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FROM ECTOTHERMY TO HETEROTHERMY: THE ENERGETICS OF THE KOWARI, DASYUROIDES BYRNEI (MARSUPIALIA: DASYURIDAE)[1]

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The development of thermoregulation and torpor was investigated in the kowari, *Dasyuroides byrnei.* Rates of cooling and oxygen consumption indicate that independent thermoregulation (euthermia) was achieved at the age of about 90 days at a body mass of 28 g. The development of endothermy was accompanied by the ability to enter torpor. Torpor in juveniles was reduced in summer at a body mass greater than 80 g. However, an increase in the tendency to enter torpor was observed in the juveniles with the approach of the following winter. In this season the torpor pattern was similar to that seen in adults.

INTRODUCTION

The ontogeny of temperature regulation in most small mammals begins with a period when they are ectothermic, and effective thermoregulation develops with increased body size and thickness of pelage. In many rodents, for example, thermoregulation develops within about 3 wk of birth (e.g., Hudson 1974; Rosen 1975; Soholt 1976).

At birth, marsupials are extremely altricial and continue their development in the protection of the mother's pouch. In the kangaroos (family Macropodidae), thermoregulatory abilities have been correlated with the development of pelage and thyroid function (Setchell 1974), but, until this stage, a constant temperature in the pouch serves to regulate body temperature of the single young. In contrast to this family, members of the Dasyuridae (marsupial insectivores and carnivores) give birth to a litter of young and have open pouches that do not afford the thermal protection of a more developed pouch, even when the young are very immature.

The species considered in this study, the kowari (*Dasyuroides byrnei*), is a desert-dwelling, presumably solitary, dasyurid which rears five to six young in each litter (Aslin 1974). During the first 30 days after birth the young are completely covered by pouch folds. From this time until detachment from the teat at around 56 days, progressive exposure occurs, even though the eyes are unopened and pelage is sparse. After permanent attachment to the teat has been abandoned, the young may be left in the nest while the mother forages. At about 105–110 days of age (when body mass reaches about 40 g), weaning occurs, and the young become virtually independent (Aslin 1974).

In the present study we determined at what age young kowaris become endothermic. Since weaning occurs at a body mass of less than half of adult size, and many small endotherms use torpor for energy conservation, we investigated whether the development of independent thermoregulation in juvenile kowaris was accompanied by the ability to enter and arouse from torpor. The developmental and seasonal tendency for torpor was also compared to adults in which torpor has not been described previously.

MATERIAL AND METHODS

ANIMALS

Five female and three male adult kowaris and a female with six pouch young, supplied by the Institute of Medical and Veterinary Science, Adelaide, South Australia, were used in this study. The biology of this

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laboratory colony has been described by Aslin (1980). The animals were individually housed in cages provided with wood shavings and nest boxes. Water and a mixture of canned and dried dog food were available ad lib. *Tenebrio* larvae and an egg/gelatine mixture were fed as a supplement about once every 2 wk. Since litters of this species are difficult to maintain (Aslin 1980), the female with the pouch young was housed in an isolated room at an ambient temperature (T_a) of 23 C under a natural photoperiod. All the other animals, including the juveniles after weaning, were maintained in outside pens at the Flinders University, Adelaide, under natural photoperiod and temperature fluctuations.

DEVELOPMENT OF THERMOREGULATION

Two methods were used to assess the thermoregulatory status of the young; the rate of heat production, measured indirectly as oxygen consumption ($\dot{V}O_2$), and the rate of change in body temperature (T_b) at a constant environmental temperature. Levels of $\dot{V}O_2$ were measured in individual animals at ambient temperatures of 20, 25, 30, and 35 C. The measurements were commenced when the animals were 58 days old, the time when they first became detached from the nipple, and continued until weaning at around 110 days. For these measurements, the animals were placed in metabolic chambers and air was drawn through at flow rates which kept the ambient O_2 concentration above 20%. The chamber sizes were increased from 0.15–0.35 to 1.2–3.0 liters as the animals grew. Each chamber had ports for incurrent and excurrent gas and a thermocouple. Airflow was controlled by a pump which drew air sequentially through the chamber, a column which removed CO_2 and water, a rotameter, and an Applied Electrochemistry S3A Oxygen Analyser. Rates of oxygen consumption were calculated using equation (4d) of Withers (1977). All measurements were taken during the animals' period of inactivity (daytime) after they had been in the chamber for at least 60 min. This time is greater than the time to reach 99% equilibrium for any of the chamber and flow combinations. Body temperatures were determined with a 0.5-mm-diameter thermocouple inserted 1.5 cm into the rectum immediately after the animal was removed from the chamber. The young were taken from the mother immediately before the measurement period and were therefore most likely not postabsorptive. Steady levels of oxygen consumption usually occurred within 1 h after the animals had been placed into the chamber and were defined as less than 5% variation in $\dot{V}O_2$ over a 15-min period.

