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Circadian rhythms of body temperature and locomotor activity in the
antelope ground squirrel, *Ammospermophilus leucurus*

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ABSTRACT

We studied circadian rhythms of body temperature and locomotor activity in antelope ground squirrels (*Ammospermophilus leucurus*) under laboratory conditions of a 12L:12D light-dark cycle and in constant darkness. Antelope ground squirrels are diurnally active and, exceptionally among ground squirrels and other closely related members of the squirrel family in general, they do not hibernate. Daily oscillations in body temperature consisted of a rise in temperature during the daytime activity phase of the circadian cycle and a decrease in temperature during the nighttime rest phase. The body temperature rhythms were robust (71% of maximal strength) with a daily range of oscillation of 4.6 °C, a daytime mean of 38.7 °C, and a nighttime mean of 34.1 °C (24-h overall mean 36.4 °C). The body temperature rhythm persisted in continuous darkness with a free-running period of 24.2 hours. This pattern is similar to that of hibernating species of ground squirrels but with a wave form more similar to that of non-hibernating rodents. Daily oscillations in body temperature were correlated with individual bouts of activity, but daytime temperatures were higher than nighttime temperatures even when comparing short episodes of nocturnal activity that were as intense as diurnal activity. This suggests that although muscular thermogenesis associated with locomotor activity can modify the level of body temperature, the circadian rhythm of body temperature is not simply a consequence of the circadian rhythm of activity.

Keywords: *Ammospermophilus*; Body core temperature; Circadian rhythm; Locomotor activity; PIT tag thermometry

1. Introduction

Circadian rhythmicity of body temperature is ubiquitous in mammals and birds. In a thermoneutral environment, the body temperature of some species oscillates less than 1 °C on a daily basis, but as much as 5 °C in others (Aschoff, 1983; Refinetti and Menaker, 1992). In energetically challenging situations, such as low ambient temperature or seasonally limited food availability, some small species of mammals and birds exhibit daily torpor, in which body temperature may decline by 10 °C or more on a daily basis (Ruf and Geiser, 2015).

Ammospermophilus leucurus is particularly interesting from the perspective of thermal biology because, unlike many other Holarctic (Northern Hemisphere) ground squirrels and related members of the squirrel family's Tribe Marmotini (Helgen et al., 2009; Hoffmann et al., 1993), the antelope ground squirrel does not hibernate (Chappell and Bartholomew, 1981; Karasov, 1983; Kenagy and Bartholomew, 1985). It ranges widely across arid environments in western North America from the Great Basin and Mojave Desert southward into the Sonoran Desert and throughout the Baja California Peninsula (Hall, 1981).

Despite the unique thermal physiology of *A. leucurus*, the circadian rhythmicity of its body temperature has not been studied under controlled laboratory conditions. A hibernator of similar body size, the thirteen-lined ground squirrel (*Ictidomys tridecemlineatus*) exhibits a large amplitude in the oscillation of its body temperature while housed in the laboratory under conditions approximating thermal neutrality prior to the first torpor bout of the hibernation season (Refinetti, 1996; Russell et al., 2010). We have undertaken the current comparative study in order to learn whether quantitative characteristics of the body temperature rhythm of the antelope ground squirrel resemble those of hibernators such as the thirteen-lined ground squirrel or those of non-hibernating rodents such as the laboratory rat (Honma and Hiroshige, 1978; Ikeda and Inoué, 1998; Nagashima et al., 2003). We describe here the daily rhythmicity of body

temperature and its interrelationship with the rhythmicity of locomotor activity in the antelope ground squirrel housed in the laboratory under a light-dark cycle as well as under constant darkness.

2. Methods

2.1. Subjects

Antelope ground squirrels were born in the laboratory to dams captured while pregnant in Owyhee County, Idaho (Idaho Department of Fish and Game permit number 160812). Ten animals from four different litters (5 males and 5 females) were used in this study. The squirrels were four months old and weighed about 125 g, typical of adult body weight, at the beginning of the study. They were housed individually in polycarbonate cages with wire tops (36 cm length, 24 cm width, 19 cm height) lined with cellulose bedding (Comfort Bedding, BioFresh, Ferndale, WA). The cages were kept inside light-tight, ventilated individual chambers maintained at 25 ± 0.5 °C with 20 ± 5 % relative humidity. Food (Purina Rodent Diet 5001, Lab Diet, St. Louis, MO) and water were available *ad libitum*.

