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Daily Torpor and Thermoregulation in the Small Dasyurid Marsupials *Planigale gilesi* and *Ningaui yvonneae*

Fritz Geiser[A] *and R. V. Baudinette*[B]

[A] Department of Zoology, University of New England, Armidale, N.S.W. 2351, Australia.
[B] School of Biological Sciences, Flinders University, Bedford Park, S.A. 5042, Australia.

Abstract

Torpor in endotherms has only been observed in small species, suggesting that body mass determines the occurrence of torpor. The present study investigates the influence of body mass on the occurrence of torpor and also the pattern of torpor (i.e. minimum body temperature, metabolic rate, and the duration of torpor). The two small dasyurid marsupials *Planigale gilesi* (8·3 g) and *Ningaui yvonneae* (11·6 g) entered torpor frequently when food was available; withdrawal of food increased the occurrence of torpor to almost 100%. Minimum body temperatures during torpor in both species were lower and the torpor duration was longer than for most larger dasyurid species studied so far. These findings suggest that the thermal stress on these very small species exerts a strong selective pressure to enhance daily torpor episodes for reduction of heat loss to the environment.

Introduction

Daily torpor, reflected by brief (<24 h) reductions of body temperature (T_b) and metabolism, has been observed in many small mammals and birds. At low air temperatures (T_a), these small endotherms may save large amounts of energy by abandoning regulation of T_b at high values (Lyman *et al.* 1982). Because small species have high mass-specific metabolic rates and lack large fat stores, their internal energy reservoirs deplete in a relatively short time while normothermic, and new fuels must be supplied from external sources. However, a constant supply of surplus food is unlikely in the wild, especially for insectivorous species which have to deal with large fluctuations in prey availability. Furthermore, insectivorous species cannot avoid food fluctuations by food caching. It is therefore adaptive to lower the T_b and metabolic rate during periods of inactivity when the animal is not supplementing internal energy stores.

These energetic constraints may be the reason why pronounced heterothermy has been observed only in small endotherms of body mass <10 kg (Bartholomew 1986; French 1986). However, within the large range of body masses of mammalian heterotherms between 2 g in shrews and 10 kg in the badger (Frey 1980; Harlow 1981), there is a considerable variation in rates of heat loss and extent of fat stores due to difference in size. It is therefore likely that the occurrence of torpor and also the patterns of torpor (i.e. frequency, depth, and length of torpor) are influenced by body mass.

The potential influences of body mass on the pattern of torpor are poorly understood. We therefore investigated torpor in the very small dasyurid marsupials *Planigale gilesi* (8·3 g) and *Ningaui yvonneae* (11·6 g) and compared the results with those previously reported on larger dasyurids. We were particularly interested in whether the small species show longer torpor and lower body temperatures than the larger dasyurid marsupials.

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Materials and Methods

Animals

P. gilesi is one of the smallest marsupials and is found in the deserts east from Lake Eyre. It is a largely nocturnal species which lives in soil cracks along creek channels and floodouts (Read 1983, 1985). The diet appears to consist of invertebrates and small vertebrates (Read 1983). Torpor has been observed in the laboratory (Dawson and Wolfers 1978).

The animals used in the present study (two males and three females) were the offspring of a wild caught female which had been obtained from Coopers Creek. They were kept at a T_a of 22°C and a natural photoperiod. In spring (September) they were transferred to a constant T_a of 19°C and a photoperiod of LD 12 : 12 (light from 0600–1800 h), which is similar to the natural photoperiod at that time of the year. Animals were kept under these conditions for 3 weeks before the experiment commenced and throughout the experimental period of September to November 1984.

Ningaui spp. are only slightly larger in body size than *Planigale* spp. *N. yvonneae* was only recently described and is found in the mallee areas of southern Australia (Kitchener *et al.* 1983). It has only been collected from habitats with spinifex (*Triodia* spp.) which it appears to use as shelter (Coventry and Dixon 1984). *N. yvonneae* is a nocturnal species which appears to feed on invertebrates (McKenzie 1983). Torpor has not been described previously in this genus.

