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## Ecology of natural hibernation in the marsupial mountain pygmy-possum (*Burramys parvus*)

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**Abstract** The hibernating marsupial mountain pygmy-possum (*Burramys parvus*, 40 g) has to raise its slow-growing offspring during a short alpine summer. Only females provide parental care, while after mating males emigrate to marginal habitats often at lower altitudes which can sustain only low possum densities. We predicted that the hibernation strategies in mountain pygmy-possums are distinct from those of similar-sized placental hibernators, because of the developmental constraints in marsupials and because hibernation differs between the sexes. Using temperature-sensitive radio transmitters, we studied the hibernation patterns of free-living male and female mountain pygmy-possums living in a north- and a south-facing boulder field (Kosciusko National Park) for two consecutive winters. Individual possums commenced hibernation several months before the snow season. As in other hibernators, torpor in the mountain pygmy-possum was interrupted by periodic arousals which occurred most often during the late afternoon. Torpor bouts initially lasted a few days when the hibernacula temperature ( $T_{hib}$ ) ranged from 4 to 7°C. As the hibernation season progressed, torpor bouts became longer and possum body temperatures ( $T_b$ ) approached 2°C. The  $T_b$ s of females were significantly lower and torpor bouts were longer in the second half of the hibernation season than in males. Between torpor bouts, both sexes were often active and left hibernacula for periods of up to 5 days. Especially during the first months of the hibernation season, possums also frequently changed hibernacula sites probably in an attempt to select a site with a more suitable microclimate. Emergence from hibernation was closely coupled

with the disappearance of snow from the possum habitat (September 1995, October 1996) and the limited fat stores probably dictate an opportunistic spring emergence. However, in 1995, spring was early and males emerged significantly earlier than females. In 1996, when snow melt was delayed, this difference vanished. Testes are regressed in males during hibernation and the time needed for testes growth and spermatogenesis favours an earlier emergence for males which was probably achieved by their preference for the more sun exposed north-facing boulder field. A sexual dimorphism in hibernation strategies and spring emergence therefore enables mountain pygmy-possums to cope with their harsh alpine environment.

**Key words** Alpine · Natural hibernation · Marsupial · Pygmy-possum · Torpor

### Introduction

Many mammals are confronted with seasonal changes in food availability. Large animals with their low mass-specific metabolic rate are able to sustain their energy demands during times of food shortage by metabolising body fat stores. In contrast, small animals with their high mass-specific metabolic rate, unfavourable surface to volume ratios and small fat stores can sustain normal metabolism only for short periods, in extreme cases only for a few hours. If food shortage is associated with low winter temperatures, energy demands for thermoregulation become prohibitively high.

To overcome these energetic constraints, many small mammals (<10 kg) employ hibernation as an energy-saving strategy. However, in relatively large hibernators, like many of the well-studied sciurid rodents, favourable climatic conditions and food availability often do not determine the onset and end of hibernation, which are

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predominantly governed by an endogenous circannual rhythm (Pengelley and Fisher 1957, 1963; Mrosovsky 1980). Emergence in spring can therefore occur before snow melt and before fresh food becomes available, but the large body size of these species enables them to survive prolonged normothermic periods on body fat. The early emergence and breeding season ensures that juveniles have time to gain sufficient body fat before the next hibernation season. Since a functional reproductive system and hibernation seem to be incompatible in male sciurid rodents (Liddle and French 1982; Barnes et al. 1986, 1987), these time constraints for reproduction also lead to distinct differences in hibernation strategies and timing of emergence between the sexes (Kenagy 1989; Young 1990; Michener 1992; Arnold 1993). In contrast, most smaller hibernating mammals with their rapid juvenile growth rate are not subjected to these reproductive time constraints, but are also not able to survive prolonged normothermic periods without feeding. Accordingly, the few data available for small placental hibernators suggest a more opportunistic timing of the hibernation season (French 1986).

It appears that the small marsupial mountain pygmy-possum (*Burramys parvus*, Marsupialia ca. 40 g) follows patterns of small placental hibernators since, at least in captivity, an endogenous circannual rhythm shows little persistence and the expression of hibernation can vanish completely (Geiser et al. 1990; Mansergh and Scotts 1990; Körtner and Geiser 1995, 1996). However, in contrast to most placental mammals, the juvenile development of marsupials is slow (Tyndale-Biscoe 1973). Thus the small alpine mountain pygmy-possum, which experiences very short summers, is subjected to similar reproductive time constraints as the much larger ground squirrels and marmots. Accordingly, sex-related differences in torpor bout length and minimum body temperature ( $T_b$ ) similar to ground squirrels have been recorded under laboratory conditions (Geiser and Broome 1991). Furthermore, it appears that, unlike other mammalian hibernators, male and female possums are segregated for most of the year except for the short spring mating season when males visit female home ranges. Females usually occupy the best habitats, which are often situated at higher altitudes or on south-facing slopes, while males are generally confined to marginal habitats often at lower altitudes (Mansergh and Scotts 1986; Mansergh and Broome 1994). Given these differences in altitude and aspect between the habitat typically occupied by males and females, together with energetic and reproductive constraints, the annual life cycle and hibernation patterns of mountain pygmy-possums should be distinct for males and females and should include features characteristic for both small and large hibernators. To test this hypothesis we investigated a free-ranging population of mountain pygmy-possums over two consecutive winters, monitored climatic variables in relation to hibernation and placed particular emphasis on comparing male and female hibernation strategies.