2.2. Procedure

All procedures were approved by the Boise State University Animal Care and Use Committee under Protocol No. 006-AC16-014.

Body temperature was monitored continually with a temperature-sensitive PIT tag system. Passive integrated transponders (PIT) are radio-frequency microchips housed inside glass ampoules the size of a grain of rice that are widely used for animal identification. LifeChip PIT tags with bio-thermo technology (Destron Fearing, Eagan, MN) are temperature-sensitive tags with resolution better than 0.1 °C in the range of 32 to 42 °C. The PIT tags were injected intraperitoneally with a sterile 12-gauge needle while the animals were under isoflurane

anesthesia. The signal from the transponders was monitored by a custom-designed antenna system connected to an RM310 reader and an SM303 multiplexer (Biomark, Boise, ID).

Locomotor activity was monitored with Konlen passive infrared motion sensors (Light in the Box, Seattle, WA). Temperature and activity data were continually recorded with a desktop computer and saved in 6-min bins (0.1 h intervals).

The squirrels were studied under the vivarium temperature of 25 ± 0.5 °C. This ambient temperature is slightly below the thermoneutral zone of *A. leucurus* (30 to 34 °C) as determined by Dawson (1955). Vivarium temperatures are often maintained below the thermoneutral zone for laboratory rodents (David et al., 2013), and, in our particular case, the lower ambient temperature may have led to a slight overestimation of the daily range of oscillation of body temperature. An overestimation is possible because the range of oscillation of body temperature is extended in some species at ambient temperatures below thermoneutrality (Refinetti, 1997).

Illumination was controlled by a programmable electronic timer (ChronTrol XT, ChronTrol Corp., San Diego, CA) that activated white-light-emitting-diode units (Backup Trailer Light, Online-LED-Store, Ontario, CA) generating an illuminance of approximately 600 lux, as measured 8 cm above the cage floor. Data were collected from each animal for three or more weeks under a 12L:12D light-dark cycle and three or more weeks in constant darkness. The 10 animals were studied simultaneously in separate individual chambers. Data collection was started early in August and completed by mid October 2017.

2.3. Data analysis

Individual time series were analyzed by cosinor rhythmometry (Nelson et al., 1979; Refinetti et al., 2007) for five rhythmic parameters: mesor (mean level), amplitude (half the range of daily excursion), acrophase (time of the daily peak), period (the duration of each cycle), and robustness. Rhythm robustness refers to the strength of rhythmicity and is closely related to

the stationarity of the time series. Robustness is independent of amplitude, except at the extreme low end of the range, because a rhythm with zero amplitude also has zero robustness. Rhythm robustness was computed as the percentage of total variance accounted for by the cosine fit (Refinetti et al., 2007).

For the purpose of standardization, 10-day segments were selected for analysis after stable entrainment was achieved (as defined by at least 20 consecutive days with less than 30-min variability of daily activity onsets). Temperature files were filtered for removal of recording artifacts prior to analysis. A reading was considered an artifact if it registered less than 32 °C or more than 42 °C without being preceded by a lowering or rising trend. Artifactual readings (which were fewer than 2% of the readings in a data set) were replaced by the immediately-preceding temperature reading.

Locomotor activity was quantified as the number of changes in the passive infrared detection signal (“counts”) per 6-min bin. For the analysis of the effect of locomotor activity on body temperature, Pearson correlation coefficients were calculated for the activity and temperature data from each animal. For further analysis, the data sets were separated into day and night segments. In each segment, the mean body temperature in temporal bins with different levels of activity was determined. This procedure allowed the computation of separate regressions of temperature on activity for the daytime and the nighttime.

