Seasonality of torpor and thermoregulation in three dasyurid marsupials

Fritz Geiser* and R.V. Baudinette

School of Biological Sciences, Flinders University, Bedford Park 5042, South Australia

Summary. Seasonal variation in the pattern of torpor and temperature regulation was investigated in the closely related arid zone dasyurid marsupials *Sminthopsis crassicaudata* (17 g), *S. macroura* (24 g), and *Dasyuroides byrnei* (120 g). The tendency to enter torpor was greater, torpor commenced earlier, torpor duration was longer, and body temperatures (T_b) were lower in *Sminthopsis* spp. than in *D. byrnei*. The minimum mass-specific rate of oxygen consumption ($\dot{V}_{O_2}$) of torpid animals was similar among the three species despite the differences in minimum T_b. The mass-specific oxygen consumption of normothermic animals was reduced during winter when compared with the summer values in all species, but there was no seasonal variation in normothermic T_b in any species. The tendency to enter torpor was increased during winter. Torpid *Sminthopsis* spp. had lower values of T_b and $\dot{V}_{O_2}$ during winter than during summer; *D. byrnei* did not show seasonal changes in these variables. These results suggest that seasonal changes in the pattern of thermoregulation and torpor in small dasyurids may be more distinct than in larger species.

Introduction

Torpor in warm-blooded animals is expressed by a lowering of body temperature (T_b) and metabolism both of which can be actively raised to the initial high values after a torpor episode. This ener-

Abbreviations: RMR resting metabolic rate; *BMR* basal metabolic rate

* Present address: Department of Zoology, University of Adelaide, Adelaide 5001, South Australia

gy conserving state of lethargy allows these "heterothermic endotherms" to survive periodic shortages of energy and water. Because relative heat loss is inversely related to body mass in endotherms (Brody 1945), torpor occurs mainly in small species, which may not be able to accumulate enough energy stores to maintain a constant high T_b during cold exposure.

Considering that both cold exposure and food shortage occur predominantly during winter it is not surprising that the pattern of thermoregulation in many heterothermic mammals shows a seasonal change. Such thermoregulatory changes are most pronounced in seasonal hibernators that show strong annual rhythms of activity (homeothermy) and hibernation (heterothermy) (Pengelley 1967). In species that enter daily, rather than prolonged, torpor the occurrence of dormancy is more opportunistic; however, even in these species the frequency of torpor is reduced during summer (Lynch et al. 1978; Heldmaier and Steinlechner 1981a). The lower proclivity to entering torpor in summer is accompanied by higher T_b's during torpor than in winter (Gaertner et al. 1973; Lynch et al. 1978; Tannenbaum 1985) suggesting that the "set point" at which T_b is regulated during torpor may vary seasonally.

Because our knowledge about seasonal changes of the physiology of daily torpor is very restricted we investigated how variables of torpor in dasyurid marsupials may be modified by season. The species we studied were *Sminthopsis crassicaudata* (body mass 14–22 g), *S. macroura* (body mass 19–30 g), and *Dasyuroides byrnei* (body mass 96–140 g), three closely related marsupials which have overlapping distribution ranges and similar life histories (Lee et al. 1982; Aslin 1983; Morton et al. 1983).

Materials and methods

Animals. The fat-tailed dunnart, *Sminthopsis crassicaudata*, occurs widely in southern Australia and is mainly found in semi-arid and arid habitats. It is nocturnal and is found in soil cracks and unter stones (Morton 1978). Its diet consists mainly of invertebrates, with a large proportion of spiders and insects (Morton et al. 1983). Torpor in the wild and in captivity have been described (Godfrey 1968; Morton 1978). The animals (16 males and 12 females) used in the present study were obtained from a laboratory colony at the Genetics Department, Adelaide University, with the exception of two individuals which had been wild caught.

The stripe-faced dunnart, *Sminthopsis macroura* is found in arid and semi-arid parts of central and northern Australia. The animal's behaviour in the field is largely unknown, but in the laboratory, *S. macroura* readily enters torpor (Geiser and Baudinette 1985). In captivity, the animal is largely nocturnal (O'Reilly et al. 1984). Food habits in the wild are similar to that of *S. crassicaudata*, but a larger proportion of termites are used as prey items (Morton et al. 1983). Animals used in the present study (10 males, 14 females) were obtained from laboratory colonies at the Arthur Rylah Institute, Heidelberg, Victoria, and from the Evolutionary Biology Unit, South Australian Museum, Adelaide.

The kowari, *Dasyuroides byrnei* is found in the gibber deserts of south-western Queensland. It lives in burrows, appears to be nocturnal and solitary, and has a diet consisting of insects and small vertebrates (Aslin 1983). Torpor has been previously described in this species (Geiser et al. 1986a). The animals used in the present study (8 males, 7 females) were obtained from a laboratory colony at the Evolutionary Biology Unit, South Australian Museum.

Experiments were conducted on adults only, between autumn 1983 and summer 1985. The austral seasons are defined as: spring, 1 September–30 November; summer, 1 December–28 February; autumn, 1 March–31 May; and winter, 1 June–31 August. Animals were held outside at the Flinders University of South Australia (34°56'S, 138°36'E), exposed to natural photoperiod and temperature fluctuations (Fig. 1). They were housed individually in cages provided with hardwood shavings and boxes containing nesting material. Animals were fed ad libitum a mixture of dried and canned commercial pet food and water. *Tenebrio* larvae and an egg-gelatine mixture were provided every two weeks.

