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Effect of photoperiod and ambient temperature on activity patterns and body weight cycles of mountain pygmy-possums, *Burramys parvus* (Marsupialia)

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(With 5 figures in the text)

The mountain pygmy-possum *Burramys parvus* shows strong seasonal rhythms of reproduction and activity in summer, pre-hibernation fattening in autumn and hibernation in winter. We investigated whether photoperiod or air temperature (T_a) or interactions of these environmental factors influence activity patterns, fattening and onset of hibernation. In January 1993, 10 *Burramys* held under long photoperiod were divided into two groups. One group was maintained under the previous long photoperiod (LD 14·5 : 9·5; $n = 5$), the other was transferred to short photoperiod (LD 9·5 : 14·5; $n = 5$). The T_a was reduced in steps lasting at least one month from 12 to 8 to 4 and to 2 °C. All individuals showed pronounced daily activity rhythms and were mainly nocturnal. Individuals under short photoperiod maintained their nocturnal activity pattern irrespective of T_a. In contrast, most individuals under long photoperiod at T_a 4 and 2 °C temporarily showed a free-running activity rhythm and began their activity period during the day. Body weight and total daily activity were negatively correlated. Individuals with low body weight (<50 g) generally were more active and showed longer activity periods than heavy animals. Under both photoperiods these lean individuals often extended their activity periods into the light phase. While in the first year after capture all animals showed pre-hibernation fattening and hibernation, a second body mass cycle was observed in only five individuals and this was independent of T_a and photoperiod. However, total daily activity in these individuals decreased with increasing body weight. Our study shows that photoperiod has little influence on seasonal changes of activity, body weight and hibernation of *Burramys*. Low T_a has some effect on activity patterns of *Burramys* held under long photoperiod. Body weight and activity of *Burramys* were interrelated suggesting that pre-hibernation fattening occurs during a time of reduced activity and thus low energy expenditure.

Contents

Introduction

Annual body weight cycles and hibernation of many placental hibernators are highly persistent. Circannual rhythms may continue for several years even when animals are maintained under constant laboratory conditions without a seasonal Zeitgeber (Pengelley & Fisher,

FIG. 1. The mountain pygmy-possum (*Burramys parvus*).

1957; Mrosovsky, 1971, 1986). In other species annual rhythms are less pronounced and persist only if animals are exposed to seasonal changes of ambient temperature and photoperiod (Mrosovsky, 1971; Jallageas, Mas & Assenmacher, 1989). In both hibernators that rely on endogenous rhythms and in hibernators that use environmental cues for timing of seasonal physiological changes, hibernation generally begins after a period of pre-hibernation fattening (Mrosovsky, 1971) which is characterized by a decrease of activity and energy expenditure (Mrosovsky, 1971; Ward & Armitage, 1981; Körtner, 1991).

The rare marsupial hibernator *Burramys parvus* (Fig. 1), the mountain pygmy-possum, is confined to altitudes between 1400–2200 m of the Snowy Mountains of south-eastern Australia (Calaby, 1983; Caughley, 1985; Broome & Mansergh, 1990; Mansergh & Scotts, 1990). The habitat of *Burramys* is characterized by harsh winters with snow cover lasting for several months from about May to October. *Burramys* appears to undergo a seasonal change of body weight with fattening in autumn followed by a prolonged hibernation season during winter similar to placental hibernators (Broome & Mansergh, 1990; Mansergh & Scotts, 1990). Fat storage from pre-hibernation fattening, which occurs in both the field and laboratory, is sufficient to cover the metabolic cost for six to seven months of hibernation (Fleming, 1985; Broome & Mansergh, 1990; Geiser & Broome, 1993). Extensive fattening appears to be a prerequisite for hibernation in

Burramys (Fleming, 1985; Geiser & Broome, 1991), perhaps because heavy individuals are more likely to survive the winter (Mansergh & Scotts, 1990).