## Materials and methods

### Study area and trapping

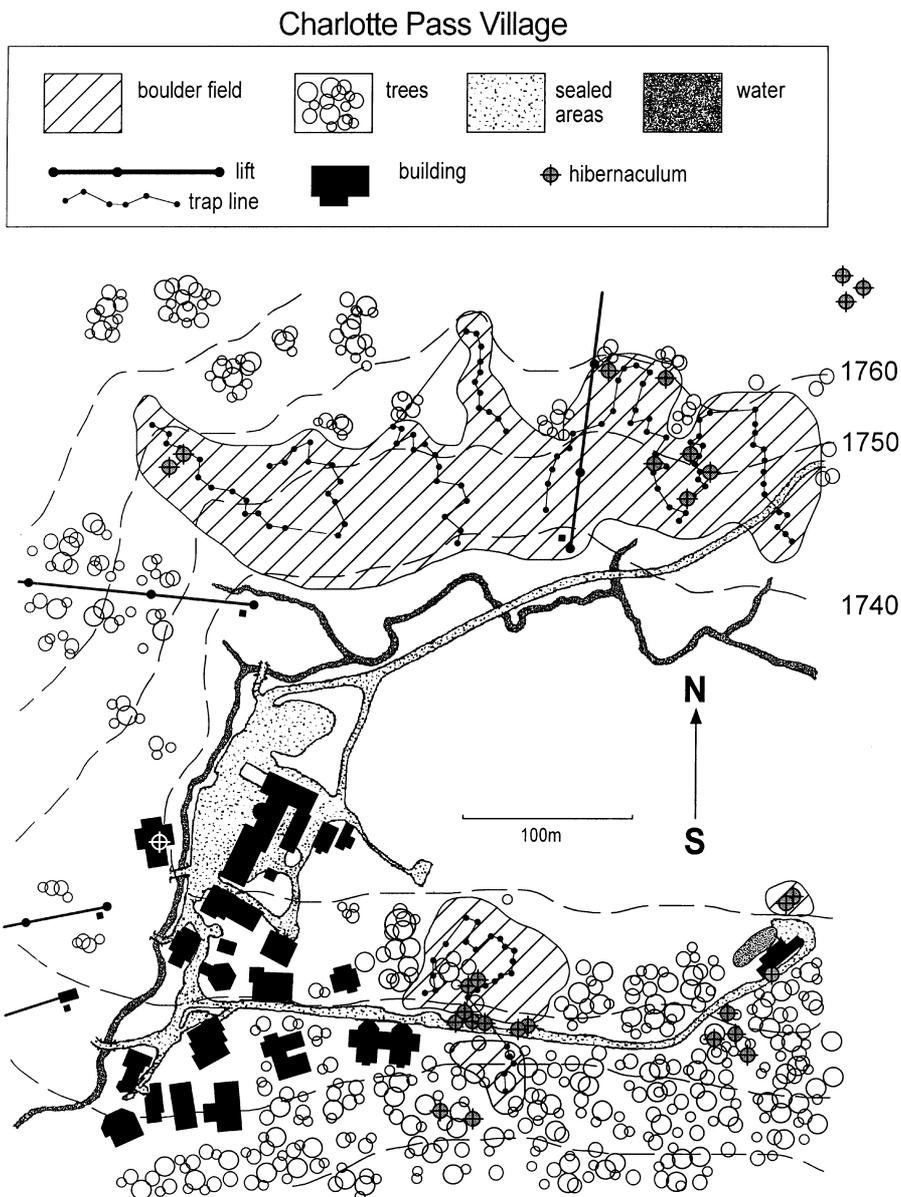
We studied the hibernation patterns of free-ranging mountain pygmy-possums during the winters of 1995 and 1996. The study area was situated next to Charlotte Pass Village in Kosciuszko National Park, New South Wales, Australia [36°44'S, 148°33'E; elevation 1750 m (mountain pygmy-possums distribution 1500–2200 m)] (Fig. 1). Elliott traps (similar to Sherman traps) were set along five trap lines (25 traps each) covering the major boulder fields on the north and south side of the valley (Fig. 1). Traps were baited with walnuts, and Dacron fibre material was provided as insulation. Each trap was placed inside a plastic bag which functioned as a rain cover. Since some possums loose mass when trapped successively, traps were set for no more than three consecutive nights. Autumn trapping was conducted from 18 April to 3 May 1995 (542 trap nights) and from 28 March to 12 May 1996 (467 trap nights). Spring trapping commenced as soon as areas within the boulder fields were free of snow, but since during the initial period of trapping most sections of the trap lines were still under snow, temporary trap stations were established in adjacent snow-free patches. Spring trapping started on 16 September 1995 (745 trap nights) and 8 October in 1996 (608 trap nights). In both years, trapping was terminated by early November. Traps were also frequently set in several buildings of the village during both winters, and occasionally we attempted to trap individuals carrying transmitters during arousal periods in the hibernation season.