Experimental details. Diurnal fluctuations in oxygen consumption ($\dot{V}_{O_2}$) were determined over an air temperature (T_a) range of about 5–32 °C. In *S. crassicaudata*, 62 tests of mean duration 21.2 ± 1.9 h were conducted in summer and 40 tests of 20.1 ± 2.6 h in winter; for *S. macroura*, 23 tests of 20.1 ± 2.1 h in summer and 33 tests of 20.8 ± 1.4 h in winter; and for *D. byrnei*, 39 tests of 21.1 ± 2.1 h in summer and 36 tests of 21.0 ± 2.3 h in winter. These measurements began in the afternoon 2–3 h before the lights switched off. The photoperiod in all experiments matched local sunrise and sunset. Food and water were not available during measurements of $\dot{V}_{O_2}$. Measurements of $\dot{V}_{O_2}$ were used to determine the metabolic rate of normothermic, inactive animals measured when a variation of less than 5% over at least 15 min occurred after an inactive period of at least 30 min (RMR); the minimum metabolic rate of torpid animals was determined at times of constant $\dot{V}_{O_2}$ over at least 30 min (the $\dot{V}_{O_2}$ of *S. crassicaudata* during torpor and normothermia are those reported by Geiser et al. 1986b). Furthermore, the duration of torpor and the time required to arouse from torpor to normothermia were derived from these measurements (the $\dot{V}_{O_2}$ peak during arousal was assumed to
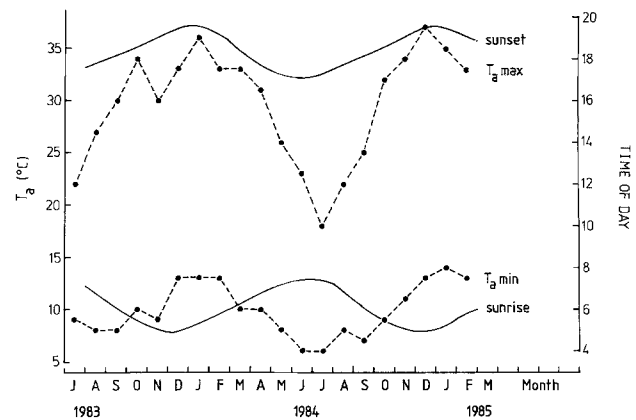

Fig. 1. Monthly minima and maxima of air temperature (T_a), and the times of sunrise and sunset during the experimental period. T_a was measured in the animal holding pens with a minimum-maximum thermometer. Sunrise and sunset represent certified times by the Bureau of Meteorology, Adelaide. The austral seasons are defined as: spring: 1 September–30 November; summer: 1 December–28 February; autumn: 1 March–31 May; and winter: 1 June–31 August

be the endpoint of the arousal period). Additional measurements of shorter periods were used to determine the $\dot{V}_{O_2}$ of postabsorptive, normothermic, inactive animals at T_a around and above thermoneutrality during their inactive period (daytime). All measurements were conducted in a quiet controlled-temperature room ($T_a\pm0.5$ °C) that was acoustically isolated from the recording equipment; animals were observed by video camera during the experiments.

A Servomex Model OA 184 paramagnetic oxygen analyzer was used for the $\dot{V}_{O_2}$ measurements together with a Rikadenki potentiometric recorder. $\dot{V}_{O_2}$ was determined from the difference between the oxygen content in two parallel open flow circuits (room air reference *vs* the animal). Flow rates of dried air in the open flow system were adjusted and measured with calibrated rotameters to 0.3–0.4 l/min (*S. crassicaudata*), 0.3–0.5 l/min (*S. macroura*), and 0.6–1.2 l/min (*D. byrnei*). Carbon dioxide was not scrubbed from the system because the absorbant caused large pressure drops in prolonged experiments and thereby changed the partial pressure recorded in the analyzer cell. All volumes were corrected to dry standard temperature and pressure (STPD) and rates of oxygen consumption were calculated using equation 3a of Withers (1977). An RQ of 0.85 was assumed which would result in a maximum error of 3% if the RQ value was actually 1 or 0.7. Repirometers were 3 l for *Sminthopsis* spp. and 7 l for *D. byrnei*. For the calculation of mass specific $\dot{V}_{O_2}$ during prolonged experimental periods, the animals were weighed before and after the experiments and body masses were interpolated assuming a constant rate of loss.

Temperature in the respiratory chamber was measured with two thermocouples; one connected to an Omega 871 Digital Thermometer and used for point readings and the other connected to an Omega MCJ-T Thermocouple Connector and the Rikadenki recorder. T_b was measured with 0.5 mm diameter thermocouples inserted into the rectum (20–25 mm *Sminthopsis* spp.; 30–40 mm *D. byrnei*). All thermocouples were calibrated against a mercury thermometer traceable to a national standard.

Means of samples are expressed $\pm$ the standard deviation (SD). *N* = number of individuals; *n* = number of determinations.

Table 1. Frequency of induced torpor (food and water not provided) and spontaneous torpor (food and water ad libitum) in *Sminthopsis crassicaudata*, *S. macroura*, and *Dasyuroides byrnei*

Species	Season	N	n	Torpid	Normo-thermic	% torpid
Induced torpor:						
S. crassicaudata	summer	15	59	45	14	76
	winter	17	24	23	1	96
S. macroura	summer	9	16	13	3	81
	winter	9	24	24	0	100
D. byrnei	summer	8	25	20	5	80
	winter	11	35	29	6	83
Spontaneous torpor:						
S. crassicaudata	spring	6	65	8	57	12
	summer	14	77	10	67	13
	winter	9	103	14	89	14
S. macroura	spring	9	18	3	15	17
	summer	15	49	6	43	12
	autumn	15	45	13	32	29
	winter	15	97	29	68	30
D. byrnei	spring	13	90	4	86	4
	summer	12	71	1	70	1
	winter	13	165	16	149	10

