Development of thermoregulation in the sugar glider *Petaurus breviceps* (Marsupialia: Petauridae)

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Abstract

Young, relatively undeveloped sugar gliders *Petaurus breviceps* have been observed to be left alone in the nest while the mother forages and may be subject to considerable thermal or energetic stress. As no information is available on the development of thermoregulation in this species, which begins reproduction in winter, we measured resting metabolic rate (RMR), body temperature (T_b) and thermal conductance over a range of ambient temperatures (T_a) in 10 sugar gliders from *c.* 55 days of age until they had grown to adult size. Sugar gliders were unable to maintain a stable T_b over a T_a range of 30–15 °C until the age of 95–100 days, although they raised RMR somewhat as T_a decreased. Further growth resulted in a steady decrease in mass-specific RMR, an increase in T_b and a substantial decrease in thermal conductance. Our study shows that young gliders below the age of 100 days rely largely on heat produced by adults to maintain a high T_b, but are well able to cope with regular falls in T_b of > 10 °C and a concomitant decrease of RMR. This thermal tolerance and reduction in energy expenditure should allow the mother to forage and replenish her own body fuels while her offspring are left alone in the nest.

Key words: *Petaurus breviceps*, development, thermoregulation, metabolic rate, body temperature, conductance

INTRODUCTION

Thermoregulation is a complex process involving the integration of a number of physiological systems, including the muscular, nervous and endocrine. Further, insulation and body size also play an important role in retaining any heat produced. In many small mammals, these systems are not fully developed at birth and, because of a low thermogenic capacity and high heat loss, the young are poikilothermic until the thermoregulatory processes begin to function. The development of thermoregulation can happen within a few days, weeks or even months after birth, but is usually established by the time of weaning (Reynolds, 1952; Morrison & Petajan, 1962; Shield, 1966; Hudson, 1974; Maxwell & Morton, 1975; Dolman, 1980; Geiser, Matwiejczyk & Baudinette, 1986; Geiser & Kenagy, 1990). This process generally occurs in conjunction with an increase in body size and pelage (Morrison & Petajan, 1962), and the activation of the thyroid gland (Setchell, 1974; Hulbert, 1988). Marsupials represent an extreme case in mammals as the young are born in a very altricial state and have an extended period of development in the

mother's pouch (Dawson, 1983). Consequently, the time from conception to weaning in marsupials and their rate of development is much slower than that of most placental species (Lee & Cockburn, 1985) and this has significant implications on their thermal biology and energy expenditure during development.

The sugar glider *P. breviceps* is a small (140–160 g) Australasian marsupial that is locally common in regions where tree hollows are available and food sources are plentiful (Suckling, 1995). In south-eastern Australia litters of either one or two young are born between June and January (Fleay, 1947; Smith, 1979; Suckling, 1995) after 16 days gestation, and at an average birth mass of only 194 mg (Smith, 1971). Like other marsupials, sugar gliders are hairless when born, with only the forelimbs and olfactory organs showing reasonable development. By age 60–68 days, the young cannot be fully contained within the pouch. However, at this stage they are still predominantly unfurred (Smith, 1979). We have also observed slightly furred, relatively undeveloped young alone in nest boxes. Consequently, given that ambient temperatures (T_a) in some regions the gliders inhabit often drop below 0 °C during the reproductive season in winter and spring, the possibility exists that the young of this species frequently become hypothermic before the full development of endothermy.

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Although patterns of development and field observations suggest that young sugar gliders may face thermal and energetic stress for some time, no information is available on how their thermal capacity changes with development and how this affects energy use. We, therefore, investigated how energy expenditure, thermal conductance and maintenance of body temperature (T_b) changed with development, and how they are affected by the thermal conditions of their environment.

MATERIAL AND METHODS

Ten juvenile sugar gliders that had been born in captivity were used in this study. These gliders were either first (8 of the 10) or second generation offspring of gliders caught in the New England Tablelands region. All gliders were maintained in their family groups in 3 aviaries at the University of New England under natural photoperiod and temperature conditions. Each aviary contained 2 nest boxes and some large branches. Smaller branches with fresh eucalypt leaves were provided at regular intervals. An excess of food and water was provided daily for each family group. Food consisted of a mixture of high protein cereal, honey and water, which was occasionally supplemented with vitamins (Pentavite infant vitamins). In addition, fresh apple and carrot were given every second day, while mealworms (Tenebrio larvae) were also provided occasionally.

Pouches of all mature female gliders were checked weekly for the presence of young. However, because of the small size of the neonates (10.8 mm crown–rump, 194 mg; Smith, 1971, 1979), combined with the increased aggression of females before and after birth, young were sometimes not detected for a few weeks. Therefore, ages had to be determined using head length and the regression equation provided by Smith (1979), as this parameter has been found to be the most reliable for estimating age in sugar gliders to an age of 100 days.