Since the pygmy-possum population in Charlotte Pass is also the focus of an ongoing population study by the National Parks and Wildlife Service (Broome and Mansergh 1989), most of the animals were already individually marked with ear tags. We ear-tagged all previously untagged individuals captured. Trap location, body mass, sex, age, and testis size for males (length and width) were recorded.

### Radio tracking and $T_b$

In 1995, 10, and in 1996, 11 adult possums (12 females, 9 males) were fitted with temperature-sensitive radio collars (Sirtrack: single stage, 3.5 g, frequency 150.060–150.580 MHz). These animals were kept in captivity for several days to test the transmitter arrangement and then were released at the site of capture. Prior to attachment, transmitters were calibrated in a water bath using a mercury thermometer ( $\pm 0.1^\circ\text{C}$ ). After release we took manual temperature readings at least twice a day using a Regal 2000 tracking receiver (Titely Electronics) and a stopwatch. If the temperature reading differed by more than  $1^\circ\text{C}$  from the previous one, indicating an ongoing or recent arousal, the location of the animal was also determined. Since two readings per day are not sufficient to determine with precision the time of arousal from and entrance into hibernation, we deployed two types of automatic systems which allowed temperature sampling at 10- or 30-min intervals. The first system consisted of a notebook computer controlling a scanning receiver (FRG9600, Yeasu) via the serial port and an 11-bit analog-to-digital converter (PICO ADC-11, Pico Technology). The software used for data acquisition was a modified program originally written by Thomas Ruf and Barry Lovegrove. This system was connected to a three-element Yagi antenna (Titely Electronics) set up in one of the ski lodges. With increasing snow cover, the transmitter signals became too weak to be processed from this base station, at which point a second mobile system was developed which was the only one used in 1996. This second recording system consisted of a modified scanner receiver (i.e. using the signal detect output of the radio chip; Uniden Bearcat UBC60XLT or Netsat Pro-44, Tandy) and a custom-designed data logger based on a microprocessor (BASIC Stamp, Parallax) powered by a 4- or 7-AmpH gel battery (battery life 3 or 5 weeks). The data loggers measured the interval between two transmitter "clicks" and stored the data on an 8-kbyte EEPROM. One

Fig. 1 Study area, Charlotte Pass Village, Kosciusko National Park



recording unit for each transmitter was placed in a waterproof box close to the hibernating animal. Due to the short detection range (<10 m), these units had to be moved if animals changed hibernacula. Data were down-loaded onto a notebook computer at 1- to 4-week intervals.

Since the transmitter was attached to a collar, the temperature we recorded represents skin temperature, but gives a reasonable estimate of the core  $T_b$  (Audet and Thomas 1996; Barclay et al. 1996). Activity periods were characterised by pronounced fluctuations in the recorded temperature. However, during rest and torpor, pygmy-possums, like most hibernators, curl up into a tight ball and in this position the transmitter is situated in the “centre” of the animal’s body; the reading therefore, should represent a good estimate of core  $T_b$ . The measurement should be particularly precise during hibernation when the temperature gradient between  $T_b$  and ambient temperature is minimal. Since the main focus of the study was to measure torpid individuals, we refer to the transmitter readings as  $T_b$ . Nevertheless, we are aware of the limitations of this technique especially during normothermia.

Transmitter readings from animals which died during the hibernation season or possibly lost the collar were used to assess

ambient temperatures of hibernacula ( $T_{hib}$ ) (transmitters from 1995 functioned through 1996).