While the yearly patterns of activity, pre-hibernation fattening and hibernation of *Burramys* appear to be strongly seasonal, it is not known whether these annual cycles are controlled by environmental cues or by an endogenous circannual rhythm. Previous observations suggest that hibernation in *Burramys* may be opportunistic because individuals occupying home ranges in and around ski huts tend to be active during winter (Mansergh & Scotts, 1986). Moreover, individuals kept in captivity for breeding appear to be less seasonal than individuals in the wild (Thomas, 1982; Mansergh & Scotts, 1990) and laboratory-bred mountain pygmy-possums neither undergo seasonal body weight changes nor hibernate (Geiser *et al.*, 1990).

The aim of our study was to investigate whether annual cycles of activity, body weight and hibernation persist in captivity. We determined whether seasonal changes of activity patterns and fattening of *Burramys* are entrained by changes of photoperiod and ambient temperature and how activity and fattening are interrelated.

Materials and methods

Ten mountain pygmy-possums (*Burramys parvus*) were trapped in April 1992 on Mt. Kosciusko, Kosciusko National Park, at an altitude of about 2160 m. As the overall population of *Burramys* is estimated to be only about 2000 individuals and the species is considered endangered, a permit for only 10 individuals was issued. At the time of capture, the group consisted of 4 juveniles (born in the previous summer), 2 sub-adults (second year) and 4 adults (older than 2 years) (details in Table I). Animals were transferred to the University of New England, Armidale, New South Wales and were kept in temperature-controlled cabinets (air temperature, $T_a \pm 0{\cdot}5$ °C). Possums were maintained individually in polyethylene cages (29 × 22 × 13 cm), containing sawdust and paper shredding as bedding. Water and food (canned baby food, high protein baby cereal, walnuts, sunflower seeds and apples), which was varied daily, were provided *ad libitum*, except from May to September 1992 when possums were hibernating. However, when body weight was approaching 40 g during the hibernation season food was provided. When animals were normothermic, cages were cleaned in weekly intervals.

During the first year in captivity (1992), animals were subjected to an annual cycle of T_a with highest temperature of 14 °C in summer and lowest temperature of 2 °C during midwinter. Until mid-December 1992 the light/dark cycle in the cabinets was adjusted to the natural photoperiod at Kosciusko National

TABLE I

Details of experimental animals

Animal No.	Sex	Age group at capture	Body weight at capture (g)	Photoperiod
C1	female	adult	68	long
B14	female	adult	39	
B5	male	sub-adult	39	
B18	female	juvenile	29	
C15	male	juvenile	31	
B7	male	juvenile	35	short
B119	female	adult	34	
C10	female	juvenile	31	
B120	male	adult	48	
B22	male	sub-adult	37	

Park. From mid-December until late January 1993 animals were maintained under unaltered long photoperiod LD = 14·5 : 9·5 h. In late January 1993, after one and a half months in constant long photoperiod, 2 groups of matched sex and body weight were established. Five of the *Burramys* were transferred to short photoperiod LD = 9·5 : 14·5 h while the other 5 were maintained under previous long photoperiod. These light regimes resemble the shortest and longest photoperiod experienced by the animals in their natural habitat. For both groups the photoperiod was not changed for the rest of the experiment, but the T_a was lowered from 12 °C (28 January to 1 March) to 8 °C (1 March to 1 April), 4 °C (1 April to 4 June) and finally to 2 °C (4 June to 23 July). This decline of T_a is similar to that in their natural habitat during autumn and early winter. To test whether the animals could hibernate, food was removed from animals heavier than 56 g at the end of the experiment. Since it is known that individuals with body weight below 50 g do not enter torpor (Geiser & Broome, 1991) and because of the risk of killing animals, food was not withdrawn from animals lighter than 50 g.

The body weight of the animals was recorded in weekly intervals during the cage-cleaning procedure. Animals were checked daily for signs of torpor. Animals were considered torpid when they were curled into a tight ball, respiration rate was low and the animals did not respond to a puff of air.