The animals used in the present study (1 male and 2 females) were trapped in the Big Desert, Victoria in spring (September) and were transferred to the laboratory where they were kept at T_a 19°C and a photoperiod of LD 12 : 12 for 5 weeks before the experiments started. Measurements were carried out in October and November 1984.

Animals were kept individually in cages provided with hardwood shavings and boxes containing nesting material. They were fed *ad libitum* with water and a mixture of dried and canned pet food which was changed daily. *Tenebrio* larvae and an egg-gelatine mixture were fed as a supplement.

Experimental details

Rates of oxygen consumption ($\dot{V}O_2$) were measured in a 3-litre respirometer with a Servomex Model OA 184 paramagnetic oxygen analyser over about 1-day periods at constant T_a's. These measurements began in the afternoon 2–3 h before lights off. T_a was measured by a thermocouple in the respirometer. $\dot{V}O_2$ was determined from the difference between the oxygen content in two parallel open flow circuits (room air vs. air in animal cage). Flow rates of dried air (about 400 ml min^{-1}) were adjusted and measured with calibrated rotameters (for further details, see Geiser and Baudinette 1987). The metabolic rate of normothermic resting animals (RMR) was taken when variation over 15 min was less than 5% after an inactivity period of at least 30 min; the minimum metabolic rate of torpid animals was determined at times of constant $\dot{V}O_2$ of at least 30 min. The time of entry into torpor, the duration of torpor in undisturbed animals and the time required to rewarm from torpor to normothermia (the peak $\dot{V}O_2$ during arousal was assumed to be the endpoint of the arousal episode) were derived from these measurements. The photoperiod was LD 12 : 12 (light from 0600–1800 h) during all measurements of $\dot{V}O_2$ and food and water were not provided. Body temperatures of normothermic and torpid animals were determined by 2 cm rectal insertion of a calibrated thermocouple read from a Kane-May digital thermometer. Torpor was defined as $\dot{V}O_2$ <75% of the resting $\dot{V}O_2$ at the same T_a (Hudson and Scott 1979) or a reduction of T_b below 30°C (Wallis 1976). N = number of individuals; n = number of observations.

Table 1. Spontaneous torpor in *Planigale gilesi* and *Ningaui yvonneae*

Food and water were available *ad libitum*. Observations were made in the morning at about 0900 h. Torpor was determined by observation of coordination and touch and if necessary by measurement of T_b; animals with T_b's of <30°C were considered torpid. N = number of individuals; n = number of observations

Species	T_a (°C)	n	Torpid	Normothermic	% Torpid
P. gilesi (N = 5)	19	25	8	17	32
N. yvonneae (N = 3)	19	17	5	12	29
N. yvonneae (N = 3)	16	9	5	4	56

Results

The tendency to enter torpor was high in both *P. gilesi* and *N. yvonneae*. Both species frequently exhibited torpor in their holding cages at T_a 19°C when food and water were freely available (spontaneous torpor) (Table 1). In *N. yvonneae* the occurrence of spontaneous torpor increased when T_a was lowered to 16°C (Table 1). Spontaneous torpor was observed in the morning; in the afternoon animals were usually normothermic. When food was withheld, the incidence of torpor increased in both species (induced torpor). Apart from

