heat production by both shivering thermogenesis and NST. Given this, it is of interest to determine at what point during their rapid development endothermy occurs. This article examines the development of endothermy by measuring the $\dot{V}O_2$ (metabolic rate) of *P. gunnii* in response to NE and to cool ambient temperature. It is hypothesized that the onset of thermoregulation will be correlated with pelage appearance and that *P. gunnii* will exhibit NST, as do several other Tasmanian marsupials.

Material and Methods

Animals

Six lactating eastern barred bandicoots with young were acquired from the wild near Hobart, Tasmania (43°S, 147°E). Animals were maintained indoors during the experiment. All experiments performed were approved by the University of Tasmania Animal Ethics Committee (permit A6212) acting in accord with the Australian Code of Practice. A trapping permit was also obtained from the Tasmanian Parks and Wildlife Service (FA 01133).

Measurements

Eight pouch young (both female and male; two pairs from the same litter) were used throughout this experiment. For each of our experiments, six to eight animals were used. Young were removed from their mother for $\dot{V}O_2$ measurements. Because bandicoots are nocturnal, measurements were obtained during the day between 1100 and 1500 hours, when the mothers were normally at rest. The $\dot{V}O_2$ of the young was measured at 35°C. Animals were then injected with NE intramuscularly in the rump at a dosage of 400 mg kg⁻¹ (Rose et al. 1998). These animals were measured in the same way in the week following their vacation from the pouch (week 9).

$\dot{V}O_2$ was measured in one of two Perspex chambers (volumes 300 mL and 2 L) that were submerged in a water bath. Temperature could be controlled by thermostat between 0° and 40°C. Air was pumped into the chamber at rates of 225, 250, 400, and 500 mL min⁻¹ or 1.5 L min⁻¹ as required. The air passed through a 1-m-long coiled copper pipe inside the water bath, ensuring that air entering the chamber was at a similar temperature to that of the water bath. The difference in O₂ concentration between the ambient air and the expired air leaving the chamber was measured by passing it through indicating soda lime and drying tubes before it entered an oxygen analyzer

(AMETEK S-3A/11, two channels and N-37M oxygen sensor). The "washout" period was approximately 30 min.

Each animal was left in the apparatus for at least 1 h, until the difference in O₂ concentration per minute had stabilized (for a minimum period of 5 min), before recording of O₂ concentration began. $\dot{V}O_2$ was calculated using the equation of Depocas and Hart (1957; more recently used and adapted in Withers 2001).

$\dot{V}O_2$ was obtained at two ambient temperatures, 35° and 25°C. We regarded 35°C as equivalent to pouch temperature. This was confirmed by measuring average pouch temperatures of three lactating females (35.2° ± 0.2°C). Previous work has shown that the rectal temperature of females with pouch young is quite similar to the pouch temperature (Reynolds 1952; Bartholomew 1956; Morrison and Petajan 1962; Shield 1966; Gemmell and Johnston 1985). Subsequently, we decreased ambient temperature by 10° to 25°C (as in Rose et al. 1998), which we considered a thermal "shock/stress," particularly for unfurred pouch young. Any response to this decrease in ambient temperature could be considered endothermic, as could a response to the injection of NE. Body mass of each animal was obtained before all measurements starting from the week before experiments started (week 4).

Statistical Analysis

Statistical tests were performed using SPSS 11 for Macintosh. $P < 0.05$ was considered significant. All values are presented as mean ± SEM.

A regression was undertaken between the body mass (g) and

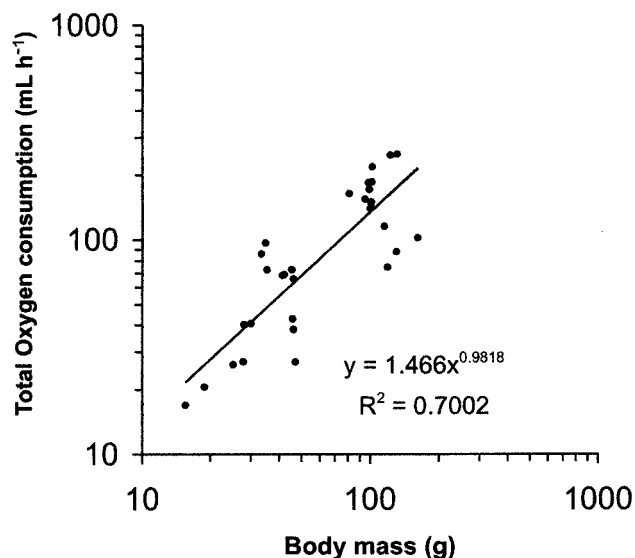


Figure 1. Log-log plot of the change in total oxygen consumption (mL h⁻¹) as body mass (g) increases (ambient temperature = 35°C) during pouch life and for 1 wk afterward.