The activity of each animal was monitored continuously for 170 days as described by Ruf *et al.* (1991). Passive infrared sensors (PIR; Jaycar Electronics LA-5017) were placed on top of each cage and activity events were summed up over 30-minute periods and stored on a data logger (Electronic Services Unit, University of New England, Armidale). PIR recordings were also used for measuring the duration of torpor bouts. PIRs monitor the temperature profile over an angle of 90°. The measuring area of the PIR is divided into several units and every change of the detected temperature profile caused by the movement of an animal, which has a higher radiation than the surroundings triggers the device. Because even a small temperature gradient between the moving object and the surroundings is detected, the sensitivity of PIRs is independent of T_a.

For data processing the activity data were transferred to a personal computer. Activity data recorded 2 h after daily feeding or cage cleaning were rejected. Double plots of activity data were created by a modified program written by B. Lovegrove and T. Ruf. For total daily activity, activity counts were summed up over a 24-hour period. If activity counts were recorded within a 30-minute measuring interval, the animal was considered to be active and the time active/day was derived from the sum of those 30-minute measuring intervals. A repeated measures ANOVA was performed for activity vs. T_a of both experimental groups. Least squares regression was performed between body weight and daily activity to determine possible correlations between these variables. The data were analysed for both single individuals, groups and all individuals. If not given on an individual basis, data are expressed as mean ± S.E.

Results

When trapped in April 1992 the body weight of only one possum had exceeded 50 g (C1, adult female: 68 g). During the following four to five weeks all animals fattened and body weight reached a mean maximum of 73·3 ± 3·2 g (Fig. 2). During the following hibernation season all animals lost weight. Body weight at termination of the hibernation season was 38·0 ± 0·9 g. From August to September most animals gained some weight but body weight remained below 60 g. A second body weight cycle with maximum values above 60 g was observed in only three animals under short photoperiod and two animals under long photoperiod (Fig. 2). However, one of these animals (C1) had already started gaining weight in November 1992 and therefore entered the experiment with a body weight above 80 g. None of the other possums had commenced body weight gain before the start of the experiment in January 1993. The occurrence of a second fattening period in captivity was not related to sex and age. However, only the heaviest individuals within their age class prior to the first hibernation season (i.e. adult > 84 g; sub-adult > 62 g; juvenile > 72 g) performed a second body weight cycle. In these individuals, body

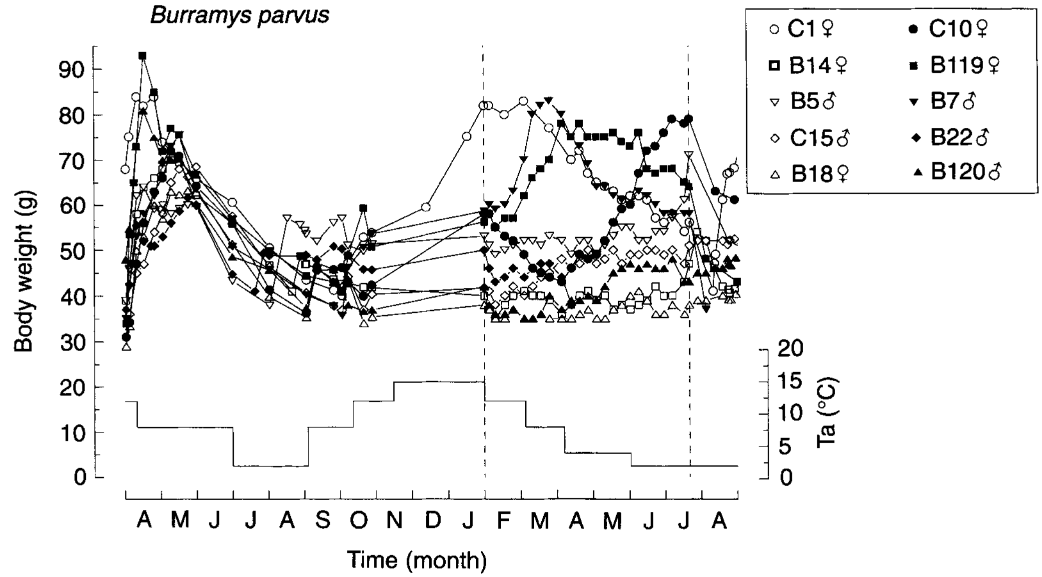

FIG. 2. Body weight of 10 captive *Burramys* over 17 months. Period of photoperiodic treatment (short photoperiod: closed symbols; long photoperiod: open symbols) is indicated by the two vertical dashed lines. Changes in T_a are illustrated by the line at the bottom of the graph.