Gliders are permanently attached to the teat from birth until 40–65 days of age (Smith, 1979). Therefore, to ensure that the young gliders could reattach to the teat, gliders were not removed from their mothers until they were observed partly out of the pouch (age 60–68 days; Smith, 1979). At this stage of development, some fur, or at least pigment, was present on the young animals. Measurements of body mass, metabolic rate and T_b were then taken at approximately weekly intervals until the gliders could at least maintain a stable T_b over a T_a range of 30–15 °C, after which occasional measurements were taken until the gliders had obtained an adult mass.

Very young gliders were transferred from the aviary to the laboratory with their mothers, removed from the teat, and immediately placed into respirometry chambers at T_a 30 °C to measure metabolic rate and T_b. However, once young were completely out of the pouch they were transferred alone to the laboratory on the morning of the measurement. A T_a of 30 °C was chosen as it is within the thermoneutral zone (TNZ) of adult gliders (Fleming, 1980) and would probably cause little thermal stress to the young, although pouch temperatures are probably slightly higher. The gliders then remained at this T_a for c. 1 h before the T_a was reduced in 5 °C steps of c. 1 h each. This procedure was subsequently repeated until either T_a 15 °C was reached, or metabolic rate or T_b decreased significantly, indicating that the animals were becoming hypothermic.

Resting metabolic rates (RMR) were measured as rate of oxygen consumption ($\dot{V}O_2$) using open-flow respirometry. Food and water were not available to the animals for the duration of these measurements. Animals were placed individually into respirometry chambers within a temperature-controlled cabinet (± 0.5 °C). Flow rates were adjusted with rotameters and measured with mass-flowmeters (Omega, FMA 5606, Stamford). Oxygen content of the dried expired air was measured with either a 1- or 2-channel oxygen analyser (Ametek Applied Electrochemistry S-3A/I and S-3A/II, Pittsburgh, respectively). With the 1-channel oxygen analyser, solenoid valves switched channels in 3-min intervals. This permitted the measurement of up to 3 animals and a reference in succession, with each channel measured once every 12 min when all chambers were occupied. The 2-channel system permitted continuous measurements of 2 animals simultaneously, with readings taken every 3 min and a reference reading every 30 min. Since very young gliders had a tendency to become hypothermic quickly, the 2-channel analyser was primarily used for the early measurements as it provided more frequent readings (1 reading every 3 min compared to every 6, 9 or 12 min, depending on the number of animals used, with the 2-channel analyser), which allowed a safer monitoring of an animal's condition.

Initially, respirometry chambers of 0.5 l, with flow rates around 10–13 l h^{-1}, were used, and 99% equilibrium of the system was achieved after 10–13 min. However, as the gliders increased in size, they were subsequently placed in larger chambers (1–3 l) with concomitant increases in flow rate. T_a was measured to the nearest 0.1 °C with a calibrated thermocouple inserted 1 cm into the respirometry chamber. Thermocouple output was amplified by a digital thermometer (Omega DP116).

The analogue outputs from the mass-flowmeter, oxygen analyser and digital thermometer were interfaced to a personal computer where data acquisition and processing were performed with software written by B. Lovegrove, T. Ruf and G. Körtner. Rates of oxygen consumption were calculated, after dry standard temperature and pressure gas values were calculated, using equation 3a of Withers (1977). A respiratory quotient (RQ) of 0.85 was assumed, which would give a maximum error of 3% if the RQ value was actually 0.7 or 1.0 (Withers, 1977).