3. Results

All animals exhibited significant daily rhythmicity of body temperature and locomotor activity, as determined by cosinor rhythmometry ($p < 0.00001$). Four-day segments of the records of body temperature of two representative squirrels are shown in Fig. 1. The animal whose records are shown in the top panel (Fig. 1A) exhibited a daily range of oscillation of body

temperature of almost 4 °C. Its body temperature typically started to rise at around the time of lights-on, declined briefly by about 2 °C around the middle of the light phase, and finally fell to the nocturnal low around the time of lights-off. The squirrel whose records are shown in the lower panel (Fig. 1B) did not show a decrease in body temperature during the middle of the day, but the general form of its oscillation of body temperature was otherwise similar to that of the first animal.

The remaining eight squirrels had temperature rhythms similar to those shown in Fig. 1. Four of the ten animals exhibited a large temperature decrease (~ 2 °C) lasting 30 to 60 min, during the middle of the day, but this did not occur every day, and it did not occur at the same time of day over successive days. Thus, when 10 consecutive days for all 10 squirrels were averaged into one day to yield an educed rhythm, the oscillatory pattern was smooth, with no midday decrease (Fig. 2). This educed rhythm was characterized by a sharp rise in temperature starting an hour before lights-on and a more gradual fall in temperature starting two hours before lights-off and reaching the nighttime trough about three hours after lights-off. As a natural consequence of the averaging process, the amplitude of the daily oscillation was smaller in the educed rhythm than in the rhythms of the individual squirrels.

The results of the quantitative analysis of the time series are summarized in Table 1. Each parameter was computed for each of the ten squirrels using 10 consecutive days with 240 data points per day under a 12L:12D light-dark cycle. Values shown in the table are the means (and standard errors) for the 10 animals. The overall mean body temperature was 36.4 °C with a mean range of oscillation of 4.6 °C (with a daytime high of 38.7 °C and a nighttime low of 34.1 °C), an amplitude of cosinor fit of 1.4 °C, and rhythm robustness of 71%. The mean acrophase (time of peak temperature) was 6.4 hours after lights-on, amounting to about the middle of the light phase of the environmental cycle.

When the squirrels were kept in constant darkness, their temperature rhythms free-ran, as exemplified by the records of two squirrels in Fig. 3. The mean free-running period of all 10 squirrels was 24.2 hours (Table 1), the shortest being 23.8 h and the longest 24.4 h.

The oscillatory pattern of locomotor activity was very similar to the oscillatory pattern of body temperature, as exemplified in Fig. 4. This four-day segment of records for a representative squirrel shows large daily oscillations of both body temperature (Fig. 4A) and activity (Fig. 4B). Variations in body temperature were generally correlated with variations in locomotor activity, with correlation coefficients ranging from 0.67 to 0.83 ($p < 0.0001$) in the ten squirrels (2400 data points in each time series).

A more detailed analysis of the relationship between body temperature and locomotor activity is provided in Fig. 5. For each animal, the mean body temperatures associated with different levels of activity were calculated separately for the light phase and the dark phase of the light-dark cycle. More intense activity is associated with higher body temperatures, but for a given activity level the temperature is generally higher during the light phase than during the dark phase for all 10 animals.

4. Discussion

Under conditions approximating thermoneutrality in the laboratory, antelope ground squirrels exhibited a robust daily rhythm of body temperature that persisted with an average period of 24.2 hours in constant darkness. With a mean robustness of 71%, the body temperature rhythm of the antelope ground squirrel is on the high end of the range of robustness for rodent body temperature rhythms in general (Refinetti, 2004). In a manner consistent with the diurnal activity habit of this species, the body temperature rhythm in the laboratory peaked in the middle of the light phase of the daily light-dark cycle.

