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Daily torpor and thermoregulation in *Antechinus* (Marsupialia): influence of body mass, season, development, reproduction, and sex

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Summary. Season and body mass influence torpor in mammals. However, the effects of the two factors are often difficult to distinguish because body mass in many species changes with season. The present study attempted to separate seasonal and body mass related alterations of torpor. Adult female *Antechinus stuartii* and *A. flavipes* (Marsupialia), which were about half the size of males of the respective species, showed longer and deeper torpor than males. When the two species were compared, torpor in *A. stuartii*, the smaller species, was more pronounced than in *A. flavipes*. Juveniles of both species had lower body temperatures and longer torpor durations than adults. Torpor was most pronounced in juvenile males during summer; in winter, when males had grown to adult size, the use of torpor was reduced. Seasonal changes in torpor of adults were not distinct. These results suggest that the influence of body mass on torpor in these *Antechinus* species is stronger than that of season.

Key words: *Antechinus* – Body mass – Season – Torpor – Thermoregulation

Hibernation and daily torpor in mammals and birds are expressed by periodic reductions of body temperature (T_b) and metabolic rate which, after a torpor episode, are actively raised by the animal to high endothermic levels. Energy expenditure during torpor is substantially reduced and it appears that heterothermy in these small endotherms is an important adaptation for survival of food shortages and adverse environmental conditions (Hudson 1978; Lyman et al. 1982). So far pronounced heterothermy has only been observed in small (<10 kg) species. Small endotherms are unable to survive starvation for long periods because they have relatively high mass-specific metabolic rates and lack the large fat stores that are available to large species (Bartholomew 1986; French 1986). Body mass therefore appears to have a strong influence on the use of torpor. However, the impact of body mass on depth and length of torpor, which determine the extent of energetic savings, is at present poorly understood.

Seasonal alterations of climate also strongly influence thermoregulation of heterothermic mammals. Daily torpor is more frequent and more pronounced in winter than in summer in rodents and marsupials (MacMillen 1965; Gaertner et al. 1973; Lynch et al. 1978; Heldmaier and Steinlechner 1981; Geiser and Baudinette 1987). However, the frequent use of daily torpor in heterothermic mammals during winter is often accompanied by a substantial reduction of body mass (Morton 1978a, b; Heldmaier and Steinlechner 1981). Therefore it is difficult to ascertain whether such alterations in the pattern of torpor result directly from seasonal influences or simply from changes in body size.

The present study attempted to separate seasonal and body mass related alterations of torpor in the closely related forest dwelling dasyurid marsupials *Antechinus stuartii* and *A. flavipes*. Both species are insectivorous and have been previously observed in torpor (Wallis 1976; Geiser 1985). Torpor was investigated in juveniles after endothermy had been achieved, and in adults of both species. *Antechinus* are monoestrous with a highly synchronised mating period in winter (Woolley 1966; McAllan and Dickman 1986). Because all *Antechinus* males die after mating and most females die after the young have been reared most individuals in wild populations are less than one year of age (Lee et al. 1982).

Materials and methods

Four male and four female *A. stuartii* and seven females with pouch young that reared eleven young (5 males, 6 females) were wild caught in the Gosford area of New South Wales (about 100 km north of Sydney). Two male and three female *A. flavipes* and two pregnant females that reared nineteen young (6 males, 13 females), were caught in the Myponga area of South Australia (about 100 km south of Adelaide). Animals were transported to the Flinders University, Adelaide, and kept in outdoor pens under natural photoperiod and temperature (Geiser and Baudinette 1987). Experiments on these animals were conducted between the austral winter 1983 and summer 1985. Adults and juveniles after weaning were kept individually in cages provided with hard wood shavings and boxes containing nesting material. Animals were fed ad libitum with water and a mixture of dried and canned pet food which was exchanged daily. *Tenebrio* larvae and an egg-gelatine mixture were provided once every two weeks.

Torpor in adults and recently weaned juveniles was monitored by measurement of the rate of oxygen consumption ($\dot{V}O_2$) over 1-day periods. $\dot{V}O_2$ was measured in a 3-liter repirometer with a Servomex Model OA 184 paramagnetic oxygen analyzer at constant air temperatures (T_a) that were measured by thermocouple in the respirometer;

food and water were not provided during these measurements. The photoperiod matched local sunrise and sunset for the respective time of year. $\dot{V}O_2$ was determined from the difference between the oxygen content in two parallel open flow circuits (room air vs. the animal). Flow rates of dried air (about 500 ml/min) were adjusted and measured with calibrated rotameters. Calibrations and calculations were performed as described (Geiser and Baudinette 1987). The $\dot{V}O_2$ of normothermic resting animals (RMR) was determined when a variation of less than 5% over 15 min occurred after an inactive period of at least 30 min; the minimum metabolic rate of torpid animals was determined at times of constant $\dot{V}O_2$ over at least 30 min. Furthermore, the duration of torpor in undisturbed animals were derived from measurements of $\dot{V}O_2$. For determination of T_b of torpid animals, $\dot{V}O_2$ measurements were interrupted. Body temperatures during $\dot{V}O_2$ measurements and in animals held in the outside pens were determined by 3 cm rectal insertion of a calibrated thermocouple probe read from a Kane-May digital thermometer.

