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Rhythmicity of torpor in a marsupial hibernator, the mountain pygmy-possum (*Burramys parvus*), under natural and laboratory conditions

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Abstract Circadian rhythms have been observed in most mammals, but their importance and function remain controversial with respect to daily cycles during hibernation. We investigated the timing of arousals from and entries into hibernation for both free-living and captive mountain pygmy-possums (*Burramys parvus*). Under both natural and laboratory conditions most arousals and entries were entrained with the light-dark cycle. Entries occurred mainly during the night and arousals preferably around dusk, which coincides with the onset of the normal activity phase for the nocturnal pygmy-possums. This entrainment prevailed throughout the hibernation season although only the laboratory animals were constantly subjected to photoperiodic stimuli, whereas under natural conditions hibernacula are shielded from photic cues and diurnal temperature fluctuations. Nevertheless, possums left their hibernacula frequently throughout winter and were occasionally trapped close to the snow surface suggesting that during the periods of post-arousal normothermia they can be exposed to environmental stimuli. It thus appears that the synchronisation with the photocycle was governed by a temperature-compensated circadian clock which was reset periodically during short activity periods. For the mountain pygmy-possum, entrainment with the photocycle probably has two functions:

1. Entrainment ensures that foraging bouts during the hibernation season remain synchronised with the dark phase.

2. Information about the prevailing climatic conditions sampled during short activity periods enables them to time final spring emergence from hibernation when

snow melt begins and ensures that the breeding season can commence as early as possible.

Key words Arousal · Entry · Circadian rhythms · Hibernation · Marsupial · Mountain pygmy-possum · Torpor bouts

Abbreviations T_a air temperature · T_b body temperature

Introduction

The timing of activity and rest in animals is under most circumstances controlled by an endogenous clock. This clock is periodically reset by environmental cues such as photoperiod and daily temperature fluctuations (Bünning 1986). If these synchronising stimuli from the environment are lacking, the normal daily activity patterns will persist in most cases, but the resulting free-running endogenous cycles usually deviate somewhat from exact 24-h periods and thus are referred to as circadian rhythms (Aschoff and Pohl 1970).

Although circadian rhythms have been observed in most mammals, the importance and function of endogenous clocks remain controversial with respect to daily cycles during hibernation. Hibernators can abandon normal activity cycles for several months and it may appear that during this time a functional circadian system is of little ecological importance, and the question as to its persistence is purely of physiological interest. Indeed many hibernators are shielded from most environmental variables in deep underground burrows, where they remain until spring emergence. However, some opportunistic hibernators exploit intermittent favourable weather conditions for foraging even in winter (Van der Merwe 1973; Fowler and Racey 1990; Körtner and Geiser 1998) and could benefit from a functional Zeitgeber as it would ensure that arousals coincide with the normal activity period. If the circadian clock is to remain functional, a high degree of temperature compensation is paramount, because body temperatures (T_b)

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during the hibernation season can range from below 0 °C during torpor to about 38 °C during normothermia (Barnes 1989; Geiser and Ruf 1995). The known occurrence of minute circadian fluctuations in T_b or metabolic rate during torpor in some mammals (Menaker 1959; Pohl 1961; Grahn et al. 1994) has demonstrated that temperature compensation can be achieved to some extent. On the other hand, the expression of torpor can interfere with the precision and periodicity of the circadian system (French 1977a; Thomas et al. 1993; Grahn et al. 1994). Unfortunately, available results are inconsistent even for closely related species and may range from apparent arrhythmicity (Kristoffersson and Soivio 1964; Twente and Twente 1965; Thomas 1993) to a persistent, fully temperature-compensated circadian system with a rhythmicity of about 24 h (Twente and Twente 1987). To complicate the issue further, hibernating animals may not even respond to photoperiodic cues as their free-running rhythms persist when exposed to a daily photocycle (Pohl 1967, 1987). Some of the discrepancies between studies might be explained by different experimental designs, data analysis and possibly laboratory artefacts. However, species-specific differences in the over-wintering strategies employed by different hibernators may also explain some of the variance.

To address these questions we investigated the hibernation patterns of the mountain pygmy-possum (*Burramys parvus*, Marsupialia). These possums are restricted to the high altitudes of the Australian alps, hibernate in rock crevices for up to 6 months, and interrupt hibernation frequently by short activity periods when they may forage outside their hibernacula (Mansergh and Broome 1994; Broome and Geiser 1995; Körtner and Geiser 1996, 1998). Given that hibernating mountain pygmy-possums are more aware of their environment than most known hibernators, we predicted that a circadian system would persist and would be entrainable to a light-dark cycle. Since these assumptions imply an ecological significance of the circadian system during the hibernation season, we considered it desirable to verify results obtained in the laboratory by field observations. A comparison between field and laboratory conditions gained additional importance since most studies investigating the circadian system during hibernation have been carried out in the laboratory. The few data available from field research (Thomas 1993) seem to contradict laboratory findings from a closely related species (Twente and Twente 1987), raising the question whether unintended daily disturbances explain some of the discrepancies.

To resolve whether the contradictory results are explained by differences between species or laboratory artefacts, we studied the periodicity of arousals from and entry into hibernation in free-ranging *B. parvus* for two consecutive winters. In comparison we investigated individuals maintained in the laboratory under short photoperiod and a temperature regime resembling that of their natural habitat.