The mean body temperature of 36.4 °C and range of oscillation of 4.6 °C are comparable to those previously recorded under laboratory conditions in other species of ground squirrels such as the golden-mantled ground squirrel (Lee et al., 1990), thirteen-lined ground squirrel (Refinetti, 1996), and arctic ground squirrel (Williams et al., 2011). This value of mean body temperature is a full degree lower than, and the range of oscillation is twice as broad as, the values recorded from the laboratory rat (Ikeda and Inoué, 1998) and Nile grass rat (McElhinny et al., 1997). Yet, the body temperature rhythm of the antelope ground squirrel was very consistent from day to day and resembled the regularity observed in rats and mice (Castillo et al., 2005; Honma and Hiroshige, 1978; Ikeda and Inoué, 1998; Weinert and Waterhouse, 1998). The temperature rhythm of antelope ground squirrels did not exhibit the large fluctuations observed at the beginning of the hibernation season in thirteen-lined ground squirrels kept under comparable indoor environmental conditions at the same time of the year (Refinetti, 1996; Russell et al., 2010). This finding is consistent with the fact that *Ammospermophilus leucurus* does not hibernate (Chappell and Bartholomew, 1981; Karasov, 1983; Kenagy and Bartholomew, 1985), as do most other ground squirrels and many closely related members of the squirrel family.

In a study of arctic ground squirrels (*Urocitellus parryii*), the mean level of body temperature in the wild started to decline gradually more than a month before the first torpor bout of the hibernation season (Sheriff et al., 2012). Although our time series were relatively short, we did not observe a gradual decline of body temperature in anticipation of winter in antelope ground squirrels, which is again consistent with the fact that *Ammospermophilus leucurus* does not hibernate.

The fact that increases in body temperature were closely associated with locomotor activity suggests that episodes of exercise-induced thermogenesis might be the cause of

oscillations in body temperature. However, in agreement with a previous comparative study of seven rodent species (Refinetti, 1999), we found that, whereas higher activity levels are associated with higher body temperatures, the daily rhythm of activity and rest cannot account for the daily oscillation in body temperature because a given activity level is associated with higher temperatures during the light phase than during the dark phase of the light-dark cycle in this diurnal species. Thus, the thermogenic effect of physical activity is reflected in an elevation of body temperature, but this effect is superposed on a more complex heat-exchange mechanism that is responsible for the circadian rhythmicity of body temperature. Although the heat-exchange mechanism responsible for the body temperature rhythm has not been extensively studied, a study in laboratory rats has shown that the daily oscillation in body temperature is due not to a daily oscillation in heat production per se, or in heat dissipation per se, but to the temporal coordination of heat production and heat loss (Refinetti, 2003). That is, both heat production and heat loss oscillate on a daily basis in very close temporal proximity, and the oscillation of body temperature results from small variations in the balance of heat production and heat loss.

The squirrel family Sciuridae represents a large group of nearly 300 species within the mammalian Order Rodentia that dates back to the Eocene (nearly 50 million years) as an independent lineage of mostly diurnally active species (Koprowski et al., 2016). Within the entire family only the Holarctic (Northern Hemisphere) lineage of the Tribe Marmotini is recognized to include hibernators, whereas other Tribes Sciurini and Xerini (and corresponding subfamilies) of temperate and tropical latitudes in both Northern and Southern Hemispheres do not hibernate, and these include various tree squirrels, flying squirrels and African ground squirrels. Most, but not all species of marmots, prairie dogs, ground squirrels, and chipmunks

(Tribe Marmotini as defined by Hoffmann et al., 1993; and with a more recent revision of ground squirrels by Helgum et al, 2009) are hibernators.