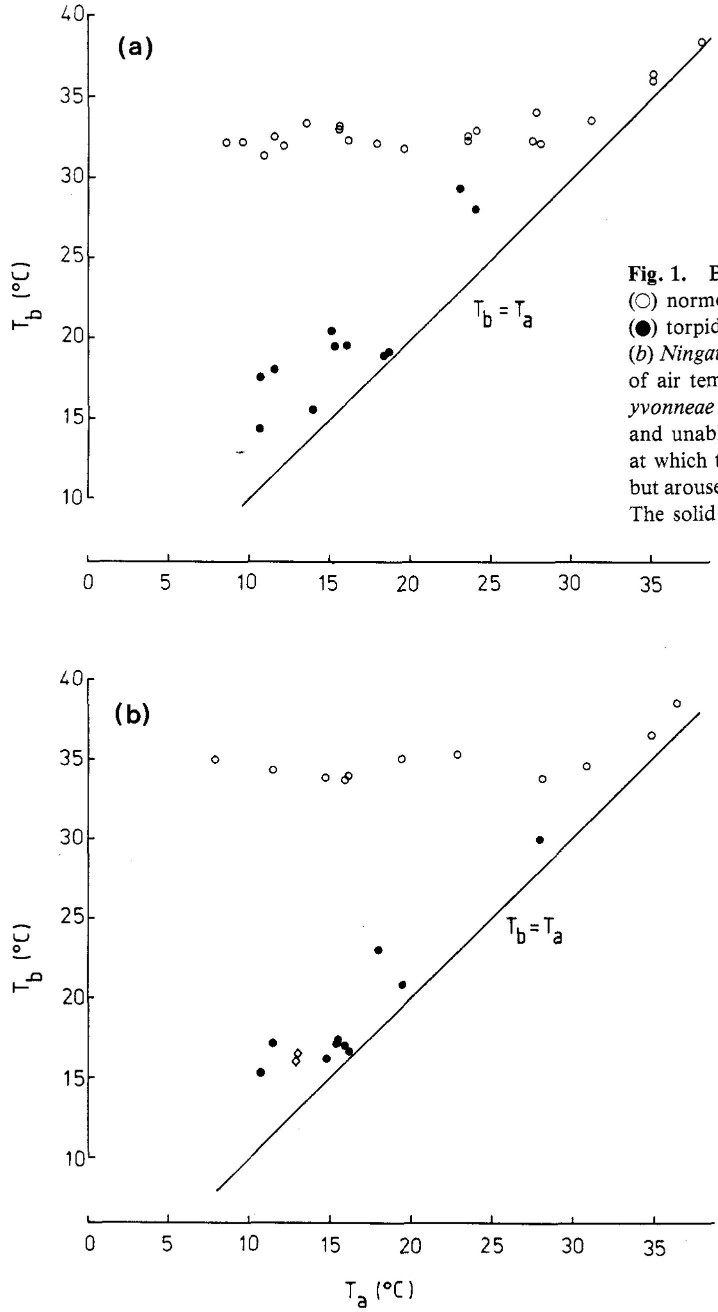

Fig. 1. Body temperatures (T_b) of (○) normothermic, inactive and (●) torpid (*a*) *Planigale gilesi* and (*b*) *Ningaui yvonneae* as a function of air temperature (T_a). Two *N. yvonneae* were hypothermic (◇) and unable to arouse at the T_a at which they had entered torpor, but aroused after partial rewarming. The solid line represents $T_b = T_a$.

one exception in each species, individuals of both species entered torpor in all 1-day $\dot{V}O_2$ measurements when food and water were not available and T_a was less than 20°C. The highest T_a at which induced torpor was observed ($\dot{V}O_2$ < 75% of resting values) was 30·2°C in *P. gilesi* and 28·0°C in *N. yvonneae*. Entry into induced torpor usually occurred in darkness between 1900 h and 0500 h with a mean ± s.d. of 2255 ± 3·8 h (n = 29) in *P. gilesi* and 0027 ± 3·8 h (n = 14) in *N. yvonneae*.

Bouts of induced undisturbed torpor lasted between 2 and 15·3 h in *P. gilesi* and the mean was 8·8 ± 2·4 h (n = 21; T_a 10–27°C). In *N. yvonneae* torpor lasted 4 to 12·3 h and the mean was 7·5 ± 2·9 h (n = 6; T_a 9–28°C). The longest torpor bouts of both species were observed at T_a's close to their minimum T_b during torpor.

Body temperature of resting normothermic animals was stable between T_a 7 and 32°C (Fig. 1). The mean T_b of normothermic *P. gilesi*, 32·6 ± 0·7°C, was significantly lower than the 34·4 ± 0·6°C measured in normothermic *N. yvonneae* ($P < 0·001$; *t*-test). During torpor, T_b decreased with T_a and values of ΔT (T_b–T_a) of less than 2°C were observed between T_a 14 and 20°C in both species (Fig. 1). Below 14°C, ΔT increased to > 3·6°C in both species, suggesting that T_b was regulated at or above a specific minimum. The lowest individual T_b (minimum T_b) measured during torpor was 14·3°C in *P. gilesi* and 15·3°C in *N. yvonneae*. Two individuals of *N. yvonneae* were hypothermic and could not arouse after a disturbance at the T_a at which they entered torpor. Both animals aroused after partial rewarming and survived.

