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## DEVELOPMENTAL THERMOENERGETICS OF THE DASYURID MARSUPIAL, *ANTECHINUS STUARTII*

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Although conception-to-weaning times in dasyurid marsupials are extremely long and neonates very small, little is known about their growth and thermoenergetics. We studied the growth pattern of *Antechinus stuartii* from birth to after weaning in relation to thermoregulatory capabilities and energetic cost of lactation in the female. Litter size was 1–8 young. Growth rate was slow for age 0–40 days, increased until weaning at about 100 days of age, and then slowed again. At weaning, males were 18% heavier than females (*t*-test,  $P < 0.01$ ). Energy expenditure of females increased significantly by about 30% during late lactation, compared with early or postlactation. Overall, maternal investment increased with increasing litter size. Total energy expenditure from birth to weaning was 2,373 kJ for small litters (1–3 young) and 4,580 kJ for large litters (8 young). However, at weaning, young from small litters were about 30% heavier than young from large litters. Ability of young *A. stuartii* to thermoregulate improved with age. At 60 days age, young were poikilothermic after cold exposure, but by 79 days, physiological thermoregulation was established.

**Key words:** *Antechinus stuartii*, development, energy expenditure, lactation, marsupial, maternal investment, metabolic rate, thermoenergetics, thermoregulation

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A difference between marsupials and placentals is their mode of reproduction. Marsupials tend to have a short gestation period, young are born in an extremely altricial state and are very small (neonate litter mass about 0.1% of maternal body mass,  $M_b$ —Hayssen et al. 1985). Most energy and nutrient transfer occurs during the subsequent prolonged lactation period when young spend much of their developmental life in a pouch (Hayssen et al. 1985; Russell 1982; Tyndale-Biscoe and Renfree 1987). In contrast, many placental mammals are precocial at birth (neonate litter about 15.5% of maternal  $M_b$ ), and time of gestation plays a much more important role in nutrient and energy transfer than in marsupials (Hayssen et al. 1985; Tyndale-Biscoe and Renfree 1987). Overall, the conception-to-weaning

period in marsupials is about twice that of placentals (Lee and Cockburn 1985) and this has implications for daily energy and nutrient requirements. Moreover, the small size and slow growth of young marsupials has implications for their development of endothermic thermoregulation.

Comparisons of marsupials and placentals suggest that daily maternal energy use for reproduction is much lower in marsupials (Thompson and Nicoll 1986). However, total energy allocation from conception to weaning of marsupials and placentals appears to be similar (Nicoll and Thompson 1987; Russell 1982; Thompson and Nicoll 1986). Currently, quantitative data on thermoenergetics of marsupial development and reproduction are largely restricted to medium or large species of the orders Didelphimorphia, Peramelina, and

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Diprotodontia (Gemmell and Johnston 1985; Morrison and Petajan 1962; Shield 1966; Thompson and Nicoll 1986). In contrast, published information on development of thermoregulation in carnivorous and insectivorous marsupials (order Dasyuromorphia), which exhibit some of the slowest developmental rates for their body size (Hayssen et al. 1985) and contain the smallest marsupials with minute neonates ( $M_b$  approx. 5–18 mg—Tyndale-Biscoe and Renfree 1987), is presently restricted to a single species, the kowari (*Dasyuroides byrnei*—Geiser et al. 1986). There is also some conflicting evidence with regard to reproductive cost of the brown antechinus, *Antechinus stuartii*, in the field. Field metabolic rates, which represent the sum of all energy costs including that for thermoregulation and foraging, are reported to increase during late lactation in *A. stuartii* (Green 1997), whereas they are also reported not to change (Green and Crowley 1989).

The aim of the present study was to provide detailed information on the growth patterns of *A. stuartii* from birth to weaning in relation to thermoregulatory capabilities, and to quantify energy use of females and their young at different stages of the reproductive cycle and under different thermal regimes.