Antelope squirrels (four species in the Genus *Ammospermophilus*) are among the exceptional members of the Tribe Marmotini that do not hibernate, and *A. leucurus* has the broadest geographic range of any of the *Ammospermophilus*. While hibernation is an effective strategy for dealing with energy shortages in highly seasonal environments in many species, the milder environmental conditions of the deserts inhabited by *Ammospermophilus* and their broad, omnivorous diet have been suggested as the bases of a strategy for successful year-round activity and survival without resorting to hibernation. In fact, antelope ground squirrels initiate their breeding season in late winter in order to produce young by early spring, before the onset of summer drought (Kenagy and Bartholomew, 1985). Although many laboratory studies have been conducted on *A. leucurus* (DeCoursey, 1973; Kenagy, 1978, 1981; Kenagy and Bartholomew, 1979; Kenagy and Vlek, 1982; Pengelley, 1966; Pengelley et al., 1976; Pohl, 1983, 1998), no previous study has investigated the circadian rhythmicity of its body temperature. In the present study, we found that under conditions approximating thermoneutrality in the laboratory, antelope ground squirrels exhibited a robust daily rhythm of body temperature that was as stable as that of non-hibernating rodents but had mean and amplitude similar to that of hibernators during the euthermic stage of the annual cycle. Further studies may prove useful in clarifying whether there is some form of annual variation in the body temperature rhythm of this species, especially under seasonal oscillation of photoperiod and ambient temperature. Although antelope ground squirrels do not enter hibernation, they may exhibit small annual changes in the regulation of body temperature.

Conflict of interest

The authors declare that they have no conflict of interest.

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Table 1. Parameters of the Body Temperature Rhythm

	Mean \pm SEM
Mesor (mean level)	36.42 \pm 0.12 °C
Amplitude	1.43 \pm 0.09 °C
Range	4.55 \pm 0.20 °C
Acrophase	6.35 \pm 0.28 HALO
Robustness	71 \pm 2%
Period	24.20 \pm 0.05 h

HALO: hours after lights on

Figure captions

Fig. 1. Four-day segments of body temperature recordings in two representative squirrels. The dark and white horizontal bars above the graphs denote the dark and light phases of the prevailing 24-hour light-dark cycle.

Fig. 2. Generalized, educed rhythm of body temperature of the antelope ground squirrel, based on data for 10 individuals. For each six minutes of a day, the body temperature readings of all 10 squirrels were averaged over 10 consecutive days. The standard errors of the mean are plotted in two-hour intervals to avoid cluttering the figure. The dark and white horizontal bars above the graph denote the dark and light phases of the prevailing light-dark cycle.

Fig. 3. Plots of the free-running rhythm of body temperature of two representative squirrels maintained in constant darkness. (A) free-running period 24.1 hours; (B) free-running period 24.4 hours. Each line corresponds to a day, and consecutive days are plotted on consecutive lines. For each 6-min interval, a small vertical dark mark is plotted (resulting in a solid black bar) for all times when the body temperature was above the daily mean ; the space is left blank during the portion of the day when body temperature was below the daily mean.

Fig. 4. Four-day segments of simultaneous records of body temperature and locomotor activity of a representative squirrel. The dark and white horizontal bars above the graphs denote the dark and light phases of the prevailing light-dark cycle.

Fig. 5. Mean body temperature as a function of activity level (changes detected in passive infrared signals) for each of the 10 squirrels (A through J). In each panel, open circles denote data from the light phase of the light-dark cycle and dark circles denote data from the dark phase of the light-dark cycle.