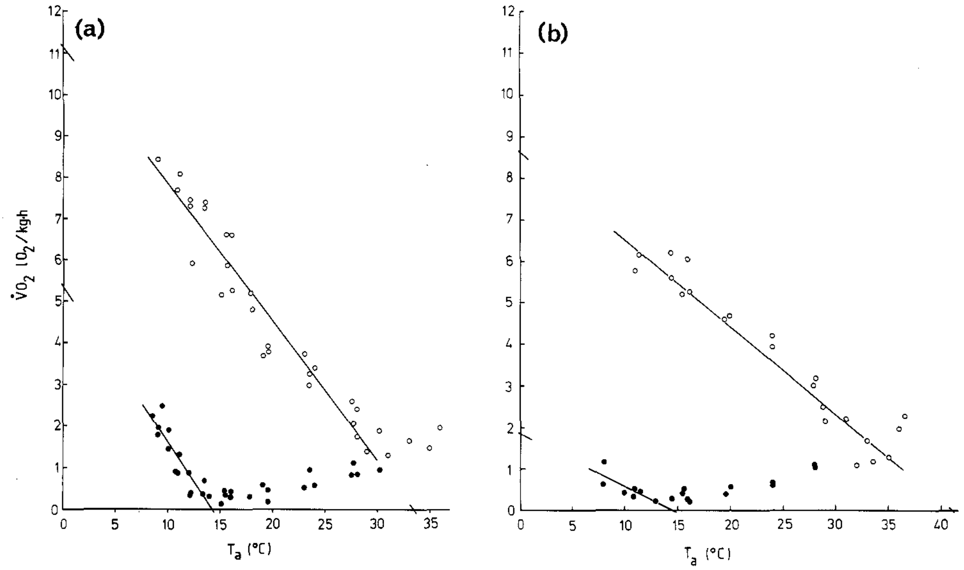

Fig. 2. Rates of oxygen consumption ($\dot{V}O_2$) of (○) normothermic, inactive and (●) torpid (*a*) *Planigale gilesi* and (*b*) *Ningaui yvonneae* as a function of air temperature (T_a). Lines were fitted by least squares regression and the equations are:

P. gilesi; normothermic, inactive: $y = 11·11 - 0·33x$; $r = -0·96$
in torpor: $y = 5·32 - 0·38x$; $r = -0·88$
N. yvonneae; normothermic, inactive: $y = 8·64 - 0·21x$; $r = -0·97$
in torpor: $y = 1·85 - 0·13x$; $r = -0·76$

Rates of oxygen consumption of *P. gilesi* and *N. yvonneae* were strongly dependent on T_a (Fig. 2). Basal metabolic rates were 1·43 ± 0·16 l O_2 kg^{-1} h^{-1} (n = 5; T_a 29–35°C) in *P. gilesi* and 1·35 ± 0·26 l O_2 kg^{-1} h^{-1} (n = 4; T_a 32–35°C) in *N. yvonneae*; both values are close to the predicted standard metabolic rate for a marsupial of the respective body mass (MacMillen and Nelson 1969; Dawson and Hulbert 1970). The lower critical temperature of the thermoneutral zone was approximately 28–29°C in *P. gilesi* and about 32°C in *N. yvonneae*. Below thermoneutrality the $\dot{V}O_2$ of normothermic, resting animals increased as T_a decreased in both species; the line relating these values extrapolated to the abscissa at 33·4°C (*P. gilesi*) and 41·0°C (*N. yvonneae*). These intercepts were 0·8 and 6·6°C, respectively, above the mean resting T_b.

