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Hibernation in the mountain pygmy possum *Burramys parvus* (Marsupialia)

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(With 3 figures in the text)

Mountain pygmy possums *Burramys parvus* (40 g) disappear from their Mt. Kosciusko boulder fields from May to October/November and it is assumed that they hibernate during this time. However, laboratory studies did not observe the characteristic hibernation pattern of placentals, which, throughout the hibernation season, show long bouts of torpor (several days to weeks) that are interrupted by short (< 1 day) normothermic periods. We investigated the pattern of hibernation in juvenile ($N = 8$) and adult ($N = 8$) male and female *B. parvus* in the laboratory at an air temperature that was similar to that in the field during winter. Adults commenced hibernation earlier and hibernated longer (about seven months) than juveniles (about five months). All adult individuals hibernated whereas only six of the eight juveniles did so. Hibernating animals showed distinct seasonal changes in the duration of torpor bouts. Torpor bouts were short (about five days) at the beginning, long (12–20 days) during the middle, and short again at the end of the hibernation season. Normothermic periods were usually shorter than one day. The pattern of the seasonal change of torpor bout duration differed between juveniles and adults and between sexes. Body temperature during mid-hibernation was regulated at about 2 °C in females and 3 °C in males and the metabolic rate was similar to that of hibernating placentals.

Contents

Introduction

Hibernation is found in a number of mammalian orders. This physiological adaptation to seasonal changes of climate and food availability is expressed by a substantial reduction of body temperature (T_b), metabolism and other physiological functions (Lyman *et al.*, 1982). However, hibernating mammals do not remain torpid throughout the hibernation season. Torpor bouts during which T_b falls below 10 °C for several days or weeks are interrupted by endothermic arousals that are followed by short (< 1 day) normothermic periods (Wang, 1978; French, 1985; Barnes *et al.*, 1986).

Most of the work on hibernation has been conducted on placental mammals from the northern hemisphere (Lyman *et al.*, 1982). Because detailed information about hibernation on the other

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mammalian groups (monotremes and marsupials) is sparse, it is often assumed that they do not hibernate in the classical sense. However, these mammals have to cope with a similar range of seasonal stresses as do placentals and it is not unlikely that they could have evolved similar physiological responses to the same energetic problems.

To provide conclusive data on the subject we investigated the torpor pattern of the marsupial mountain pygmy possum *Burramys parvus*. This species is confined to altitudes of 1400–2200 m of the Snowy Mountains of south-eastern Australia (Calaby, 1983; Broome & Mansergh, 1990). *Burramys* had a much wider distribution range in the past, but extant populations have been reduced to a total of only about 2000 individuals living in boulder fields that are covered by snow for up to five months during the austral winter. It is assumed that they hibernate because animals disappear from their habitat from May to October (Mansergh, 1984). However, laboratory studies (Dimpel & Calaby, 1972; Fleming, 1985) did not observe the hibernation pattern of long torpor bouts interrupted by short normothermic periods that are so characteristic for hibernating placentals. Therefore, we investigated the pattern of torpor in *B. parvus* in the laboratory under environmental conditions that were similar to those experienced by animals in the wild. We compared juvenile and adult males and females to determine whether intraspecific differences in the pattern of hibernation, that have been observed in placental mammals (French, 1982), also occur in marsupials.

Materials and methods

Eight adults (4 males and 4 females), and 8 juveniles of the year (4 males and 4 females) were caught in late March 1989 near Charlotte Pass in Kosciusko National Park at an altitude of about 1800 m. Animals were transferred to the University of New England, Armidale, New South Wales, at an altitude of about 1000 m, and maintained in temperature-controlled cabinets (air temperature, $T_a \pm 0{\cdot}5$ °C) and a photoperiod of LD 9·5:14·5 light from 07:30 to 17:00 h EST, which is close to the shortest photoperiod experienced by wild populations. Water was freely available throughout the experiment. Food was provided ad libitum during the time of fattening, but was removed during most of the hibernation season (see Figs 1 and 2). Food was exchanged daily and consisted of high protein baby cereal with honey and water, canned baby food, apples, carrots, walnuts and sunflower seeds. Calcium and vitamins were mixed into the food. Animals were weighed at regular intervals; in torpid individuals this induced premature arousals in 23% of observations. The decline of T_a from 12 to 2 °C shown in Fig. 1 for adults was similar to that in autumn in their natural habitat. In juveniles, T_a had to be raised from 2 to 8 °C for a short time period in autumn because they did not enter torpor and lost weight (Fig. 2). However, juveniles began to hibernate when T_a was reduced again to 2 °C later in the season. All animals that hibernated in the laboratory survived the experiments and were released in November at their site of capture.