To determine the rate of cooling, the animals were removed from the nest, fitted with a thermocouple inserted 1.5 cm into the rectum and taped to the tail, placed in an open container in a constant-temperature room (16.5 ± 0.5 C); then body temperatures were measured for periods of 30 min. The apparent cooling constants were determined from the regression coefficients of the plot of the logarithm of the percent temperature differential at the beginning of the exposure period against time (see Soholt 1976).

TORPOR

After weaning at 110 days, the juveniles were separated from the parent. From 116 days to 13 months of age, levels of $\dot{V}O_2$ were measured over 18–24-h periods from individual animals of eight age groupings. The circuit for monitoring changes in $\dot{V}O_2$ was similar to that used for the immature animals, except in this case a Servomex model OA 184 paramagnetic oxygen analyzer was used. Oxygen consumption was determined from the difference between the oxygen concentration in two parallel circuits, one as control and one containing the animal, and monitored on a Rikadenki chart recorder. Chamber sizes of 3 and 7 liters were used, and flow rates were maintained through calibrated rotameters. For calculations of mass-specific $\dot{V}O_2$ during prolonged periods, measurements of body mass were taken before and immediately following the run and interpolated assuming a constant rate of loss (see fig. 6*C* for weight loss). Experiments to determine the ability to enter torpor were conducted in a quiet, constant-temperature room remote from the recording equipment. The ambient temperature used was 15.6 ± 1.0 C, the photoperiod was representative of sunrise and sunset at that time of the year, and no food and water were provided.

Additional measurements of oxygen consumption were taken in adult kowaris during winter (July/Aug.). Body temperatures were taken from 0.5-mm-diameter thermocouples inserted rectally for 30 mm, and the temperature read from a Comark Electronic Thermometer. Animals exhibiting a rate of oxygen consumption 25% or more below the level expected for normothermic inactive animals at the T_a's in question (75% or less of resting values; T_b less than 31 C) were considered to be torpid. This is consistent with the definition of Hudson and Scott (1979). At body temperatures below 31 C, motor control was clearly different from normothermic animals.

CALIBRATIONS AND STATISTICS

All thermocouples were calibrated against a precision mercury thermometer traceable to a national standard. Oxygen analyzers were calibrated against room air and nitrogen (Servomex) or room air and an electronic span (Applied Electrochemistry). The calibration of rotameters was taken from a spirometer. All gas volumes were corrected to dry volumes under standard conditions of temperature and pressure (STPD). Means of samples are expressed as ±SD: statistical differences between samples were determined by a Student's t-test and assumed significant at the 95% level ($P < .05$).

RESULTS

At 58 days animals were blind and naked until, at 76 days, fur had developed and eyes were open (for details, see legend of fig. 1). The rate of growth was similar in males and females until the age of 120 days. Above 120 days males were heavier than females, and about 80% of the adult mass was reached at 200 days in both sexes. The