T_b were determined by inserting a 38 standard wire gauge copper/constantan thermocouple probe 15–20 mm rectally and reading from an Omega HH-71T electronic
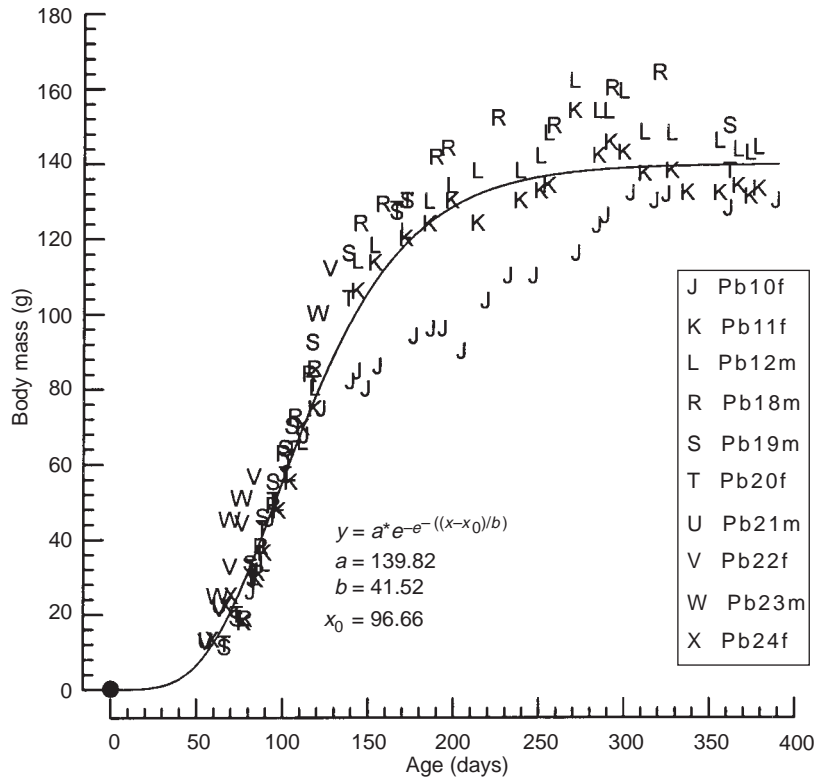
Fig. 1. Growth of *Petaurus breviceps* born in captivity, measured as body mass (g). Data were fitted with a Gompertz curve which was highly significant ($P < 0.001$). m and f, male or female gliders, respectively; ●, birth mass of gliders (0.2 g) as determined by Smith (1971).

thermometer. All thermocouples were calibrated, to the nearest 0.1 °C, over a temperature range of 10–40 °C in a waterbath against a precision mercury thermometer (R6578, Dobros, Australia). Initially, T_b were measured immediately after removal of the animal from the chamber, once stable metabolic measurements had been obtained, at each T_a (after *c.* 1 h). Animals were returned to the chamber within 1 min. However, once a glider's eyes opened and it became more aware of its surroundings, the animal took longer to settle after each disturbance. Consequently, the possibility existed that metabolic rates would be higher than normal because of the animal's agitation. Therefore, T_b were only determined at the beginning and end of each measurement once T_b were generally stable over the T_a range of 30–15 °C.

Thermal conductance, a measure of the rate at which heat is lost from a body to the environment, was calculated using data from metabolic rates and temperature according to the following formula, adapted from the Newtonian cooling equation (Schmidt-Nielsen, 1990):

$$C = MR/(T_b - T_a),$$

where C = thermal conductance, MR = metabolic rate, and $(T_b - T_a)$ = the differential between body and ambient temperature.

After plotting the standardized residuals to ensure homoscedasticity, regression lines were fitted using the least squares method. The slopes and elevations of multiple regression lines were compared using analysis of covariance (ANCOVA) (Zar, 1984).

RESULTS

Body mass of the juvenile gliders increased with time and, given a birth mass of 0.2 g (Smith, 1971), displayed a typical sigmoidal growth curve (Fig. 1). At birth, gliders were small and hairless with relatively large heads and well-developed forelimbs. Initial growth was slow compared to the later stages of development, as by the age of 60 days gliders had only increased their mass by *c.* 13 g, i.e. *c.* 0.2 g day^{-1} assuming a birth mass of 0.2 g (Smith, 1971). At this stage the eyes were still closed and the gliders only had a covering of short, fine fur on the dorsal surface, with bare underside, patagium, legs and tail. Co-ordination did not appear to be well developed as the animals had trouble righting themselves, although they could move around quite freely. Although they were more often partially exposed when attached to their mother, they could still be fully enclosed within the pouch at this age.