Data for induced torpor were taken from the measurements of $\dot{V}_{O_2}$ at T_a 4–20 °C (see Fig. 3). Observations of spontaneous torpor were made in the morning at about 0900 h. Significant differences between summer and winter in the frequency of torpor were observed in *S. crassicaudata* and *S. macroura* (induced torpor) and in *S. macroura* and *D. byrnei* (spontaneous torpor) ($P < 0.05$; equality test of two percentages). N = number of individuals; n = number of observations

Results

Distinct differences in the tendency to enter torpor were observed in the three species investigated (Table 1). In all species torpor was more frequent when food was withdrawn (induced torpor) than when food and water were available (spontaneous torpor). Spontaneous torpor was observed only in the morning. Both *Sminthopsis* species showed a greater tendency to enter torpor than *D. byrnei*, the largest species (Table 1). The frequency of induced torpor by food and water deprivation during the measurements of $\dot{V}_{O_2}$ at T_a 4–20 °C (compare Fig. 3) in *Sminthopsis* increased from about 80% in summer to 100% in winter. Of the 7 individual *S. crassicaudata* that were tested under these conditions in both seasons 3 remained normothermic throughout the experiment in summer whereas all but one individual entered torpor in winter. In contrast, *D. byrnei* showed no seasonal variation in the tendency to enter torpor after food deprivation. Spontaneous torpor in the outdoor facilities

Table 2. The time of onset of torpor and torpor duration in *Sminthopsis crassicaudata*, *S. macroura*, and *Dasyuroides byrnei*

Species	Season	Relative time (h)	Torpor duration (h)
S. crassicaudata	summer	-1.2 ± 3.0 (14)	5.4 ± 2.5 (12)
	winter	-3.0 ± 3.0 (17)	5.9 ± 3.0 (8)
S. macroura	summer	-2.4 ± 2.7 (8)	5.5 ± 3.4 (8)
	winter	-3.1 ± 2.6 (11)	6.0 ± 2.8 (11)
D. byrnei	summer	$+1.1 \pm 1.7$ (8)	2.7 ± 1.9 (8)
	winter	-0.9 ± 1.3 (9)	2.7 ± 1.9 (12)

The time of torpor onset was defined as the time at which a decrease in $\dot{V}_{O_2}$ that resulted in a torpor bout was observed. Relative time represents the time in relation to 'lights on'; $-$ indicates that torpor occurred before the lights switched on; $+$ indicates torpor entry after the lights switched on. The onset of torpor relative to the onset of light occurred significantly earlier in winter than in summer in *S. crassicaudata* and *D. byrnei* (t-test; $P < 0.05$) and torpor onset in *D. byrnei* occurred later than in the *Sminthopsis* species ($P < 0.01$; Kruskal-Wallis one-way nonparametric ANOVA and Mann-Whitney U-test). Mean torpor duration did not show significant seasonal changes in any species (t-test). Torpor duration in the *Sminthopsis* species was significantly longer than in *D. byrnei* ($P < 0.05$; Kruskal-Wallis one-way nonparametric ANOVA and Mann-Whitney U-test). Numbers of individuals are shown in parentheses

was more frequent during winter in *D. byrnei* and *S. macroura*; spring and autumn values were intermediate (Table 1). *S. crassicaudata* did not show this seasonal variation in spontaneous torpor.

Induced torpor in *Sminthopsis* spp. commenced earlier than in *D. byrnei* and in both summer and winter torpor began before the onset of light (Table 2). In *D. byrnei*, the onset of torpor occurred before the lights switched on in winter and after the lights switched on in summer. Significant seasonal differences in the timing of torpor relative to the time of lights on were observed in *S. crassicaudata* and *D. byrnei* ($P < 0.05$; Mann-Whitney U-test). The time of torpor onset did not appear to be related to T_a in any species.

Torpor bouts were shorter than 24 h in all three species. The mean duration of torpor did not show seasonal variation in either species and was between 5.4 and 6.0 h in *Sminthopsis* spp. which was significantly longer than the 2.7 h in *D. byrnei* (Table 2; $P < 0.05$; Mann-Whitney U-test). Torpor duration was not strongly dependent on T_a; however, the longest torpor bouts were observed between T_a 10 and 20 °C in all species.