Materials and methods

Study area, trapping and animal husbandry

The field study was conducted next to Charlotte Pass Village in Kosciuszko National Park, New South Wales, Australia (36°44' S, 148°33' E; elevation 1750 m) during the winters of 1995 and 1996. The laboratory study was conducted at the University of New England, Armidale, in 1996.

All animals were trapped using Elliott traps (similar to Sherman traps) baited with walnuts. Dacron fibre material was provided as insulation and for protection from rain, each trap was placed inside a plastic bag. Trapping for the field study was conducted from 18 April 1995 to 29 April 1995 (542 trap nights) and from 28 March 1996 to 12 May 1996 (467 trap nights). Traps were set along five trap lines (25 traps each).

Animals for the laboratory study were obtained from a separate population close to Mt. Kosciuszko summit. In a single night (3 April 1996) six adult males were trapped (40 traps) and transferred to the University of New England 3 days later. An adult female with an injured foot from the Charlotte Pass area was added to the group since we were worried about its survival in the wild. This animal recovered quickly in captivity. Possums were housed individually in cages provided with sawdust and shredded paper for bedding. Cages were placed in a temperature-controlled cabinet (accuracy: ± 1.5 °C) and the photoperiod was set to L:D 9.5:14.5, the shortest photoperiod in the natural habitat of the possums. The light in the cabinet caused a small daily fluctuations in air temperature (T_a) of about 0.5 °C. To simulate the temperature conditions experienced in the wild the T_a was set to 10 °C (29 April–7 May), 5 °C (6 May–3 June), 3 °C (4 June–6 October), and until the end of the experiment (25 October) to 8 °C. This species is known to hibernate in the laboratory under these environmental conditions; its hibernation pattern is temperature-sensitive, and use of hibernation appears to be opportunistic (Geiser and Broome 1991, 1993; Körtner and Geiser 1995). During pre-hibernation, fattening possums were provided with food ad libitum (carrots, walnuts, sunflower seeds, canned baby food and high protein cereal with honey and water). Later when the animals hibernated, food was withheld. However, the body mass of the possums was recorded in regular intervals and possums which approached a body mass of 40 g or terminated hibernation were provided with food. Water was available throughout the experiment. After the end of the experiment (7 November) the possums were released at the site of capture.

Body temperature measurements

Field study

For the field study 10 (1995) and 11 (1996) adult possums 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 were released afterwards at the site of capture. Prior to attachment, transmitters were calibrated in a water bath against a mercury thermometer (± 0.1 °C). After release we took manual transmitter readings at least twice a day using a Regal 2000 tracking receiver (Titley electronics) and a stopwatch, to monitor physiological state, location and movement of the animals. To determine the precise timing of entry into and arousal from torpor, we used two automatic systems which allowed temperature sampling at 10 or 30 min intervals. Initially we used a stationary computer-controlled scanner receiver set up in one of the ski lodges (Körtner and Geiser 1998). When snow cover increased, the transmitter signals became too weak to be processed from this base station and therefore mobile recording units were used for the rest of the study (Körtner and Geiser 1998). These mobile units consisted of custom-made data loggers, a modified scanner receiver (Uniden Bearcat) and a 12 V gel battery. One recording unit for

each transmitter was placed in a waterproof, insulated container close to the hibernating animal. The short detection range enabled us also to record absence of possums from their hibernaculum, but these units had to be moved if an animal changed the location of its hibernaculum. Data were down-loaded onto a notebook computer at 1–4 week intervals.

Since the transmitter was attached to a collar, the temperature we recorded represents skin temperature, which can be a reasonable estimate of core T_b (Audet and Thomas 1996; Barclay et al. 1996) particularly when resting or hibernating animals are in a curled-up position with the transmitter pressed against the belly. Although transmitter readings from active animals were less reliable, temperature records permitted precise determination of arousal from and entry into torpor because values change by more than 30 °C between normothermia and torpor (Körtner and Geiser 1998).

Temperature readings from transmitters which had been lost or from animals which had died during the hibernation season were used to assess T_b of hibernacula (transmitters from 1995 functioned through 1996). Precipitation data for Charlotte Pass were obtained from the Meteorological Institute in Sydney.

Laboratory study

The seven captive possums were implanted under Isoflurane anaesthesia with calibrated temperature transmitters (Minimitter Inc, model XM ± 0.1 °C). After the surgery possums were allowed to recover for at least 2 weeks at high temperatures (~ 20 °C) before being placed in the temperature cabinet set to 10 °C to induce hibernation. Transmitter signals were received via ferrite rod antennae placed under each cage and multiplexed to a receiver. The audio signal from the receiver was then transformed to a square wave signal after the background noise had been electronically subtracted. Data acquisition, data storage and channel multiplexing was performed by a personal computer equipped with a 12 bit analog to digital converter. T_b of all animals were recorded in 6 min intervals. The software was initially developed by Thomas Ruf and Barry Lovegrove and was modified by the authors.

