THE THERMAL PHYSIOLOGY OF THE MOUNTAIN PYGMY-POSSUM *BURRAMYS PARVUS* (MARSUPIALIA: BURRAMYIDAE)

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The Mountain Pygmy-possum *Burramys parvus* is restricted to the Australian alpine region. Laboratory studies of the thermo-physiology of this species found that body temperature (T_b) was tightly regulated at 36.1°C, but animals quickly become hyperthermic at ambient temperatures (T_a) above 30°C, causing the thermal neutral zone to be truncated. Basal metabolic rate was 2.15 W kg $^{-0.75}$ (mean body mass 44.3 g) and weight-specific thermal conductance was 0.112 ml 0_2 g^{-1} h^{-1} $°C^{-1}$. These values are 9% and 44% lower, respectively, than the mass predicted value for a marsupial, showing that the overall rate of energy expenditure is considerably reduced in this species. Huddling also reduces individual rates of energy expenditure. *Burramys parvus* enters prolonged bouts of deep torpor lasting up to one week, during which T_b is very low and close to T_a and the rate of oxygen consumption greatly reduced. Spontaneous arousal occurred from a T_b as low as 6°C and the overall rate of rewarming was 0.17 °C/min. Attainment of a critical body mass appeared to be necessary before an animal would enter torpor. *Burramys parvus* shows physiological adjustments similar to that described in many placental mammals from cold climates and this species represents a true marsupial hibernator.

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THE comparative thermophysiology of many northern hemisphere placental mammals has been studied in detail with particular attention being given to arctic mammals (reviews: Hart 1964, 1971 and Miller 1978). The physiological adjustments found in placentals from cold environments have been used to infer general correlations between climate and single physiological parameters (Scholander *et al.* 1950, Irving *et al.* 1955, Hart 1964, McNab 1966 and Withers *et al.* 1979). These generalized placental 'adaptations to cold' include increased insulation of the surface layers, peripheral cooling, increased body size, a basal metabolic rate higher than predicted by mass, increased summit metabolism and the ability to become torpid.

Burramys parvus Broom is the only marsupial restricted to the alpine and subalpine habitats of southeastern Australia. Localised, low-density populations have been recorded from Mt Hotham and the Bogong High Plains in Victoria and in the Kosciusko National Park in New South Wales (Mansergh 1984). Fossil remains close to the modern form of *B. parvus* have been found in owl deposits at much lower altitudes (Broom 1896 and Wakefield 1972). These deposits are Pleistocene and Recent in age indicating that this species had a much wider distribution in the recent past.

Extant populations are strongly associated with peri-glacial boulder streams which are usually shrub covered (Gullen and Norris 1981). This habitat would provide an extensive sub-nivean environment during the five months of the year that the ground is usually snow-covered. The ecology of *B. parvus* is reviewed by Kerle (1984) and Mansergh (1984). This study describes thermoregulation and torpor in *B. parvus* as an example of a small marsupial adapted to a cold environment.

METHODS

METABOLIC MEASUREMENTS OF NORMOTHERMIC ANIMALS

The animals used in this study were obtained from two sources. Five captive-bred adults were obtained from a colony in Canberra. The original stock for this colony came from a number of sub-alpine localities within the Kosciusko National Park, N.S.W. A further three adult female *B. parvus* were live-trapped at Mt Hotham, Victoria. One female had four pouch young when captured and these were successfully reared. The animals were housed as pairs or individuals in steel mesh cages (1 m) in a constant temperature room. The female with pouch young was housed in a large cage (1.5 x 2 x 1 m) in the same constant temperature room. All cages contained nestbox-metabolic chambers fitted with thermocouples for the continuous measurement of fur surface temperature (Godfrey 1968). The *B. parvus* were maintained on a diet of raw peanuts, sunflower seed, and commercial baby food with added vitamin powder. A calcium supplement was added to the drinking water which was available *ad libitum*.

Oxygen consumption rate ($\dot{V}O_2$, indicated hereafter by symbol VO_2) was measured continuously using an open-circuit system connected to a paramagnetic oxygen analyser (see Fleming 1980 for details). The oxygen consumption of individuals and groups was determined by the following procedure. Animals were weighed to the nearest 0.1 g and placed in an air-tight perspex metabolic chamber equipped with inlet and outlet ports and a wire mesh platform. Single animals were measured in a 0.5 l metabolic chamber with a flowrate of about 300 ml air min^{-1} and groups of four animals were measured in a 1.2 l chamber with a flowrate of about 900 ml air min^{-1}.