*Antechinus stuartii* is a small (20–35 g) insectivorous marsupial (family Dasyuridae) with a highly synchronized reproductive life history. Mating within a population occurs over about 2 weeks in late winter and early spring (McAllan and Dickman 1986) and is associated with an increase in locomotor activity in males (Körtner and Geiser 1995). After the mating period, all males die, leaving only pregnant females in the population (Woolley 1966). Gestation in *A. stuartii* lasts for approximately 27 days, and neonates weigh only about 16 mg (Marlow 1961; note: *A. stuartii* is listed as *A. flavipes*). This species has a particularly long conception-to-weaning period and slow growth; the young remain in the

pouch from birth to approximately 50 days age, after which they are nest young until weaning at approximately 100 days age (Marlow 1961).

#### MATERIALS AND METHODS

Ten pregnant female *A. stuartii* were live-trapped (in Elliott box traps, Elliott Scientific, Upwey, Victoria, Australia) during 3–23 September 1998 at about 1,000 m altitude on the Northern Tablelands near Armidale, New South Wales, Australia. Animals were housed at the University of New England, Armidale, in plastic cages (30 by 50 by 40 cm) with sawdust bedding and a nest box containing shredded paper. Animals were fed daily a mixture of macerated cat food pellets and canned dog food. Mealworms were supplied once or twice weekly and water was made available ad libitum. Air temperature ( $T_a$ ) was maintained at  $22 \pm 2^\circ\text{C}$  and photoperiod was natural. Females and most of their young were released at their site of capture when young reached 120 days age. However, 7 juvenile males and 7 juvenile females from litters of  $>3$  young were kept for further body mass measurements.

Females were checked for pouch development and birth of young every 2–3 days. Day of birth was considered as day 0. Immediately after birth to about 160 days, crown–rump lengths of 3 randomly selected young from each litter (1 for the litter with a single young) were measured weekly with vernier calipers. Females with their litter were also weighed at regular intervals, until young were seen to be unattached from the teat at 70 days. From that time, young and mothers were weighed separately, and sex of the young was noted. During the pouch stage we estimated body mass of females by assuming a linear mass change between the last  $M_b$  measurement before birth and the female  $M_b$  after young were left in the nest. This estimate of the female  $M_b$  was subtracted from the total  $M_b$  of female and pouch young to estimate litter mass and mass of individual young.

Two systems, based on the same oxygen sensor, were used to measure  $\text{VO}_2$ . Oxygen consumption was measured with 1 of 2 oxygen analyzers, a single-channel (S-3A/I, Ametek Applied Electrochemistry, Pittsburgh, Pennsylvania) and a dual-channel (S-3A/II, Ametek) analyzer, as described by Geiser et al. (1996). Animals (alone or with litters) were placed in 1-

liter respirometry chambers with dry air flowing through it at a rate of about 400 ml/min, as measured with a mass flowmeter (FMA-5606, Omega, Stamford, Connecticut). These chambers were then placed in a temperature-controlled cabinet maintained to within 0.5°C. Temperature inside the chamber ( $T_a$ ) was measured to the nearest 0.1°C by a calibrated thermocouple. Thermocouple output was amplified by a digital thermometer (Omega DP116, Omega). Analog outputs from the flowmeter, oxygen analyzer, and thermometer were interfaced with a personal computer via a 14-bit analog-to-digital card (Bartels et al. 1998). Both systems were calibrated so that data could be pooled.

Metabolic rates (MR) were measured weekly (using both systems) as rate of oxygen consumption ( $\dot{V}O_2$ ) of each female and her litter at a  $T_a$  of 30 and 20°C for 2 h each. A  $T_a$  of 30°C is within thermoneutrality of adults, and  $T_a$  20°C represents a mild cold load (Wallis 1976). These chambers were then placed in a temperature-controlled cabinet maintained to within 0.5°C. MR was averaged over approximately 30 min for both systems after it became minimal and stable.

Food or water was not available to animals in the metabolic chambers. A linear decrease in  $M_b$  during the measurement was assumed for calculation of mass-specific MR according to equation 3a of Withers (1977).

To estimate energy costs of lactation, mass-specific MR of 3 females (each with 8 young) was measured at a  $T_a$  of 30°C at 3 stages of growth. Measurements were conducted during early lactation (days 7–13, when females had pouch young), late lactation (days 62–93, females without young), and post lactation (days 107–116, females without young). Resting MR for each animal was averaged over 1–1.5 h when  $\dot{V}O_2$  was minimal and stable.