$\dot{V}O_2$ (mL h^{-1}) for pouch young. Changes with age in $\dot{V}O_2$ as a result of temperature or injection with NE were tested using a two-factor repeated-measures ANOVA with Fisher's PLSD post hoc tests (Rose et al. 1998); body mass was used as a covariate. The independent variable was age and repeated-measures $\dot{V}O_2$ at the two ambient temperatures or before and after NE injection. Furthermore, regressions were plotted for the mean of the weekly differences in metabolic rate of pouch young at the two ambient temperatures and before and after NE injection (at 35°C).

Results

Oxygen Consumption

Figure 1 shows total $\dot{V}O_2$ of pouch young and juveniles (9 wk) as a function of body mass in a log-log plot. The increase in $\dot{V}O_2$ is rapid, as indicated by the steep slope of the line ($y = 1.466x^{0.9818}$; $R^2 = 0.7002$).

Age and Ambient Temperature

There were significant differences in $\dot{V}O_2$ over time ($F_{4,32} = 3.2$, $P = 0.025$) and with ambient temperature ($F_{4,1} = 18.1$, $P = 0.0002$); there was also significant interaction ($P = 0.001$; Fig. 2). The $\dot{V}O_2$ of 5-wk-old pouch young at 25°C was 0.59 $\text{mL g}^{-1} \text{h}^{-1}$. This increased to a maximum $\dot{V}O_2$ of 1.54 $\text{mL g}^{-1} \text{h}^{-1}$ at 8 wk, measured at 25°C. The $\dot{V}O_2$ of 5-wk-old pouch young at 35°C was 0.90 $\text{mL g}^{-1} \text{h}^{-1}$, while at pouch vacation

it was 1.42 $\text{mL g}^{-1} \text{h}^{-1}$. At 9 wk, the metabolic rate measured at 25°C reached levels similar to those of adults (0.59 vs. 0.51 $\text{mL g}^{-1} \text{h}^{-1}$; Ikonomopoulou and Rose 2003). Post hoc tests indicated that the differences in $\dot{V}O_2$ at week 5 were significantly different from those in all other weeks of pouch life. Plotting the mean difference in $\dot{V}O_2$ due to ambient temperature against week of pouch life resulted in a straight line with positive slope ($y = 0.1686x - 1.289$; $R^2 = 0.7384$; Fig. 3a), indicating that the ability to produce heat at lower ambient temperature gradually increased with age.

Norepinephrine

There was a significant difference due to NE injection ($F_{4,1} = 16.7$, $P = 0.0003$), although overall there was a not a significant difference due to age ($F_{4,32} = 2.36$, $P < 0.074$). In the before-and-after NE treatment, there was also significant interaction ($P = 0.001$). Post hoc tests did not show a significant effect on $\dot{V}O_2$ of animals 5–7 wk old but did for animals 8–9 wk old. Plotting the mean difference in treatment against week of pouch life led to a straight line with positive slope ($y = -0.2123x + 1.23$; $R^2 = 0.91$; Fig. 3b), indicating that the ability to produce heat in response to NE gradually increased with age.

Mass

Young grew rapidly, almost doubling their mass each week between weeks 4 and 7 (Fig. 4), for an overall increase from