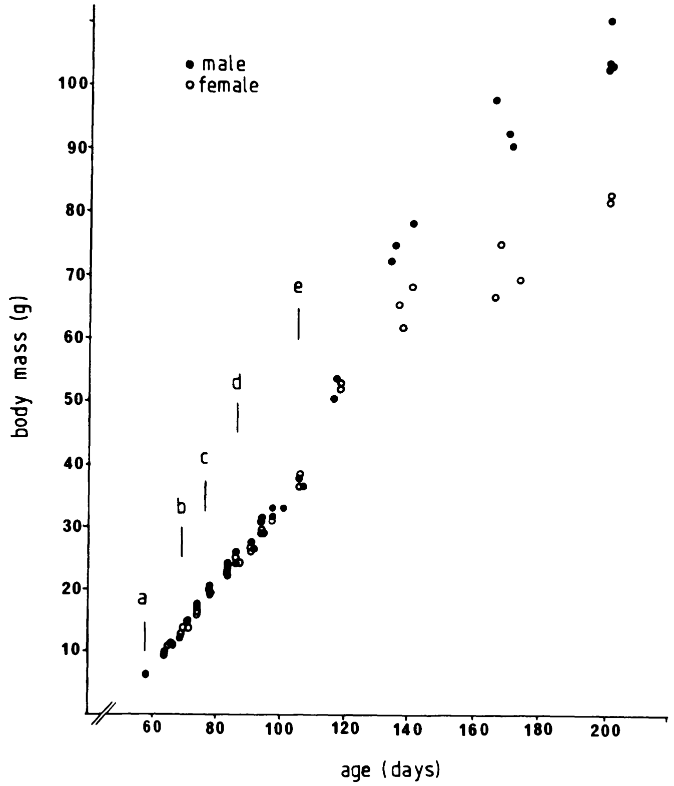

FIG. 1.—The increase in body mass of kowaris after the first detachment from the teat until the age of 200 days. The difference between males (●) and females (O) became apparent after weaning. The external appearance as indicated by the dashes was (a) blind naked; (b) partly furred; (c) open eyes, furred, teeth emerging; (d) teeth present; (e) of adult form.

rate of development in this litter is in close agreement with data from Aslin (1974).

DEVELOPMENT OF THERMOREGULATION

Thermoregulatory ability in kowaris develops extremely slowly. The change in T_b between day 59 and day 106 measured at T_a = 16.5 C is shown in figure 2. Cooling at 59 days was rapid but gradually decreased with age, until at 105/106 days the young remained homeothermic. An extrapolation of the apparent cooling constants derived from these data (fig. 3) indicates that endothermy is achieved at a body mass of about 28 g and at an age of 90 days, about 2 wk after fur had developed (fig. 1). The zero value of the apparent cooling constant at 105/106 days is excluded from this regression (fig. 3).

Rates of oxygen consumption at rest and equilibrium T_b's of young kowaris were measured at T_a = 20, 25, 30, and 35 C between days 58 and 118 (fig. 4). The increase in $\dot{V}O_2$ between 84 and 98 days at T_a 20 and 25 C was associated with an increase in $\Delta T(T_b - T_a)$ and is consistent with results from the cooling experiments. At T_a = 30 C, the main increase in ΔT was observed at about day 90, but $\dot{V}O_2$ was changed only slightly. At 35 C, both $\dot{V}O_2$ and ΔT were largely independent of the age of the animal.

The body temperatures below the age of 70 days ranged between 21.2 C at T_a 20 C, 25.0–29.6 C at T_a 25 C, 30.1–32.1 C at T_a 30 C, and 35.1–35.8 C at T_a 35 C. Between 70 and 80 days, T_b was increased to values between 22.6–24.8 C at T_a 20 C and 28.3–29.9 C at T_a 25 C, while at T_a 30 and 35 C, values similar to the younger animals were observed. At about 85 days, T_b's were still less than 30 C at T_a 20 and 25 C; at T_a 30 and 35 C, T_b ranged between values of 32.4 and 35.8 C. Above 90 days, all T_b's