Normothermic T_b's in animals resting at T_a < 30 °C were similar in all three species, about 34 °C, and no seasonal changes were observed (Fig. 2, Table 3). In animals that had entered torpor at the T_a at which T_b was measured, T_b during
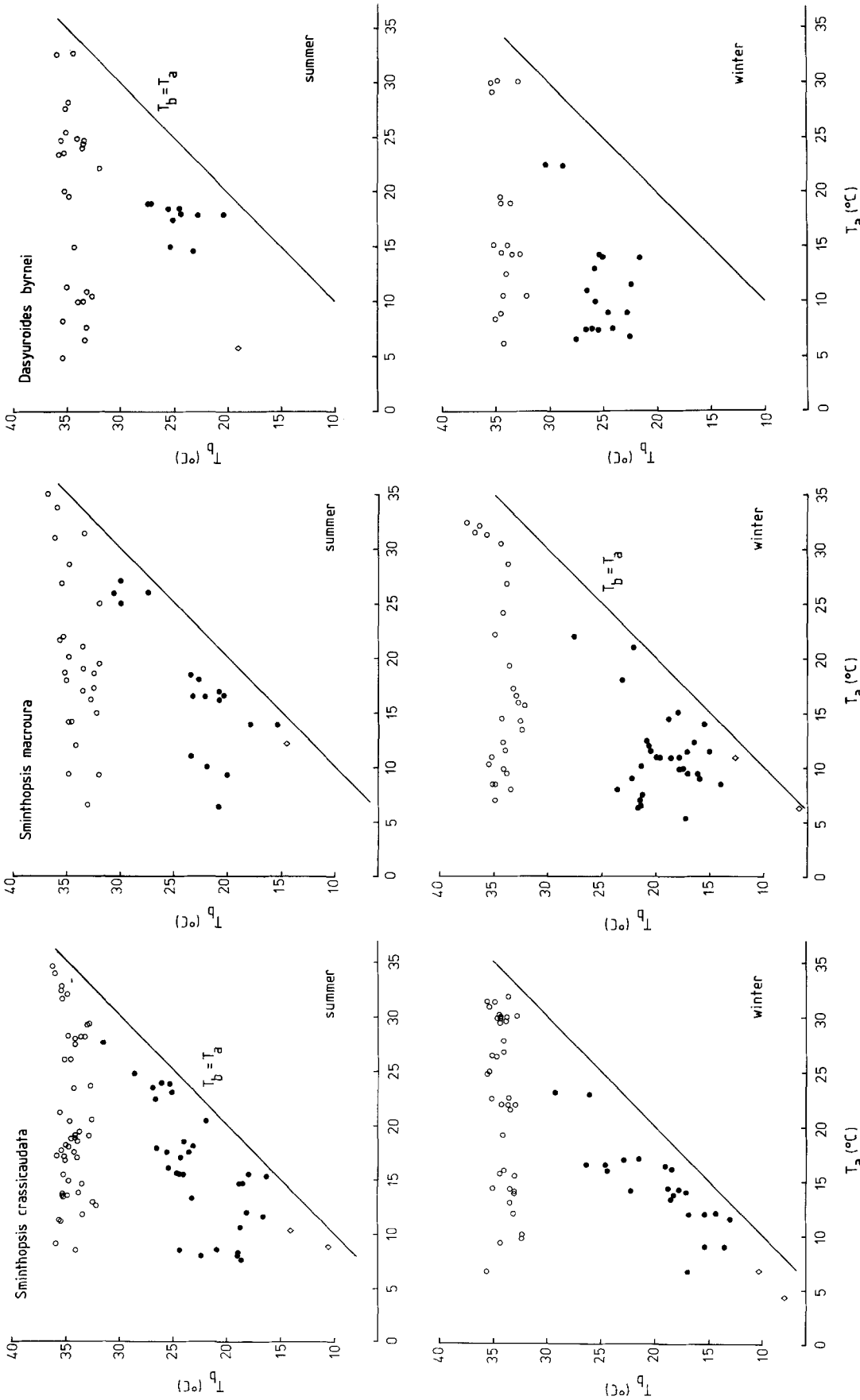
Fig. 2. Body temperatures (T_b) as a function of air temperature (T_a) in normothermic, inactive (o), torpid (●), and hypothermic (◇) dasyurid marsupials in summer (upper) and winter (lower). Animals with a $T_b < 31$ °C were considered to be torpid because they showed a conspicuous loss of coordination. Each point represents an individual measurement of T_b. The constructed solid line represents $T_b = T_a$

Table 3. Body temperatures (T_b) and rates of oxygen consumption $(\dot{V}_{O_2})$ during normothermia and torpor in *Sminthopsis crassicaudata, S. macroura,* and *Dasyuroides byrnei*

Species (Season)		T_b rest (°C)	BMR (l O_2/kg h)	T_b torpor (°C)	$\dot{V}_{O_2}$ min (l O_2/kg h)	Body mass (g)
S. crassicaudata	(s)	34.3±1.0 (14)	1.25±0.20 (6)	20.2±2.5 (10)	0.40±0.16 (8)	17.7± 2.1 (19)
	(w)	34.1±0.9 (15)	1.22±0.15 (8)	16.9±2.4 (12)	0.29±0.10 (12)	17.3± 2.5 (15)
S. macroura	(s)	33.9±1.3 (11)	1.07±0.10 (5)	20.7±2.3 (11)	0.57±0.22 (5)	22.0± 2.3 (11)
	(w)	34.0±0.9 (11)	1.01±0.26 (6)	18.4±2.2 (13)	0.33±0.13 (8)	26.9± 3.4 (13)
D. byrnei	(s)	34.3±1.1 (8)	0.70±0.11 (6)	24.6±2.2 (9)	0.44±0.04 (6)	118.2±14.7 (9)
	(w)	34.2±0.9 (9)	0.78±0.12 (5)	25.4±1.1 (7)	0.40±0.03 (5)	115.0±12.9 (13)

Values represent means±SD. The body masses (with number of individuals) are the corresponding values for the $\dot{V}_{O_2}$ measurements in Fig. 3. Significant seasonal differences were observed in $\dot{V}_{O_2}$ min and the T_b during torpor in *S. crassicaudata* and *S. macroura* (*t*-test; $P<0.05$), but not in *D. byrnei*. The mean T_b during torpor of the three species in both seasons were determined from measurements that had been taken below the T_a of the $\dot{V}_{O_2}$ intercept in torpor; i.e. the highest T_a below which individuals of each species regulated T_b during torpor (see Fig. 3). Numbers of individuals are shown in parentheses. (s) = summer, (w) = winter

torpor decreased with T_a and the difference between these temperatures $(\varDelta T)$ was usually >1 °C. The lowest T_b's (13.0 °C, *S. crassicaudata*; 14.0 °C, *S. macroura*) were observed in winter. In summer the minimum T_b's were 16.3 and 15.0 °C, respectively. The mean T_b's during torpor in the *Sminthopsis* species were significantly lower during winter than during summer $(P<0.05$; *t*-test), but not in *D. byrnei* (Table 3). The minimum T_b of *D. byrnei* was 20.4 °C and T_b during torpor was greater than in *Sminthopsis* spp. $(P<0.001$; *t*-test). At T_a below the seasonal T_b minimum of each species, an increase in $\varDelta T$ during torpor occurred; the absolute values of T_b's of torpid animals in this range of T_a were also increased. Individuals that further decreased T_b were unable to arouse at the T_a at which they had entered torpor. However, most hypothermic individuals completed arousal after partial rewarming.