The chamber was placed in a lighted constant-temperature cabinet regulated within ± 0.5°C of the desired setting. Temperature within the chamber was recorded on a Leeds and Northrup Speedomax W multipoint recorder. Dried room air passed through a copper heat exchanger before entering the metabolic chamber. Oxygen consumption rates were determined on resting post-absorptive animals held in the metabolic chamber for more than 1 hour at a selected T_a. The minimum metabolic rate for a T_a was calculated from the lowest value of the fractional difference lasting for at least 5 min. All measurements were made between 0800 and 1900 h. $V0_2$ was calculated from the equations of Withers (1977) with all gas volumes corrected to STP.

METABOLIC MEASUREMENTS OF TORPID ANIMALS

The initial study on torpor was made in the Department of Zoology, Australian National University, Canberra in 1976. Three captive-bred adults which had been maintained in a large outdoor cage were individually housed in a 2 x 1 x 1 m cabinet made from 50 mm thick polystyrene foam. The cabinet was placed in an isolated room and a constant temperature of 5-8°C was maintained within the cabinet by the daily renewal of tubs of crushed ice placed above the animal cages. A little light penetrated from an external light source set at 14 hours dark, 10 light.

Animals were supplied with a nestbox-metabolic chamber made from a hemispherical lidded plastic bowl (diameter = 100 mm) with a perspex entrance tube attached (30 x 50 mm). Torpor was detected by continuously monitoring temperature within the nest (Godfrey 1968). Oxygen use during torpor was measured by drawing air through a small hole in the lid, over the animal and out through a rubber bung, which was used to seal the entrance tube. The air was dried and sampled for oxygen content every two minutes with a Beckman

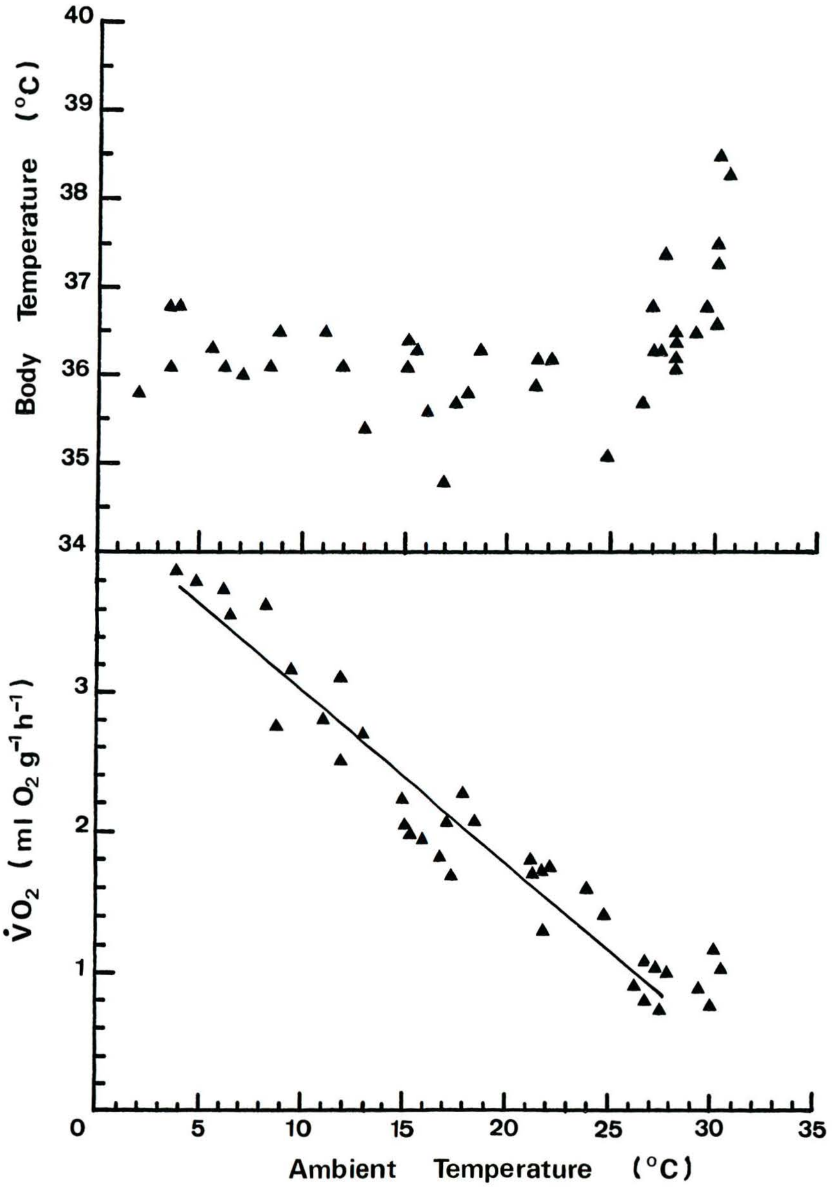

Fig. 1. The relationship of body temperature and oxygen consumption rate to ambient temperature for individual *Burramys parvus*. The solid line in the lower part is the regression equation $VO_2 = 4.24\text{-}0.123\ T_a$.