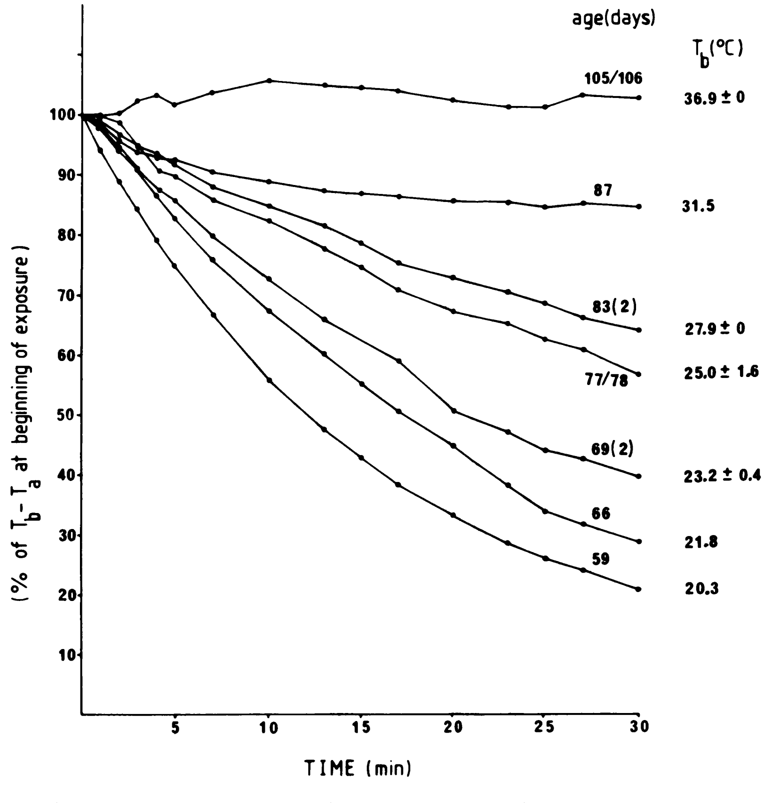

FIG. 2.—Change in body temperature of kowaris between 59 and 106 days. All measurements were taken over 30 min at 16.5 ± 0.5 C. Age and body temperatures (T_b) after 30-min exposure are indicated for each experiment. Duplicate determinations are indicated in brackets. For 77/78 days and 105/106 days, the measurements were pooled.

were greater than 32.0 C, independent of T_a.

TORPOR

Shortly after weaning, the $\dot{V}O_2$ of the young kowaris was measured over 18–24-h periods at T_a 15.6 ± 1.0 C. The depicted animals (a male and a female; fig. 5) showed a period of activity after being placed in the chamber. This was followed by a resting period, with $\dot{V}O_2$ values around 1.8 and 2.0 liter O_2/kg h, respectively, at times between 1800 and 2000 hours. After the lights were switched off, $\dot{V}O_2$ increased to maximum levels of 5.8 and 6.8 liter O_2/kg h during the activity period. Torpor commenced in the morning and resulted in minimum $\dot{V}O_2$ of 0.42 and 0.28 liter O_2/kg h. At 1245 hours, an increase in $\dot{V}O_2$ occurred in the female; however, when examined at 1530 hours, this individual was still in torpor with a T_b of 25.4 C. This torpor bout of about 11.5 h was, despite the interruption by the T_b measurement, the longest observed for this species. For the male, the increase in $\dot{V}O_2$ and T_b was measured after the disturbance by the measurement of T_b. Both the $\dot{V}O_2$ and T_b increased rapidly, and the arousal rate was 0.46 C/min. All animals used in this study could arouse at T_a 15.6 C using endogenous heat production.

In figure 6*A*–*C* the $\dot{V}O_2$ maxima at night, the arousal peaks, the resting $\dot{V}O_2$ (inactive normothermic animals) with 75% of this value and the daily minima of such measurements (fig. 5) are compared with the duration of torpor, the body mass, and the weight loss of the juveniles during their development. The maximum levels of $\dot{V}O_2$ and arousal peaks (mean with SD) in juveniles were similar, and both decreased with age (fig. 6*A*). The resting $\dot{V}O_2$ of the