Rates of oxygen consumption of normothermic, resting dasyurids (RMR) were strongly temperature dependent and increased linearly in all species in both summer and winter as T_a decreased below thermoneutrality (Fig. 3). During summer, the lines relating resting metabolic rate (RMR) and T_a were significantly higher in elevation than in winter (F-test; $P<0.01$). The intercepts of these lines with the abscissa (T_a) were within 3.2 °C of the mean T_b determined. No significant seasonal differences could be detected in the basal metabolic rate (BMR) (Table 3).

In the range of T_a's below the thermoneutral zone and above the T_a at which T_b was regulated, torpid animals decreased $\dot{V}_{O_2}$ steadily with decreasing T_a (Fig. 3). The mean values of $\dot{V}_{O_2}$ of the three species in torpor ranged from 0.3–0.6 l O_2/kg h (Table 3). In *Sminthopsis* spp., the minimum

$\dot{V}_{O_2}$ during torpor in winter was significantly lower than in summer $(P<0.05$; *t*-test); only a slight reduction in the $\dot{V}_{O_2}$ minima during winter was observed in *D. byrnei*. When the $\dot{V}_{O_2}$ minima during torpor of 7 individual *S. crassicaudata* that had been measured in both summer and winter were compared within a T_a range of 3 °C for each individual, the summer animals showed a 1.6-fold increase in $\dot{V}_{O_2}$ over the winter animals and the means in summer were significantly greater than during winter $(P<0.05$; *t*-test). In *D. byrnei* most individuals were used in summer and winter, but no significant seasonal differences in $\dot{V}_{O_2}$ during torpor could be detected. A linear increase in $\dot{V}_{O_2}$ below a critical T_a was observed in all species (Fig. 3). The lines relating $\dot{V}_{O_2}$ of torpid dasyurids and T_a (at T_a's below which $\dot{V}_{O_2}$ during torpor increased, in the *Sminthopsis* species – this temperatures varied seasonally; in *D. byrnei* the increase of $\dot{V}_{O_2}$ occurred below T_a 15 °C in both seasons) were significantly lower in elevation during winter than in summer $(P<0.01$; F-test). In the *Sminthopsis* species this shift was more pronounced than that observed for the RMR. The intercepts of these derived lines with the abscissa occurred at a lower temperature during winter than in summer in *Sminthopsis* spp., suggesting a shift in the set point at which T_b is regulated during torpor. This was not the case in *D. byrnei*. The intercepts of these lines with the abscissa were within 1.9 °C of the minimum T_b determined for each species and season.