Table 1. Spontaneous torpor in *Antechinus stuartii* and *A. flavipes*

Species	Season	n	N	Torpid	Normothermic	%Torpid	T_a min (°C)	T_a max (°C)
A. stuartii	summer	19	10	0	19	0	13	35
	autumn	51	10	0	51	0	8	33
	winter	57	10	4	53	7	6	22
A. flavipes	summer	18	9	0	18	0	13	35
	autumn	46	9	2	44	4	8	33
	winter	63	9	6	57	10	6	22

Food and water were available ad libitum. Observations were made in the morning at about 0900 h. Only females entered torpor spontaneously. n = number of observations; N = number of individuals. T_a min and T_a max represent minimum and maximum air temperatures recorded in the outdoor pens in the respective season, for further climatic details see Geiser and Baudinette (1987). The austral seasons are given in Figure headings

Results

The occurrence of daily torpor in *Antechinus stuartii* and *A. flavipes* was dependent on food availability and air temperature. Individuals of both species occasionally entered torpor in their outdoor enclosure when food and water were provided ad libitum (spontaneous torpor; Table 1). Spontaneous torpor was only observed in females when T_a was low in autumn and winter and was never observed in males.

Withdrawal of food and water increased the incidence of torpor in both species (induced torpor). When food and water were withheld for about 24 h during measurements of $\dot{V}O_2$ at T_a 11–18° C (90% of measurements were taken at T_a 15±1° C) torpor was observed in all seasons (Table 2). However, the tendency to enter torpor differed between species and sexes and was dependent on the developmental state of the animals. In summer, juvenile female *A. stuartii* at a mass of less than 18 g usually became hypothermic (were unable to arouse from torpor at the T_a they had entered torpor and required partial rewarming), whereas the males at the same time with a mass of about 21 g showed a very high incidence of torpor. (Body masses are given in Figs. 1, 2). Both male and female juvenile *A. flavipes*, with a body mass >23 g in summer, entered torpor frequently. In autumn, induced torpor was common in male and female *A. stuartii*, and female *A. flavipes*. In contrast, the tendency towards entering torpor in this season was reduced in male *A. flavipes*, which had reached a body mass of about 50 g, and remained low for the rest of the experi-

Table 2. Induced torpor in *Antechinus stuartii* and *A. flavipes*

Species	Season	Sex	n	N	Torpid	Normothermic	Hypothermic	%Torpid
A. stuartii	summer	female(j)	3	3	1	0	2	30
		male(j)	4	4	3	0	1	75
	autumn	female	14	6	12	0	2	86
		male	10	6	8	2	0	80
	winter	female	14	8	12	1	1	86
		male	13	6	6	6	1	46
	spring	female	5	4	4	0	1	80
		female(lac)	3	3	0	3	0	0
		male	1	1	0	1	0	0
	summer	female	8	8	7	0	1	88
		male	1	1	0	1	0	0
A. flavipes	summer	female(j)	5	4	4	1	0	80
		male(j)	5	4	4	1	0	80
	autumn	female	6	5	5	1	0	83
		male	6	3	1	3	0	17
	winter	female	9	6	5	4	0	56
		male	3	3	1	2	0	33
	spring	female	4	3	2	2	0	50
		male	1	1	0	1	0	0
	summer	female	5	4	1	4	0	20

Data were taken from the 1-day measurements of $\dot{V}O_2$. Food and water were withheld and T_a was 11–18° C (90% of measurements were taken at T_a 15±1° C). n = number of observations; N = number of individuals; (j) = juveniles; (lac) = lactating. Hypothermic animals were unable to arouse from torpor at the T_a they had entered torpor and required partial rewarming. Low numbers of adult males in spring and summer are due to male die-off. A reduction of the metabolic rate by more than 25% below the RMR was defined as torpor (Hudson and Scott 1979)