E2 paramagnetic oxygen analyser. To measure the very low rates of oxygen use during torpor, the nestbox-metabolic chamber was sealed for up to 1 hour, then unsealed and oxygen use recorded until the value prior to sealing was reached. The area under the curve was integrated over time to measure total oxygen use.

The induction of torpor in *B. parvus* was attempted at the Department of Zoology, Monash University, under three different conditions. For the first winter (1978), five animals were housed in a constant temperature room set at 7 ± 2 °C with the light regime identical to natural photo-period. Torpor was monitored from outside the constant temperature room by continuously recording nestbox temperature. The constant temperature room also housed other species being used for other experimental work. For the second winter, four animals were kept in the same constant temperature room in 0.30 x 0.45 x 0.15 m tubs with wire mesh tops and nestbox-metabolic chambers. The tubs were placed within a cabinet (2 x 1 x 1 m) made from 5 cm thick polystyrene foam to reduce disturbance by noise. For the third winter, the polystyrene cabinet was placed in an isolated room and cooled by a silent refrigeration unit with a remote cooling coil. The cooling coil was immersed in a supersaturated salt solution within the polystyrene cabinet and connected to the refrigeration unit by flexible hoses. Two animals were placed in wire topped tubs with nestbox-metabolic chambers.

BODY TEMPERATURE

Body temperature (T_b) was measured with a silastic-sheathed thermocouple inserted into the rectum to a depth of 2-3 cm. Rectal thermocouples were connected to either a Leeds and Northrup Speedomax multipoint recorder (accuracy, ± 0.25°C) or a Comark Electronic thermometer Type 1624 (accuracy, ± 0.1°C). T_b of single animals was measured within 30 seconds of removal from the metabolic chamber. Respiration rate was measured by a pressure transducer connected to the metabolic chamber and the output was displayed on a Grass polygraph.

STATISTICAL ANALYSIS

All averaged data is presented as Mean ± Standard Deviation (n = number of measurements, N = number of individuals). Areas under oxygen consumption curves were determined by finding the area of an irregular polygon. Linear regressions were fitted by the least squares method and inflexion points were determined by a programme called TURNPOINT (Fleming 1985).

RESULTS

NORMOTHERMIC: INDIVIDUALS

Burramys parvus strictly regulate their body temperatures at ambient temperatures (T_a) between 2°C and 28°C (Fig. 1). Within this range T_b is 36.1 ± 0.53 °C (n = 28, N = 6). A pronounced inflexion in the body temperature curve occurs at T_a = 28.0 °C with T_b increasing at a rate of 0.68 °C per degree T_a. *B. parvus* were noticeably stressed by $T_a > 29$ °C. The animals lay on their flanks, their ears were fully-expanded, the naked tail was engorged with blood and saliva was spread on the forepaws. The only indication of active cooling was dampness and matting of fur around the scrotum. Exposure to a T_a of 33°C for less than one hour was found to be lethal.

The metabolic response of individual *B. parvus* is shown in Fig. 1. The lower critical temperature (T_{lc}), as determined by TURNPOINT, is 27.7 °C. Only two VO_2 measurements were made at T_a higher than 30 °C as the animals quickly became hyperthermic. These measurements indicate that the upper critical temperature (T_{uc}) is about 30 °C within the narrow thermal neutral zone (TNZ), the rate of oxygen use is 0.83 ± 0.14 ml O_2 g^{-1} h^{-1} (n = 6,