Statistics

Timing of arousal from and entry into hibernation were tested using a Raleigh test. Data sets were also tested for periodic time intervals ranging from 21–29 h (step 0.5 h) using a contingency test δ^2 (Canguilhem et al. 1994). Correlations against time of day were performed using circular statistics, i.e. a parametric linear-angular correlation (Zar 1996); plotted against a linear time axis these regressions appear as a sine curve. Data for ' n ' the number of individuals or ' N ' the number of observations are presented as means \pm SEM.

Results

The body mass of adult possums in the field prior to hibernation ranged from 45 g to 69 g and body mass declined by approximately 40% over winter. In the laboratory pre-hibernation body mass ranged from 62 g to 76 g.

Hibernation patterns

Possums hibernated under both field and laboratory conditions. In the field the hibernation season lasted from April/May to September/October. The hibernation season in the laboratory commenced in early June and

was terminated in September. As in other mammalian hibernators, hibernation in the mountain pygmy-possum was interrupted by frequent arousals. On some occasions arousals of several individuals in the field were synchronised and occurred after periods of heavy rain. During these rain storms rapid temperature changes of hibernacula were observed which most likely triggered arousals. Noise of rushing water and dampness might also have been contributing factors. In most individuals both in the field and in the laboratory, hibernation began with short torpor bouts of less than 24 h. On average, torpor bout length increased as the hibernation season progressed and decreased again towards spring. However, in one free-ranging individual prolonged periods of post-arousal normothermia late in the hibernation season were followed by several successively longer and deeper bouts. The longest individual torpor bouts were 16.1 days in the field and 17.7 days in the laboratory.

Timing of entries into and arousals from torpor

Under both field and laboratory conditions, entries into torpor and arousals were entrained with the day-night cycle (Fig. 1). Arousals were observed mainly around the beginning of the dark phase (field: 1817 hours, $r = 0.5$ (length of the mean vector), $N = 211$, $P < 0.001$; laboratory: 1804 hours, $r = 0.33$, $N = 52$, $P < 0.01$), whereas entries occurred preferably near midnight (field: 0023 hours, $r = 0.45$, $N = 223$, $P < 0.001$; laboratory: 0257 hours, $r = 0.6$, $N = 59$, $P < 0.01$).

In the field, the time that elapsed between consecutive arousals or entries therefore tended to be close to multiples of 24 h. The residuals, i.e. the deviation from 24-h rhythms, showed a normal distribution with a centre near zero (mean deviation, entries: -4.09 min, $r = 0.38$, $N = 158$, $P < 0.001$; arousals: -49.05 min, $r = 0.53$, $N = 192$, $P < 0.001$) (not shown). Under laboratory conditions, however, only residuals for entries into torpor showed a non-random distribution (mean deviation: $+50.10$ min, $r = 0.44$, $N = 47$, $P < 0.001$). Residuals for arousals were random, reflecting the smaller sample size, but also more scatter in the data set possibly caused by disturbance in the laboratory (not shown).

Entries into torpor, in both field and laboratory, which had occurred during the last part of a night or during the day (about 0400 hours to 1700 hours) tended to result in a phase advance (i.e. the following entry occurred earlier than the previous one) (Fig. 2). Phase delays (i.e. the following entry occurred later than the previous one) were more frequent, if entries had occurred during the late afternoon or early part of the night (about 1700 hours to 0400 hours). Both regressions for field and laboratory were significant ($P < 0.001$) (Note: time shifts > 8 h were excluded because of the uncertainty for the direction of the shift).

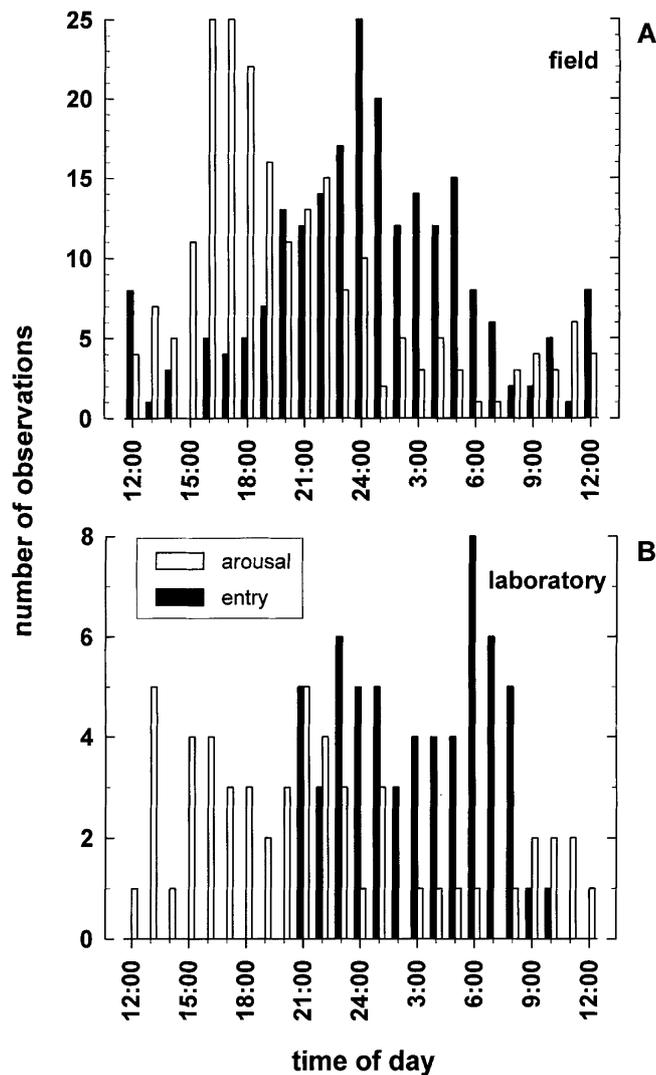


Fig. 1 Frequency distributions of timing for torpor entries and arousals in *Burrumys parvus* in the field (A) and laboratory (B). Photoperiod in the laboratory was L:D 9.5:14.5, lights from 0730 hours to 1700 hours. All variables showed a significant non-random distribution for mean values (see Results)