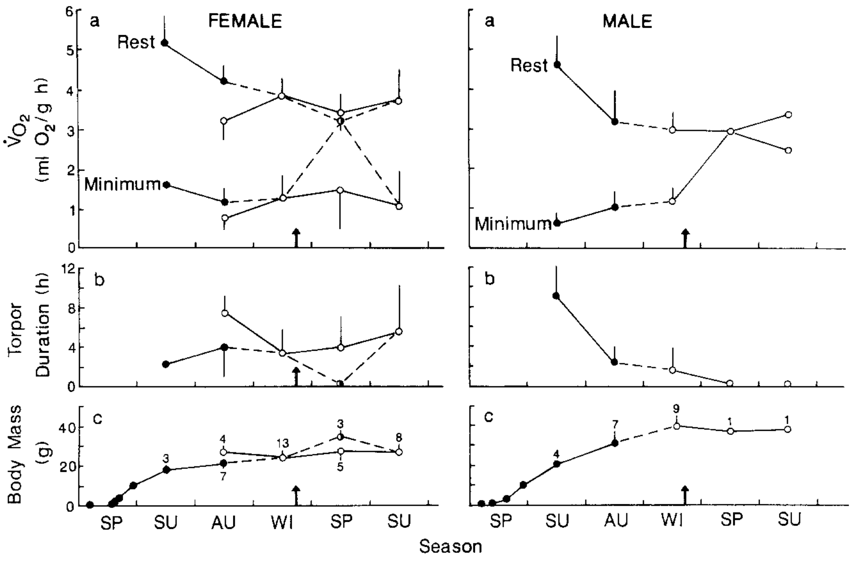

Fig. 1a–c. Rate of oxygen consumption ($\dot{V}O_2$) (**a**), duration of torpor (**b**), and body mass (**c**) of female and male *Antechinus stuartii* at different seasons of the year: spring (SP; September-November), summer (SU; December–February), autumn (AU; March–May), and winter (WI; June–August). Food and water were not provided and T_a was 15 ± 1° C. The symbols indicate juveniles (●), adults (○), and females with pouch young (◑). Solid lines combine animals remaining in the same status, broken lines combine animals which changed status from one season to the next. Numbers of determinations are given in (**c**); all values are shown with SD. The mating period is indicated by an arrow

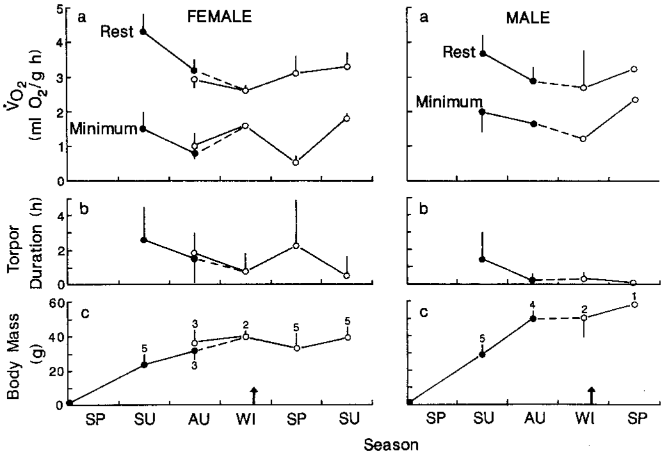

Fig. 2a–c. Rate of oxygen consumption ($\dot{V}O_2$) (**a**), duration of torpor (**b**), and body mass (**c**) of female and male *Antechinus flavipes* at different seasons of the year: spring (SP; September–November), summer (SU; December–February), autumn (AU; March–May), and winter (WI; June–August). Food and water were not provided and T_a was 15 ± 1° C. The symbols indicate juveniles (●) and adults (○). Solid lines combine animals remaining in the same status, broken lines combine animals which changed status from one season to the next. Numbers of determinations are given in (**c**); all values are shown with SD. The mating period is indicated by an arrow

ment. A similar reduction in the occurrence of torpor was observed in male *A. stuartii* and female *A. flavipes* in winter. Non-lactating adult *A. stuartii* females showed a similar frequency of torpor throughout the year when their body mass was above about 20 g; lactating females did not enter torpor.

Torpor duration, resting metabolism (RMR), the minimum metabolic rate during torpor, and body mass of male and female *A. stuartii* at T_a 15 ± 1° C differed throughout the yearly cycle (Fig. 1). The mass-specific RMR decreased with growth and remained fairly stable when the animals reached adult body mass. The minimum $\dot{V}O_2$ during torpor in nonlactating female *A. stuartii* did not show a clear yearly cycle. Lactating females did not lower metabolic rate below RMR values. In male *A. stuartii*, the lowest mass-specific $\dot{V}O_2$ during torpor was observed in juveniles, although they had the smallest body masses and thus the highest RMR's, and the minimum $\dot{V}O_2$ increased with growth. In female *A. stuartii* the duration of torpor was >2 h throughout the year and the longest torpor bouts were observed in autumn. Adult male *A. stuartii* remained torpid for <2 h, whereas juvenile males in summer had the longest torpor duration of about 9 h.