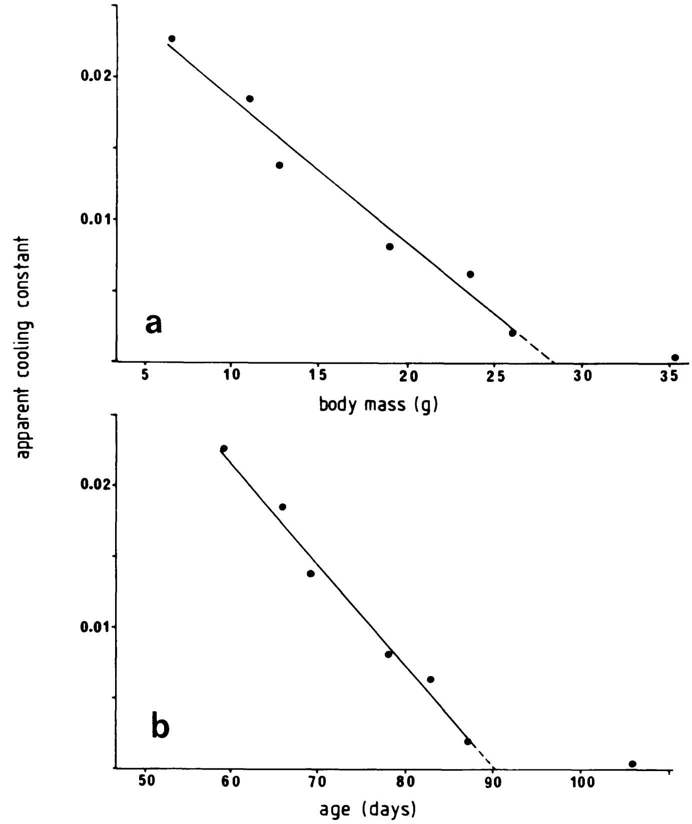

FIG. 3.—Apparent cooling constants (log °C/min) of kowaris at different body masses (*a*) and ages (*b*). The apparent cooling constants were obtained from regression analysis of each cooling curve in fig. 2 (Soholt 1976). A linear of regression analysis relating the apparent cooling constant with both body mass and age (excluding the value at 105/106 days, which was approximately zero), results in a correlation coefficient < .98.

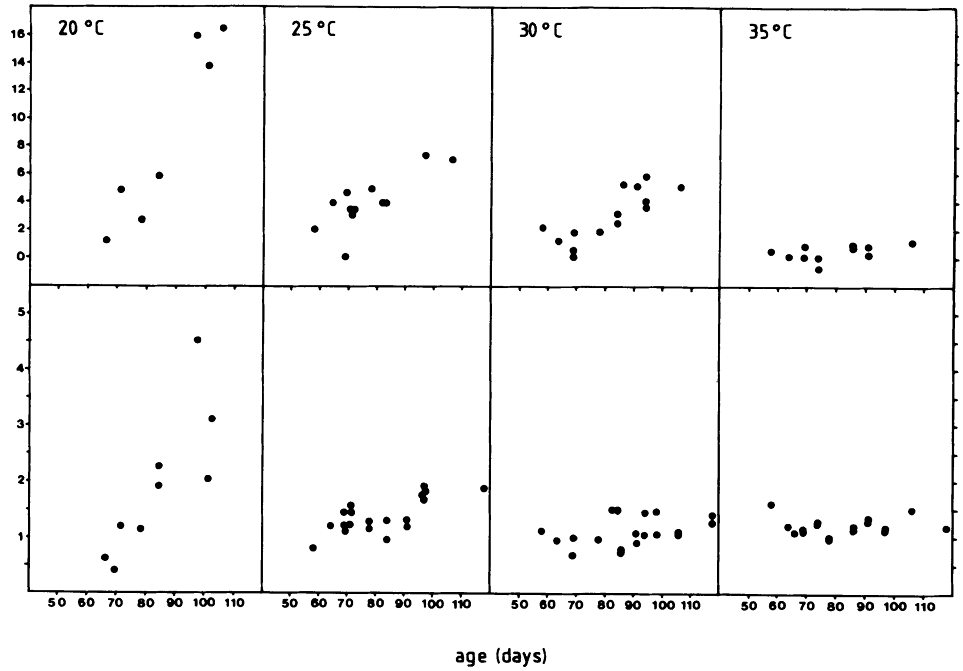

FIG. 4.—Steady-state oxygen consumption rates ($\dot{V}O_2$) and $\Delta T(T_b - T_a)$ of kowaris at different ages. The ambient temperatures for these measurements are indicated in the upper left-hand corners.

juveniles decreased steadily from 2.8 liter O_2/kg h (October) at about 50 g body mass to about 1.62 liter O_2/kg h (March), with the exception of an increase in $\dot{V}O_2$ in January, and remained fairly stable above a body mass of 100 g (fig. 6*A*, *C*). The resting