Periodicity in individual possums

For six possums in the field and two possums in the laboratory more than 10 multi-day torpor bouts each were recorded and 50% ($n = 3$, field; $n = 1$ laboratory) tested positive for a 24-h periodicity (contingency test δ^2 ; $P < 0.01$). For the remaining three possums in the field a 24-h periodicity also seemed to prevail, but P -values were slightly greater than 0.01, which is the suggested significance threshold for the contingency test (Canguilhem et al. 1994). One individual in the field which had tested overall positive for 24-h periodicity showed an additional significant periodicity of 23.5 h. When data for this individual were analysed separately for pre-snow and snow cover conditions, the 24-h periodicity during the snow-free part of the hibernation season was shortened to 23.5 h after the study area was

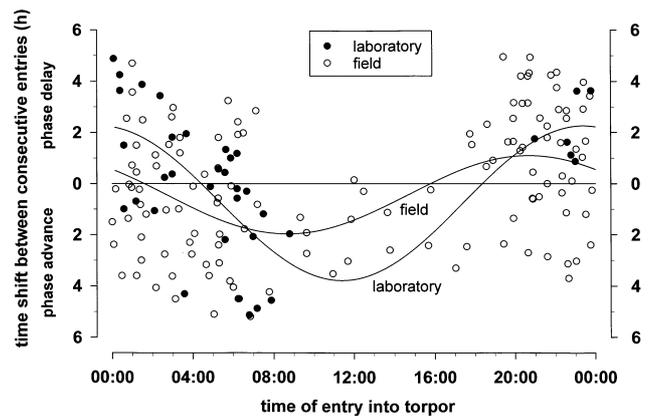


Fig. 2 Time shifts between consecutive entries of *Burrumys parvus* in the field (open symbols) and laboratory (closed symbols). Timing of entries was regressed against time of day using a parametric linear-angular correlation. Plotted against a linear, rather than on a circular time axis, these regressions appear as a sine curve. Entries into torpor which occurred during the last part of the night or during the day (about 0200–1800 hours) generally resulted in a phase advance, while phase delays were observed if entries occurred during the late afternoon or early part of the night (about 1800–0200 hours); both regressions were significant ($P < 0.001$)

covered with substantial snow (Fig. 3). At this point in time compressed snow caused by snow grooming blocked any access to the surface.

Activity and entrainment to the day-night cycle

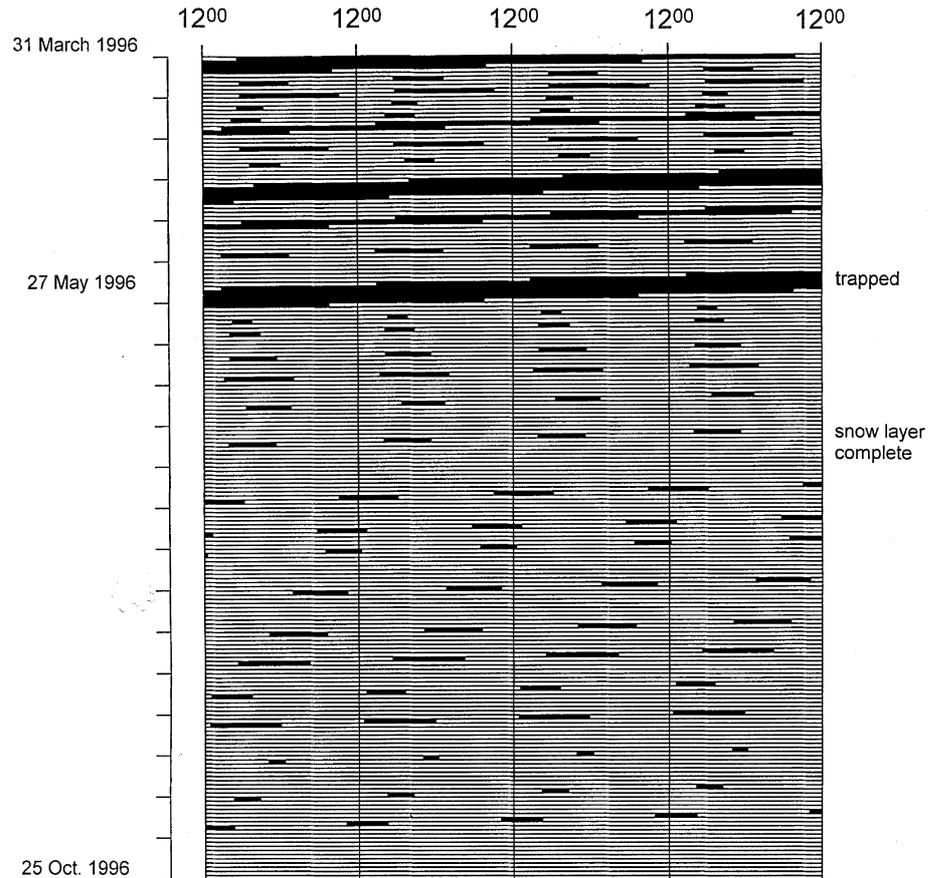
Normothermic periods interrupting hibernation varied in length under both field and laboratory conditions. Under natural conditions, long activity periods (> 24 h, 15.6%) occurred mostly during the initial snow-free part of the hibernation season, particularly during warm weather spells. It appears that these long normothermic periods were associated with foraging, since animals could be trapped easily during such occasions. However, activity prevailed throughout the hibernation season and possums left their hibernaculum after at least 66.9% of all arousals, but often for only a few hours. Activity might have been even more common given that the data loggers operated in 30 min intervals. Possums also frequently changed their hibernaculum, but how often this occurred differed considerably (0–12 times) among individuals.