From ages 60 to 110 days, juvenile gliders substantially increased their mass, growing at a rate of *c.* 1 g day^{-1}, after which the rate of increase began to taper off (Fig. 1). From ages 70 days onward, young gliders could no longer be fully enclosed within the pouch, but would firmly hold on to their mother's fur while suckling. The physical characteristics of the gliders
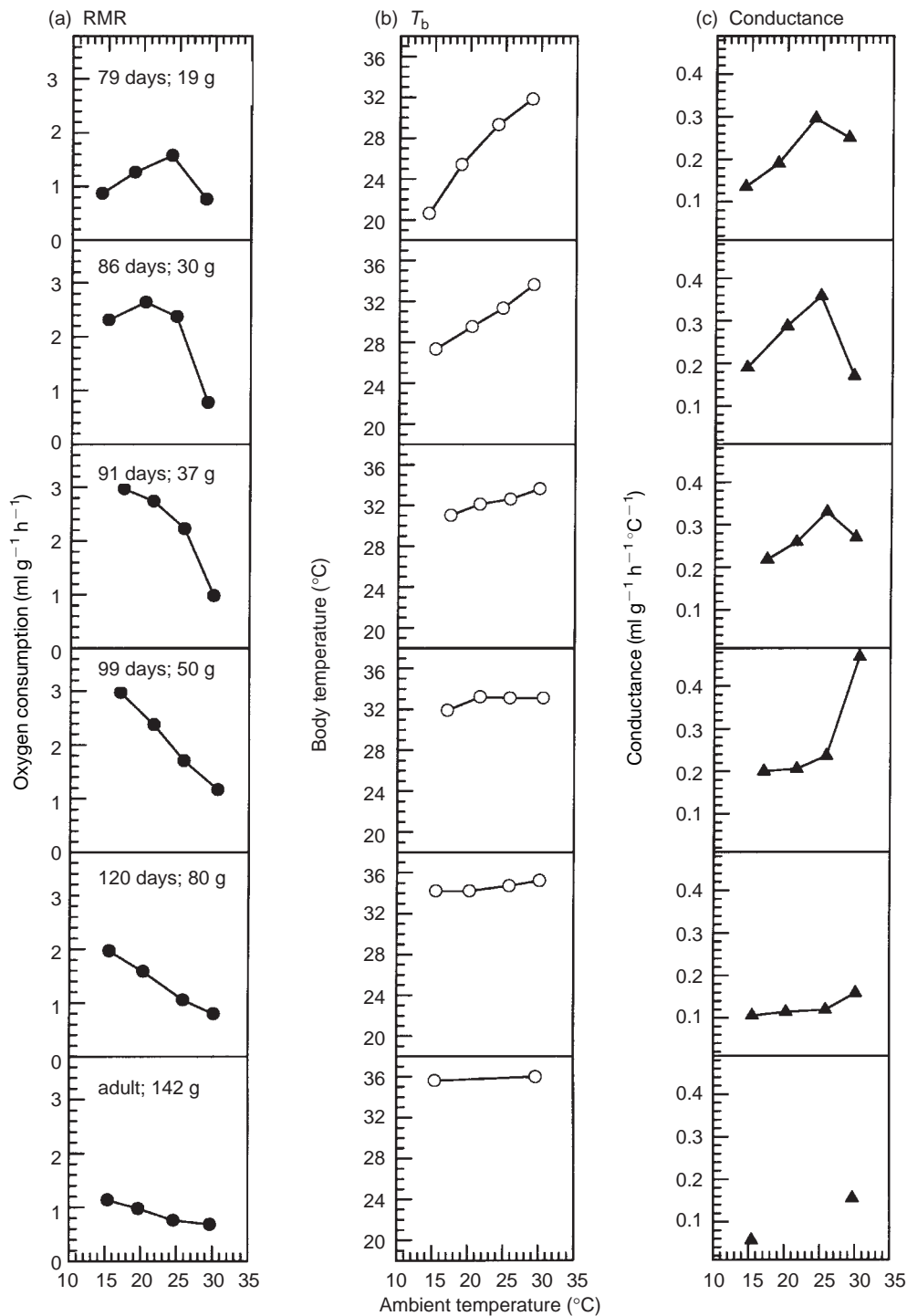
Fig. 2. Development of: (a) resting metabolic rate (RMR); (b) body temperature (T_b); (c) conductance in a young glider (Pb12), born 16 August 1995. The glider was initially placed in the chamber in the morning at ambient temperature (T_a) 30 °C for *c*. 1 h, after which T_a was reduced in 5 °C steps, remaining at each T_a for 1 h. To avoid elevating RMR, T_b and calculated conductance of the adult glider were only obtained before and after the measurement. As conductance of the adult glider is a curvilinear response, no line was drawn between the two points.

rapidly developed over this time: eyes opened, fur grew to cover the entire body, and co-ordination improved, resulting in animals that resembled young adults by age 110 days. It is at this age that juvenile gliders first leave the nest and start to rely on their own resources (Fleay, 1947; Smith, 1973).