The duration of torpor bouts in hibernating individuals was determined by observing daily at 09:00–10:00 h the displacement of sawdust from the back of the animals that occurs when they arouse. All undisturbed torpor bouts of all individuals were used to calculate the mean duration of torpor bouts over a particular time interval. When torpor bouts extended over 2 months the torpor bout was included in the month in which the longer part of the bout occurred. The metabolic rate (measured as oxygen consumption, $\dot{V}O_2$) and minimum T_b, the species-specific minimum at which T_b is regulated during torpor (Heller & Hammel, 1972), of hibernating animals were determined when they had been hibernating for at least 2 months. These values are lowest during the central part of the hibernation season (Geiser *et al.*, 1990). Adults were measured between 10 and 21 July, juveniles between 14 and 27 August. For these measurements, hibernating animals were transferred from their holding chambers at T_a 2 °C to a respirometer vessel at T_a $2{\cdot}0 \pm 0{\cdot}5$ °C. The T_a, measured by thermocouple in the respirometer, was slowly decreased by less than 0·02 °C/min when the $\dot{V}O_2$ had stabilized. The minimum T_b and minimum T_a was measured at the time when the increase in $\dot{V}O_2$ was observed that prevents a further drop of T_b in the torpid animal (Geiser *et al.*, 1990). The minimum T_b was determined by a 4-cm rectal insertion of a 38 Gauge thermocouple probe that was calibrated to the nearest 0·1 °C and read with an Omega Model HH-71 T Microcomputer thermometer. To maximize heat exchange with the air during the cooling experiment, we suspended the animals in a plastic mesh hammock in the respirometer vessel (Geiser *et al.*, 1990). Because the sensitivity to disturbance increases towards the end of a torpor bout, cooling experiments were performed between days 2 and 4 of a torpor bout. Premature arousal occurred after the cooling experiments and T_b measurements in 79% of the observations. $\dot{V}O_2$ was measured, after removal of water from the air stream, with an Applied Electrochemistry S-3A/II oxygen analyser. The flowrate of dry air through the 0·75-litre respirometer vessel was 80 ml/min. The $\dot{V}O_2$ at T_a $2{\cdot}0 \pm 0{\cdot}5$ °C was integrated over 1 hour, corrected to STP and calculated according to Withers (1977).

Numeric values in the text are expressed as mean ± 1 standard deviation.

Results

Burramys parvus showed a prolonged hibernation season in the laboratory. The pattern of hibernation differed substantially between juveniles and adults and between sexes (Figs 1 and 2). Adults commenced hibernation earlier (late April) than juvenile males (late May/June) and females (late June). Six adults entered torpor at T_a 8 °C, the other two only entered torpor after T_a was lowered to 2 °C. All adults at a body mass of 70–80 g commenced hibernation when food was freely available. In contrast, only two of the male juveniles (body mass 62 and 68 g) started to hibernate in May when food was available. All other juveniles that had a body mass of 50–63 g in May entered torpor only after withdrawal of food in late June when body mass ranged from 62–69 g. One juvenile of each sex did not fatten (body mass was always < 55 g) and both individuals never entered torpor, although food was withheld from them several times.

The hibernation season of adults was longer than that of juveniles (Figs 1 and 2). Adults hibernated for about seven months, juvenile males for 5–6 months and juvenile females for about five months. Although most individuals commenced hibernation when food was freely available in autumn, all individuals ceased to hibernate after food was offered in spring. We do not know whether the animals would have continued to hibernate if no food had been provided as has been observed in several placental hibernators (French, 1986).