Several individuals at low T_a were unable to maintain a constant "high" $\dot{V}_{O_2}$ during torpor and $\dot{V}_{O_2}$ steadily declined after an initial constant level of 1–2 h (Fig. 3). These animals were unable to arouse without partial rewarming.
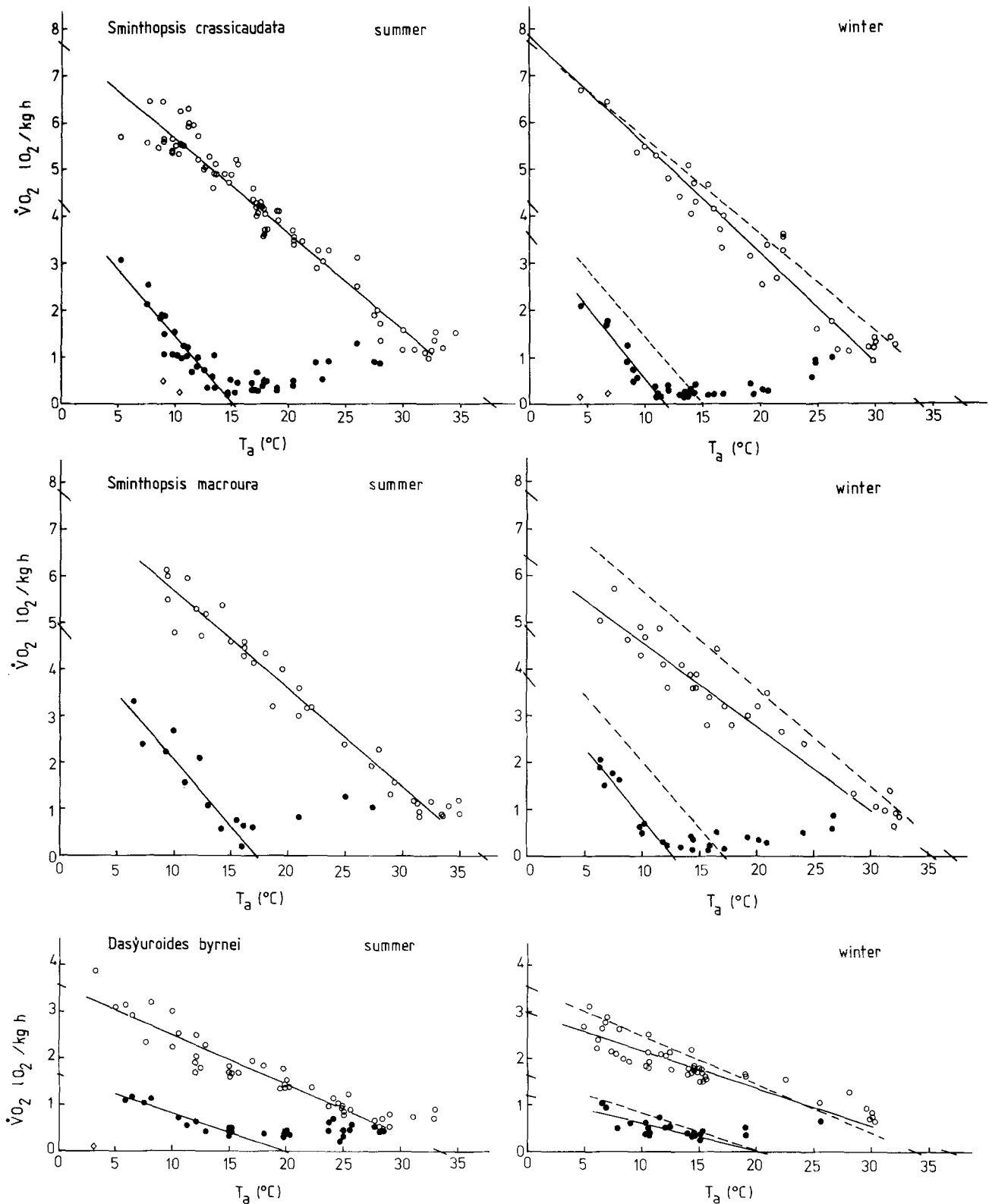
Fig. 3. Rates of oxygen consumption ($\dot{V}_{O_2}$) as a function of air temperature (T_a) of the three dasyurids in summer and winter. The symbols indicate: normothermic, inactive (o); $\dot{V}_{O_2}$ minima during torpor that were constant over at least 30 min (●); and animals in hypothermia (◇). Lines were fitted by least squares regressions to the $\dot{V}_{O_2}$'s that were increased due to thermoregulation during both normothermia and torpor. In the *Sminthopsis* species this thermoregulatory increase of $\dot{V}_{O_2}$ during torpor showed strong seasonal changes; in *D. byrnei* it occurred below T_a 15 °C in both seasons. The equations are: *S. crassicaudata*, summer: $y = 7.82 - 0.23x$; $r = -0.96$ (normothermic, inactive), $y = 4.28 - 0.29x$; $r = -0.92$ (in torpor); winter: $y = 7.69 - 0.20x$; $r = -0.96$ (normothermic, inactive), $y = 3.58 - 0.30x$; $r = -0.95$ (in torpor). *S. macroura*, summer: $y = 7.81 - 0.21x$; $r = -0.97$ (normothermic, inactive), $y = 4.95 - 0.28x$; $r = -0.87$ (in torpor); winter: $y = 6.38 - 0.18x$; $r = 0.93$ (normothermic, inactive), $y = 3.84 - 0.30x$; $r = -0.96$ (in torpor). *D. byrnei*, summer: $y = 3.53 - 0.10x$; $r = -0.94$ (normothermic, inactive), $y = 1.65 - 0.08x$; $r = -0.95$ (in torpor); winter: $y = 2.92 - 0.08x$; $r = -0.84$ (normothermic, inactive), $y = 1.20 - 0.06x$; $r = -0.73$ (in torpor). The broken lines in the winter graphs represent the summer values
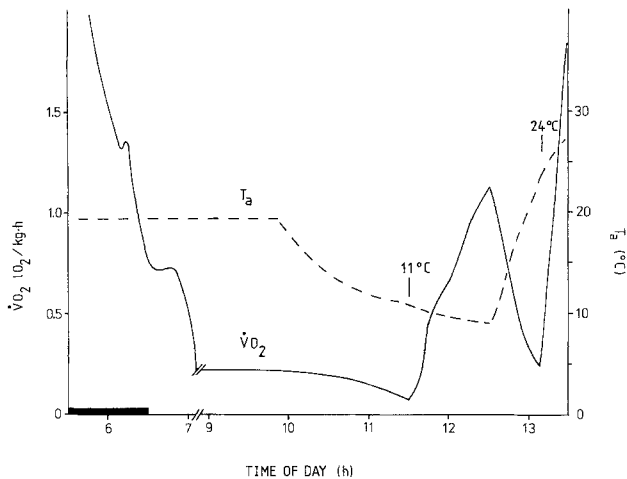
TIME OF DAY (h)

Fig. 4. The rate of oxygen consumption ($\dot{V}_{O_2}$; solid line) of an individual torpid *S. crassicaudata* exposed to a changing air temperature (T_a; broken line). The T_a's at which an increase in $\dot{V}_{O_2}$ occurred are indicated. The increase in $\dot{V}_{O_2}$ that occurred after cooling was reversed and the T_a was increased suggests that the increase in $\dot{V}_{O_2}$ below $T_a = 11$ °C was due to thermoregulation, not arousal. Arousal was induced when T_a reached 24 °C. The abscissa represents the local time, the dark bar indicates the period of darkness. The $\dot{V}_{O_2}$ between 0700 and 0900 h was constant and was omitted

When torpid *S. crassicaudata* were cooled, their $\dot{V}_{O_2}$ showed an increase at a critical T_a (Fig. 4). The mean T_a at which an increase in $\dot{V}_{O_2}$ was observed during cooling was 15.0 ± 0.9 °C ($N = 7$) in summer and 11.5 ± 0.8 °C ($N = 7$) in winter; these means were significantly different ($P < 0.001$; t-test). For three individuals cooling experiments during torpor were performed in both seasons and $\dot{V}_{O_2}$ increased at T_a 16.0 ± 0.6 °C in summer and T_a 11.9 ± 0.4 °C in winter. These results further support the view of a seasonal shift in the "set point" at which T_b is regulated during torpor (see Fig. 3). Reduction of T_a below these critical temperatures resulted in arousal in half the animals, while the others remained torpid but increased $\dot{V}_{O_2}$.