The rate of increase in mass of one glider (Pb10) was notably lower than that of the other gliders from age 120 days onward (Fig. 1). The mother of this individual died at approximately the same time. Therefore, it is possible that the lack of certain nutrients found in her milk may have slowed the rate of growth in this glider.
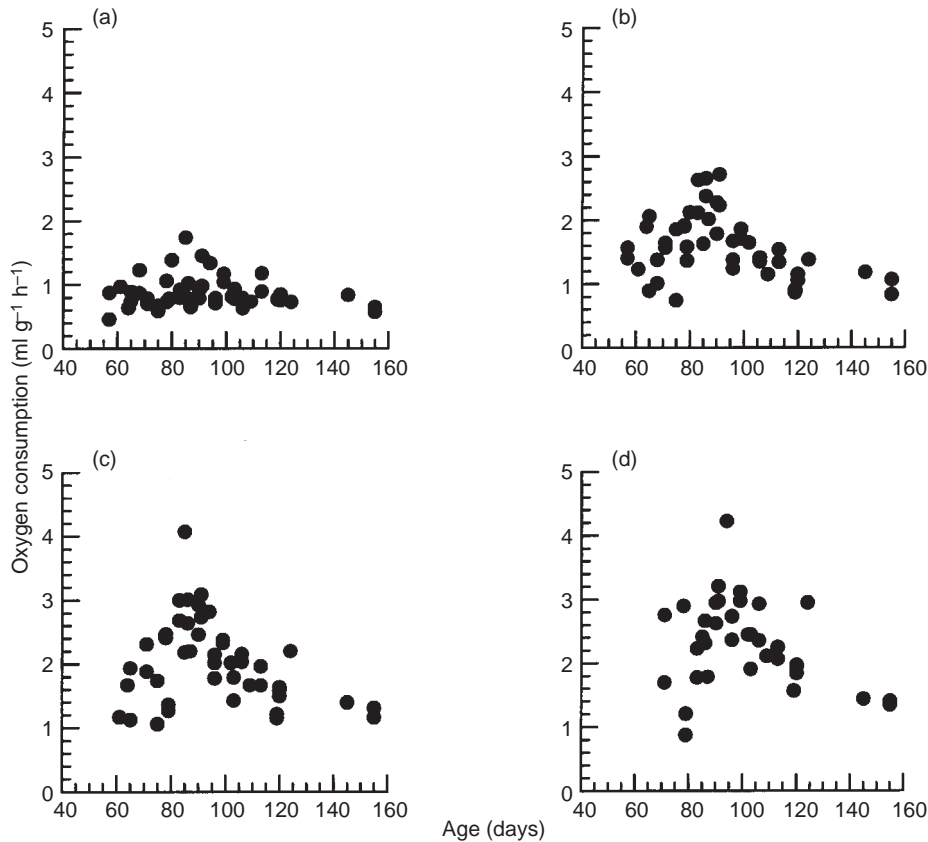
Fig. 3. Changes with age in resting metabolic rates (RMR) of juvenile *Petaurus breviceps* at ambient temperatures (T_a): (a) 30 °C; (b) 25 °C; (c) 20 °C; (d) 15 °C.

However, the glider did eventually reach adult mass and gave birth to a single young in her second breeding season.

Of the seven litters born, four were of single young (Pb10, Pb18, Pb23, & Pb24), and there was an equal proportion of five males and five females. Each of the three litters of two young consisted of a male and a female. Apart from the one female glider mentioned above, males and females displayed no difference in their rates of increase in mass, at least until age 150 days ($F = 1.20$, d.f. $= 1,63$, $P = 0.28$, ANCOVA). Nor was there any difference in the mean mass of males and females at any given age below 150 days ($F = 1.72$, d.f. $= 1,64$ $P = 0.20$, ANCOVA). No difference was observed in the rate of increase in mass between those gliders that were born in litters of one or two young.

All sugar gliders showed the same pattern of change in RMR, T_b and thermal conductance. As shown for one representative individual (Pb12, Fig. 2), RMR, T_b and conductance as a function of T_a underwent substantial changes during development. RMR at 79 days increased when T_a was lowered from 30 to 25 °C, but T_b declined with T_a over the entire range measured. Despite T_b dropping to as low as 20 °C, there did not seem to be any noticeable affect on the co-ordination of the animal. RMR increased with age until 120 days, when the highest values were observed at most T_a; RMR declined thereafter. T_b became less and less T_a-dependent, and around 100 days T_b was constant, although about 3 °C lower than in adults. Conductance from 79–91 days increased when T_a was lowered from 30 to 25 °C, probably because the animals were shaking or shivering. From 99 days, conductance declined with T_a in a similar pattern to that in adults.

RMR as a function of age at the four T_a showed three major stages (Fig. 3). At 55–80 days RMR was relatively low. The highest rates were observed between 80 and 100 days, but RMR declined thereafter to adult values. The peak in mass-specific RMR was least pronounced at T_a 30 °C, but became more obvious at the lower T_a at which RMR was raised substantially at most ages.

The $T_b - T_a$ differential (ΔT) also increased significantly with age and decreasing T_a (Fig. 4). At T_a 30 °C, ΔT was small and seemed to increase more or less linearly. At the lower T_a, ΔT showed an initial steep increase until about day 80 or 90 after which age the change became less pronounced.