#### Ambient temperature and precipitation

Temperature patterns in the boulder fields between rocks and shrubs (depth 0.5–1.5 m) on the north and south side of the valley were recorded for winter 1996 with two custom-made data loggers each equipped with eight monolithic temperature transducers (AD592; accuracy  $\pm 0.35^\circ\text{C}$ ). Air temperature (ca. 1 m above the ground) was measured using one channel of each of these data loggers and with a min/max thermometer affixed to a tree. Precipitation data for Charlotte Pass were obtained from the Meteorological Institute in Sydney.

#### Statistics

The sex ratios for the two boulder fields were analysed for autumn and spring trapping with a multiple comparison using a Tukey-type

posteriori test (Zar 1996). Timing of arousal and entry into hibernation were tested using a Raleigh test. We assessed differences in hibernation patterns between males and females by a two-factor ANOVA (time and sex) and by comparing second-order polynomial fits. Sex differences in spring emergence were analysed using a Moods median test. Regressions were calculated using the least-squares method. Data are presented as means  $\pm$  SE.

## Results

### Climatic conditions

Daily fluctuations in air temperature were well buffered under shrubs and rocks in the boulder fields and daily temperature fluctuations were virtually eliminated after a substantial snow cover developed. The measured temperatures in the top region of the boulder fields were then close to 0°C (Fig. 2). The locations possums chose to hibernate were even better insulated, since changes in  $T_{hib}$  were normally slow and daily temperature fluctuations were generally absent even without snow. At the start of the hibernation season (around April in both years),  $T_{hib}$  ranged between 4 and 7°C and decreased steadily until the end of June (Fig. 3). Even during mid-winter,  $T_{hib}$  never fell below 0.6°C and was usually between 1.5 and 2.5°C.  $AT_{hib}$  below 1°C was observed only twice for brief periods in August and September 1995 after some unseasonal heavy rain storms caused rapid snow melt. In 1996, a similar phenomenon was observed in September/October, but this was less pronounced (Fig. 3). In general, rapid changes in  $T_{hib}$  were associated with heavy rainfall which caused a temperature decrease when snow was present due to snow melt, whereas rain without snow cover usually resulted in a temperature increase.

In 1995, lasting snow cover was established in June, whereas in 1996, the first substantial snow falls did not occur until the beginning of July (Fig. 3). Snow melt began in mid-August during 1995 and by the end of

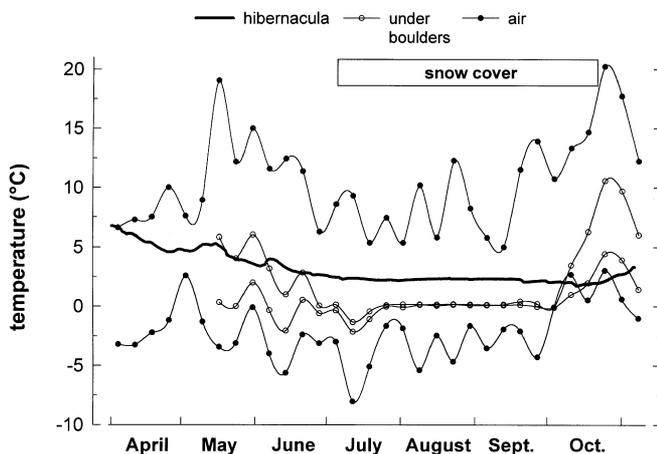


Fig. 2 Average weekly minimum and maximum air temperature and temperature under shrubs and boulders. The average temperature at the hibernacula level is illustrated as a solid line

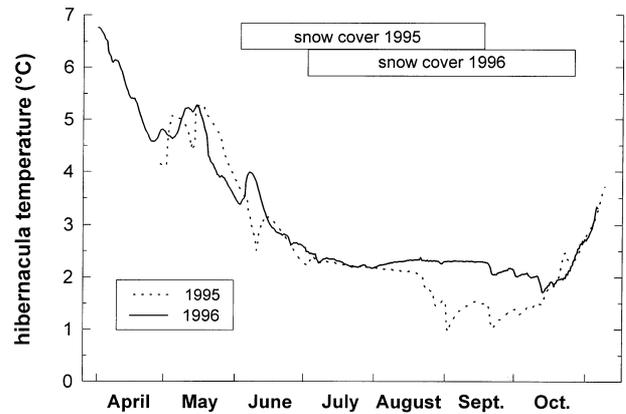


Fig. 3 Hibernacula temperature patterns for 1995 and 1996. The curves represent the average for up to six transmitters