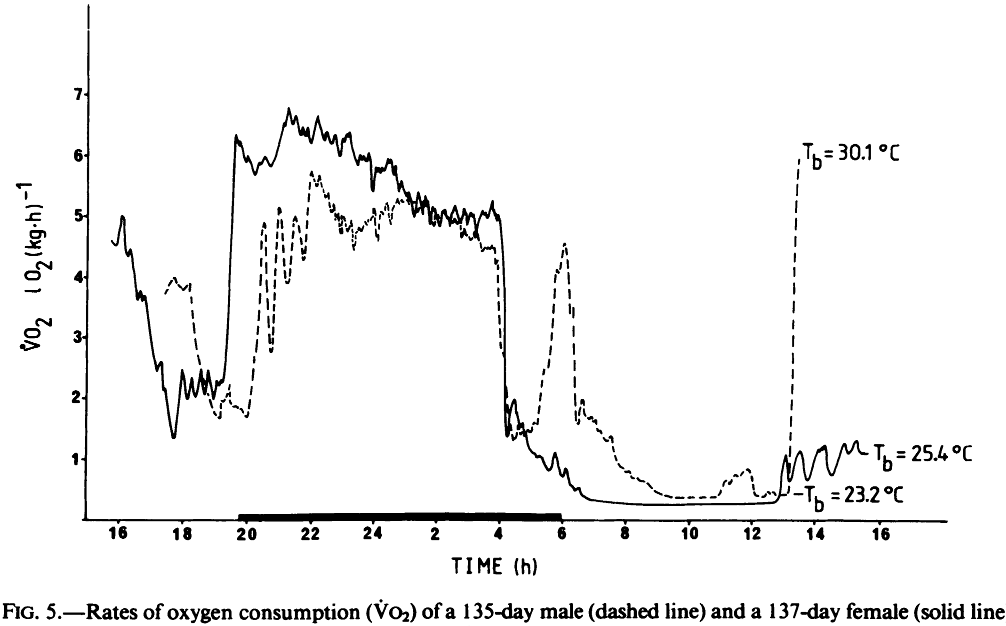

FIG. 5.—Rates of oxygen consumption ($\dot{V}O_2$) of a 135-day male (dashed line) and a 137-day female (solid line) juvenile kowari. The dark bar indicates the period of darkness. The body temperatures (T_b) are indicated in °C at the end of the measurements.

$\dot{V}O_2$ for the adults in winter was 1.7 ± 0.2 liter O_2/kg h ($n = 9$; body mass 121 ± 16 g), a value similar to that observed in juveniles.

Torpor below a body mass of about 80 g (October/November), as shown by the individual daily $\dot{V}O_2$ minima, was deeper (mean 0.59 ± 0.22 liter O_2/kg h; $n = 8$) than in heavier animals (0.83 ± 0.43 liter O_2/kg h; $n = 6$; December). In January (summer), even the juvenile females, which showed a strong tendency to enter torpor