The length of normothermic periods which were shorter than 24 h correlated significantly with the timing of arousal from torpor, both in the field and in the laboratory (Fig. 4). Normothermic periods were on average the shortest when the arousals had occurred in the first hours of darkness and were longer after arousals in the second half of the night or during the day.

Discussion

Our study shows that mountain pygmy-possums remain entrained to the day-night cycle throughout the hiber-

Fig. 3 Quadruple plot of normothermic periods (*dark bars*) of an individual *Burramys parvus* between 31 March 1996 and 25 October 1996. This individual hibernated in an overgrown part of a boulder field, but initially this possum was encountered regularly being active in the adjacent open boulder field, after arousals. Consequently both entries and arousals remained synchronised with the day-night cycle until June. In early July the access to the open part of the boulder field became blocked by deep compressed snow, and both entries and arousals became free-running with a periodicity of less than 24 h



nation season both in the laboratory and in the field. Arousals from and entries into torpor predominantly followed a 24-hour periodicity, so that arousals occurred around the onset of the nocturnal activity period of

pygmy-possums. However, a free-running circadian rhythm was observed in one field individual for the latter part of the hibernation season when the access to the surface was blocked due to snow grooming.

The similarities in the timing of entry into and arousal from torpor in the laboratory and field may appear surprising because only the animals in the laboratory were constantly exposed to daily changes of illumination and, to a lesser degree, temperature. Under natural conditions mountain pygmy-possums hibernate in rock crevices situated in deep boulder fields. Although such hibernacula seem to provide less protection than the excavated underground burrows of many other hibernators, they are often situated in the overgrown periphery of boulder fields. Here soil and shrubs provide insulation and protection while the gaps between the underlying boulders provide access for the possums. Such underground hibernacula can be found up to 50 m from the closest open boulder field and consequently most hibernacula are shielded from the photocycle and daily temperature fluctuations (Walter 1996; Körtner and Geiser 1998). Therefore, arousals after extended torpor periods must have been triggered by a temperature-compensated circadian clock. Although entries and arousals clearly followed a daily rhythm, we were, however, unable to detect small daily fluctuations of T_b in torpid free-ranging possums, possibly due to the external transmitter arrangement. Such fluctuations have

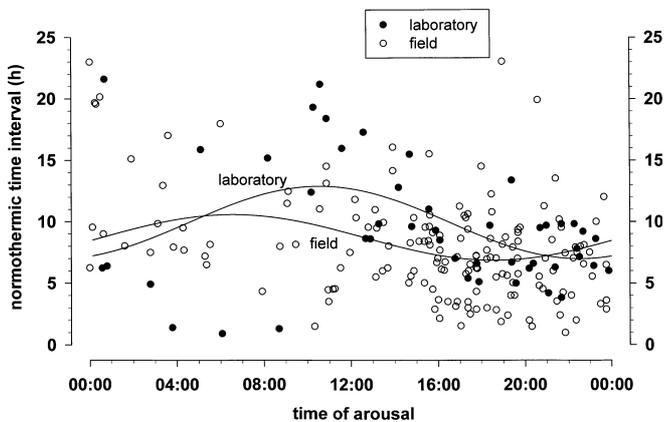


Fig. 4 The length of the normothermic time intervals of *Burramys parvus* in the field (*open symbols*) and laboratory (*closed symbols*) in relation to the time of arousals. The duration of normothermic periods was regressed against time using a parametric linear-angular correlation. Plotted against a linear, rather than on a circular time axis, these regressions appear as a sine curve. Normothermic periods were long when arousals occurred early in the day and short when they occurred in the late afternoon or the first half of the night; both regressions were significant ($P < 0.01$)

been observed in other hibernating species and have been used as evidence for a circadian organisation of hibernation (Menaker 1959; Pohl 1961; Grahn et al. 1994). Nevertheless, the precision of timing of arousals in pygmy-possums suggests an accurate pacemaker and the free-running 23.5-h period of one individual is still more precise than that of many non-hibernating mammals (Lohmann 1967). Overall, the circadian clock of pygmy-possums also appears to be more stable than in hibernating golden-mantled ground squirrels (*Spermophilus lateralis*) which show considerable bout to bout fluctuations in period length (Grahn et al. 1994). Despite this relative stability of the circadian clock, even a small daily error in pygmy-possums will accumulate over a torpor bout of up to 2 weeks, causing at least partly the scatter in the timing of arousals and possibly entries. Venturing close to the snow surface and sampling the photic conditions after arousals is therefore crucial for resetting the clock of pygmy-possums and for maintaining entrainment. That these adjustments were made after an arousal is further supported by the fact that the length of the normothermic periods correlated with the timing of the preceding arousal. The relative long normothermic periods after early arousals and the short normothermic periods after late arousals could achieve re-synchronisation.