Antechinus flavipes showed a similar seasonal pattern of RMR, minimum $\dot{V}O_2$, and torpor duration at T_a 15 ± 1° C (Fig. 2). However, RMR in *A. flavipes*, the larger species, was lower and the duration of torpor was shorter than in *A. stuartii*. Adult female *A. flavipes* showed no clear seasonal shifts in the depth and duration of torpor, however, induced torpor was less frequent in summer than in the other seasons. Juvenile male *A. flavipes* showed distinct torpor periods whereas torpor in adult males was very shallow.

Body temperatures during torpor (minimum T_b) and body masses in adults differed significantly between the two species and sexes ($P < 0.025$; one-way ANOVA). In contrast, the normothermic T_b's of males and females of both species was similar (about 35° C). The lowest mean minimum T_b, 24.8 ± 1.7° C, was measured in female *A. stuartii*, which had the lowest body masses. Male *A. flavipes*, the heaviest animals, had a mean minimum T_b of 31.6 ± 0.1° C, which was significantly lower than the normothermic T_b of 35.1 ± 1.4° C ($P < 0.01$; *t*-test). Male *A. stuartii* and female *A. flavipes* had intermediate minimum T_b's and body masses.

The pattern of torpor in *Antechinus* appeared to be predominantly a reflection of size. Therefore I tested whether the minimum T_b, the torpor duration, and the $\dot{V}O_2$ during torpor can be explained by body mass, independently of season. The minimum T_b of both species showed a direct linear relationship with body size and explained 54% (58% when juveniles were excluded) of the variation in body temperature during induced torpor (Fig. 3). The duration of torpor showed an inverse relationship with body mass and when both variables were log-transformed 59% of the variation in torpor duration could be explained by body mass (Fig. 4). In contrast, the mass-specific $\dot{V}O_2$ during torpor in *Antechinus* was not related with body mass ($r^2 = 0.004$; $P > 0.8$; $N = 39$).

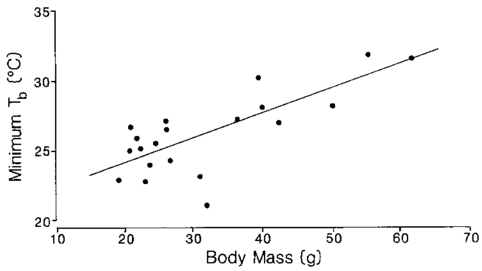

Fig. 3. Minimum T_b as a function of body mass in *Antechinus stuartii* and *A. flavipes* juveniles and adults. Linear regression analysis resulted in the equation $y = 20.85 + 0.17x$; $r^2 = 0.54$; $P < 0.0001$; $N = 20$. Each point represents a mean or a single determination for each individual. Two individuals were used twice, as juveniles and as adults. When juveniles were excluded from regression analysis, the equation was only slightly altered: $y = 20.03 + 0.18x$; $r^2 = 0.58$; $P < 0.0005$; $N = 14$

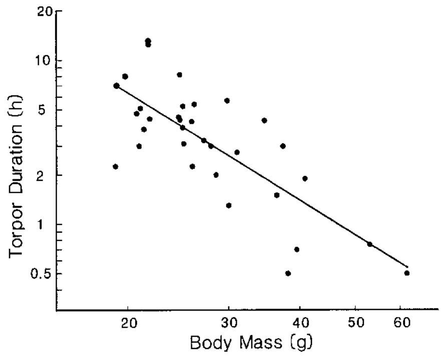

Fig. 4. Logarithmic plot of torpor duration as a function of body mass in *Antechinus stuartii* and *A. flavipes* juveniles and adults. Linear regression analysis resulted in the equation $\log_{10} y = 3.64 - 2.18 \log_{10} x$; $r^2 = 0.59$, $P < 0.0001$; $N = 33$. Each point represents a mean or a single determination for each individual. Six individuals were used twice, as juveniles and adults

Discussion

The present study reveals significant interspecific, developmental, seasonal, and sexual differences in the pattern of heterothermy in *Antechinus stuartii* and *A. flavipes*. Torpor was more pronounced in juveniles than in adults, and females of both species entered torpor more frequently than the males. Most of these differences could be explained by body mass; seasonal influences appear to be less important.