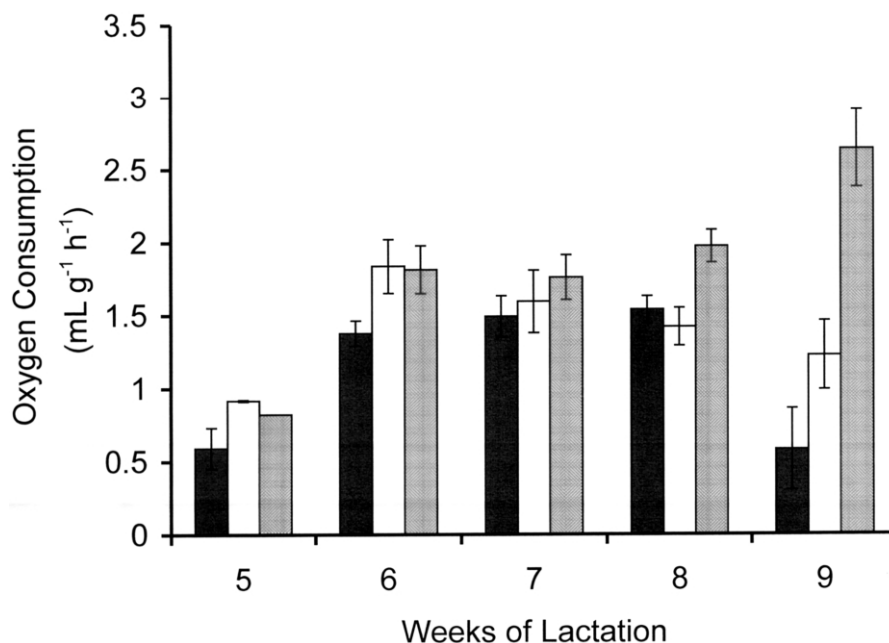


Figure 2. Oxygen consumption measurements ($\text{mL g}^{-1} \text{h}^{-1}$; \pm SEM) for *Perameles gunnii* at 25°C (black bars), at 35°C (white bars), and after NE injection (gray bars) during the pouch life (5–8 wk) and for 1 wk afterward ($N = 6$ –8). Data presented as mean \pm SE.

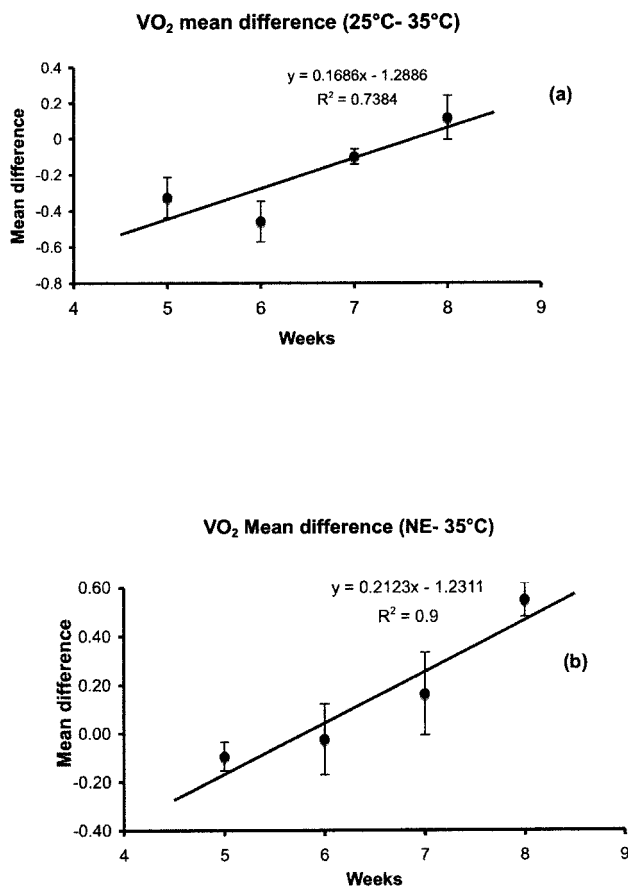


Figure 3. Linear plot of the mean differences (\pm SE) in metabolic rate between ambient temperatures of 25° and 35°C (a) and between periods before and after norepinephrine injection (b).

14.8 to 93.7 g. From week 6, fur was detected. Between weeks 4 and 8, there was a linear relationship between mass and age ($y = 27.53x - 19.586$; $R^2 = 0.9812$).

Discussion

$\dot{V}O_2$ at 25°C was lower than that at 35°C for pouch young that were 5–6 wk old. This and the fact that NE had no effect on $\dot{V}O_2$ indicate that pouch-young *Perameles gunnii* up to 6 wk of age are unable to thermoregulate by increasing heat production. In a similar study, Rose et al. (1998) studied the onset of endothermy in young Tasmanian bettongs and showed that metabolic rate was lower at 22°C than at 35°C for young up to the age of 10 wk, which was two-thirds of the way through pouch life.

The effect of NE on the metabolic rate of *P. gunnii* at 7 wk is a sign that thermoregulatory heat production might be possible, and it is at this time that the eastern barred bandicoot begins to leave and return to the pouch. By 8 wk, eastern barred bandicoot young are almost weaned. $\dot{V}O_2$ at 25°C was higher

than that at 35°C, demonstrating that the young were then able to increase their metabolic rate in response to a thermal stress. At this time, the application of NE resulted in a significant increase in $\dot{V}O_2$. Loudon et al. (1985) found that NE had a minor effect on the $\dot{V}O_2$ of pouched Bennett's wallaby up to 250 g (100 d old) but that a significant increase was evoked for animals after this age. Rose et al. (1998) made a similar finding for the Tasmanian bettong. However, the metabolic rate of the eastern barred bandicoot near pouch vacation is higher than that of the adult. This may be in part because of differences in the surface area to body mass ratio that is always greater in younger/smaller animals of the same species (Munn and Dawson 2001).