The duration of torpor bouts changed with season in all animals. Torpor bouts were short at the beginning of the hibernation season and long in the central part of the hibernation season. Adult males showed a decrease in the duration of torpor bouts from August to October and a slight increase again in November. Adult females showed a close to constant duration of torpor bouts from July to November. In the juveniles, the seasonal change of torpor bout duration was more pronounced than in adults and both juvenile males and females did not show a prolonged period during which torpor bout duration was stable.

The T_a had an additional effect on the bout duration. The rise of T_a to 8 °C in November resulted in a shorter bout duration. Food availability did not seem to have a strong impact on the seasonal change in the duration of torpor bouts in early hibernation.

In adult females, the torpor bouts were longer ($P < 0{\cdot}05$; *t*-test) than those of males from September–November (Fig. 1). This resulted in fewer arousals in females ($16{\cdot}3 \pm 1{\cdot}3$ times) than in males ($21{\cdot}3 \pm 2{\cdot}9$ times) over the 174 days of food withdrawal ($P < 0{\cdot}01$; *t*-test). The longest bout for an adult female was 19 days and the longest bout for an adult male was 16 days. In early hibernation, the duration of torpor bouts was longer in juvenile males than in females because two of the three males commenced hibernation earlier than the females and thus were in a later state of hibernation when females began to hibernate (Fig. 2). In late hibernation, the torpor bouts of the

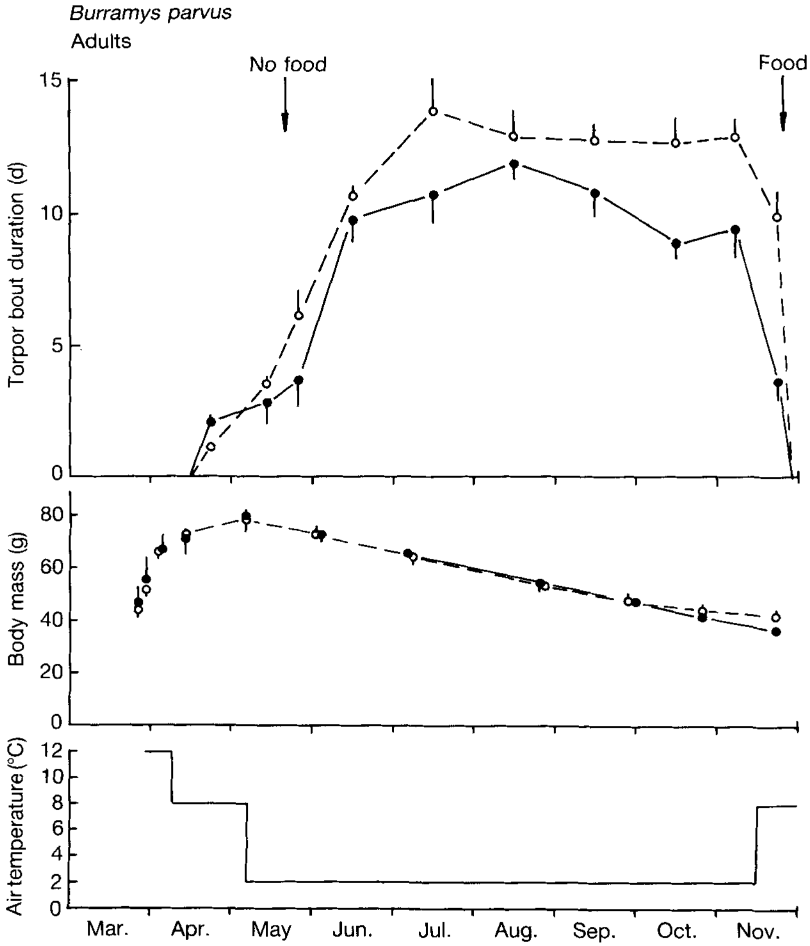

FIG. 1. Seasonal patterns of the duration of torpor bouts and body mass of adult *Burramys parvus* females (○- - -○) and males (●——●), and the T_a at which the animals were maintained. All undisturbed torpor bouts of all hibernating individuals were used to calculate the mean duration of torpor bouts over a particular time interval. When torpor bouts extended over two months the torpor bout was included in the month in which the longer part of the bout occurred. Values are means with S.E. for four individuals/sex except for April when they represent three individuals/sex.

juvenile females seemed to be longer than those of males, although the values did not differ significantly because of low numbers and high variability (Fig. 2). The longest individual torpor bouts in juveniles were 20 days in females and 18 days in males. The mean of the two longest consecutive torpor bouts observed within the hibernation season of each individual differed significantly between sexes in adults ($P < 0{\cdot}01$; *t*-test) and between all juveniles and adults ($P < 0{\cdot}05$; *t*-test; Tables I and II).