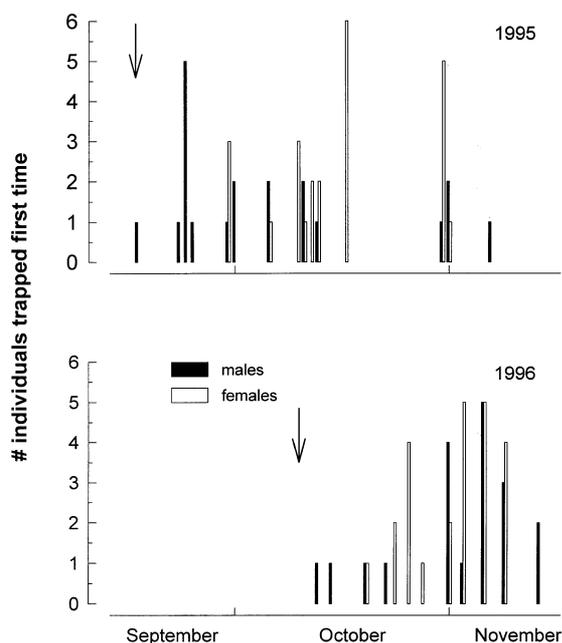
September most of the snow had disappeared. In 1996, about 30% of the boulder fields were still covered by snow at the end of October. Snow depth was quite variable due to constant drifting and differences in sun exposure and in some cornices snow piled up to more than 20 m. The deepest snow cover over a hibernaculum was only slightly more than 3 m.

### Trapping and survival

During autumn trapping, 15 individuals were caught in 1995 and 30 individuals in 1996. In both years, the majority (1995: 12/15; 1996: 20/30) were females. However, the male-female distribution was significantly different between the two boulder fields (multiple comparison,  $P < 0.05$ ). While the bigger south-facing boulder field harboured the majority of the population, most of these were females (11 females:3 males, 1995; 17 females:2 males, 1996). In contrast, in the smaller north-facing boulder field, males were more abundant (4 females:7 males, 1996, in 1995, trapping commenced too late and only a single female was trapped).

Only one juvenile was trapped in 1995, whereas 16 juveniles were captured in 1996. During autumn, the number of trapped individuals decreased successively and trapping was terminated on 3 May 1995 and 12 May 1996.

In spring, trapping success gradually increased as the snow cover receded. Timing of snow melt and the first appearance of possums in traps, presumably reflecting their emergence from hibernation, were closely coupled. The time of these events varied considerably between the two years of the study. In 1995 with an early snow melt, the first possum was trapped by mid-September (Fig. 4) and by the end of October all but one had emerged. In 1996, with an unusually late snow melt, emergence from hibernation was considerably delayed. The first possum was not trapped until mid-October and most did not appear before the beginning of November. In 1995, males appeared significantly earlier than females



**Fig. 4** Spring emergence from hibernation for both years. In 1995 with an early snow melt, males emerged significantly earlier than females. The arrow indicates the start of trapping

(median test,  $P < 0.01$ ), but in 1996 there was no detectable difference between the sexes in the timing of emergence (Fig. 4).

In both years, more individuals were captured in spring than in autumn (1995: 23 females, 20 males; 1996: 23 females, 19 males) and the sex ratio was only slightly biased towards females, a significant change when compared with the autumn. The higher trap success for both sexes in spring indicates that by March/April several possums were already hibernating. However, the relatively high percentage of males encountered in the south-facing boulder field (19 females:11 males, 1995; 23 females:15 males, 1996) and the fact that in the spring of both years, several previously unmarked adult males were caught confirms the spring immigration of males from outside the monitored areas. In contrast, the sex ratio in the north-facing boulder field remained unaltered (4 females:9 males, 1995; 0 females:4 males 1996). Although spring immigration was substantial, little migration occurred between the two boulder fields (1 female) possible due to the village blocking the path (Fig. 1). It appeared that male immigration into the south-facing boulder field must be ascribed to one or more small male populations outside the study area. The fact that two males initially caught in the north-facing boulder field (spring 1995) were retrapped in a summer survey several kilometres outside the valley illustrates the possible extent of the migration.

The extensive spring migration potentially complicates capture-recapture studies in this species. We therefore did not calculate winter survival from total numbers, but only for individuals previously trapped in the autumn. Survival for these animals was 40%

( $n = 15$ ) in 1995 and 44.2% ( $n = 30$ ) in 1996. These numbers are probably an underestimate, particularly as far as males are concerned. However, due to the small numbers of males trapped in the autumn (1995: 3; 1996: 9 including both adults and juveniles) it was impossible to calculate reliable sex-specific survival rates.

### Reproductive state

All possums trapped in the autumn were in a non-reproductive state, but the pouch of some females was still slightly enlarged, indicating recent weaning of offspring. Testes at this time of the year were small (approximately  $0.5 \times 0.6$  cm). However, three males inhabiting one of the buildings went through a period of testis growth in June 1995 after they had terminated hibernation after only a few short torpor bouts. A juvenile female residing in the same building in 1996 also discontinued hibernation prematurely, but did not show any signs of reproductive activity.