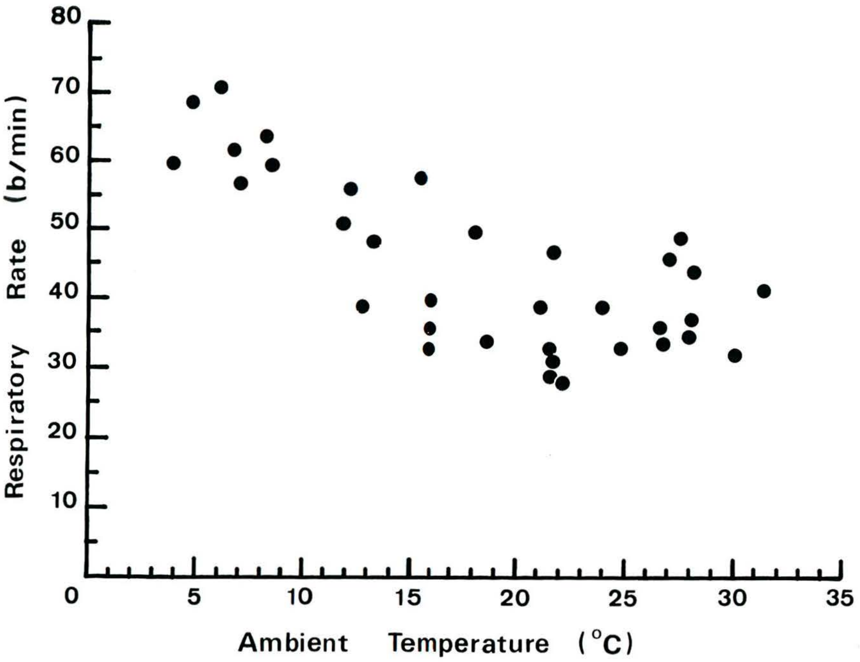

Fig. 2. The relationship of respiratory rate with ambient temperature for *Burramys parvus.*

N= 4; body mass 44.29 ± 13.81 g, n =6) which is a standard metabolic rate of 2.15 W kg $^{-0.75}$ (assuming R.Q. = 0.86).

The change in VO_2 as T_a increases from 3 °C to 27 °C is described by the linear regression equation:

VO_2 (ml 0_2 g $^{-1}$ h $^{-1}$) = 4.24 — 0.123 T_a $r^2 = 0.93$, n = 37, N = 5, $p < 0.001$ $S_{y.x} = 0.24$, $S_b = 0.006$).

A mass specific measure of the insulative properties of fur and surface tissues can be calculated from $V0_2$ and T_b (McNab 1980). For *B. parvus* the mean mass specific thermal conductance at T_a less than T_{lc} is 0.112 ± 0.013 ml 0_2 g^{-1} h^{-1} °C $^{-1}$ (n = 22).

The respiratory frequency of *B. parvus* as a function of T_a is shown in Fig. 2. The minimum breathing rate of about 33 breaths/min^{-1} was reached at $T_a = 18°C$ and the breathing rate started to increase at $T_a > 27°C$. High breathing rates and panting were not observed.

NORMOTHERMIC: GROUPS OF FOUR ANIMALS

The measurements of $V0_2$ of a group of four *B. parvus* were made at T_a less than T_{lc}. The huddling behaviour of *B. parvus* differs markedly from that observed in two other species of small possums. At T_a close to the TNZ, the animals lay on their flanks, but not in contact. As T_a decreased, the animals assumed a curled posture with the head held under the body; usually individuals were not in contact. At low T_a (i.e., 5°C), the curled posture was maintained and the animals formed a tight group with their flanks and backs in contact. At no time did individuals lie across each other as observed in Sugar Gliders (*Petaurus breviceps*) and Feathertail Gliders (*Actobates pygmaeus*) (Fleming 1980, 1985).

The metabolic response of a group of four *B. parvus* is shown in Fig. 3. There is little difference between the $V0_2$ of individuals alone and that of groups at higher T_a, but as T_a decreases a difference becomes apparent. The regression equation for $V0_2$ of a group of four as a function of T_a is:

$V0_2$ (ml 0_2 g^{-1} h^{-1}) $= 3.4 - 0.091\ T_a$ ($r = 0.82$, $n = 23$, $p < 0.001$; $S_{y.x} = 0.29$, $S_b = 0.009$).

The T_b of groups was not measured, but the mass specific thermal conductance was calculated from $V0_2$ and T_a measurements by assuming $T_b = 36.2$ °C. The mean thermal conductance for a group of four *B. parvus* was 0.096 ± 0.013 ml 0_2 g^{-1} h^{-1} $°C^{-1}$ ($n = 20$).

TORPOR

At Monash University torpor was recorded on only one occasion during the three winters in which observations were made. The continuous monitoring of nest temperature showed that an adult female *B. parvus* had entered torpor during the first winter for a period of 12.5 h with $T_a = 9.0$°C. Food had been available *ad libitum* and body mass was 45.1 g. Subsequent attempts to induce torpor centred on the reduction of environmental noise and disturbance. No attempt was made to induce torpor by starvation.