Body mass of all individuals that hibernated approximately doubled during the pre-hibernation period. Adults increased their body mass from 43·7 ± 4·0 g at capture to 78·1 ± 8·5 g (females) and

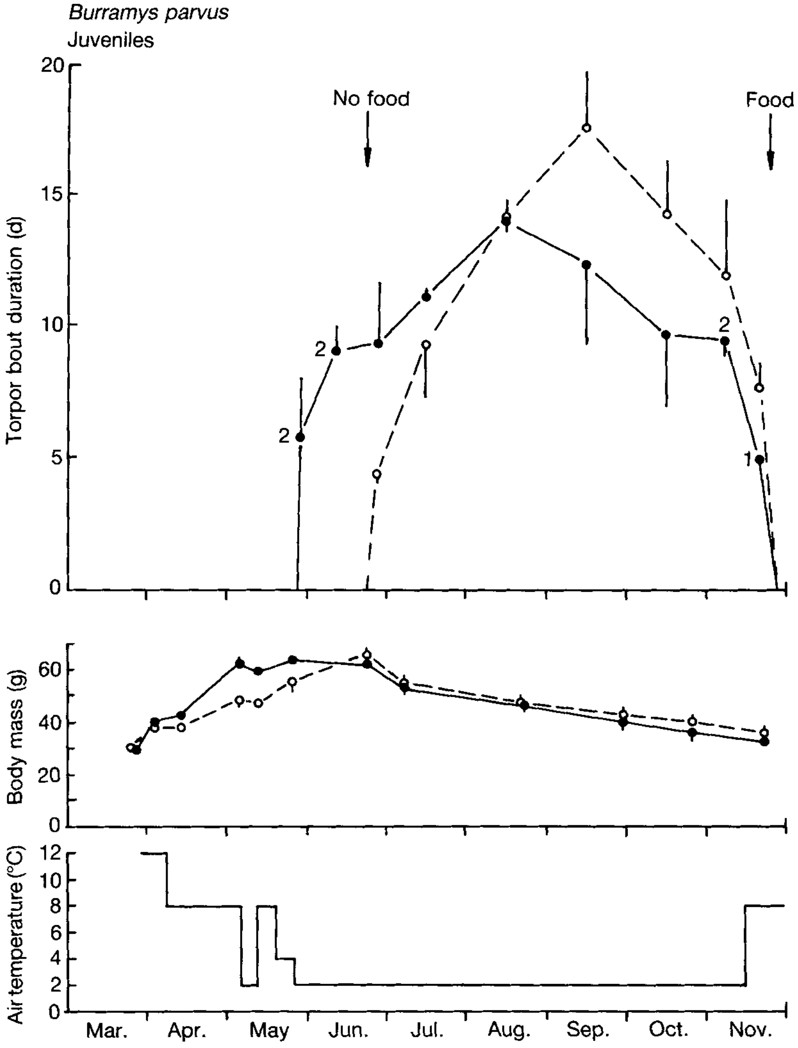

FIG. 2. Seasonal patterns of the duration of torpor bouts and body mass of juvenile *Burramys parvus* females (O– – –O) and males (●——●), and the T_a at which the animals were maintained. All undisturbed torpor bouts of all hibernating individuals were used to calculate the mean duration of torpor bouts over a particular time interval. When torpor bouts extended over two months the torpor bout was included in the month in which the longer part of the bout occurred. Values are means with S.E. for three individuals/sex or as indicated in the figure. Two of the males became very light towards the end of the hibernation season and therefore were removed from the temperature cabinet before the other individuals.

46·3 ± 12·3 g to 79·8 ± 5·5 g (males). Juvenile females increased their body mass from 30·3 ± 2·3 to 65·6 ± 3·9 g, males from 29·5 ± 1·7 to 63·4 ± 3·3 g (Figs 1 and 2).