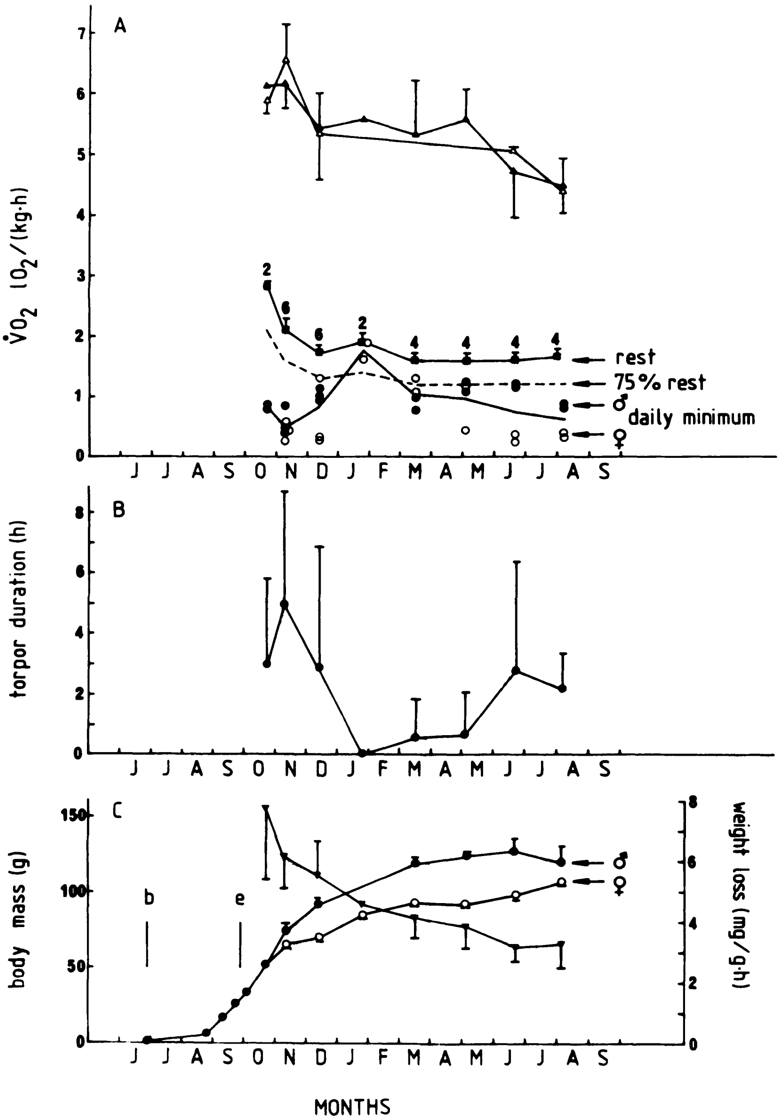

FIG. 6.—*A*, Rates of oxygen consumption ($\dot{V}O_2$) of juvenile kowaris determined from 18–24-h measurements at different times of the year. The symbols represent the arousal peaks (Δ mean with SD), daily maxima (▲ mean with SD), resting values (■ mean with SD), 75% of the resting value (– – –) and the daily minima (individuals; ● males, O females). The numbers adjacent to the resting values are the numbers of 18–24-h measurements on individual animals from which all the data presented in fig. 6*A*–*C* were derived. *B*, The duration of torpor bouts (hours, mean with SD) of juvenile kowaris determined for 18–24-h measurements for both sexes at different times of the year. *C*, The body mass (●, O) and the weight loss (▼ mg/h g body mass at beginning of experiment) for juvenile kowaris. Below a body mass of 55 g, the values of males and females were pooled (●). Above 60 g, the difference between males (●, mean with SD) and females (O, mean with SD) became apparent. Birth (*b*) and euthermia (*e*) are indicated.

in November/December, remained normothermic. The tendency of juveniles to enter torpor again increased with the slow growth to adult body mass and with the approach of winter. In July/August (winter), the metabolism during torpor was statistically similar in the adults (mean: 0.88 ± 0.4 liter O_2/kg h; $n = 9$) and juveniles (mean: 0.62 ± 0.3 liter O_2/kg h; $n = 4$).

In figure 6*B* the duration of the torpor bouts of the juveniles over the period of the experiment is compared. Torpor lasted between a mean of 3–5 h below body mass of 85 g and was reduced in January. The length of torpor increased with the approach of winter, and, in July/August, the duration of torpor in juveniles (mean 2.2 ± 1.2 h) was similar to that in the adult animals (mean 1.8 ± 2.1 h). The weight loss in juveniles appears independent of the daily $\dot{V}O_2$ minima and the duration of torpor, and decreased with increasing body mass (fig. 6*C*).

Body temperatures during torpor ranged between 19.7 and 26.5 C in juveniles and between 21.6 and 25.4 C in adults.

DISCUSSION

The development of thermoregulation in the kowari is a gradual process. At 58 days of age, when the young may be left in the nest while the mother forages (Aslin 1974), virtually no thermoregulatory ability is present. Endothermy develops slowly over the next 4–5 wk in association with the development of fur and, apparently more important, increasing body mass. Body temperatures at different T_a are not maintained at the same level during the various experimental periods—suggesting that the "setpoint" is not gradually increased with growth. It appears that the metabolism of the young becomes more and more endothermic until a normothermic T_b can be maintained even during exposure to low T_a. The slow development of thermoregulation implies that young kowaris are potentially exposed to passive fluctuations of T_b for about 60 days, from day 30, when they protrude from the pouch (Aslin 1974), to day 90, when endothermy is achieved. This development of endothermy is extremely slow when compared with similar-sized placentals, even when the gestation period of 30–35 days (Woolley 1971) is added to the period of development and used as a comparison (see Morrison and Petajan 1962; Hissa 1968). The development of independent thermoregulation after 100 days, as for *Dasyuroides byrnei* (including the gestation period), has been observed for much larger placentals like pigs and porcupines, and even the opossum (*Didelphis marsupialis virginiana*), which weighs about 5 kg, shows a faster rate of development (Morrison and Petajan 1962). The advantage in such a slow development of thermoregulation may be that nutrients are utilized for growth spread over a long time period rather than for thermoregulation (Bartholomew 1982). Endothermy is only achieved shortly before the young become independent, at a time when good food availability is most likely.