During the Canberra study, the three *B. parvus* were housed in the polystyrene cabinet for 135 days during the winter. Thirteen episodes of torpor were recorded, six of which were not disturbed and are detailed in Table 1. The remaining seven episodes were interrupted to measure $V0_2$

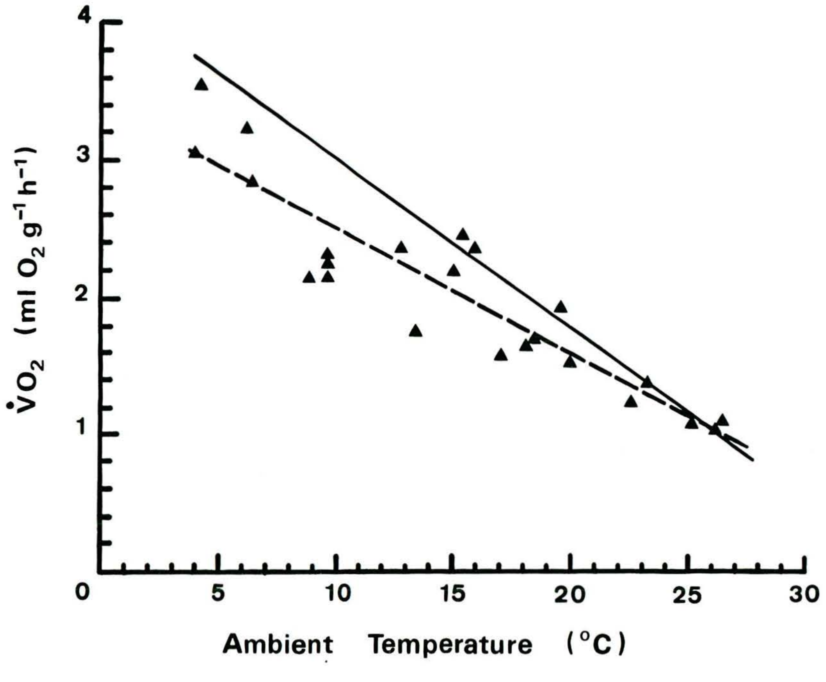

Fig. 3. The relationship of oxygen consumption rate with ambient temperature for groups of four *Burramys parvus*. Solid line is the regression line for individuals. Dashed line is the regression line for groups of four, namely: $VO_2 = 3.4\text{-}0.091\ T_a$.

and T_b during arousal. VO_2 and T_b during torpor are given in Table 2. Overall arousal rates at $T_a = 8°C$ varied from 0.17 to 0.22 °C/min with a mean rate of 0.17 ± 0.03 °C/min ($n = 5$). The fastest rate measured over a 20 min period was 0.44 °C/min. *Burramys parvus* appears to enter torpor only when body mass has attained a critical level (Fig. 4). Torpor did not occur while body mass was below 50 g. Partial starvation of one animal over 18 days, causing a weight loss of 43%, did not induce torpor and complete starvation of a second animal for 48 hr also did not induce torpor (Fig. 5).

DISCUSSION

NORMOTHERMIC INDIVIDUALS

The body temperature of *B. parvus* is tightly regulated at $T_a < 28°C$ unlike that of the possums *Cercartetus nanus* and *Acrobates pygmaeus*, which show large variation in T_b (Bartholomew and Hudson 1962 and Fleming 1985). The diurnal lability of T_b was not measured directly, but the continuous measurements of T_{skin} of of *B. parvus* did not show the cyclical variation that has been observed in other pygmy possums and small dasyurids (Bartholomew and Hudson 1962, Godfrey 1968, Wallis 1976, Morton and Lee 1978 and Fleming 1985). In contrast to their strictness of regulation at low T_a, *B. parvus* become rapidly hyperthermic at $T_a > 28°C$. This intolerance of high temperature is not shared by *C. nanus* or *A. pygmaeus* or other small marsupials, which are able to survive T_a of 38° C and higher (Robinson and Morrison 1957, Bartholomew and Hudson 1962 and Fleming 1985).