When animals had commenced hibernation, body mass decreased throughout the rest of the hibernation season. The weight loss over the entire hibernation season was similar between juveniles and adults and sexes and ranged between 0·19 g/d in adult females and 0·22 g/d in juvenile

TABLE I

The minimum T_b, minimum T_a, $\dot{V}O_2$ at T_a 2 °C, and body mass of adult ***Burramys parvus***

Sex	N	Minimum T_b (°C)	Minimum T_a (°C)	$\dot{V}O_2$ at 2 °C (ml O_2/g h)	Bout duration (days)	Body mass (g)
Females	4	2·0±0·2	0·6±0·3	0·021±0·007	15·9±1·5	63·2±7·6
Males	4	2·7±0·2	1·2±0·1	0·029±0·006	12·6±1·5	62·3±2·2
t-test		$P<0·01$	$P<0·01$	ns	$P<0·01$	ns

Numeric values are means ± S.D. Bout duration represents the mean of the mean of the two longest consecutive torpor bouts during the hibernation season of each individual. Body masses were determined during the $\dot{V}O_2$ measurements. The minimum T_b and minimum T_a are the values measured when the torpid animal increased its metabolic rate to prevent a further drop in T_b. N = number of individuals

males. However, the weight loss of adult females in the second half of the hibernation season, when their torpor bouts were longer than those of males, was less (0·15 ± 0·02 g/d) than that of the males (0·20 ± 0·02 g/d) ($P<0·05$; *t*-test). In juveniles a similar trend was observed between sexes during the time when no food was available (females 0·13 ± 0·03 g/d; males 0·17 ± 0·02 g/d).

The minimum T_b and minimum T_a of torpid individuals during the central part of the hibernation season also differed between adult males and females (Table I). Adult females had significantly lower minimum T_bs and minimum T_as than the males ($P<0·01$; *t*-test; Table I). The $\dot{V}O_2$ did not differ significantly between sexes, but the females showed slightly lower $\dot{V}O_2$s than the males. The lowest individual T_b measured in adults was 1·8 °C in a female and 2·5 °C in a male. In the juveniles, no significant differences could be observed between these variables, however, as in adults, the minimum T_b and the minimum T_a of the females showed a trend to lower values than in the males (Table II). The lowest individual T_b measured in juveniles was 2·1 °C in a female and 2·8 °C in a male. The difference between the mean minimum T_b and the minimum T_a ranged between 1·3 and 1·5 °C in all groups. The duration of torpor bouts did not seem to be affected by the cooling experiments; mean torpor bout duration increased by 1·0 ± 3·6 days from the last uninterrupted bout before to the first uninterrupted bout after the cooling experiment.

The $\dot{V}O_2$ of hibernating individuals showed an interesting fluctuation of high $\dot{V}O_2$ alternating with low $\dot{V}O_2$ (Fig. 3). These fluctuations were caused by the breathing pattern of the animals, which alternated between periods of polypnoea during the $\dot{V}O_2$ increase and apnoeas during the $\dot{V}O_2$ decrease, which represents the wash out of CO_2 from the respirometer. The amplitude and

TABLE II

The minimum T_b, minimum T_a, $\dot{V}O_2$ at T_a 2 °C, and body mass of juvenile ***Burramys parvus***

Sex	N	Minimum T_b (°C)	Minimum T_a (°C)	$\dot{V}O_2$ at 2 °C (ml O_2/g h)	Bout duration (days)	Body mass (g)
Females	3	2·6±0·7	1·3±0·2	0·024±0·002	16·7±3·0	46·9±5·4
Males	3	3·0±0·2	1·7±0·5	0·020±0·003	16·5±1·3	46·2±3·4

Numeric values are means ± S.D. Bout duration represents the mean of the mean of the two longest consecutive torpor bouts during the hibernation season of each individual. Body masses were determined during the $\dot{V}O_2$ measurements. The minimum T_b and minimum T_a are the values measured when the torpid animal increased its metabolic rate to prevent a further drop in T_b. Variables did not differ significantly between sexes ($P>0·05$; *t*-test). N = number of individuals