Figure 1

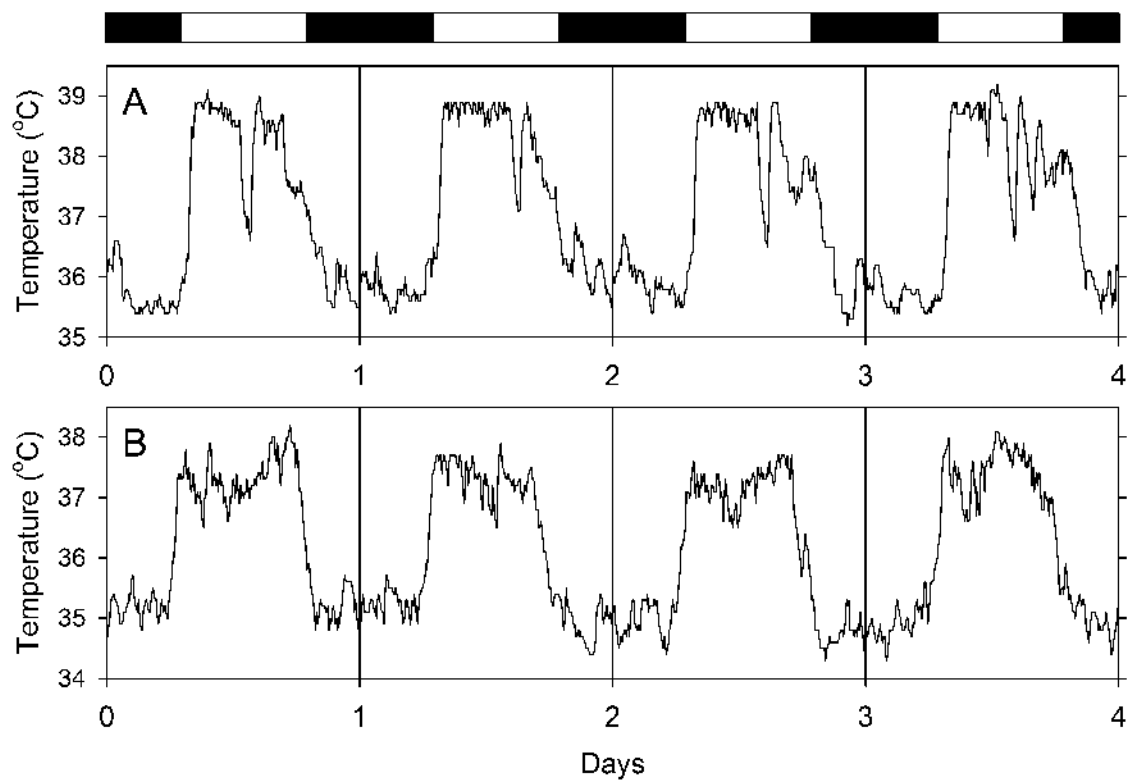


Figure 2

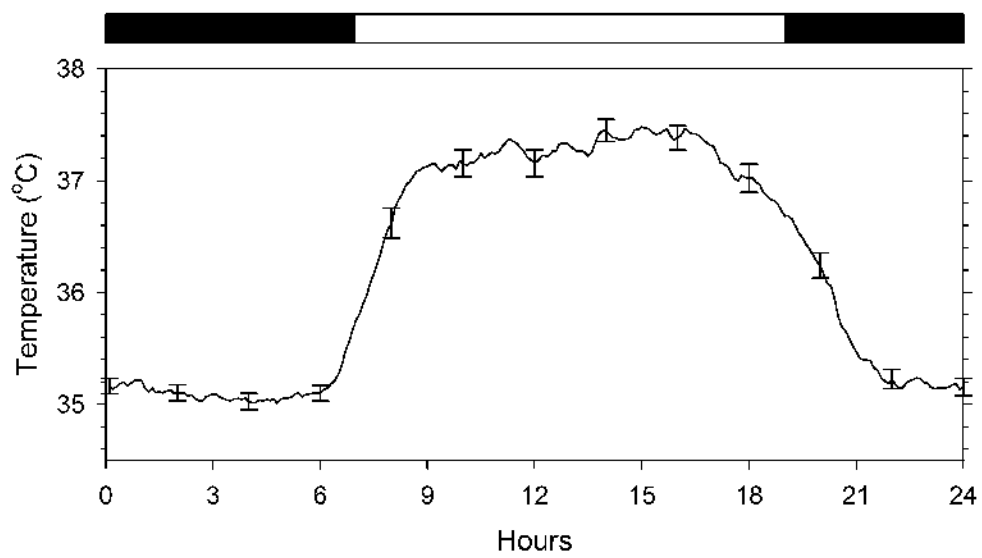