The mass specific thermal conductance of *B. parvus* (0.112 ml 0_2 g^{-1} h^{-1} $°C^{-1}$) is 44 % lower than the weight predicted value (Fleming 1982). The fine dense fur

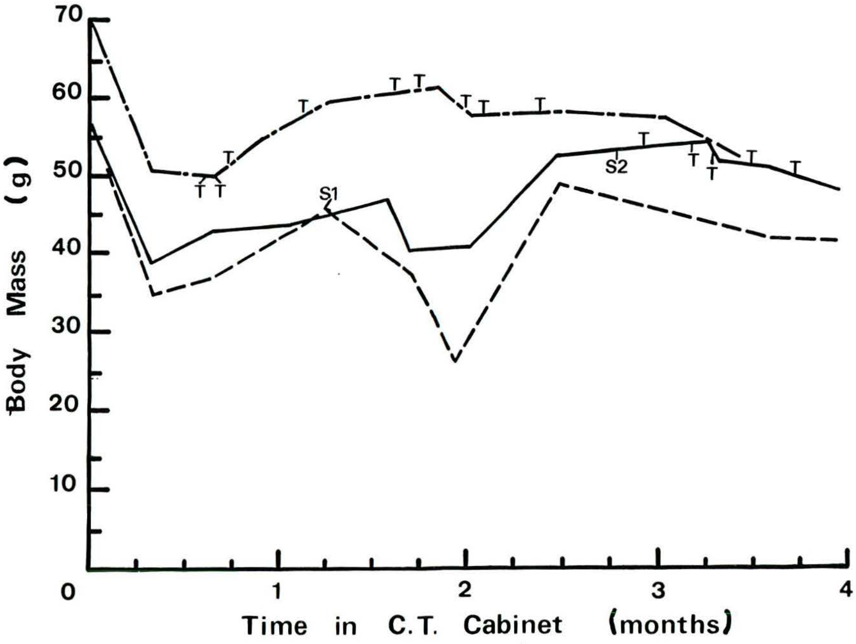

Fig. 4. The changes in body mass associated with episodes of torpor for three *Burramys parvus* maintained at an air temperature of 5-8 °C. T, marks the initiation of an episode of torpor. S1, food rationed for 18 days (dashed line); S2, food withdrawn for 2 days (solid line).

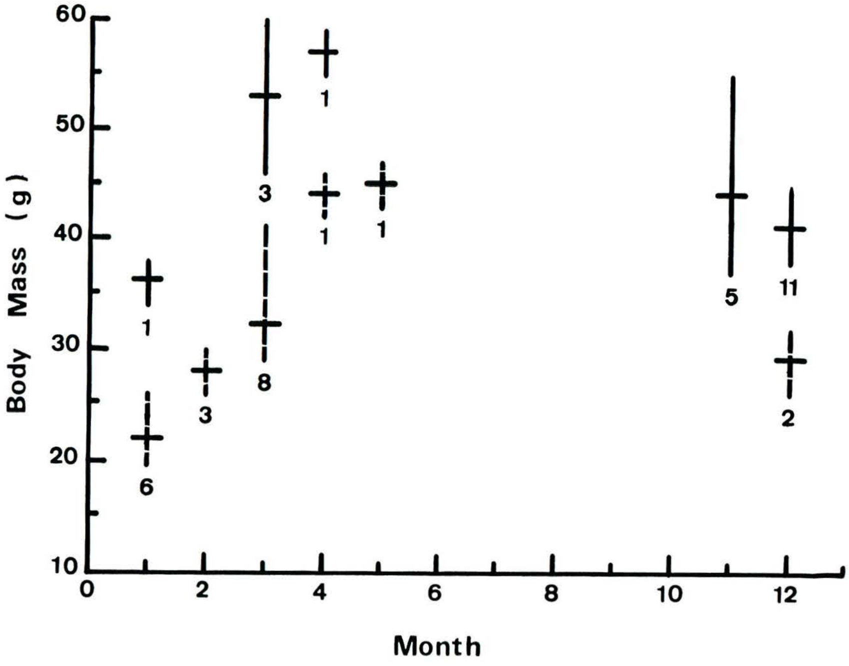

Fig. 5. The seasonal changes in body mass of wild caught adult (solid bars) and juvenile (slashed bars) *Burramys parvus.* The bar is the mean body mass, the vertical line connects the range and sample size is given below this range. (Data from Dixon 1971, Gullan and Norris 1981, Green pers. comm. and Fleming pers. obs.).

of this species probably accounts for most of the insulation because there is very little subdermal fat (Dimpel, personal communication). The SMR (2.15 W kg $^{-0.75}$) is also reduced, being 91% of the mass predicted value (Fleming 1982). This gives an overall metabolic response (Fig. 1) which considerably reduces the energy expenditure of *B. parvus* at all T_a. This is reflected by T_{lc} for *B. parvus* which is three degrees lower than the mass predicted value of 30.6°C (Fleming 1980). As a consequence, absolute food requirements would be reduced at time of food shortage and survival time on body fat reserves would be increased.