Total energy expenditure of *A. stuartii* females and their young was estimated from  $\dot{V}O_2$  values at  $T_a$  30 and 20°C. Whole-animal MR was measured weekly, and derived values (milliliters per hour) were multiplied by the total number of hours between measurements. We assumed that 1 liter of  $O_2$  produced the equivalent of 20.1 kJ/l (Schmidt-Nielsen 1997). These energy expenditure values were then summed over the 100 days from birth to weaning.

To determine development of thermoregulation, the mass-specific MR was measured week-

ly for young from 3 litters of 8 young each (3 young per litter;  $n = 9$  young), from 62 to 93 days age (each litter was measured on a separate day at 7-day intervals, beginning with days 62, 64, and 65). Individual young in metabolic chambers (50-ml plastic syringes) were placed in a water bath at 30°C ( $T_a$  in chamber measured with a calibrated thermocouple) at a flow rate of 200 ml/min. After 2 h, metabolic chambers were transferred to a temperature-controlled cabinet at  $T_a$  20°C for a further 2 h.  $M_b$  of young was recorded before and after measurements, and a linear decrease in  $M_b$  during the period of measurement was assumed.

Because the young were very small (approximately 5 g) at the beginning of measurements, we measured eye surface temperature ( $T_{eye}$ ) rather than rectal body temperature ( $T_b$ ) before and after measurements using an infrared digital thermometer (resolution, 1°C; OS-600, Omega). Eye surface temperature predicts rectal  $T_b$  of small dasyurids reliably (Song and Geiser 1997).

Numerical values in the text are presented as means  $\pm 1$  SE for  $n$  individuals. A Gompertz, 3-parameter equation, as used by Zullinger et al. (1984), was used to describe growth data of young:

$$M_b = Ae^{-e^{-K(\text{age}-I)}}$$

where  $M_b$  is body mass (g) at a given age,  $A$  is asymptotic mass,  $K$  is growth rate constant ( $\text{days}^{-1}$ ), and  $I$  is age at inflection point (days). Linear regressions were fitted by the least squares method. As mass-specific MR of females and litters at  $T_a$  20°C changed over time, the point of transition of MR versus age was determined by the intercept of the 2 regressions with the smallest sum of the residual sum of squares (Yaeger and Ultsch 1989). The age from which  $T_{eye}$  of young *A. stuartii* remained stable for 2 h at  $T_a$  20°C was estimated by linear regression analysis. Age and  $T_{eye}$  were regressed beginning at 85–93 days, when the regression was not significant, and values of younger animals were added until the regression became significant. The age for which the regression remained nonsignificant was considered to be the minimum age for constant  $T_{eye}$ . A repeated measures analysis of variance (ANOVA) followed by a Student–Newman–Keuls (SNK) test for paired comparisons was used to compare data statistically for different lactation stages.

## RESULTS

Body mass of 10 pregnant females at capture was  $21.0 \pm 1.0$  g and increased slightly in the 1st week of captivity (Fig. 1a). On day 0 (birth of young), mean  $M_b$  for females and pouch young was  $26.7 \pm 1.0$  g. Initially,  $M_b$  of females plus litters increased slowly at a rate of about 0.1 g/day during days 0–40, after which mass gain increased rapidly at a rate of about 0.8 g/day until day 70. Starting on day 70, females were weighed independent of their young. Mean  $M_b$  of females at day 80 was  $34.3 \pm 2.9$  g and slowly decreased until 120 days, to a mean mass of  $26.4 \pm 1.1$  g, similar to the  $M_b$  when young were born.

Initially 6 litters of 8 young, 2 litters of 6 young, 1 litter of 3 young and 1 litter of 1 young were recorded, and mean litter size was  $6.4 \pm 0.8$ . Two young, both from litters of 8, died on approximately day 40. Of the 62 young that survived, 34 were male and 28 female.