Surprisingly, exposure to a light-dark regime in the laboratory, thereby increasing the frequency of photoperiodic stimuli in comparison to the field, neither improved the precision of timing of arousals nor entries in pygmy-possums. Observations of only weak entrainment to the photocycle have also been made for several species under laboratory conditions. In the European hamster (*Cricetus cricetus*), for example, entries into torpor were entrained, but arousals occurred apparently at random or were free-running (Canguilhem et al. 1994; Wollnik and Schmidt 1995; Waßmer and Wollnik 1997). Both Turkish hamsters (*Mesocricetus brandti*) and dormice (*Glis glis*), also exposed to a photocycle, showed free-running torpor patterns in the laboratory (Pohl 1967, 1987, 1996). Overall, these observations suggest that many hibernators do not perceive or use light stimuli when torpid and that in some species, the sensitivity to photoperiodic entrainment appears to be impaired even during normothermic periods. This lack of sensitivity to a photocycle might to some extent be related to the absence of the normal daily melatonin cycle in hibernating mammals (Florant et al. 1984; Janský et al. 1989).

In contrast to photoperiodic cues, changes in T_a are likely to be perceived even during torpor (Lyman and O'Brien 1972) and sudden substantial changes in T_a after rain storms can induce arousal in mountain pygmy-possums (Körtner and Geiser 1998). However, the thermal sensitivity seems to depend on several factors including T_b , but also increases towards the end of a torpor bout (Twente and Twente 1965). The sole effect of T_a fluctuations upon observed torpor patterns is therefore difficult to quantify. Nevertheless, it is likely

that the changing sensitivity during a torpor bout for temperature fluctuations and possibly noise contributes to the greater scatter in timing of arousals than timing of torpor entry, in pygmy-possums as well as in other hibernators (Canguilhem et al. 1994; Waßmer and Wollnik 1997). It appears, therefore, that timing of arousals is predominantly determined by an endogenous Zeitgeber; however, premature arousals triggered by natural or artificial disturbances may mask this underlying periodicity.

The apparent ability of hibernators to perceive environmental cues during the hibernation season raises the question as to the importance of photoperiod and temperature sensitivity under natural conditions. As far as photoperiod is concerned, exposure to photic cues during torpor is unlikely especially in those species that hibernate and remain in underground burrows throughout the winter like ground squirrels and marmots (Bibikow 1968; Michener 1992). For these hibernators lack of food is seasonally predictable, therefore foraging attempts after the hibernation season has commenced are futile. Synchronising arousals with outside day-night cycles is therefore of little advantage. Nevertheless, the beginning and end of the hibernation season in these species must occur at an appropriate time and this is apparently achieved by an endogenous circannual clock (Pengelley and Fisher 1957; Barnes and Ritter 1993). This circannual clock may, however, be linked to the circadian system (Pengelley and Fisher 1957, 1963; Mrosovsky 1971). Such a link would explain why the hibernation patterns of some ground squirrels and hamsters show a circadian periodicity with only weak or no entrainment to the photocycle (Strumwasser 1959; Pohl 1967, 1987; Strumwasser et al. 1967). Without being able to use the photocycle as environmental cue, sensitivity to temperature changes gains additional importance, because it allows animals to adjust spring emergence according to the prevailing climatic conditions (Davis 1977; French 1977a; Michener 1977; Mrosovsky 1980; Arnold et al. 1991; Murie and Harris 1982).

Of course not all hibernators spend the entire winter in underground burrows. For many insectivorous hibernators, food availability fluctuates as the activity of their prey is temperature-dependent and therefore less seasonally predictable. Hibernacula of these species are often situated in small rock crevices, in tree hollows, grass nests or under leaf litter and make foraging during normothermic periods possible. Accordingly, winter activity has been reported not only for mountain pygmy-possums, but also for echidnas, hedgehogs and bats (Brigham 1987; Fowler and Racey 1990; Grigg et al. 1992; Broome and Geiser 1995; Körtner and Geiser 1996, 1998) and might apply to several other species. For these hibernators, which exploit favourable weather conditions for foraging, a circadian clock entrained with the photocycle is obviously most important.

Occasional activity outside the hibernaculum also gives these hibernators the option to survey the external

climatic conditions in more detail, instead of relying purely upon slow changing soil temperatures. One has to bear in mind that predictable seasonal environments such as those in parts of Northern America and Eurasia are not universal to all regions harbouring mammalian hibernators. Temperate regions, in which the severity and length of winter can be highly variable, demand a high degree in flexibility in the timing of hibernation. Such a flexibility, which enables hibernators to optimise the time available for reproduction, can be achieved by regularly sampling the external climatic conditions.