Figure 3

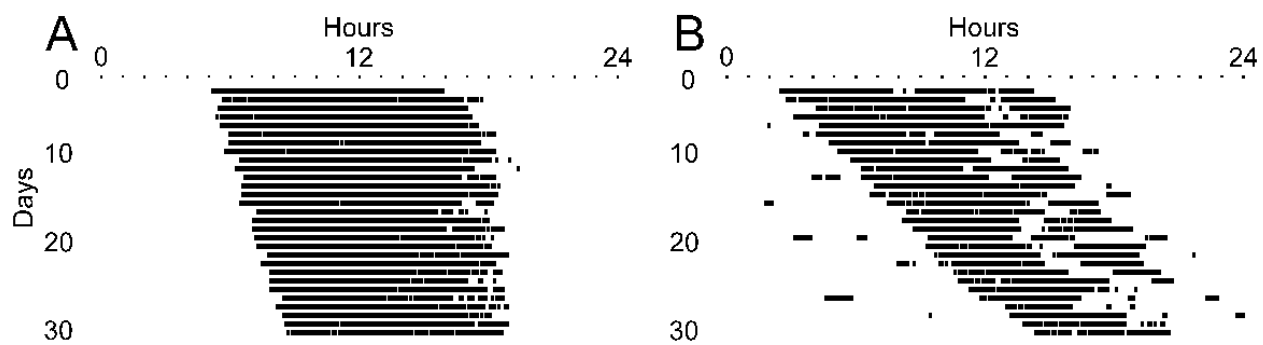


Figure 4

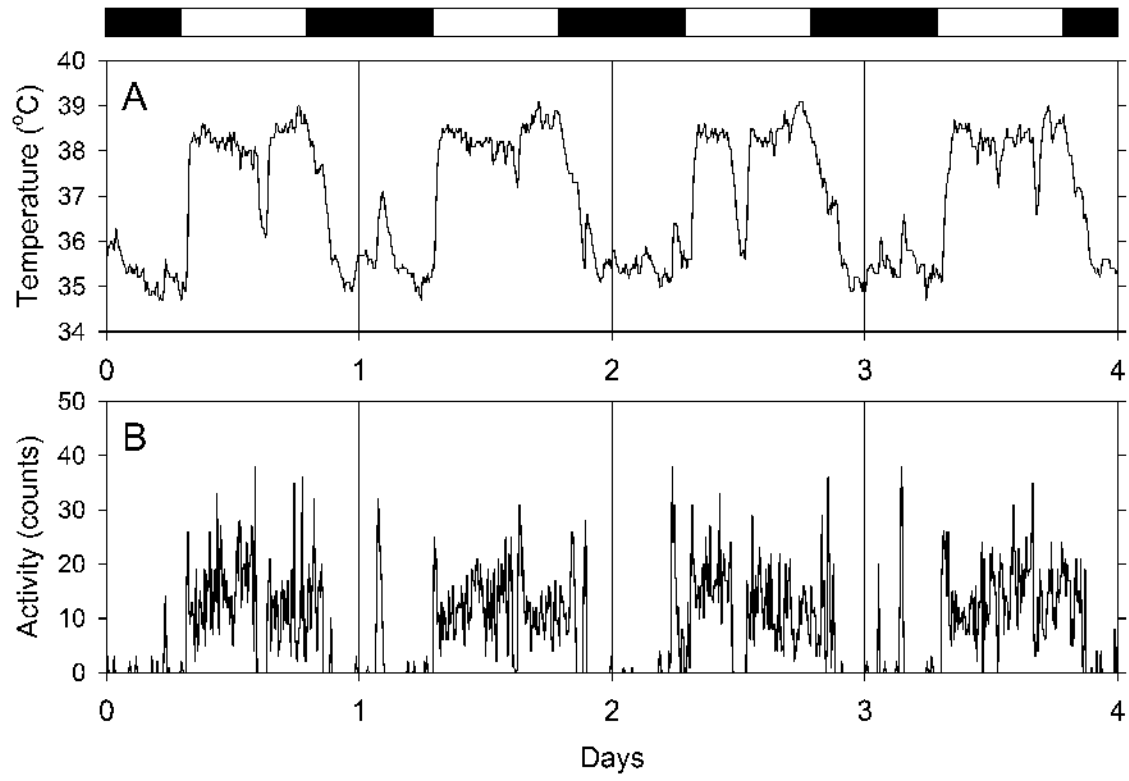


Figure 5