weight gain was not entrained by low T_a but the onset occurred randomly throughout the experiment. After maintaining peak body weight for several weeks, three of these five individuals lost body weight again, which was not necessarily accompanied by torpor. Two animals did not complete the weight cycle within the period of the experiment. All the remaining individuals showed little or no sign of body weight change in the second year.

All animals kept in short photoperiod were active mainly during the dark phase (Fig. 3). Activity was either equally distributed over the dark phase or a distinct activity peak was observed at the beginning or the end of the dark phase. However, for all individuals small bursts of activity were monitored throughout the day and the two most active possums (B120, Fig. 3 and B22, not shown) regularly extended their main activity period into the light phase.

A change in the activity patterns after the transfer from long to short photoperiod at the beginning of the experiment was observed in three individuals (B7, B119, C10) with a relatively low daily activity (Fig. 3). These individuals shifted their activity period towards the end of the extended dark phase within the first week after the photoperiod was changed. After this initial phase, the activity period was either extended towards the beginning of the dark phase (B7, B119) or shifted from late in the dark phase to early in the dark phase (C10). After this apparent acclimation to short photoperiod was completed in all individuals, the onset of the activity period was entrained to the beginning of the dark phase; the end of the activity period was more variable (Fig. 3). T_as ranging from 12 to 2 °C had no apparent influence upon the activity patterns of *Burramys* maintained under short photoperiod (ANOVA), although a decline of daily activity at low T_a seemed to occur in some individuals (C10, B119).

Possums held under long photoperiod substantially altered their activity patterns at low T_as (Fig. 4). At T_as above 4 °C the activity patterns were similar to those observed under short

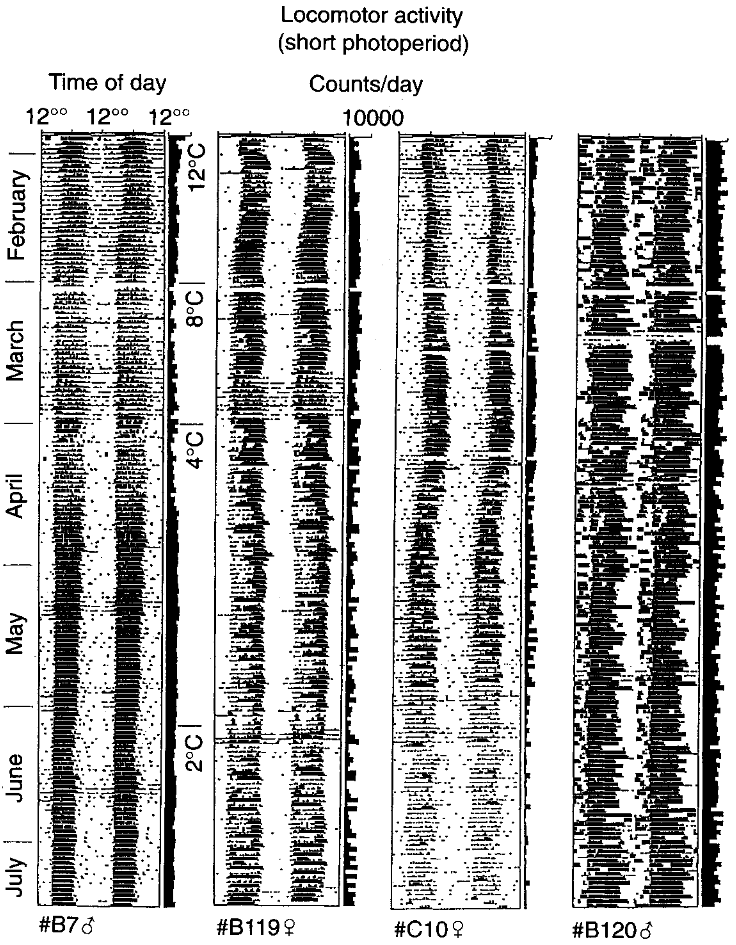

FIG. 3. Daily double plots of locomotor activity for four animals over 170 days in short photoperiod. The sum of activity counts per day is given as a horizontal bargraph next to each plot and the changes in T_a are indicated.