It appears that a functional circadian system which may assist in the seasonal timing of hibernation persists in most mammalian hibernators. The degree to which the circadian system is sensitive to entrainment by external stimuli, however, is likely to be variable and appears to depend on the different hibernation strategies that are employed. Hibernators which spend the winter in deep underground burrows must obviously rely predominantly on a circannual clock. In contrast, hibernators that use relatively exposed hibernacula, live in unpredictable environments, and display opportunistic hibernation patterns are more likely to use environmental cues for organisation of their yearly cycle.

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References

- Arnold W, Heldmaier G, Ortman S, Pohl H, Ruf T, Steinlechner S (1991) Ambient temperatures in hibernacula and their energetic consequences for alpine marmots (*Marmota marmota*). *J Therm Biol* 16: 223–226
- Aschoff J, Pohl H (1970) Rhythmic variations in energy metabolism. *Fed Proc* 29: 1541–1552
- Audet D, Thomas DW (1996) Evaluation of the accuracy of body temperature measurement using external transmitters. *Can J Zool* 74: 1778–1781
- Barclay RMR, Kalcounis MC, Crampton LH, Stefan C, Vonhof MJ, Wilkinson L, Brigham RM (1996) Can external radio-transmitters be used to assess body temperature and torpor in bats? *J Mammal* 77: 1102–1106
- Barnes BM (1989) Freeze avoidance in a mammal: body temperatures below 0 °C in an arctic hibernator. *Science* 244: 1593–1595
- Barnes BM, Ritter D (1993) Patterns of body temperature changes in hibernating arctic ground squirrels. In: Carey C, Florant GL, Wunder BA, Horwitz B (eds) *Life in the cold*. Westview, Boulder, pp 119–130
- Bibikow DI (1968) Die Murmeltiere (Gattung *Marmota*). Die Neue Brehm Bücherei, A. Ziemsen, Wittenberg Lutherstadt
- Brigham RM (1987) The significance of winter activity by the big brown bat (*Eptesicus fuscus*): the influence of energy reserves. *Can J Zool* 65: 1240–1242
- Broome LS, Geiser F (1995) Hibernation in free-living mountain pygmy-possums, *Burramys parvus* (Marsupialia: Burramyidae). *Aust J Zool* 43: 373–379
- Bünning E (1986) Evolution der circadianen Rhythmik und ihre Nutzung zur Tageslängenmessung. *Naturwissenschaften* 73: 70–77
- Canguilhem B, Malan A, Masson-Pévet M, Nobelis P, Kirsch R, Pévet P, Le Minor J (1994) Search for rhythmicity during hibernation in the European hamster. *J Comp Physiol B* 163: 690–698
- Davis DE (1977) Role of ambient temperature in emergence of woodchucks (*Marmota monax*) from hibernation. *Am Midl Nat* 97: 224–229
- Florant GL, Rivera ML, Lawrence AK, Tamarkin L (1984) Plasma melatonin concentrations in hibernating marmots: absence of a plasma melatonin rhythm. *Am J Physiol* 247: R1062–R1066
- Fowler PA, Racey PA (1990) Daily and seasonal cycles of body temperature and aspects of heterothermy in the hedgehog *Ericaneus europaeus*. *J Comp Physiol B* 160: 299–307
- French AR (1977a) Periodicity of recurrent hypothermia during hibernation in the pocket mouse, *Perognathus longimembris*. *J Comp Physiol A* 115: 87–100
- French AR (1977b) Circannual rhythmicity and entrainment of surface activity in the hibernator, *Perognathus longimembris*. *J Mammal* 58: 37–43
- Geiser F, Broome LS (1991) Hibernation in the mountain pygmy possum *Burramys parvus* (Marsupialia). *J Zool (Lond)* 223: 593–602
- Geiser F, Broome LS (1993) The effect of temperature on the pattern of torpor in a marsupial hibernator. *J Comp Physiol B* 163: 133–137
- Geiser F, Ruf T (1995) Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. *Physiol Zool* 68: 935–966
- Grahn DA, Miller JD, Houng VS, Heller HC (1994) Persistence of circadian rhythmicity in hibernating ground squirrels. *Am J Physiol* 266: R1251–R1258
- Grigg GC, Augee ML, Beard LA (1992) Thermal relations of free-living echidnas during activity and in hibernation in a cold climate. In: Augee ML (ed) *Platypus and echidnas*. The Royal Zoological Society of New South Wales, Sydney, pp 160–173
- Janský L, Vanecek J, Hanzal V (1989) Absence of circadian rhythmicity during hibernation. In: Malan A, Canguilhem B (eds) *Living in the cold II*. John Libbey Eurotext, London, pp 33–39
- Körtner G, Geiser F (1995) Effect of photoperiod and ambient temperature on activity patterns and body weight cycles of mountain pygmy-possums, *Burramys parvus* (Marsupialia). *J Zool (Lond)* 235: 311–322
- Körtner G, Geiser F (1996) Hibernation of mountain pygmy-possums (*Burramys parvus*) in the Australian alps. In: Geiser F, Hulbert AJ, Nicol SC (eds) *Adaptations to the Cold: Tenth International Hibernation Symposium*. University of New England Press, Armidale, pp 31–38
- Körtner G, Geiser F (1998) Ecology of natural hibernation in the mountain pygmy-possum (*Burramys parvus*). *Oecologia* 113: 170–178
- Kristoffersson R, Soivio A (1964) Hibernation in the hedgehog (*Ericaneus europaeus* L.). The periodicity of hibernation of undisturbed animals during the winter in a constant ambient temperature. *Ann Acad Sci Fenn Ser A5* 80: 5–22
- Lohmann M (1967) Ranges of circadian period length. *Experientia (Basel)* 23: 788–790
- Lyman CP, O'Brien RC (1972) Sensitivity to low temperature in hibernating rodents. *Am J Physiol* 222: 864–869
- Mansergh IM, Broome LS (1994) *The mountain pygmy-possum of the Australian alps*. New South Wales University Press, Sydney