The daily $\dot{V}O_2$ minima during torpor of both species decreased steadily at T_a's below and above the minimum T_b. The mean $\dot{V}O_2$ of torpid *P. gilesi* was $0·36 \pm 0·14$ l O_2 kg^{-1} h^{-1} (T_a 15–20°C) and $0·30 \pm 0·09$ l O_2 kg^{-1} h^{-1} (T_a 13–16·2°C) for *N. yvonneae* (Fig. 2). At T_a 13–15°C, the $\dot{V}O_2$ of torpid individuals of both species was less than 5% of that in normothermic resting animals. The $\dot{V}O_2$ during torpor increased parallel to that in normothermic resting animals below a critical T_a (about 13°C) in both species (i.e. the slopes were indistinguishable; *F*-test). The line relating T_a and $\dot{V}O_2$ during torpor below 13°C intersected the abscissa at 14·1°C (*P. gilesi*) and 14·5°C (*N. yvonneae*). These temperatures were within 0·8°C of the minimum T_b's determined rectally.

Table 2. Arousal rates of *Planigale gilesi* and *Ningaui yvonneae*

The fastest arousal rates were determined over time periods of at least 10 min at T_b's above T_a. n.d. = not determined. Arrows indicate that animals were transferred from the T_a they had entered torpor to a T_a at which arousal rate was determined. Food during the night prior to the measurement was either available (+) or not available (–)

Species	T_a (°C)	T_b initial (°C)	T_b end (°C)	Overall arousal (°C min^{-1})	Fastest arousal (°C min^{-1})	Food available
P. gilesi	15·3	19·5	30·2	0·54	0·62	–
	17·0	26·4	34·2	0·60	n.d.	+
	13·5→20	25·9	35·2	0·93	n.d.	–
	13·5→20	24·2	35·5	0·71	0·95	–
N. yvonneae	10·8	15·3	22·8	0·15	n.d.	–
	15·5	15·6	31·3	0·40	0·50	+
	15·5	17·2	33·6	0·57	n.d.	+
	15·9	17·0	30·0	0·11	0·30	–
	17·0	22·0	37·4	0·58	0·69	+
	18·5→24	18·6	34·5	0·64	0·82	+

The rate of rewarming from torpor decreased with T_a in both species (Table 2). The fasted arousal rates determined over periods of at least 10 minutes were 0·95°C min^{-1} in *P. gilesi* and 0·82°C min^{-1} in *N. yvonneae*. The fastest overall rewarming rates were only slightly less than the fasted arousal rates over 10 min. The data do not allow the conclusion that food withdrawal in the night before the measurement of rewarming affects the arousal rates, although measurements in *N. yvonneae* suggest a slower rewarming in starved animals.

The time required to rewarm from torpor to normothermia increased exponentially with decreasing T_a (Fig. 3). In both species, arousal times after disturbance by measurement of T_b were significantly faster ($P < 0·01$; *F*-test) than when the animals aroused spontaneously in the afternoon.

Both species showed good coordination at low T_b. The movements of *P. gilesi* at T_b 27·4°C were difficult to distinguish from those of normothermic animals and rapid movements were observed in this species at a low T_b of 20°C. *N. yvonneae* were observed to eat mealworms at T_b 20°C although they were less coordinated than *P. gilesi* at the same T_b.