Body mass of young showed a sigmoidal increase with age (Fig. 1b). For the first 40 days,  $M_b$  increased slowly; growth was rapid between 40 and 100 days, and slowed again after weaning. Increases in  $M_b$  were described by a Gompertz growth equation (males,  $P < 0.01$ ,  $r^2 = 0.93$ ; females,  $P < 0.01$ ,  $r^2 = 0.97$ ; Fig. 1b). Dimorphism in  $M_b$  between males and females became apparent after day 80, and variation in  $M_b$  from day 80 was greater in males than in females. At weaning, males had a higher mean  $M_b$  ( $14.1 \pm 0.3$  g,  $n = 34$ ) than females ( $11.6 \pm 0.2$  g,  $n = 28$ ;  $t$ -test,  $d.f. = 55$ ,  $T = 6.13$ ,  $P < 0.01$ ), which represents 31.3% of adult male  $M_b$  (45 g; Marlow 1961) and 41.5%, of mean  $M_b$  ( $28.0 \pm 1.0$  g) of adult females. At 300 days (the last recordings), males also had a higher mean  $M_b$  ( $38.3 \pm 1.6$  g,  $n = 7$ ) than females ( $23.2 \pm 0.6$  g,  $n = 7$ ;  $t$ -test,  $d.f. = 8$ ,  $T = 8.96$ ,  $P < 0.01$ ). The Gompertz growth rate constant ( $K$ ) was 0.016 for males and 0.031 for females. The inflection point at which growth is maximal, as determined by the

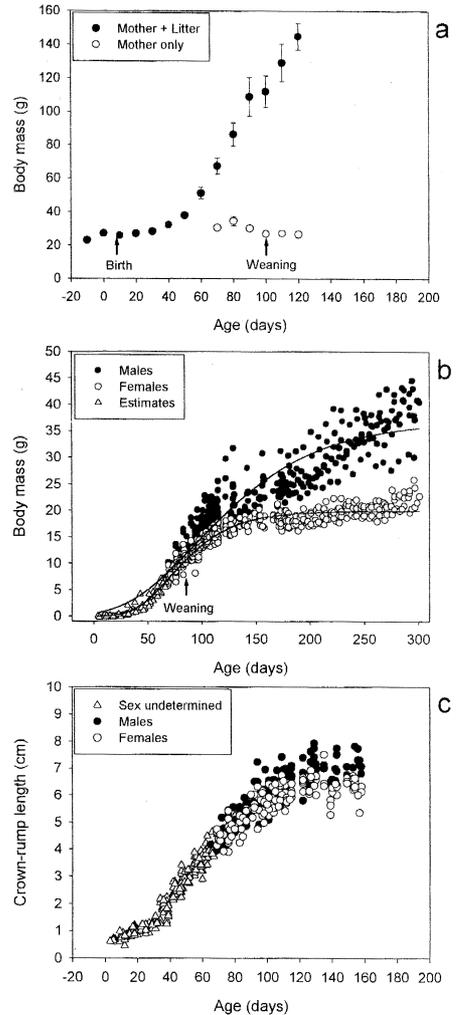


FIG. 1.—Growth of *A. stuartii* young. a) Mean body mass of 10 females and their young (closed circles) as a function of age of young, and mean mass of 10 females without young (open circles), after young detached from nipples and females could be weighed separately. Horizontal line indicates  $\pm 1$  SE. b) Body mass of individual young. Mass was calculated for ages 0–70 days (see text—open triangles) and measured mass for males (closed circles) and females (open circles) for ages 70–300 days. Line is Gompertz 3-parameter equation, fitted to each set of data: males ( $M_b = 36.874 \exp\{-\exp[-0.016(\text{age} - 93.954)]\}$ );  $r^2 = 0.93$ ,  $P < 0.01$ ); females ( $M_b = 19.928 \exp\{-\exp[-0.031(\text{age} - 70.417)]\}$ );  $r^2 = 0.97$ ,  $P < 0.01$ ). c) Crown-rump lengths of 3 randomly selected young from each of the 10 litters. Sexes could not be determined for ages 0–70 days (triangles).

Gompertz equation, occurred at 94 days for males and at 70 days for females.

Crown-rump length showed a pattern similar to  $M_b$  (Fig. 1c). Mean length at 5–12 days age was  $0.68 \pm 0.02$  cm ( $n = 20$ ). Length increased slowly up to 40 days of age and then increased more rapidly up to 100 days. At 101–106 days mean length was greater for males ( $6.24 \pm 0.12$  cm,  $n = 17$ ) than for females ( $5.92 \pm 0.11$  cm,  $n = 14$ ;  $d.f. = 28$ ,  $T = 2.31$ ,  $P = 0.04$ ).