- Menaker M (1959) Endogenous rhythms of body temperature in hibernating bats. *Nature* 184: 1251–1252
- Michener GR (1977) Effect of climatic conditions on the annual activity and hibernation cycle of Richardson's ground squirrels and Columbian ground squirrels. *Can J Zool* 55: 693–703
- Michener GR (1992) Sexual differences in over-winter torpor patterns of Richardson's ground squirrels in natural hibernacula. *Oecologia* 89: 397–406
- Mrosovsky N (1971) Hibernation and the hypothalamus. Appleton-Century-Crofts, New York
- Mrosovsky N (1980) Circannual cycles in golden-mantled ground squirrels: experiments with food deprivation on effects of temperature on periodicity. *J Comp Physiol* 136: 355–360
- Murie JO, Harris MA (1982) Annual variations in spring emergence and breeding in Columbian ground squirrels. *J Mammal* 63: 431–439
- Pengelley ET, Fisher KC (1957) Onset and cessation of hibernation under constant temperature and light in the golden-mantled ground squirrel (*Citellus lateralis*). *Nature* 180: 1371–1372
- Pengelley ET, Fisher KC (1963) The effect of temperature and photoperiod on the yearly hibernating behavior of captive golden-mantled ground squirrels (*Citellus lateralis tescorum*). *Can J Zool* 41: 1103–1120
- Pohl H (1961) Temperaturregulation und Tagesperiodik des Stoffwechsels bei Winterschläfern. *Z Vgl Physiol* 45: 109–153
- Pohl H (1967) Circadian rhythms in hibernation and the influence of light. In: Fisher KC, Dawe AD, Lyman CP, Schönbaum E, South FE (eds) *Mammalian hibernation III*. Oliver and Boyd, Edinburgh, pp 141–151
- Pohl H (1987) Circadian pacemaker does not arrest in deep hibernation. Evidence for desynchronisation from the light cycle. *Experientia* 43: 293–294
- Pohl H (1996) Circadian and circannual rhythmicity of hibernation in the Turkish hamster, *Mesocricetus brandti*. In: Geiser F, Hulbert AJ, Nicol SC (eds) *Adaptations to the Cold: Tenth International Hibernation Symposium*. University of New England Press, Armidale, pp 87–93
- Strumwasser F (1959) Factors in the pattern, timing and predictability of hibernation in the squirrel, *Citellus beecheyi*. *Am J Physiol* 196: 8–14
- Strumwasser F, Schlechte FR, Streeter J (1967) The internal rhythms of hibernation. In: Fisher KC, Dawe AD, Lyman CP, Schönbaum E, South FE (eds) *Mammalian hibernation III*. Oliver and Boyd, Edinburgh, pp 110–139
- Thomas DW (1993) Lack of evidence for a biological alarm clock in bats (*Myotis* spp.) hibernating under natural conditions. *Can J Zool* 71: 1–3
- Thomas EM, Jewett ME, Zucker I (1993) Torpor shortens the period of Siberian hamster circadian rhythms. *Am J Physiol* 265: R951–R956
- Twente JW, Twente JA (1965) Effects of core temperature upon duration of hibernation of *Citellus lateralis*. *J Appl Physiol* 20: 411–416
- Twente JW, Twente JA (1987) Biological alarm clock arouses hibernating big brown bats, *Eptesicus fuscus*. *Can J Zool* 65: 1668–1674
- Van der Merwe M (1973) Aspects of hibernation and winter activity of the Natal clinging bat, *Miniopterus schreibersi natalensis* (A. Smith 1834), on the Transvaal Highveld. *S Afr J Sci* 69: 116–118
- Walter M (1996) The ecology of hibernating mountain pygmy-possums (*Burramys parvus*) in Kosciusko national park. Honours Thesis, University of Canberra
- Waßmer T, Wollnik F (1997) Timing of torpor bouts during hibernation in European hamsters (*Cricetus cricetus* L.). *J Comp Physiol B* 167: 270–279
- Wollnik F, Schmidt B (1995) Seasonal and daily rhythms of body temperature in the European hamster (*Cricetus cricetus*) under semi-natural conditions. *J Comp Physiol B* 165: 171–182
- Zar JH (1996) *Biostatistical analysis*. Prentice Hall, Englewood Cliffs, New Jersey

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