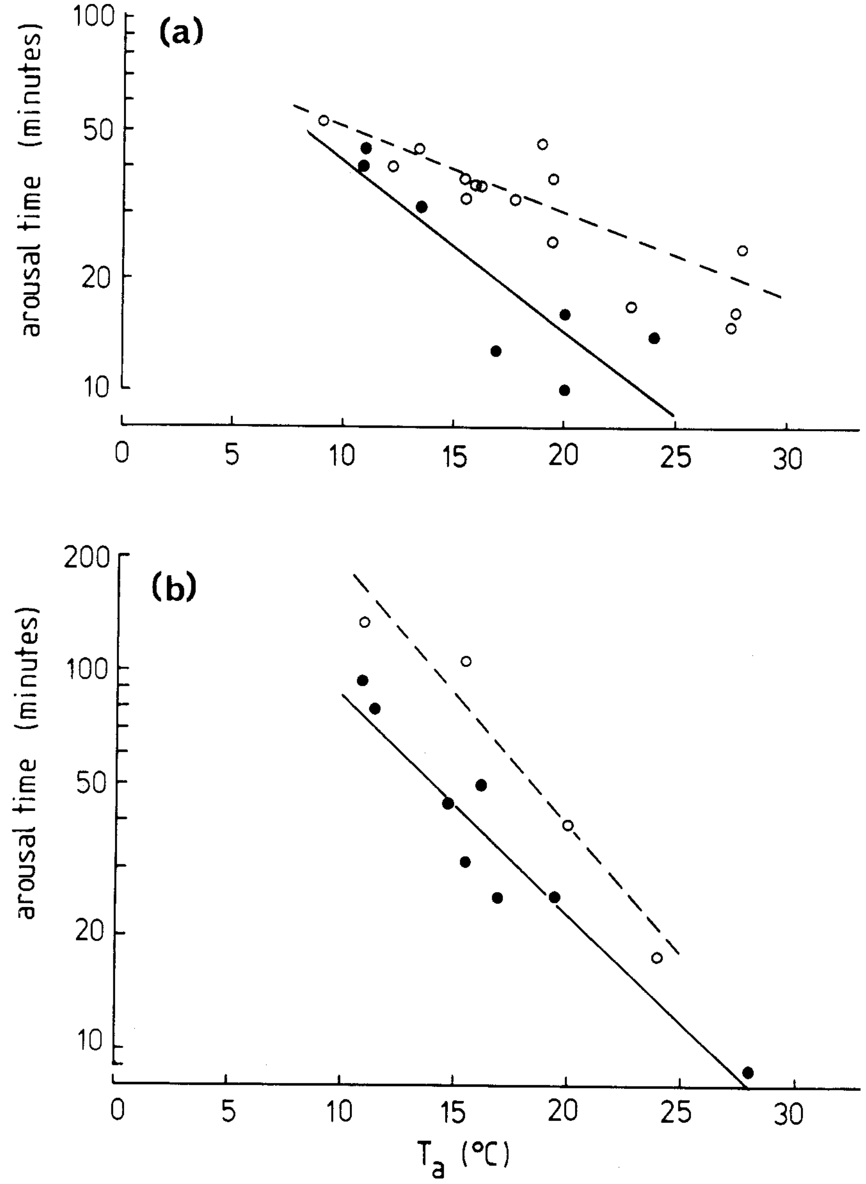

Fig. 3. Semi-logarithmic plots of the arousal times as a function of air temperature (T_a) in (*a*) *Planigale gilesi* and (*b*) *Ningaui yvonneae*. The symbols indicate (●) disturbance-induced arousal by measurement of T_b and (○) spontaneous arousal in the afternoon. Lines were fitted by least squares regression and the equations are:

Planigale gilesi;	induced:	$\log y = 2{\cdot}07 - 0{\cdot}045x$;	$r = -0{\cdot}87$
	spontaneous:	$\log y = 1{\cdot}94 - 0{\cdot}023x$;	$r = -0{\cdot}86$
Ningaui yvonneae;	induced:	$\log y = 2{\cdot}97 - 0{\cdot}069x$;	$r = -0{\cdot}97$
	spontaneous:	$\log y = 2{\cdot}51 - 0{\cdot}057x$;	$r = -0{\cdot}96$

Induced arousal was significantly faster than spontaneous arousal in both species ($P < 0{\cdot}01$; *F*-test).

Discussion

The present study shows that torpor in the tiny *P. gilesi* and *N. yvonneae* is qualitatively similar to that observed in other dasyurids, shrews, and rodents showing daily torpor (MacMillen 1965; Wallis 1976; Heldmaier and Steinlechner 1981; Nagel 1985; Geiser and Baudinette 1987). Torpor in both species began during the night and lasted for less than 24 h. However, the frequent occurrence of torpor, the low minimum body temperature and the long torpor durations in *P. gilesi* and *N. yvonneae* indicate that energetic constraints of small body mass resulted in a more pronounced torpor than in larger species.

The frequent occurrence of spontaneous torpor, about 30% of all observations at relatively high T_a of 19°C, is greater than in most other dasyurids investigated (Godfrey 1968; Morton and Lee 1978; Wallis 1976; Geiser and Baudinette 1987; Geiser 1988*b*). This observation supports the view that small heterothermic species display daily torpor more frequently than large species. Withdrawal of food and water further increased the incidence of torpor in *P. gilesi* and *N. yvonneae* to about 100% even at T_a's above 20°C. Our findings on torpor patterns in these dasyurids suggest frequent torpor in nature, where nocturnal temperatures are low and a constant surplus of food is unlikely.