The time required to arouse from torpor to normothermia showed an exponential increase with decreasing T_a in most cases (Fig. 5). The slopes relating these variables were a function of body mass: values for *S. crassicaudata* being the greatest and those for *D. byrnei* the least. In *S. macroura* a paradoxical situation was observed in winter, as arousals induced by measurement of T_b decreased in length at lower T_a's. This suggests that at low T_a arousal time during winter is shorter than during summer. Maximal arousal rates determined over a time interval of 10 min were 0.68 °C/min in *S. crassicaudata* (T_a 22 °C), 0.70 °C/min in
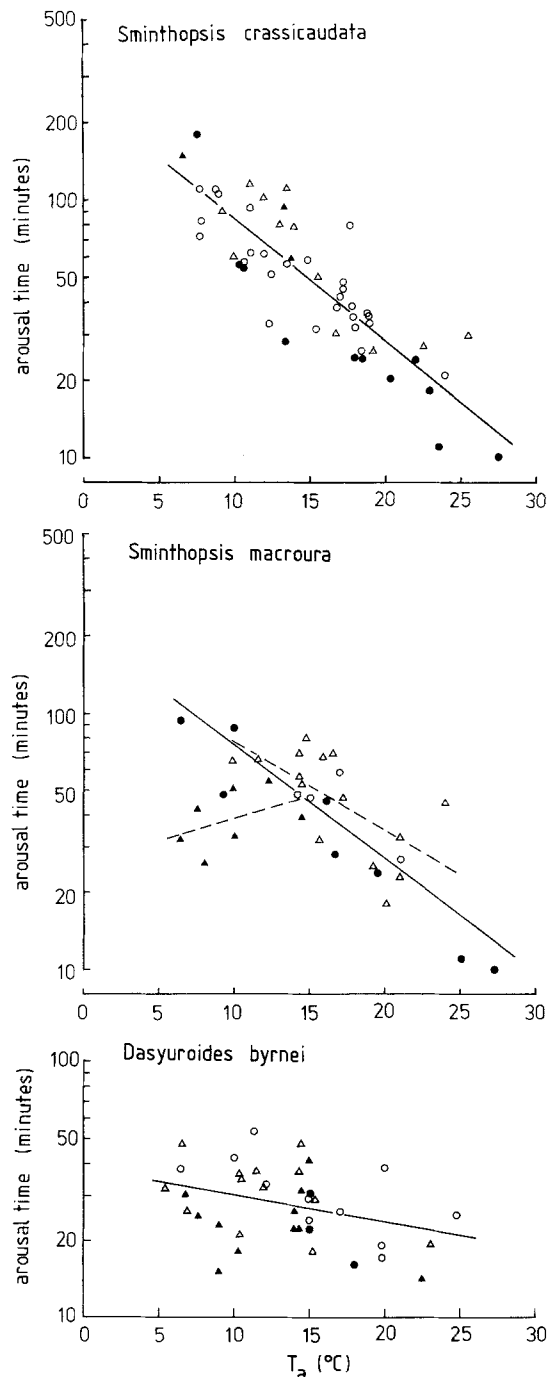

Fig. 5. Semi-logarithmic plots of the arousal times in the three dasyurids at a function of air temperature (T_a). The symbols indicate: disturbance-induced arousal in summer (●) and winter (▲); and spontaneous arousal in summer (○) and winter (△). In *S. macroura* arousals induced by measurement of T_b in summer at T_a's below 15 °C were slower than those in winter (broken line). The solid lines represent fits to all measurements in both seasons in *D. byrnei* and *S. crassicaudata* and to all measurements in summer in *S. macroura*. The lines were fitted by least squares regressions and the equations are: *S. crassicaudata*, log $y = 2.41 - 0.048x$; $r = -0.86$. *S. macroura*, summer: log $y = 2.32 - 0.046x$; $r = -0.92$; winter, induced: log $y = 1.40 + 0.018 \times$; $r = 0.46$; winter, spontaneous: log $y = 2.24 - 0.035x$; $r = -0.66$. *D. byrnei*, log $y = 1.59 - 0.011x$; $r = -0.36$

S. macroura (T_a 23 °C), and 0.55 °C/min in *D. byrnei* (T_a 9 °C).

Discussion

The present study suggests that the pattern of torpor in the three arid zone dasyurid marsupials investigated is influenced by season and perhaps body size. While in the two smaller species, *Smintopsis crassicaudata* and *S. macroura*, torpor was generally more pronounced in winter than in summer, such distinct seasonal differences were not observed in *Dasyuroides byrnei*, the largest species.

The incidence of induced torpor in the dasyurids under similar conditions was increased in both *Sminthopsis* species in winter suggesting a seasonal change in the proclivity to entering torpor. Similar seasonal changes in the tendency to entering torpor have also been observed in the small (30 g) dasyurid *Antechinus stuartii* (Wallis 1976). *Dasyuroides byrnei* lacked such seasonal differences, but this species showed an increase in spontaneous torpor in winter, most likely as a response to the colder temperatures (Fig. 1). A seasonal shift in the frequency of spontaneous torpor also occurred in *S. macroura* in agreement with observations on heterothermic placentals (Lynch et al. 1978; Heldmaier and Steinlechner 1981a). The observation of spontaneous torpor in *S. crassicaudata* during summer contrasts with findings of Morton (1978) who sampled, however, at a time of day when the present study indicates that this species would be normothermic. Spontaneous torpor throughout the year in *D. byrnei* warrants critical re-examination of reports on summer homeothermy in smaller marsupials.