photoperiod. However, in four of five possums (B14, B5, B18, C15) the activity period was generally longer than the dark phase. Only one possum (C1), which had entered the experiment with a body weight above 80 g and which had displayed prolonged torpor already before the beginning of the experiment, always maintained a relatively low daily activity and was strictly nocturnal. At low T_as (4 and 2 °C) a period of free-running activity, about 3–4 weeks, was observed in three possums (B14, B5, B18). After this free-running phase, activity became entrained again, but the animals became partly diurnal (Fig. 4). Two possums split their daily activity into two separate periods (B14, B18). The two diurnal animals (B14, B5) shifted their activity period to the dark phase again at the end of the experiment after a cage-cleaning procedure. This process was complete within two days.

The total daily activity derived from a weekly average ranged from 1000 to 8000 activity counts per day between individuals (Figs 3, 4), with lean individuals being generally more active than heavier ones (Fig. 5). In six animals ($n = 4$ short photoperiod; $n = 2$ long photoperiod), total

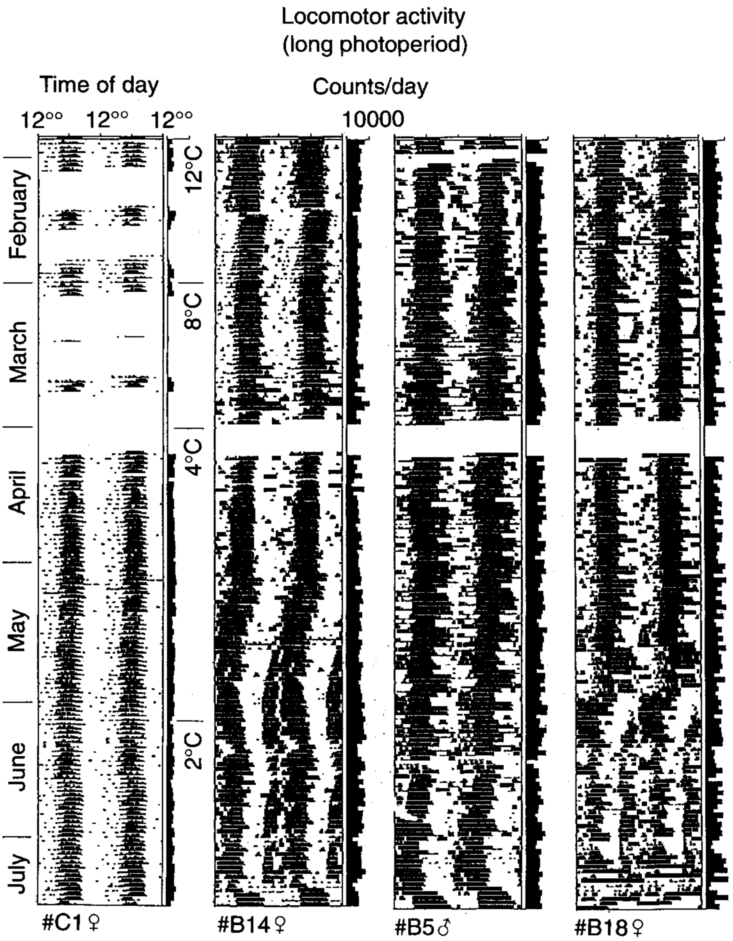

FIG. 4. Daily double plots of locomotor activity for four animals over 170 days in long photoperiod. The sum of activity counts per day is given as a horizontal bargraph next to each plot and the changes in T_a are indicated. At the beginning of April, data for seven days are missing owing to a power failure.

daily activity was significantly correlated with body weight (Fig. 5a). In three individuals no correlation between body weight and activity was observed and one individual (B5) increased its body weight too late in the experiment to have a significant impact on the regression (Fig. 2). As an average (whole data set), the total daily activity decreased by 1059 counts/day with a body weight increase of 10 g. Since the body weight of several animals changed by more than 20 g during the experiment, some individuals reduced their daily activity by more than half during periods of fattening.