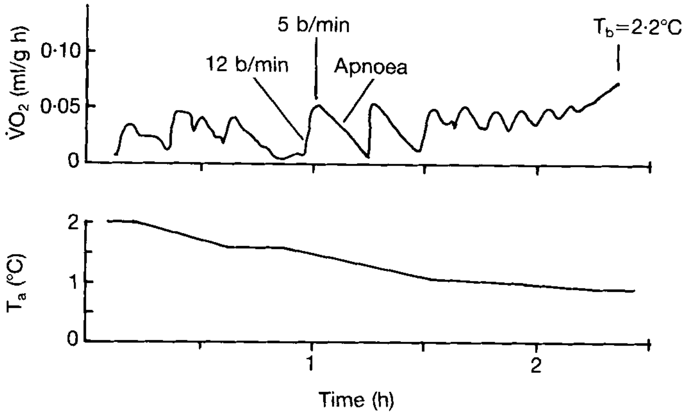

FIG. 3. Fluctuation of oxygen consumption ($\dot{V}O_2$) of a torpid *B. parvus* and the decrease of air temperature (T_a) during a cooling experiment. At T_a 2·0–1·1 °C the $\dot{V}O_2$ alternated between high and low rates because the breathing pattern changed between polypnoea (12 breaths/min) and apnoea (0 breaths/min). At lower T_as the pattern of $\dot{V}O_2$ and breathing became more regular. When an increase in $\dot{V}O_2$ and ventilation occurred, indicating onset of thermoregulation, the animal was removed immediately from the respirometer and the minimum T_b, in this example 2·2 °C, was determined. The minimum T_a, measured at the time of increase in $\dot{V}O_2$, was 0·9 °C.

interval between these fluctuations shortened before the minimum T_b was reached and they were abolished when the animals increased $\dot{V}O_2$ and started to thermoregulate.

Rewarming from torpor was rapid, but the rate of rewarming was not uniform throughout the arousal process. The fastest overall arousal rate was 0·54 °C/min and was determined at T_a 21 °C in an animal that weighed 32·7 g; initial slow rewarming rates increased to a maximum of 0·93 °C/min over a 10-min period between T_bs of 24·4 and 33·7 °C. During rewarming the animals showed intensive shivering and breathing, especially at T_bs above 22 °C. One animal ate food immediately after it had reached normothermic T_b (>35 °C) and was still very uncoordinated.

Discussion

Our study clearly shows that the pattern of hibernation in *Burramys parvus* is not different from that observed in classical placental hibernators (Lyman *et al.*, 1982). Body temperature fell to 2–3 °C, the duration of torpor bouts lasted up to 20 days and showed the characteristic seasonal changes that occur in placental mammals, and the animals hibernated successfully for up to 7 months. Moreover, the metabolic rate of torpid *B. parvus* was similar to that of placental hibernators of similar body mass (Geiser, 1988; Geiser *et al.*, 1990) and the rewarming process was rapid.

However, the pattern of torpor in *B. parvus* differed between juveniles and adults and between sexes. As in sciurid rodents (Kenagy & Barnes, 1988), juveniles commenced hibernation later than the adults. Successful hibernation requires extensive fattening in animals that rely predominantly on body fat rather than food caches for energy supply during hibernation. *Burramys parvus* fatten extensively during the pre-hibernation period. A major component of their food supply, Bogong moths *Agrotis infusa* (Mansergh & Bennett, 1989; Broome, unpubl.), is perishable so it is likely that they rely largely on fat for energy supply during hibernation. Juveniles, which are born in

November/December, have a relatively short time to reach adult size and put on enough fat for a successful hibernation season. However, the earlier entry into hibernation by adults may reduce potential competition for food resources which should allow the juveniles to forage for a longer period in autumn, put on more fat, and reduce the duration of the hibernation period.