Thermal conductance at T_a 25 °C, somewhat below the TNZ of adults, declined curvilinearly with age (Fig. 5). At 50–60 days thermal conductance was about four to five times that at 120 days and, therefore, heat loss was substantial even at this moderate T_a.
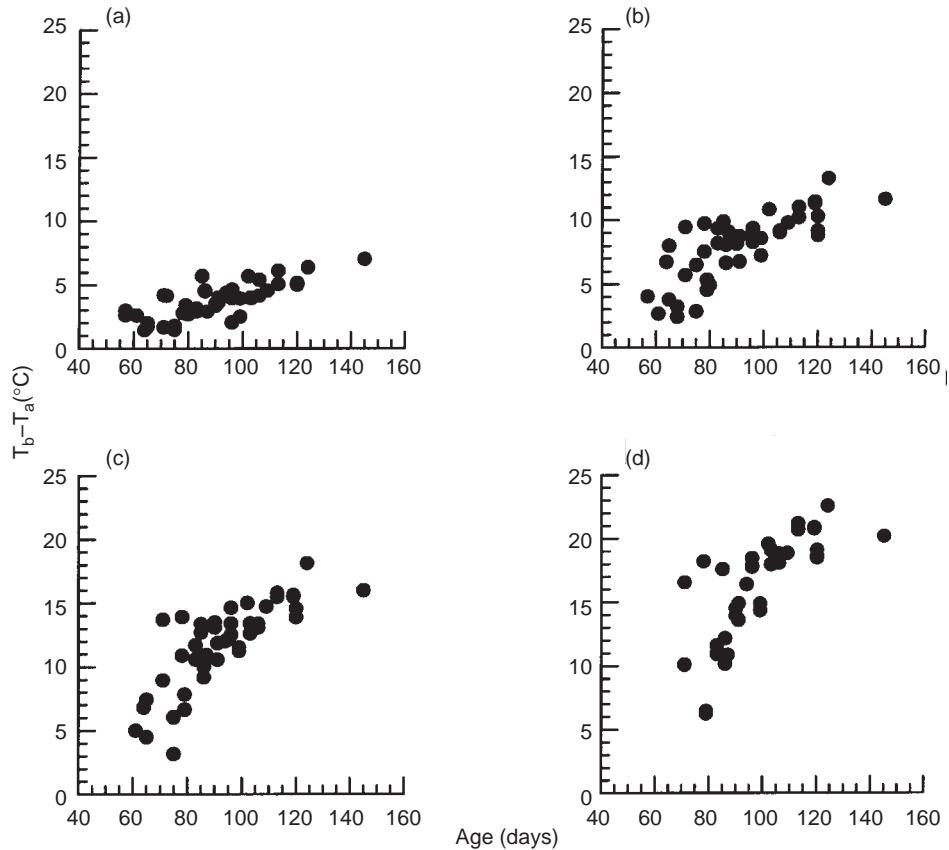
Fig. 4. Changes with age in the difference between body temperature (T_b) and ambient temperature (T_a) (ΔT) of juvenile *Petaurus breviceps* at T_a: (a) 30 °C; (b) 25 °C: (c) 20 °C; (d) 15 °C.
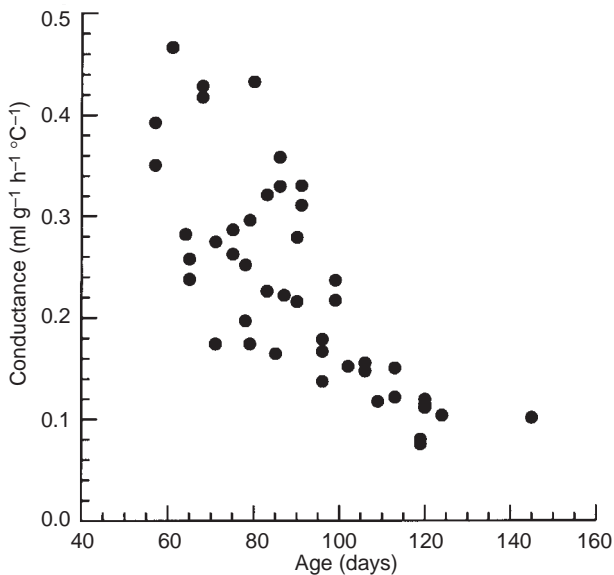

Fig. 5. Thermal conductance as a function of age in *Petaurus breviceps* at an ambient temperature (T_a) of 25 °C.

DISCUSSION

Petaurus breviceps, like all other marsupials, gives birth to altricial young. Development is slow and it takes about 250 days from birth to grow to full size. During the early stages of pouch life the young are obviously poikilothermic, and even by the age of 56 days possess only a very limited thermoregulatory ability which is restricted to T_a above 25 °C. However, by the age of 95–100 days, and when the gliders weighed only 36–42% of adult mass, an increase in heat production above that predicted for adults (Fig. 6) and heat retention meant that the gliders were able to maintain a constant T_b over a T_a range of at least 30–15 °C, although at a slightly lower T_b than that of adults. Further growth was characterized by a steady decrease in mass-specific metabolic rate to adult levels (Fig. 6) and a slight increase in T_b, presumably resulting from the decrease in conductance, until at adult mass adult levels were observed.