While the total activity of individuals decreased with increasing body weight (Fig. 5a), the time active/day for each individual remained relatively constant even when its body weight changed (Fig. 5b). However, a regression fitted to time active/day and body weight of all individuals was significant. This shows that individuals with relatively low body weights have higher activity levels and longer activity periods than animals with higher body weight.

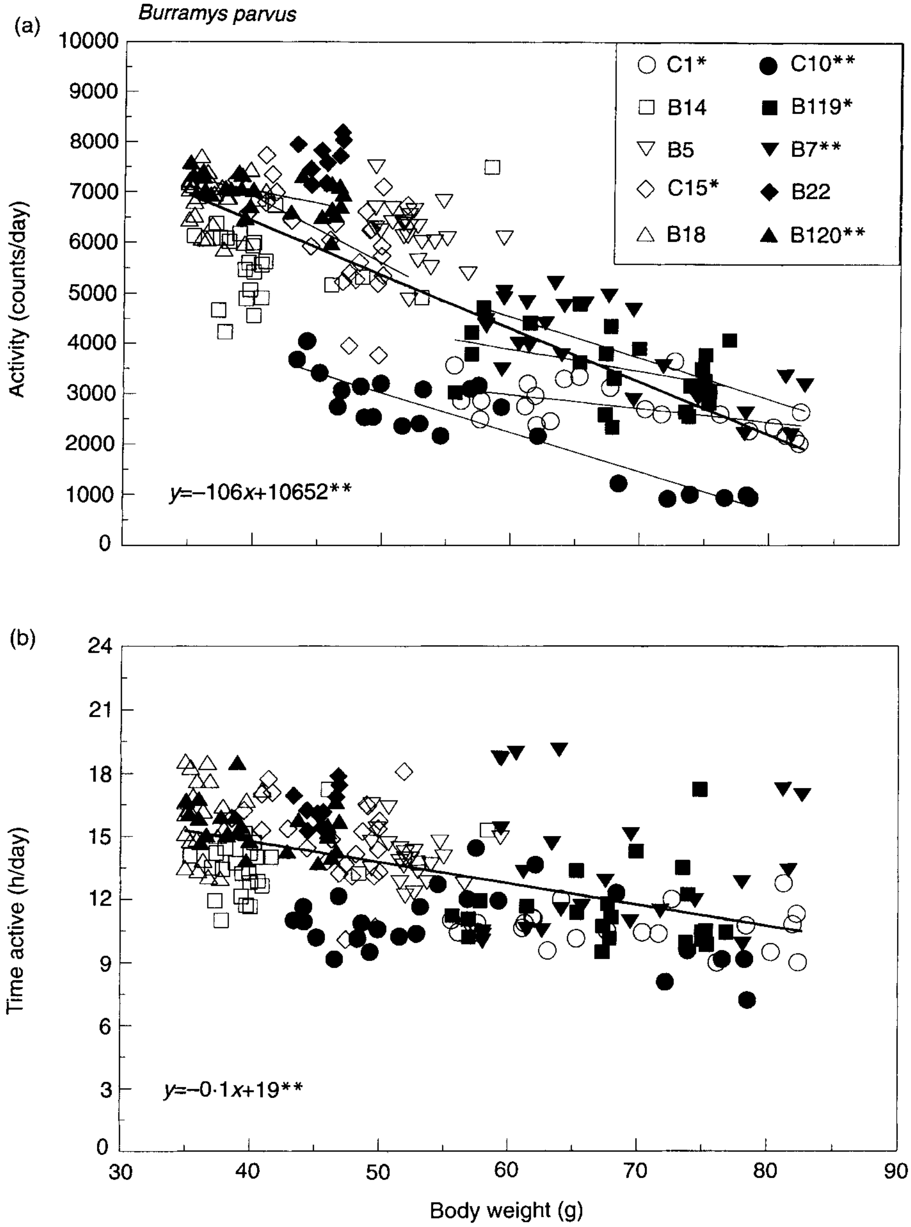

FIG. 5. (a) Total daily activity and (b) time active/day against body weight. Each data point resembles the average for one week. Closed symbols represent animals kept in short photoperiod, open symbols represent animals in long photoperiod. Equations are given for the regressions through the whole data set. Significance of the linear regressions for both individuals and the whole data set are: $*P < 0{\cdot}05$, $**P < 0{\cdot}005$.

Of the animals which reached body weights above 60 g, only one under long photoperiod showed spontaneous (food and water *ad libitum*) prolonged torpor (C1: Fig. 4). This individual showed prolonged torpor between the beginning of January and April 1993 at T_as between 14 and 4 °C. Torpor bout duration varied from several hours to 10 days and was interrupted by normothermic periods lasting from 0·5 to 4 days. One individual under short photoperiod (C10) showed spontaneous daily torpor lasting for several hours on only one occasion. However, prolonged torpor was induced in all individuals that had a body mass above 56 g after withdrawal of food (not shown).

Discussion

Daily activity patterns, photoperiod and T_a

The daily light/dark cycle is the most important environmental factor that entrains the circadian system in animals (Aschoff, 1970). However, other environmental factors, like daily fluctuations of T_a, are also considered to be important Zeitgebers (Francis & Coleman, 1990).

As in other species, the daily activity rhythm of *Burramys* is entrained by an artificial light/dark cycle in the laboratory. Under short photoperiod with a 14·5 h dark phase animals remained nocturnal even at low T_a. In contrast, under long photoperiod with a dark phase of only 9·5 h, the activity period of most animals was not entirely covered by the dark phase. This trend became more pronounced at low T_as when free-running patterns of activity were observed in three individuals (B14, B5, B18) and the animals became diurnal. Another individual (C15) remained nocturnal but activity bursts during the light phase were extended. In only one animal (C1), with a generally low activity level, the activity pattern was not influenced by the drop in T_a. Since the energy demands for thermoregulation of *Burramys* at low T_as increase dramatically (Fleming, 1985), 9·5 h of darkness were probably not sufficient for foraging and feeding. This interpretation is supported by the observation that mice (*Mus musculus*) kept at low T_a compensate their increased energy expenditure by ingesting extra quantities of food during the light phase (Bronson, 1987). *Burramys*, especially those with high activity levels and therefore high rates of energy turnover, obviously use a similar strategy to prevent an energy deficit. However, as the example of C1 shows, energy conservation achieved by a low activity level and prolonged resting periods in an insulating nest might be an alternative strategy if animals are challenged by low T_as. Since the latter option was used by only one fat individual (C1), which had recently shown prolonged torpor, the strategy of energy conservation appears to be used only by animals in a 'winter state' regardless of the photoperiodic conditions and T_a. For animals in a 'summer state' constant low T_as for long periods are unlikely to occur and therefore the combination with a short dark phase might have caused highly disturbed activity patterns. Nevertheless, *Burramys* in both 'winter and summer state' are able to maintain a positive energy balance at low T_as and if required change their daily activity patterns to establish a sufficient time-span for foraging and feeding.

Annual cycles

Activity patterns and body weight were interrelated in *Burramys parvus*. Light individuals were more active than heavy individuals. Furthermore, individuals that increased their body weight decreased their activity. As activity is energetically costly, it is possible that pre-hibernation fattening in *Burramys* may be partly caused by a decrease in daily activity, as has been suggested for ground squirrels (*Spermophilus tridecemlineatus*) (Mrosovsky, 1971). In contrast, in marmots (*Marmota* spp.) pre-hibernation fattening is mainly achieved by hyperphagia and highest rates of weight gain are observed during the peak activity season (Young, 1984; Körtner, 1991). Although marmots also show a decreased energy expenditure in the autumn, this phenomenon contributes little to pre-hibernation fattening.