The pattern of respiratory rate observed in *B. parvus* (Fig. 2) differs from that found in the similar sized *C. nanus* (Bartholomew and Hudson 1962) in two respects. At $T_a = 5°C$, the breathing rate of *B. parvus* is only double the minimum value whereas *C. nanus* has tripled its breathing rate. This reflects differences in conductance. At high T_a, the difference in patterns is more striking. The respiratory rate of *C. nanus* did not increase from minimum levels until T_a exceeded 36°C, and then breathing rate tripled by $T_a = 38°C$. *Burramys parvus* showed an increased breathing rate at $T_a = 28°C$, but this increase was accompanied by rapid hyperthermia, suggesting that these possum are unable to lower T_b by evaporative cooling.

Burramys parvus is the only mammal restricted to the Australian Alps, where snow cover may last for five months and the mean monthly maximum air temperature for summer does not exceed 16°C. The thermophysiology of *B. parvus* shows modifications similar to those described for some placental mammals from cold environments (Scholander *et al.* 1950 and Casey *et al.* 1979). The reduction in thermal con-

Date	Animal	Mass (g)	T_a (°C)	Length of episode of torpor (h)	Days active prior to next episode
12 June	4	54.7	7.5	78.8	7
9 July	4	61.2	5.5	12.5	3
21 July	4	57.5	5.5	9.0	3
24 July	4	57.5	5.5	112.6	5
19 Aug.	2	53.9	7.0	80.1	5
12 Sept.	2	50.7	6.5	154.8	—

Table 1. Episodes of undisturbed torpor for *Burramys parvus.*

ductance from the expected value falls within the range of values (33-49%) recorded for winter acclimated arctic mammals (Casey *et al.* 1979). A higher than expected BMR is usually considered adaptive to cold environments, so that a high ($\approx$ 39°C) and stable T_b can be maintained (Scholander *et al.* 1950, Bartholomew 1977 and Withers *et al.* 1979). However, *B. parvus* maintains a constant T_b of 36.2°C with a BMR that is only 63% of that predicted for an equivalent sized placental. The reduced BMR of *B. parvus* may be associated with the need to reduce energy expenditure during times of critical winter food shortage (Wang *et al.* 1973) or to facilitate entry into torpor (Morrison 1960, Hudson and Bartholomew 1964 and Hudson and Deavers 1973). Torpor is an important component of the thermal strategy of *B. parvus* (see below) so the latter interpretation is more likely.

Possibly as a consequence of these adaptations to cold, *B. parvus* is unable to tolerate heat, as is reflected in the truncation of the thermal neutral zone. It is not known if *B. parvus* undergoes a summer moult in the wild but a reduction in the insulation of the pelt would reduce the risk of hyperthermy. The diminution of the distribution of *B. parvus* that has occurred from Pleistocene times (Wakefield 1972) to the present may have resulted directly from the physiological inability of this species to cope with the general warming of the Australian climate (Galloway and Kemp 1981), leaving it isolated in the few remaining areas close to or above the snowline.

NORMOTHERMIC GROUPS

The mode of huddling in *B. parvus* differs from that observed in *A. pygmaeus* and *P. breviceps* (Fleming 1980, 1985), but the metabolic benefits of huddling are still apparent (see Fig. 3) with the regression equation for groups of four having a significantly smaller slope than the equation for single animals (t-test, $p < 0.01$). This difference in slope can lead to considerable savings at low T_a; for example, the VO_2 of a group of four at a $T_a = 0°C$ is 20% lower

Mass (g)	T_a (°C)	T_b (°C)	Method of calculation of VO_2 Area under curve	Mean	n
59.3	7.5	8.0	—	0.051	8
57.5	5.5	—	0.031	0.042	10
57.5	5.5	—	—	0.022	17
57.5	5.5	6.0	0.131	0.136	13
58.0	7.0	8.0	0.085	0.084	12

Table 2. VO_2 (ml O_2 $g^{-1}h^{-1}$) and T_b during torpor in *Burramys parvus.*

than the $V0_2$ of a single animal. The lower thermal conductance for groups of four has not led to a reduction in T_{lc} as found in other possums (Fleming 1980, 1985). This may be due to the lack of group cohesiveness at T_a close to the TNZ.