The growth rates and development observed in the current study seem to be similar to those of other sugar gliders born and reared in captivity (Smith, 1979), suggesting that the experiments conducted here did not affect the development of the young. This is in contrast to Hudson (1974), who observed reduced growth rates in neonatal rodents *Baiomys taylori* periodically removed from their mothers and exposed for 2 h to T_a 30 °C. It is probable that removal of young from their mothers has a more pronounced effect in rodents, as they grow faster than marsupials, which generally have a very slow rate of development (Tyndale-Biscoe, 1979; Lee & Cockburn, 1985). It was noticeable in sugar
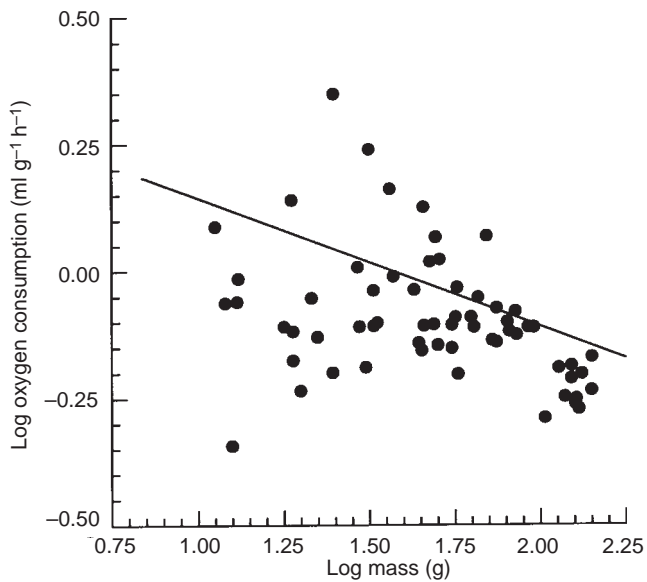
Fig. 6. Log resting metabolic rates (RMR) of juvenile gliders at ambient temperature (T_a) 30 °C as a function of log body mass. Solid line, basal metabolic rates (BMR) of adult marsupials as calculated by Hayssen & Lacy (1985): log BMR (ml g^{-1} h^{-1}) = 0.397 − 0.253 log body mass (g).

gliders, however, that although litter mates developed at the same rate, e.g. eye opening occurred within a day of each other, these same characteristics occurred at slightly different ages in individuals of different litters. However, the variation in development was generally within the ranges observed by Smith (1979).

It has been reported from observations of gliders in captivity that young at age 70 days are frequently left in the nest while the mother forages during the night (Smith, 1971). However, at this age the young gliders only have a rudimentary thermoregulatory ability which is restricted to high T_a, whereas in the New England Tablelands outside T_a may drop to as low as −6.0 °C during this period (Bureau of Meteorology, 1997). Consequently, it is possible that, in order to keep the young gliders warm, foraging of the mother is restricted to short bouts. This has been observed in the dasyurid marsupial *Phascogale tapoatafa*, which returns to the nest more frequently and for longer periods during the early nesting stage, when the young are without fur, than in later nesting stages (Soderquist, 1993). Short foraging forays might also explain the observations by Quin (1993) of the activity patterns of female sugar gliders throughout the reproductive season, during which time some free-ranging female gliders began activity later, retired earlier and displayed shorter bouts of activity throughout the night compared to gliders at other times of the year.

Thermal stress on the young gliders while the adult is away may be partially reduced by the insulation of the nest slowing the decline in nest temperature. It is also possible that other family members may remain behind with the young gliders to prevent them becoming hypothermic. In fact, this was observed on one occasion during the present study when the mother was found in one nest box with most of the other adult gliders, and her two young were found in another nest box with their grandmother. Further, if young gliders called when separated from their mother, older siblings would emerge from the nest box to investigate and attempt to take them back to the nest. Consequently, such calls may act as a cue for these older gliders to stay with the young while the mother is away.

For marsupials, the need to thermoregulate does not become necessary until the individual can no longer be contained within the pouch, as temperatures within these confines are generally within 0.5–1.0 °C of those of the mother (Morrison & Petajan, 1962; Shield, 1966; Gemmell & Johnston, 1985; Gemmell, Cepon & Barnes, 1987). Consequently, the T_b of a poikilothermic neonate will also be close to that of the adult, without the need to burn fuel for maintenance of T_b. In addition, given the naked state and small size of these animals, the rate of heat loss would be so high as to make the establishment of endothermy at this stage of development highly inefficient. Therefore, remaining poikilothermic during this stage means that nutrients can be channelled into growth and development rather than into heat production.