The increased $\dot{V}O_2$ at the age of 8–9 wk in the eastern barred bandicoot, when NE had its maximum response, may indicate NST. NST is important to eutherian neonates and is related to an increase in $\dot{V}O_2$ after injection with NE acting on brown adipose tissue (Hulbert 1988). Some marsupials are able to increase their heat production by nonshivering mechanisms that are independent of brown adipose tissue (Rose et al. 1999; Kabat et al. 2003; Rose and Ikonopoulou 2005).

The pelage of *P. gunnii* was first seen at 6 wk (the same age noted in Heinsohn 1966). Pelage development of another marsupial species, *Macropus eugenii*, occurred during the development of thermoregulation (Hulbert 1988). Rose et al. (1998) showed that the thermal conductance (an indicator of the degree of heat loss) for the young bettong remained high up to 10 wk of age, then decreased (in part as a result of fur development), and finally stabilized at 20 wk of age. Rose (1997) stated that Tasmanian species, in general, are better furred than mainland species. This was in agreement with a previous study by Hulbert and Dawson (1974) that noted that an eastern barred bandicoot in Tasmania had greater coat depth and coat insulation than six species of mainland bandicoots. In a more recent study, Ikonopoulou and Rose (2003) observed that the adult Tasmanian bandicoot has a low thermal conductance up to ambient temperature of 30°C. This may occur as a result

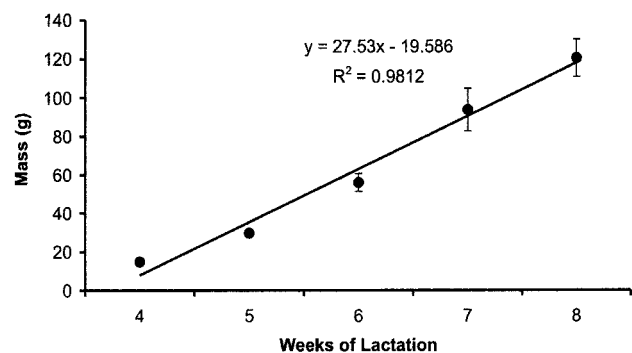


Figure 4. Changes in mass (mean \pm SE) during pouch life and plotted regression line and equation.

of environmental adaptation, since Tasmania is the coolest state in Australia.

Additional influencing factors for the onset of endothermy include thyroid hormones (Sigurdson and Himms-Hagen 1988). Peak thyroxine levels occur at the same time as the development of the pelage for *M. eugenii* (Setchell 1974). Rose et al. (1998) showed that the free-thyroxine level peaked at the time endothermy developed in the Tasmanian bettong. Johnston and Gemmell (1987), in their research studying the progression of endothermy in the bandicoot *Isodon macrourus*, noticed that the highest thyroid hormone concentrations occurred during pouch life, when endothermy developed and the ratio of thyroid gland mass to body mass was at its highest. At that stage, *I. macrourus* also had the highest plasma concentration of thyroxine (T₄; Saunders et al. 2000).

Perameles gunnii has rapid growth and a very short lactation period of 8 wk, with a sharp increase in lipids at week 8 (Ikonopoulou and Rose 2005). The increase in lipid components at the end of lactation correlates with the development of endothermy in other marsupials (Smolenski and Rose 1988; Jansen et al. 1997). The development and maintenance of endothermy requires considerable energy, and Smolenski and Rose (1988) observed an increase in lipid levels and a decrease in carbohydrate levels for two other small marsupials, *Bettongia gaimardi* and *Potorous tridactylus*, at the end of lactation.

To summarize, the metabolic rate of *P. gunnii* changes during pouch life, particularly toward the end of lactation. *Perameles gunnii* shows signs of thermoregulation by week 7 (when metabolic rate at 25°C is similar to that at 35°C). By 8 wk (the end of lactation), the eastern barred bandicoot has a higher metabolic rate than that typically found in adults, and at 9 wk old, its metabolic rate drops to adult level. Based on the increased metabolic rate after NE injection, it could be surmised that *P. gunnii* starts to thermoregulate at the age of 8 wk.

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