The achievement of endothermy in kowaris is accompanied by the ability to enter torpor. The initial high tendency in juveniles to enter torpor was reduced in summer at a body mass of about 80 g, but in the following winter torpor in juveniles and adults was similar. The development of torpor in other mammals has not been described to our knowledge. However, the ability to enter torpor after the achievement of endothermy and a short period of homeothermy has been observed in a white-toothed shrew (Nagel 1977).

The value of resting metabolism in relation to the predicted standard values has been considered important in the determination of mammalian torpor (McNab 1983). In figure 7, the resting $\dot{V}O_2$ at $T_a = 30$ C is plotted against body mass on logarith-

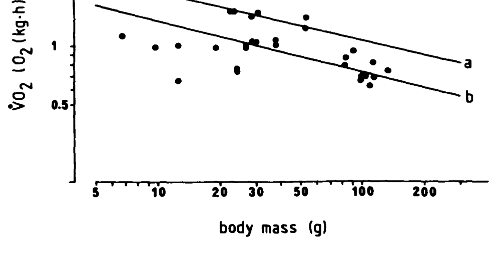

FIG. 7.—Logarithmic plot of oxygen consumption rate ($\dot{V}O_2$) versus body mass of kowaris at different ages. The ambient temperature was 30.0 ± 0.5 C. Line (*a*) represents the equation by Kleiber (1961) for placentals; line (*b*) represents the equation by MacMillen and Nelson (1969) for dasyurid marsupials.

mic coordinates and is compared with the standard metabolic rate of dasyurids (MacMillen and Nelson 1969) and placentals (Kleiber 1961). The strong ectothermic nature of kowaris below a body mass of 20 g is indicated by $\dot{V}O_2$ values lower than those predicted for dasyurids. Between 20 and 40 g, the predicted dasyurid values are exceeded, and at about 50 g $\dot{V}O_2$ values similar to those for placentals are observed. Young kowaris at this body mass entered torpor despite their high metabolic rates. The resting $\dot{V}O_2$ was decreased at 80–90 g, together with a decreased tendency to enter torpor. At a body mass above 100 g, the rate of resting $\dot{V}O_2$ was close to the prediction for dasyurids, and the tendency to enter torpor was similar to that seen in adult animals.

Little information about the natural history of the kowaris is available to date, so it is difficult to discuss the probable adaptive significance of the change in the torpor tendency during development. In ground squirrels an intraspecific, mass-dependent difference in hibernation, apparently related to reproduction, has been observed (French 1982). Similar reasons, like the establishment of territories during the dispersal of the young kowaris in summer, which is the season of main rainfall in their distribution range (Climate of Australia 1983) and consequently prey abundance, may be a factor in their mode of thermoregulation.

Like the mulgara, *Dasycercus cristicauda* (Kennedy and MacFarlane 1971), adult kowaris have a body mass of over 100 g, considerably larger than the other dasyurids (body mass < 30 g) observed in daily torpor (see Wallis 1982). The minimum $\dot{V}O_2$ during torpor of kowaris is lower than in *Antechinus stuartii* and *Planigale gilesi* (Wallis 1976; Dawson and Wolfers 1978) but similar to that of *Planigale maculata, Sminthopsis murina,* and *S. macroura* (Morton and Lee 1978; Geiser et al. 1984; Geiser and Baudinette 1985). The minimum T_b and duration of torpor is within the range of other dasyurids (T_b = 15–24 C, torpor bouts 1.5–10 h; Wallis 1982; Geiser 1985*a*; Geiser and Baudinette 1985), and it appears that kowaris enter daily, rather than prolonged, torpor. In pygmy possums (family Burramyidae), lower T_b's and much longer torpor bouts of up to 2 wk have been observed (see Geiser 1985*b*).

The mild regime which was sufficient to induce torpor in kowaris, and the frequent observation of spontaneous torpor (food ad lib.) in their outside holding facilities, suggest that both juveniles and adults enter torpor in the wild. Even sugar gliders, which often had to be starved for several days to induce torpor in the laboratory, have been observed torpid in their natural environment (Fleming 1982). The fact that torpor occurs in the relatively large kowari suggests that many more of the smaller dasyurid species than believed at present use torpor for energy conservation.

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