The T_b's and $\dot{V}_{O_2}$'s of both torpid *Sminthopsis* species were lower in winter than during summer. While lower T_b's in winter have been reported previously in torpid *Peromyscus* spp. (Gaertner et al. 1973; Lynch et al. 1978; Tannenbaum 1985) our observation of a seasonal shift in the "set point" temperature during torpor is the first recorded case in the literature. The lower T_b's should allow a greater reduction in metabolic rate during torpor in winter and thus enhance energy conservation. *Dasyuroides byrnei*, the larger species, did not show seasonal shifts in the "set point" temperature. However, despite the relatively high T_b of >20 °C, the mass-specific $\dot{V}_{O_2}$ of this species was reduced to minima similar to those of *Sminthopsis*, suggesting that a relatively small reduction in T_b is a sufficient contribution to energy conservation in *D. byrnei*. Because the BMR of *D. byrnei*, the largest species, is much lower than in the *Sminthopsis*

spp. the slight reduction in T_b during torpor results in $\dot{V}_{O_2}$ values similar to those in *Sminthopsis* at much lower T_b's. Relatively high T_b's similar to those in *D. byrnei* have also been observed in torpid *Dasycercus cristicaudata* (100 g) and *Dasyurus geoffroii* (1000 g) (Kennedy and McFarlane 1971; Arnold 1976), suggesting that larger arid zone dasyurids may not lower T_b below 15–20 °C, unlike the smaller (<50 g) species (Geiser 1985, 1986; present study). This observation indicates that the minimum T_b during daily torpor in dasyurids may be influenced by body size with the lower values occurring in the smaller species and allowing them to maximise energy savings. The increased tendency to entering torpor, longer torpor bouts, and lower minimum T_b's in half grown than in adult *D. byrnei* (Geiser et al. 1986a) supports this view. Longer and deeper torpor may contribute to energetic balance in the smaller species which lose more heat to the environment than larger species while normothermic.

The Q_{10} of oxygen consumption between normothermia (BMR) and torpor in the *Sminthopsis* species was slightly higher in winter. This would contribute further to energy conservation. The Q_{10} in both species was, however, between 1.6 and 2.5 in both seasons, suggesting that the low metabolism found during torpor in these dasyurids and also in hibernating ground squirrels (Snapp and Heller 1981) is directly due to a temperature effect rather than some suggested physiological inhibition.

Although torpor duration was significantly longer in the *Sminthopsis* than in *D. byrnei*, seasonal differences in the duration of torpor could not be observed in any species. This suggests that the seasonal adjustment of energy balance by heterothermy in these marsupials is achieved by varying the depth rather than the length of torpor. Because species that enter daily torpor forage and feed between their lethargic phases and subsequently have to digest the food, an extension of torpor duration beyond about 6 h/day may be limited.

Rewarming from torpor was faster in the *Sminthopsis* than in *D. byrnei*, the largest species, in agreement with the prediction that body mass and arousal rates from torpor are inversely related (Heinrich and Bartholomew 1971). However, in contrast to *D. byrnei* which showed similar arousal times over a wide range of T_a's, these variables varied strongly with T_a in the *Sminthopsis*. Therefore, at low T_a arousal rates should in fact be faster in small than in large species and a reversal of the inverse relationship between rewarming rate

and body mass can be predicted. Arousal rates in the three dasyurids investigated herein were similar to or faster (almost twice as fast in *D. byrnei*) than predicted for birds and mammals (Heinrich and Bartholomew 1971). These findings do not support earlier suggestions of a generally slow rewarming from torpor in marsupials.

BMR's and normothermic T_b's did not show seasonal variations in any of the species investigated and were in close agreement with earlier determinations (MacMillen and Nelson 1969; Dawson and Hulbert 1970). This is in contrast to observations in small rodents which showed seasonal fluctuations in BMR and/or T_b (Rosenmann et al. 1975; Wunder et al. 1977; Heldmaier and Steinlechner 1981b). However, unlike the dasyurids studied herein, these rodents showed strong seasonal fluctuations in body mass which partially explains the variation in BMR. RMR's below thermoneutrality in the dasyurids were significantly increased in summer. This also appears to be in contrast to the findings on some small rodents (Rosenmann et al. 1975; Wunder et al. 1977; Heldmaier and Steinlechner 1981b) which show greater or similar mass-specific metabolic rates in the winter months. This increase in mass-specific metabolism in these small rodents appears to be largely due to a 20–50% reduction in body mass and hence a decrease in total metabolism. In contrast, ground squirrels (Pohl and Hart 1965; Kenagy and Vleck 1982), and lagomorphs which increase insulation during winter (Hart et al. 1965; Hinds 1973), show a decrease in RMR during winter in agreement with the present study. Thus the overall trend appears to be a decrease in energetic costs at normothermic T_b's during winter either by increasing insulation or decreasing body size. An increased thermogenic capacity in winter enables endotherms to thermoregulate at lower T_a's (Rosenmann et al. 1975; Heldmaier et al. 1986), but could be maladaptive if it increased the metabolism under similar thermal conditions.

Thermoregulation and torpor in dasyurid marsupials are influenced by season. The ability of marsupials to change the physiology of thermoregulation and torpor on a seasonal basis underscores the adaptive nature and the ecological value of daily torpor. It would be of interest to know whether similar seasonal changes also occur in rodents and other placentals that enter shallow, daily torpor.

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