In spring, many of the early emerging males had somewhat enlarged testes, but generally within 1 week after first capture, testis size reached its maximum of about  $0.8 \times 1.1$  cm. In 1995, reproduction started early and 4 females had pouch young by 30 October 1995, 31 days after the final arousal from hibernation for one of the possums that carried a transmitter. In 1996, no pouch young were encountered by the second week of November when the study ended.

### Body mass

Body mass in mountain pygmy-possums can change rapidly and substantially. When kept in cages for several days to test the transmitter arrangement, several possums gained 2–3 g/day. Body mass also increased rapidly in the spring when possums were trapped successively. However, juveniles did not reach adult body size before their first hibernation season. The body mass of juveniles prior to hibernation was never above 50 g and was normally around 30 g, whereas adult body mass at that time ranged from 45 g to 69 g. Since it is likely that possums forage and feed during some of the longer arousal periods, data concerning body mass loss over winter are probably not a reliable estimate of fat use during hibernation. However, a relatively accurate estimate for the body mass loss over winter of 42% (67 g–38.7 g) was obtained for one transmitter-wearing adult female which left the hibernaculum only once and was trapped a few hours after final emergence.

### Hibernation patterns

The hibernation season of the mountain pygmy-possum was interrupted by frequent arousals (Fig. 5). Most arousals occurred during the late afternoon (mean 1817

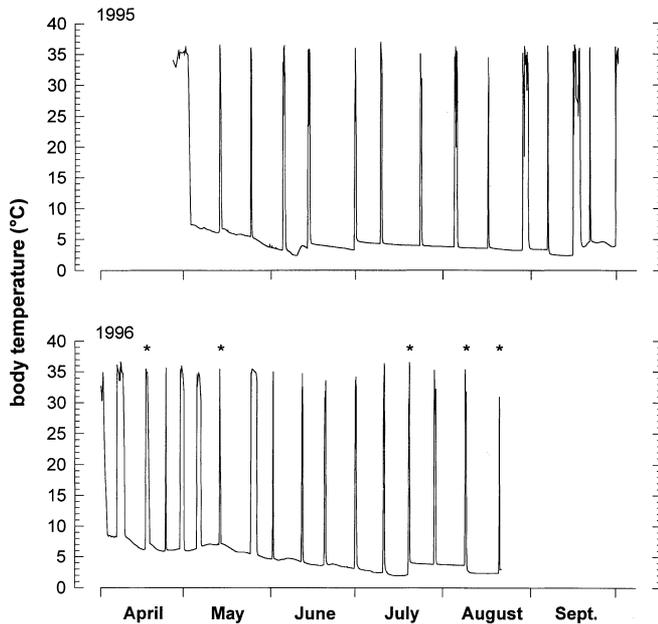


Fig. 5 Hibernation patterns of a female mountain pygmy-possum (no. 1426) in 1995 and 1996. Asterisks indicate a hibernaculum change

hours,  $P < 0.001$ ; confidence interval  $\pm 52.9$  min for  $P > 0.001$ ) and entries into torpor during the night (mean 0023 hours,  $P < 0.001$ ; confidence interval 53.7 min for  $P > 0.001$ ; Raleigh test). Especially at the beginning of the hibernation season, short bouts of less than 24 h were observed, but in one individual, prolonged torpor bouts even during mid-winter were often initiated by a sequence of short bouts that became successively longer and deeper. On average, torpor bout length increased as the hibernation season progressed. The longest torpor bouts occurred between July and August (maximum 16.1 days). Torpor bout length decreased again towards spring (Fig. 6a).  $T_b$  during torpor was lowest during mid-winter when it approached  $2^\circ\text{C}$  (Fig. 6b). Torpor bout length and minimum  $T_b$  ( $T_{b(\min)}$ ) were significantly correlated [bout length (days) =  $-0.837 * T_{b(\min)} + 10.512$ ,  $R_{\text{adj}}^2 = 0.22$ ,  $n = 199$ ,  $P < 0.001$ ]. Males maintained a higher  $T_b$  during torpor and showed on average shorter torpor bouts (Fig. 6). A two-factor ANOVA revealed a significant decrease in  $T_b$  over time and a significant time-sex interaction with females exhibiting lower  $T_b$ , but torpor bout length over this time interval did not differ between the sexes. However, due to the restriction of a two-factor ANOVA (requirements: similar sample size for both groups and a continuous data set for the same individuals over the entire time period), only six individuals could be tested for only the first 90 days of the hibernation season of 1996. Since differences in torpor bout length were likely to occur after this time period, we analysed the whole data set (0–190 days) by fitting second-order polynomials for males and females separately and for the pooled data set. In this case, the separate fits provided a significantly better model than the pooled data, demonstrating that