TORPOR

Torpor in captive *B. parvus* has been described in two studies. Dimpel and Calaby (1972) recorded three episodes of torpor during winter in an adult female kept in an unheated basement in Canberra, where T_a varied from 9 to 13 °C. This study recorded thirteen episodes of torpor in two adult male *B. parvus,* which were housed within a polystyrene cabinet cooled by ice. Both of these studies provided the captive animals with an environment that was cold, dark, humid and with little disturbance, conditions similar to those found in the subnivean environment (Pruitt 1978). The failure to induce more than one episode of torpor in *B. parvus* during the first two winters of the Monash study may have been due to excessive disturbance, noise from the refrigeration unit and a lack of seasonal acclimatization.

Acclimatization to seasonal changes in air temperature has been shown to be an important factor in the induction of torpor in a number of small mammals using winter torpor (Lyman 1954 and Gaertner *et al.* 1973). The two studies that were successful in inducing torpor in *B. parvus* both used animals that had been housed outdoors, whereas the pygmy possums used during the first two winters of the Monash study had been maintained indoors at a T_a of 22°C. For the third winter, two naturally acclimatized animals were wild-caught in early autumn and transferred immediately to the polystyrene cabinet. Their failure to enter torpor is difficult to interpret.

The pattern of torpor found in *B. parvus* shows many features common to all burramyids and other tiny possums so far studied. *Cercartetus nanus, C. concinnus* and *A. pygmaeus* (Hickman and Hickman 1960, Bartholomew and Hudson 1962, Wakefield 1970 and Fleming 1985) can all be torpid at low T_b ($<6°$) for extended periods (>24 hrs). However, *B. parvus* differs from this general pattern in the important areas of induction of torpor and the seasonal occurrence of torpor.

Starvation induces torpor in all species of small marsupial (mass <200 g) so far studied, except in *B. parvus,* where the induction of torpor appears to be a function of mass, for torpor occurred only when body mass exceeded 50 g (Fig. 4). A similar pattern of induction has been described in the small placental hibernators, the Golden Hamster (*Mesocricetus auratus*) and the Eastern Chipmunk (Lyman 1954 Wang and Hudson 1971), where increases in food storage and body weight were required for the onset of torpor. An annual cycle of change in body mass, with an increase prior to the season of torpor, is characteristic of placental mammals using prolonged torpor (Mrosovsky and Barnes 1974) and limited evidence from field work suggests that *B. parvus* fattens during late summer and autumn (Fig. 5). If there is a body mass threshold that must be exceeded before torpor can be induced, the torpor season in *B. parvus* would be confined to the part of the year when body mass is greatest; i.e., winter. Torpor has not been observed in captive *B. parvus* during spring and summer (Dimpel, pers. comm.), unlike *C. nanus* and *A. pygmaeus* which readily enter torpor throughout the year (Hickman and Hickman 1960, Bartholomew and Hudson 1962 and Frey and Fleming 1984).

The decrease in $V0_2$ during torpor at $T_a = 6°C$ (Table 2) represents a reduction in metabolic rate to a level between 0.6% and 3.9% of the normothermic rate at that temperature. When this reduction is integrated over episodes of torpor lasting up to seven days (Table 1, Dimpel and Calaby 1972), an animal would make considerable energy savings. These savings may not represent the maximum that could be attained by *B. parvus* because it was not possible to expose the animals to temperatubes lower than 6°C with the equipment available.

The two brief episodes of torpor which lasted only 9.0 and 12.5 h (Table 1) may represent test drops as they occurred three days before a longer bout of torpor. The longer episodes of torpor were separated by periods of normothermia lasting five to seven days (Table 1). If this represents the natural pattern of torpor in the wild, *B. parvus* may use these periods of activity to feed on seeds cached inside the nest or nearby (Kerle 1984). Food hoarding and extended periods of nomothermia between episodes of torpor appear to be a pattern of behaviour common to hibernators of small body size ($<$200 g) because they are unable to store sufficient body fat (Lyman 1954, Wang and Hudson 1971 and Maclean 1981).

Hibernation is a term that has been used to describe many different forms of winter thermal strategy. Concise physiologically-based definitions define hibernation as very deep torpor with body temperature below 10°C, a small T_a to T_b difference, metabolism reduced to less than 1/20th of the normothermic level and episodes of torpor which last a week or more (Lyman and Chatfield 1955, Hudson 1973 and Bartholomew 1977). This study has shown that the thermal physiology of *B. parvus* meets these criteria and that this species, therefore, qualifies as a true marsupial hibernator.

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