Whole-animal MR (milliliters of  $O_2$  per hour) of 10 females and their litters (Fig. 2a) increased with increasing age of young at  $T_a$  30 and 20°C and was always lower at  $T_a$  30°C than at  $T_a$  20°C. In accordance with growth rate of young, increase in MR was slow until an age of approximately 40 days, and then MR increased more rapidly up to 100 days of age.

Mass-specific MR (milliliters of  $O_2$  per gram per hour) of females and their litters decreased slightly with age of young at  $T_a$  30°C ( $P = 0.02$ ,  $r^2 = 0.05$ ; Fig. 2b). At  $T_a$  20°C, the relationship between MR and age was best described by fitting the data set with 2 linear regressions. From day 0 to day 39, MR was not affected by age ( $P = 0.96$ ). However, from day 42 to day 94, MR decreased with increasing age of young ( $P < 0.01$ ,  $r^2 = 0.45$ ).

To obtain a better estimate of costs of lactation, mass-specific MR of females was measured at  $T_a$  30°C. Mean MR during early lactation (days 7–13, females with young) was  $1.91 \pm 0.21$  ml  $O_2$   $g^{-1}$   $h^{-1}$ , during late lactation (days 62–93, females only)  $2.98 \pm 0.11$  ml  $O_2$   $g^{-1}$   $h^{-1}$ , and during postlactation (days 107–116, females only)  $2.12 \pm 0.26$  ml  $O_2$   $g^{-1}$   $h^{-1}$ , and these means differed (ANOVA,  $P < 0.01$ ). The 36% increase of MR of females during late lactation (despite being measured without young) in comparison with early lactation was significant (Student–Newman–Keuls,  $P < 0.05$ ), but the difference between late lactation and postlactation was not. However, when MR of females without young were compared between late and postlactation

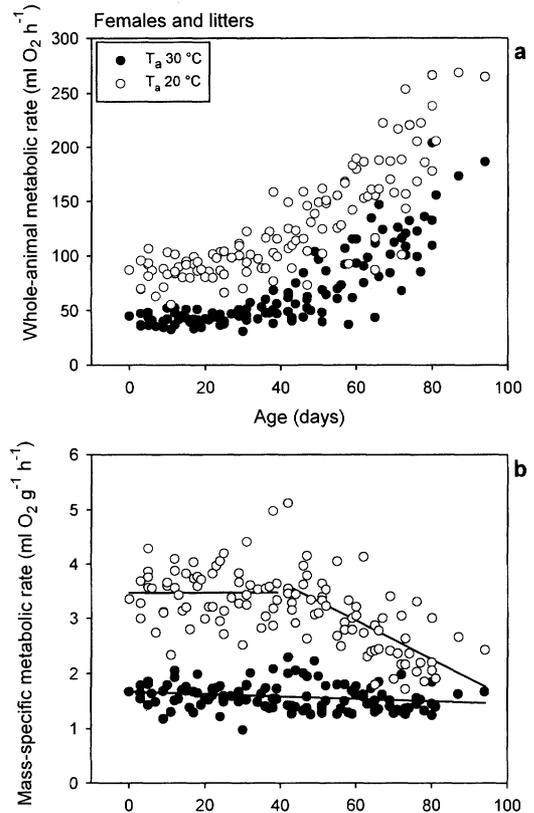


FIG. 2.—Development of physiological competency in *A. stuartii* young, as shown by a) whole-animal oxygen consumption and b) mass-specific metabolic rate (MR). Symbols show individual values for 10 females and their litters as a function of age of young at  $T_a$  30°C (closed circles) and  $T_a$  20°C (open circles). Mass-specific data at  $T_a$  30°C are linear ( $MR = 1.669 - 0.002 \times \text{age}$ ;  $r^2 = 0.05$ ,  $P = 0.02$ ). At  $T_a$  20°C, data show 2 patterns: at 0–39 days age, MR not related to age ( $P = 0.96$ ); at 42–94 days, MR decreased significantly with age ( $MR = 5.068 - 0.035 \times \text{age}$ ;  $r^2 = 0.45$ ,  $P < 0.01$ ).