The minimum T_b in adult *Antechinus* was related to body mass. Females exhibited lower minimum T_b's than the males and *A. stuartii* showed lower minimum T_b's than *A. flavipes*, the larger species. To my knowledge, the body mass related difference in the minimum T_b between species and sexes reported here has not been previously observed. Moreover, torpor duration during induced torpor of *Antechinus* was a negative function of body mass, similar to the relationship observed in placental hibernators (French 1985). Enhanced heterothermy may be required in small individuals to sufficiently reduce their high relative heat loss during cold exposure and food shortages. The extent of energetic savings during torpor in daily heterotherms is predominantly determined by the T_b and the duration of torpor (Geiser 1988). Thus, a substantial reduction of the normothermic metabolic rate can only be achieved by long torpor at low body temperatures.

The duration of torpor in *Antechinus* showed a negative relationship with body mass and the minimum T_b a positive relationship with body mass, therefore the duration of torpor and the minimum T_b should also be functionally linked (the lower the body mass, the lower minimum T_b and the longer the torpor duration). The strong influence of T_b on the duration of torpor has been previously demonstrated in ground squirrels (Geiser and Kenagy 1988). The duration of torpor and the minimum T_b of *A. stuartii* in the present study are in agreement with measurements of Wallis (1976).

As in the dasyurid marsupial *Dasyuroides byrnei* (Geiser et al. 1986) the juvenile *Antechinus* showed longer and deeper torpor than the adults. The greater relative heat loss in the juveniles associated with their small size may require longer and deeper torpor than in adults to balance their energy expenditure. Compared to adults, daily torpor in juvenile endotherms, has not been intensively studied. However, it may be a common phenomenon as is has also been observed in a placental mammal and birds (Nagel 1977; Prinzinger and Siedle 1986; Boersma 1986). Heterothermy during the development in altricial endotherms may represent an important thermoregulatory bridge between ectothermy, observed shortly after birth, and normothermy or homeothermy when adult body mass is reached and heat loss to the environment is reduced.

Lactating female *A. stuartii* did not enter torpor. This observation is consistent with the view that torpor and reproduction are mutually exclusive (Hoffman 1964). In seasonally breeding rodents the season of hibernation and reproduction are in close sequence but do not overlap (Kenagy and Barnes 1988). It appears that the females remain normothermic during the reproductive season to ensure a rapid development of the young. However, not all mammals conform to this rule. For example, bats of the genus *Miniopterus* show embryonic diapause during hibernation and the polyoestrous dasyurid marsupial *Sminthopsis crassicaudata* has been observed in torpor during lactation (Wimsatt 1969; Morton 1978a).

The pattern of torpor in *Antechinus stuartii* and *A. flavipes* did not show strong seasonal changes. This is in contrast with dasyurid marsupials of the genus *Sminthopsis* which show distinct seasonal changes in the minimum T_b and metabolic rate during torpor while body masses remained constant (Geiser and Baudinette 1987). *Sminthopsis* spp. from arid or semi-arid Australia are exposed to pronounced seasonal fluctuation in environmental temperature and the thermal stress may require a seasonal alteration of torpor. Climatic fluctuations experienced by the coastal *Antechinus* are less pronounced and seasonal acclimation may be less important.

The rodent *Phodopus sungorus* also shows strong seasonal changes in the occurrence of spontaneous torpor (Heldmaier and Steinlechner 1981). However, during winter when torpor in *P. sungorus* was observed body mass was only about half of that of summer animals (Heldmaier and Steinlechner 1981); therefore the seasonal changes in thermoregulation may be, in part, a reflection of the lower body mass. Induced torpor in *P. sungorus*, as in *Antechinus*, occurred at any time of the year (Steinlechner et al. 1986).

Only few studies have compared the seasonality of daily torpor under constant environmental conditions. Seasonal changes of daily torpor have usually been determined in the wild or under outdoor conditions (e.g. Morton 1978a; Lynch et al. 1978; Frey and Fleming 1984) and the increased incidence of torpor in winter may reflect the lower environmental temperatures rather than a seasonal acclimation of the animal. Adults of both species of *Antechinus* investigated here showed an increase in spontaneous torpor in winter when T_a was low, but no clear seasonal change could be observed in induced torpor, which was determined under constant environmental conditions. Moreover, studies conduced in the wild have not considered the possible impact of seasonal changes of body mass on torpor.

The present study demonstrates that body mass has a pronounced influence on torpor in *Antechinus*. Seasonal changes of torpor in species that show concurrent changes in body mass therefore must be carefully analyzed for the influence of size on the pattern of heterothermy.

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