A body weight cycle with pre-hibernation fattening was observed in half of the possums both under long and short photoperiod. Surprisingly, those animals which showed the highest body weight within their age class during the first fattening period after capture exhibited a second body weight cycle. It appears that the persistence of a circannual body weight rhythm and presumably the tendency for hibernation is expressed by the amplitude of body weight reached during pre-hibernation fattening.

Weight loss during the second cycle was accompanied by torpor in only one animal (C1). Therefore, the observed body weight cycle in *Burramys* appears to be rather independent of hibernation, suggesting an underlying endogenous rhythm. The cycle length, however, differed markedly between individuals since the onset of fattening and start of body weight loss during the second cycle was less synchronized and presumably free-running than during the first cycle after capture. The individual with the shortest cycle (C1) started gaining weight already in November and was the only one which at capture had a body weight above 60 g in April 1992. The individual differences of the cycle length, which seem to be apparent even in the wild, become apparently more pronounced under laboratory conditions.

Like in many placental hibernators (Pengelley & Fisher, 1957, 1963; Davis, 1967) seasonal changes in photoperiod failed to entrain the free-running circannual rhythm in *Burramys*. While T_a has a modulating influence upon the cycle length in placental hibernators (Twente & Twente, 1965; Joy & Mrosovsky, 1983) and in dormice (*Glis glis*), T_a may be the most important Zeitgeber for the annual body weight cycle and hibernation (Jallageas *et al*., 1989). The circannual system of *Burramys* seems to be fairly independent of seasonal changes of T_a. As changes of photoperiod, T_a and a combination of both do not appear to be the seasonal cues used by *Burramys*, it is likely that other environmental factors are involved. For example a decreased food availability in the field could be one factor triggering hibernation since, in captivity, fat *Burramys* enter hibernation after withdrawal of food. However, wild-caught *Burramys* establish food caches prior to the hibernation season and it is likely that they also cache food in the wild (Dimpel & Calaby, 1972; Mansergh & Scotts, 1986). It is even more unlikely that the obligatory pre-hibernation period of fattening is triggered by a decreased food availability. Since a low food availability increases the energetic cost for foraging, a shortage of food would certainly prevent body fat accumulation regardless of whether fattening is mainly achieved by hyperphagia or by a reduced energy expenditure. However, as the composition of food consumed by wild *Burramys* shows pronounced seasonal variations (Smith & Broome, 1992), some food components should act as a seasonal cue for pre-hibernation fattening. It is possible that further studies on diet composition may provide clues as to the Zeitgeber for the circannual system in *Burramys*.

In contrast to most placental hibernators, in which a free-running circannual cycle persists over several years in the laboratory (Pengelley & Asmundson, 1969; Mrosovsky, 1971), body weight cycles in about 50% of the *Burramys* had already vanished after one year in captivity. Although it was possible to induce torpor by food deprivation in *Burramys* with body weights above 56 g, prolonged spontaneous torpor was observed in only one individual under long photoperiod and with free access to food. Furthermore, seasonal changes of body weight and hibernation are also lost in laboratory-bred *Burramys* (Geiser *et al.*, 1990). Since body weight in wild individuals prior to the hibernation season varies considerably, and active lean *Burramys* are frequently encountered in and around ski huts (Mansergh & Scotts, 1986), it is still uncertain whether all individuals of the wild populations undergo seasonal hibernation. In agreement with these observations in the field, the present study indicates that some individuals do not show strong seasonal rhythms of activity, body weight and hibernation. Individual differences regarding the onset and amplitude of body weight gain were apparent already in the first months after capture and became more pronounced in the second year. The disappearance of seasonal cycles in half of the possums after one year in captivity (present study), and observed complete loss of seasonal cycles in a stock of laboratory-bred individuals (Geiser *et al.*, 1990; Mansergh & Scotts, 1990), suggest a high variance within the population and an opportunistic expression of hibernation in *Burramys*.

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