(i.e., the two data sets measured without young), this 30% decline was significant (paired  $t$ -test;  $T = 5.70$ ,  $P = 0.03$ ).

At weaning (100 days), young from small litters were heavier than those from large litters ( $P < 0.01$ ,  $r^2 = 0.88$ ; Fig. 3a).  $M_b$  ranged from 19.3 g for the single young to a mean of 15.0 g for individuals in a litter of 8.

Mean crown-rump length of individuals

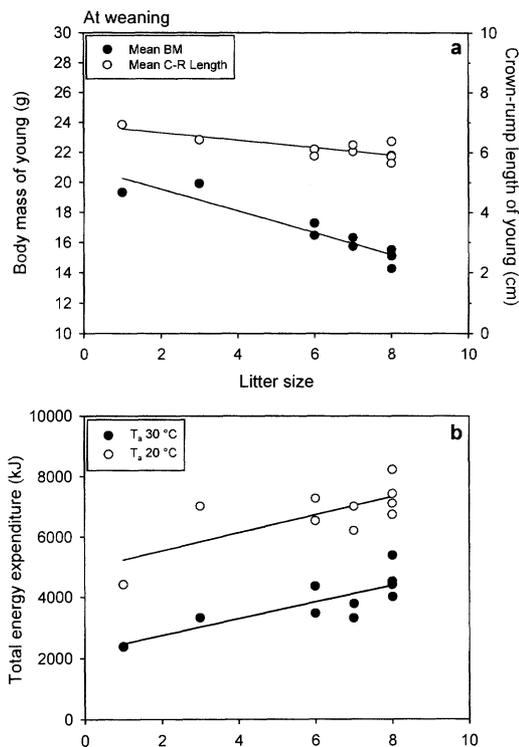


FIG. 3.—Development of *A. stuartii* young relative to litter size. a) Mean body mass of young at 100 days of age (closed circles— $M_b = 20.971 - 0.721 \times \text{litter size}$ ;  $r^2 = 0.88$ ,  $P < 0.01$ ). Mean crown-rump lengths of young from each litter size at 100 days (open circles—crown-rump length =  $6.892 - 0.123 \times \text{litter size}$ ;  $r^2 = 0.64$ ,  $P < 0.01$ ). b) Total energy expenditure of females and their litters for different litter sizes, estimated from birth to 100 days. At both  $T_a$  20°C (MR =  $4,936 + 300 \times \text{litter size}$ ;  $r^2 = 0.52$ ,  $P = 0.02$ ) and 30°C (MR =  $2,194 + 273 \times \text{litter size}$ ;  $r^2 = 0.61$ ,  $P < 0.01$ ) total energy expenditure was related to litter size.

also decreased linearly with increasing litter size ( $P < 0.01$ ,  $r^2 = 0.64$ ; Fig. 3a). Crown-rump length ranged from 6.94 cm for the single young to a mean of 5.94 cm in 8 young.

Estimated total energy expenditure of females and their litters from birth to weaning was related to litter size (Fig. 3b). Total energy expenditure was 2,373 kJ for a litter of 1 and  $4,580 \pm 291$  kJ for a litter of 8 at  $T_a$  30°C. Total energy expenditure at  $T_a$