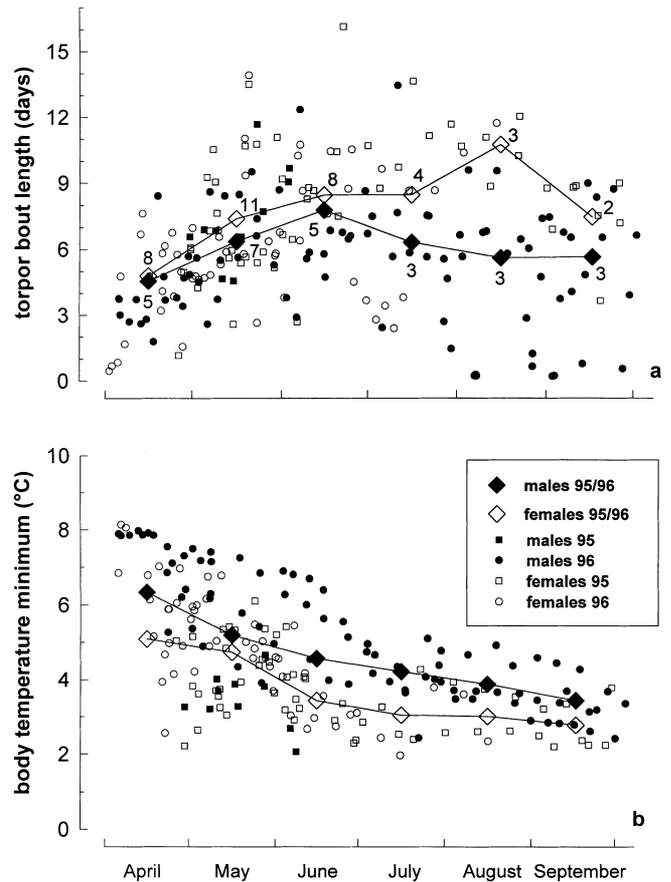


Fig. 6a,b Torpor bout length and minimum body temperature during torpor for male and female possums

torpor bout length differed between sexes ( $F = 10.45$  for 3,204 degrees of freedom).

Normothermic periods between torpor bouts were variable in length and ranged from a few hours to several days. Long normothermic periods occurred more frequently at the beginning of the hibernation season and some arousals were apparently induced by periods of warm weather combined with heavy rainfall. Although long normothermic periods became less common after an insulating snow cover was established, activity periods after arousals prevailed and possums left their hibernacula and the range of the data-recording equipment after 66.9% of all recorded arousals. It appears that activity, particularly during the extended normothermic periods, was often associated with foraging, since animals could be trapped easily during such occasions. Possums also frequently moved between hibernacula, but the number of times this occurred differed considerably (0–12) between individuals. On average, the difference in  $T_{b(\min)}$  between two consecutive torpor bouts was greater after a change in hibernaculum site ( $1.16 \pm 0.15^\circ\text{C}$ ) than when possums remained in their previous hibernaculum ( $0.04 \pm 0.04^\circ\text{C}$ ,  $P < 0.001$ ). Hibernacula of different possums were often in close proximity and some hibernaculum sites were used in

both years by the same or a different individual. However, there was no clear evidence for shared nest sites.

## Discussion

Hibernation in mountain pygmy-possums was seasonal and, as for many hibernators, began long before permanent snow cover was established. However, unlike for most seasonal hibernators, entry into hibernation varied considerably within the study population. This flexibility of entry into hibernation is most likely an adaptation to the unpredictable patterns of food availability in conjunction with climatic variables. A major dietary component, the Bogong moth (*Agrotis infusa*; body length ca. 3 cm) (Mansergh et al. 1990; Smith and Broome 1992) aestivates in enormous numbers in the Australian alps. In autumn, Bogong moths begin to emigrate from the mountain areas and the moth density can vary considerably between locations. However, this uncertainty in food availability is offset by the high energy content of the moths which allows rapid fattening, if moths are abundant. For lean possums, especially juveniles that have been born late in the year, irregular moth swarms, which are sometimes encountered as late as May, may represent an opportunity to accumulate body fat. The potential availability of moths might also have been the reason for the long normothermic periods observed during the first months of the hibernation season (Broome and Geiser 1995; present study). In contrast, it appears that foraging during mid-winter provided little success in finding food, as possums trapped during prolonged activity during winter were extremely lean. Consequently, at least four possums which showed extended activity periods late in the winter died. Thus the occurrence of foraging late in the hibernation season seems to be a response to critically low fat reserves as in some hibernating bats (Brigham 1987). Nevertheless, activity after arousals prevailed in most possums throughout the winter, but most observed activity periods were too short to be attributed to foraging, feeding and subsequent digestion which would require prolonged normothermic periods.