The expense of thermoregulation can be observed in young growing gliders. Before attaining endothermy, at *c.* 80 days of age, the total energy expenditure was only 0.5 kJ h^{-1} at T_a 15 °C, despite the very high rate of conductance. However, it is unknown if the young animal can survive alone at this T_a for more than a few hours. Subsequently, with the attainment of endothermy at the age of 100 days, there is close to a six-fold increase in energy expenditure to almost 3.0 kJ h^{-1}, virtually the same as that of an adult glider almost three times its mass.

Nagy & Suckling (1985) observed no difference between the metabolic rates of non-lactating and lactating female sugar gliders with one and two young, all estimated to be only a few weeks old. These results are in agreement with several other mammals studied during pregnancy and lactation, in which additional energetic costs for the mother were observed only in the latter half of lactation (Kenagy, Sharbaugh & Nagy, 1989; Munks & Green, 1995; Green, Merchant & Newgrain, 1997). This pattern of energetic cost to the mother during lactation can be explained by the rates of energy consumption of the developing young. During the early stages of lactation the rates of milk consumption of the young are small owing to the low growth rates, lack of thermoregulation, and hence low metabolism. Therefore, the energetic costs to the mother of maintaining the young during this period are negligible. However, once the young animals begin to thermoregulate and leave the pouch, energy demands, as seen above and, consequently, food requirements also increase, which subsequently results in the latter half of lactation being an energetically demanding time for the mother.

Between the ages of 60 and 95 days several factors contributed to the development of endothermy in

P. breviceps, the most important probably being the increase in body size resulting from the growth of the animals. This resulted in a decrease in the surface area to volume ratio, thereby reducing the amount of metabolic heat lost from the body. Heat loss was further reduced by the development of fur that grew to encompass the whole animal during this period and become an effective layer of insulation. Note that the majority of fur growth did not occur until much of the young glider's body protruded from the pouch, and it may be that this is a mechanism to prevent overheating while contained in the pouch.

In addition to reducing the relative surface area of an animal, the larger body size also acts as a factor in augmenting the absolute amount of heat produced, as an increase in muscle mass will increase the animal's shivering capacity. It was noticeable that as physical co-ordination improved, the degree of shivering at lower T_a also increased, whereas at earlier ages the animal just shook or moved its body for a short time before lying still and letting T_b decrease. However, the use of shivering is partially offset by the increase in convective heat loss that results, thus reducing its overall effectiveness to some degree.

An important change that has been observed to occur during the development of endothermy is the activation of the thyroid gland (Setchell, 1974; Hulbert, 1988). Considering that thyroid hormones are important in regulating metabolism, acting on all body cells, the observed increase in heat production from ages 60 to 100 days in *P. breviceps*, was probably the result of the activation of this gland during this period. In addition to oxidative metabolism and muscular action, a further source of heat production in neonatal placental species is non-shivering thermogenesis from the use of brown adipose tissue (BAT) (Hull, 1973). However, although BAT has been found in several marsupials (Loudon, Rothwell & Stock, 1985; Hope *et al.*, 1997), it appears to be non-thermogenic (Nicol, Pavlides & Andersen, 1997). It is possible that recently discovered uncoupling proteins that are associated with tissue other than BAT (Boss *et al.*, 1997; Larkin *et al.*, 1997) or vasoconstriction in muscle tissue (Duchamp *et al.*, 1993; Eldershaw *et al.*, 1996; Steen, Vincent & Clark, 1996) are important for non-shivering thermogenesis in marsupials, and these may also be involved in the development of thermoregulation.

Behavioural changes were also evident in the young gliders. They began to adopt the curled 'ball' posture observed in adults when they were *c.* 70 days old. This posture reduces surface area, particularly of the ventral surface and patagium which for a large period of time have much shorter fur than that of the dorsal surface, thereby reducing insulation when exposed. Simply by adopting this posture, a young opossum *Didelphis marsupialis virginiana* was able to maintain its T_b *c.* 5 °C higher than that of animals that remained outstretched (Morrison & Petajan, 1962).

At the onset of homeothermy, the T_b of the juvenile gliders was lower than that of the adult, as found in several other species (Reynolds, 1952; Rosen, 1975; Dolman, 1980). Considering that homeothermy is initially established at a markedly lower mass and when pelage is not as thick and long as that of adults, thermal conductance is much greater in these small animals. Therefore, by maintaining T_b a few degrees lower than mature individuals, juveniles can reduce their rate of heat loss by decreasing the differential between T_a and T_b.

Petaurus breviceps begins its reproductive season during winter (June–July) (Suckling, 1995; present study). It takes the young at least 100 days before they are reasonably developed and are able to thermoregulate; this is probably so the young emerge at a time of relatively favourable environmental conditions. However, before this age the young are able to cope with significant falls of T_b and metabolic rate, thus enabling the mother to forage effectively while the young gliders are left alone in the nest.

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