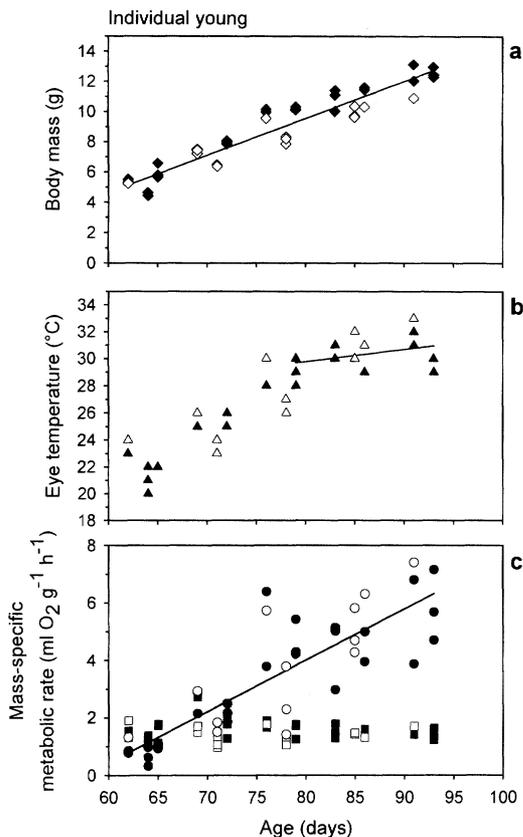


FIG. 4.—Development of *A. stuartii* young. a) Body mass, b) eye temperature (after exposure to  $T_a$  20°C for 2 h), and c) mass-specific MR (squares at  $T_a$  30°C; circles at  $T_a$  20°C) for 9 pups as a function of age. Males are denoted by closed symbols and females by open symbols ( $M_b = -10.088 + 0.245 \times \text{age}$ ;  $r^2 = 0.90$ ,  $P < 0.01$ ). From day 62 to day 78,  $T_{eye} = -2.30 + 0.386 \times \text{days}$  ( $r^2 = 0.64$ ,  $P < 0.01$ ). From day 79 to day 93,  $T_{eye} = 22.5 + 0.090 \times \text{days}$  ( $r^2 = 0.11$ ,  $P = 0.18$ ). At  $T_a$  20°C, MR =  $-10.300 + 0.179 \times \text{age}$  ( $r^2 = 0.72$ ,  $P < 0.01$ ).

20°C was parallel to that at  $T_a$  30°C, but was elevated about 2-fold.

Thermoregulatory capabilities of individual young without their mothers (days 62–93) increased with  $M_b$  from about 5 to 12 g (Figs. 4a and 4b). The ability of young to maintain  $T_{eye}$  after 2 h of exposure to  $T_a$  20°C increased linearly with increasing age until 78 days ( $P < 0.01$ ,  $r^2 = 0.64$ ). After 78 days of age,  $T_{eye}$  was independent of age.

At 62–65 days, young were hypothermic with a  $T_{eye}$  of 20–25°C. At about 70 days  $T_{eye}$  ranged from 23 to 26°C, and by 91–93 days age  $T_{eye}$  was 30–34°C. (Fig. 4b). This improvement in thermoregulation was accompanied by a linear increase of mass-specific MR with age of young at  $T_a$  20°C (Fig. 4c) over the same developmental time ( $P < 0.01$ ,  $r^2 = 0.72$ ). At 60–65 days age, MR at  $T_a$  20°C was below that of  $T_a$  30°C. However, by 90–93 days of age, young were able to increase MR in response to cold exposure. At  $T_a$  30°C, MR was independent of age (Fig. 4c).

#### DISCUSSION

Our study shows that, despite the slow rate of growth and development of *A. stuartii*, energy costs of lactation increase significantly during late lactation. This period coincides with maximum growth rate of young and time when young develop the ability to thermoregulate physiologically.

As in other dasyurids (Frigo and Woolley 1997), developmental increases in  $M_b$  and crown-rump length in *A. stuartii* are sigmoidal. Initial growth is slow, increasing during late lactation, and then slowing again after weaning. Growth patterns of many marsupials are believed to be closely correlated with their lactation pattern (Green 1984). While young are permanently attached to the nipple (0–40 days) and growth is slow, milk production rate is low and milk is relatively dilute (Frigo and Woolley 1997). The subsequent increase in growth is concomitant with the increase of milk supply and amount of milk solids (Green 1984; Settle and Croft 1982).

Development of sexual dimorphism in  $M_b$ , which is pronounced in adult *A. stuartii*, becomes apparent at approximately 80 days of age. This is likely related to the reduction in rate of growth after about 70 days in females; males continue to grow at a rapid rate up to about 95 days. At weaning, males are about 18% heavier than females and continue to grow to a mass almost twice that of females. This significant

difference in  $M_b$  between sexes is related to their distinct reproductive life histories. Large size in males is advantageous, as they compete for access to females and must survive on stored nutrients during 2 weeks of extensive mating—after which all males die (McAllan and Dickman 1986; Woolley 1966).