A possible function of these short activity periods might have been the search for other hibernacula with preferred thermal conditions. Since energy conservation in hibernating possums is optimal only in a small ambient temperature range around 2°C (metabolic rate 1% of normothermia; Geiser and Broome 1993), it may be profitable for possums to minimise thermoregulatory costs during torpor despite the energetic costs of moving between sites. Differences in thermal conditions between localities are illustrated by the observation that differences in  $T_b$  between consecutive torpor bouts were greater after the nest site had been changed. Consequently, especially during the initial months of the hibernation season when the temperature conditions in the boulder fields changed constantly, many possums frequently changed their hibernaculum. However, since

not all possums showed this behaviour, hibernacula apparently differed in quality, and the clustering of hibernacula in certain areas indicates a limitation of suitable sites. Areas with additional soil insulation (especially important before the snow season) under a road or in old overgrown boulder fields were particularly frequented, which meant that hibernacula were often outside the normal summer habitat, open boulder fields (Fig. 1). Considering the effort possums spent in selecting their hibernacula, the availability of suitable locations within or adjacent to boulder fields might well be one of the limiting factors responsible for the very restricted patchy distribution of mountain pygmy-possums (2000–3000 individuals; habitat size 10 km<sup>2</sup>; Caughley 1985).

Activity periods might have been not only important for feeding and hibernaculum selection, but might also have played a significant role in the timing of final emergence from hibernation. Since throughout the hibernation season arousals occurred preferably during the late afternoon (Körtner and Geiser 1996; present study), it is likely that possums became frequently exposed to some photoperiodic stimuli. Periodically surveying snow and weather conditions probably ensures that final emergence is closely linked with an advanced snow melt. Because snow melt differed not only between localities but overall by more than a month between the two years investigated, a flexible, opportunistic timing of final emergence appears obligatory. Given the limited fat stores of possums, food abundance is obviously a key factor in determining the end of the hibernation season. However, this is not necessarily linked with the arrival of Bogong moths per se (mid-September in both years), but more closely with a well-advanced snow melt when possums can access the moths entering the boulder fields. The importance of increased food availability for the termination of the hibernation season is also illustrated by the observation that the possums living in a ski lodge terminated hibernation in early winter with the onset of the ski season when tourists and staff provided food unknowingly.

Although emergence from hibernation and snow melt were closely correlated, males appeared in traps significantly earlier than females in 1995. This allows regrowth of testes, spermatogenesis and migration into female home ranges. In other hibernators which are also confronted with time constraints for reproduction, mating occurs either in the autumn (bats) or, if mating takes place in the spring (echidna, ground squirrels), food caches and body fat stores enable males to terminate hibernation early, even before snow melt (Fenton 1983; Kenagy 1989; Beard et al. 1992; Michener 1992). Body fat stores are not an option for a small mammal and although food-caching behaviour by mountain pygmy-possums has been occasionally observed in captivity (Calaby et al. 1971; Kerle 1984), the close correlation between snow melt and emergence for males suggests that they rely on newly arrived moths rather than stored food. Nevertheless, male possums seem to overcome

these energetic problems by selecting areas in which snow melt is early. This habitat selection of male possums for warmer environments is reflected in their higher  $T_b$  during torpor. It also appears that male possums are adapted to these higher temperatures, because a higher  $T_b$  setpoint persists even under controlled laboratory conditions, while the reduction in metabolic rate is similar to that of females (Geiser and Broome 1991). However, torpor bout length, which is the most important determinant for energy expenditure during hibernation, seems to be more dependent upon  $T_b$  than upon the metabolic rate (Geiser and Kenagy 1988). Accordingly, in free-ranging males, costly arousals occurred more frequently, at least in the second half of the hibernation season. Selecting warmer environments to increase their chance for mating in spring burdens males with higher energy demands during hibernation, which in turn seems to increase winter mortality and might contribute to the observed shorter life longevity of males (Mansergh and Broome 1994).

Our study shows that mountain pygmy-possums are not completely isolated during hibernation, but that they actively interact with their environment and are sensitive to climatic changes even during mid-winter. As in other small hibernators which have restricted body fat stores, timing of hibernation appears to be opportunistic. However, time constraints for reproduction similar to those in the much larger sciurid ground squirrels favour early reproduction and therefore early spring emergence, especially for males. Although this strategy entails higher energetic costs and probably an increased winter mortality for male mountain pygmy-possums, the sexual dimorphism in habitat selection during the hibernation season together with a high-fat diet allows this species to survive the harsh climate in the Australian alps.

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