Differences in the pattern of torpor between sexes and between adults and juveniles appear to be governed strongly by the body mass of the animals. The logarithm of body mass in all individuals was inversely related to the logarithm of the duration of the two longest consecutive torpor bouts ($r^2 = 0{\cdot}40$; $P < 0{\cdot}02$; $n = 14$) and with the minimum T_b ($r^2 = 0{\cdot}34$; $P < 0{\cdot}05$; $n = 14$). Correlations between body mass and the duration of torpor bouts have been observed previously for placental mammals (French, 1982, 1986). However, the strongest correlation was observed between the duration of the two longest torpor bouts and the minimum T_b of adults ($r^2 = 0{\cdot}68$; $P < 0{\cdot}01$; $n = 8$), supporting the view that the duration of torpor bouts is physiologically linked to the minimum T_b of the animal (Geiser *et al.*, 1990). In juveniles, no correlation could be found between the duration of torpor bout and the minimum T_b most likely because they changed bout duration (and most likely their minimum T_b) throughout the hibernation season and did not show a period of constant torpor bout duration.

Differences between sexes in the pattern of hibernation also seem to reflect the climate of their hibernacula. Adult females tend to hibernate at higher altitudes than males (Broome & Mansergh, 1990). It is likely that at higher altitudes the animals are exposed to lower T_a, which may have resulted in lower minimum T_b in the females. The lower T_b in turn may be the reason for the longer torpor bouts and lower weight loss in the females. Energetic savings during hibernation require substantial reduction of body temperature. Selection of a cold hibernaculum site allows such a reduction in T_b, however, if the T_a drops below the minimum T_b of the animal it has to increase its metabolic rate for thermoregulation (Heller & Hammel, 1972). This results in an increased energy loss and more frequent energetically expensive arousals, which may result in energy depletion before the end of the hibernation season (Geiser & Kenagy, 1987, 1988). It therefore appears that hibernators either select T_a close to or slightly above their minimum T_b to conserve the maximum amount of energy during hibernation (Twente, 1955; Barnes, 1989), or the T_a of their hibernaculum provided the selective pressure that over time resulted in an approach of the minimum T_b towards the T_a of the hibernaculum. This would result in an enhancement of energetic savings during hibernation by a reduction of the metabolic rate and long torpor bouts (Geiser & Kenagy, 1988; Barnes, 1989).

The difference in the hibernation pattern between sexes and juveniles and adults also is reflected in their survival rate in the wild. Adult females which show longer bouts, lower $\dot{V}O_2$ and lower minimum T_b than males have a better survival rate than males (Broome, unpubl.). Juveniles which commence hibernation at a lower mass than adults have a lower survival rate than adults (Broome, unpubl.).

The reduction of the metabolic rate of hibernating *B. parvus* was pronounced. The Q_{10} for $\dot{V}O_2$ between normothermia (BMR 1·12 ml/g h) and torpor was 3·0–3·3 in the experimental groups. This pronounced reduction in the metabolic rate during torpor results in a low energetic cost of torpor bouts in *B. parvus* when compared to the cost of the periodic arousals. If we assume that arousals and the associated period of normothermia lasted one day (it was somewhat shorter, but the exact time does not have a strong impact on the derived values), the metabolism of torpid adults would have used up 2·9 g body fat in males and 2·3 g fat in females from June to November, which is 8 and 7%, respectively, of the total fat loss during this time (assuming that the combustion of 1 g fat requires 2 litre of oxygen; Schmidt-Nielsen, 1979). A single normothermic period of one day required about 1·56 g fat in males and 1·85 g fat in females, which is more than half of the energy used by torpid animals during approximately 155 days of hibernation.

Hibernation in *B. parvus* appears to be seasonal. Animals fattened extensively prior to hibernation in autumn and lost weight throughout the rest of the hibernation season to approach the normal body mass of active animals in spring. Torpor occurred in autumn when food was freely available, however, in spring animals ceased hibernation after their first arousal when food had been offered. This pattern of hibernation in *B. parvus* differs from the pattern in other Burramyids. *Cercartetus lepidus* and *C. concinnus* hibernated at any time of the year with body temperatures of about 5 °C and multiday torpor bouts (Geiser, 1987). However, it is not known whether *Cercartetus* spp. show a seasonal change in the pattern of hibernation. More studies are required on *B. parvus* to ascertain whether their seasonal torpor in the wild is regulated by a circannual rhythm, as in ground squirrels (Morrison, 1964), or whether torpor is influenced by seasonal changes of food availability, temperature and photoperiod.

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