Gompertz growth constants for *A. stuartii* (0.016 males, 0.031 females) were lower, especially for males, than those calculated from the general marsupial equation of Lee and Cockburn (1985; 0.036 for males, 0.040 for females), which provides an allometric relationship between  $K$  and asymptotic  $M_b$  for marsupials. However, our constant for females is very close to that estimated by Zullinger et al. (1984) based on the data of Marlow (1961) for growth of both sexes of *A. stuartii*.

Weaning in *A. stuartii* occurs at approximately 100 days age, which is late, especially for a marsupial of its  $M_b$ , suggesting that even for marsupials, growth in *A. stuartii* is slow. As in other mammals (Mattingly and McClure 1982; Millar 1979; Randolph et al. 1977), young *A. stuartii* from small litters were about 30% heavier than those from larger litters at weaning. Crown-rump length of young also declined significantly with increased litter size, but difference between small and large litters was only about 12%. Our results differ from those reported by Settle and Croft (1982), who observed no differences in developmental rate among litter sizes in *A. stuartii*, and failure by females to raise litters of less than 3 young. However, a relationship between mass and litter size similar to that reported here has been observed for the dasyurid *Sminthopsis macroura* (Frigo and Woolley 1997).

As predicted from other mammals (Kenagy et al. 1989; Thompson 1992), the overall maternal investment in large litters in *A. stuartii* is greater than in small litters. However, as in other studies the maternal investment per individual young is greater in small than in large litters of *A. stuartii*

(Glazier 1985; Millar 1975). The reason for the negative relationship between size of young and litter size is likely due to increased energy burden of females (Kenagy et al. 1990). Females with very large litters may be unable to produce enough milk to ensure maximum growth even with free access to food, due to a limit to food intake and processing (Kenagy et al. 1990).

Development of *A. stuartii* was accompanied by an increase in energy expenditure. Whole-animal energy expenditure of females and their litters increased exponentially with age, with slow growth of young for the first 40 days and a rapid increase in body mass thereafter. In contrast, mass-specific MR at  $T_a$  20°C was constant up to 40 days and then declined. The increase in body mass and insulation of young as well as huddling apparently reduced thermoregulatory energy expenditure of the female and her litter.

Stage of lactation also affected energy expenditure. During late lactation, energy expenditure of *A. stuartii* females increased significantly in comparison with that during early lactation and with that after lactation. This has also been observed in other marsupial species (Nicoll and Thompson 1987). Late lactation coincides with a period of rapid growth of young and production of high-nutrient milk (Green 1984); so it is not surprising that energy expenditure increased, especially in large litters of 8. This differs from observations in the wild, where no increase in energy expenditure during late lactation occurred (Green et al. 1991; Green and Crowley 1989). However, in contrast to our study, which quantified energy expenditure at rest and in thermoneutrality, free-ranging *A. stuartii* also use energy for foraging and thermoregulation; so the relatively small increase of MR for lactation may have been masked. During late lactation in the wild, females use about 5,340 kJ kg<sup>-1</sup> day<sup>-1</sup> (Green and Crowley 1989), which is 39% higher than the value calculated for our study (3,250 kJ kg<sup>-1</sup> day<sup>-1</sup> for a female with 8 young at  $T_a$

20°C), but which includes foraging and thermoregulatory costs.

As for other marsupials (Geiser et al. 1986; Hulbert 1988; Morrison and Petajan 1962; Rose et al. 1998) and many other, particularly altricial, mammals (Couture 1980; Hirshfeld and Bradley 1976; Maxwell and Morton 1975; Nagel 1989), ability of young *A. stuartii* to thermoregulate improved with age. At 62–65 days, young became hypothermic after cold exposure ( $T_a$  20°C). Between 69 and 95 days, body mass and insulation increased and rate of heat loss decreased. By 79 days, physiological thermoregulation was largely established, although eye temperature was still slightly below that of adults. This period of acquisition of endothermy occurred during peaks in rates of growth and lactation. It is interesting that soon after the development of endothermy in summer, young *A. stuartii* enter torpor daily (Geiser 1988). Thus, the developmental pattern in *A. stuartii* commences with poikilothermy, which is replaced later by heterothermy once physiological thermoregulation ability is attained.

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