In addition to the frequent torpor episodes, the minimum T_b of *P. gilesi* and *N. yvonneae* are some of the lowest reported for dasyurids, many of which regulate T_b above 20°C (Kennedy and MacFarlane 1971; Wallis 1976; Geiser *et al.* 1986; Geiser 1988*b*). The T_b determined during torpor of *P. gilesi* is similar to estimates of Dawson and Wolfers (1978). Lower minimum T_b's than those observed in the two species studied here have only been observed in *Antechinomys laniger* and in winter acclimated *Sminthopsis* (Geiser 1986; Geiser and Baudinette 1987). Observations on shrews showed differences in minimum T_b between 18°C (*Crocidura russula* 10 g; Nagel 1985) and 12°C (*Suncus etruscus* 2 g; Frey 1980) also may indicate a reduction of minimum T_b with decreasing mass. A reduction of T_b to low values may be necessary in small species to enhance conservation of energy. The high mass-specific basal metabolic rate of small daily heterotherms can only be reduced to low values by a substantial lowering of T_b during torpor because they appear to lack mechanisms for temperature independent metabolic inhibition (Geiser 1988*a*).

The mean duration of torpor in *P. gilesi* and *N. yvonneae* is longer than in most other dasyurids investigated (Godfrey 1968; Wallis 1976; Geiser and Baudinette 1987; Geiser 1988*b*). These long periods of torpor, together with low T_b, would further contribute to energy conservation. The observation of longer torpor bouts in the small *P. gilesi* and *N. yvonneae* than in larger dasyurids suggests that torpor duration shows an inverse relationship with body mass not only in hibernators (French 1985), but also in daily heterotherms.

Arousal from torpor was rapid in both species. To our knowledge, the rewarming rates determined here for *P. gilesi* are the fastest yet reported for a marsupial. The rapid arousal in these two small species supports the view that body mass and rewarming rates are inversely related in endotherms (Heinrich and Bartholomew 1971). Fast arousal rates allow these small species to rewarm from low T_b's to normothermia in relatively short time intervals which may be important for escaping predators. The fastest arousal rates of both species were slightly above predicted values for vertebrates of corresponding body mass (Heinrich and Bartholomew 1971).

Body temperatures measured at or below thermoneutrality in normothermic animals differed between *P. gilesi* and *N. yvonneae*. Body temperatures determined here for *P. gilesi* were also somewhat lower than those in other members of the genus (Dawson and Wolfers 1978; Morton and Lee 1978). The large surface area in the small *P. gilesi* is accentuated by their flattened and elongate body shape. Despite their low normothermic T_b the thermal conductance below thermal neutrality in *P. gilesi* was 25–35% greater than in *N. yvonneae*. A low T_b during normothermia reduces the temperature differential with the environment and may correlate with the 'thermal liability' of the animal's shape. *P. gilesi* reduced thermal conductance at T_a 10–15°C by about 10% by regulating T_b at 32·6°C rather than at 34·4°C, the T_b of *N. yvonneae*. It is interesting that long tail weasels, *Mustela frenata*, have also sacrificed thermal efficiency by being elongate which allows them to enter rodent burrows (Brown and Lasiewski 1972). Although basal metabolic rates in *M. frenata* and *P. gilesi* are similar to those predicted on the basis of body mass, a moderate cold stress results in a marked increase in metabolism (Brown and Lasiewski 1972; Dawson and Wolfers 1978; present study). *Ningaui yvonneae* has a more spherical than cylindrical shape, which allows less heat loss even though normothermic T_b of *N. yvonneae* is regulated at a higher level than in *P. gilesi*. The body shapes in the two species investigated may reflect their habitats. *P. gilesi* lives and searches for prey in soil cracks (Read 1985); consequently a flattened body appears advantageous. In contrast, *N. yvonneae* lives on the surface of sandy soils and apparently seeks shelter in spinifex (Coventry and Dixon 1984), which provides a less stable thermal environment. Therefore reduction of heat loss by spherical shape in *N. yvonneae* may be of great importance for energy conservation.

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