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Golden hamsters are nocturnal in captivity but diurnal in nature

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Daily activity rhythms are nearly universal among animals and their specific pattern is an adaptation of each species to its ecological niche. Owing to the extremely consistent nocturnal patterns of activity shown by golden hamsters (*Mesocricetus auratus*) in the laboratory, this species is a prime model for studying the mechanisms controlling circadian rhythms. In contrast to laboratory data, we discovered that female hamsters in the wild were almost exclusively diurnal. These results raise many questions about the ecological variables that shape the activity patterns in golden hamsters and the differences between laboratory and field results.

Keywords: activity rhythms; field study; *Mesocricetus auratus*

1. INTRODUCTION

Virtually all living organisms show periodic rhythms in activity and physiological processes. Most of these rhythms have a roughly 24-hour periodicity and are synchronized with the daily light cycle, resulting in species-typical activity patterns (e.g. diurnal, nocturnal and crepuscular). Discoveries characterizing the timing of these rhythms, the biochemical and neural mechanisms involved and the mechanisms by which these patterns are entrained by environmental cues represent major achievements in science (Aschoff 1965; Pittendrigh 1993; Dunlap *et al.* 2004). In mammals, these behavioural and physiological rhythms are synchronized within an individual by pacemaker cells in the suprachiasmatic nucleus (SCN) of the brain. The length and pattern of activity are generally stereotyped for each species but differ between species, suggesting that the timing of activity is adaptive (Sharma 2003).

In contrast to the literature describing the mechanisms underlying activity patterns, the influence of extrinsic ecological variables on these patterns has been less thoroughly studied and is not well understood (Enright 1970; Halle 2000)—primarily owing to the difficulties associated with identifying and quantifying the many factors that influence activity patterns (DeCoursey *et al.* 2000). Several studies have documented shifts in activity in response to predator risk. Fenn & Macdonald (1995) observed diurnal activity in normally nocturnal wild rats (*Rattus norvegicus*) and found that the rats were active during the day to avoid predation by nocturnal foxes (*Vulpes vulpes*). Coyotes (*Canis latrans*) exposed to human persecution during the day were largely nocturnal, but when persecution ceased they exhibited more diurnal patterns of activity (Kitchen *et al.* 2000). Comparing a group of free-living, SCN-lesioned eastern chipmunks (*Tamias striatus*) with sham-lesioned and intact control chipmunks, DeCoursey *et al.* (2000) found that the SCN-lesioned group experienced significantly higher levels of predator-induced mortality than the other groups, presumably due to inappropriate activity cycles.

One of the primary mammalian species used in research on activity rhythms and their underlying mechanisms is the golden hamster (*Mesocricetus auratus*). Hamsters are important because they are strictly nocturnal in the laboratory and show a remarkable consistency in the timing of their rhythms. More than 80% of laboratory hamster activity occurs at night, regardless of the testing environment or the measure of activity (Pratt & Goldman 1986*a*,*b*). Typically, activity peaks shortly after the onset of dark followed by a gradual decline throughout the night (Gattermann 1984; Fritzsche 1987; figure 1). Individuals that are shifted from a light–dark cycle to complete darkness maintain their normal activity pattern and a regular period length. The period length can also be changed by altering the light cycle, as would occur in animals living in the wild in different seasons (Pittendrigh & Minis 1964).

Despite being a common model species in biological research, little is known about golden hamsters in the wild. In addition, the laboratory hamsters are descendents of a brother–sister pair mated in 1930 (Aharoni 1932; Murphy 1971; Gattermann *et al.* 2001). Given this, we established a research programme in southern Turkey to study hamsters in their native habitat. Our study represents the first time that the behaviour and activity patterns of golden hamsters have been recorded in the wild.

2. MATERIAL AND METHODS

(a) *Laboratory populations*

For comparing with the wild populations, we measured the activity patterns of hamsters in the Gatterman Laboratory at Martin-Luther-University, Halle-Wittenberg, Germany. The activity was measured for 21 days on 10 female golden hamsters. The study population was derived from 23 animals captured in Syria and southern Turkey in 1999; the captive animals were roughly five generations removed from their wild progenitors. The animals were 8 to 10 months old and housed in temperature-controlled rooms (ambient temperature, 22±2°C; relative humidity, 55–65%). They were exposed to an artificial light–dark cycle of 12 L : 12 D hours with lights on from 07.00 to 19.00 Central European Time. The average light intensities during the dark phase were nearly 0 lx, and those during the light phase were 200 lx. This difference between the dark and light phases is sufficient for entrainment to the light cycle. The animals were kept solitarily in macrolon cages (54×33×20 cm). To simulate a burrow, the cage was equipped with a sleeping chamber, an opaque plastic cylinder (18 cm in length and

The authors dedicate this manuscript to Rolf Gattermann who died from cancer in 2006.

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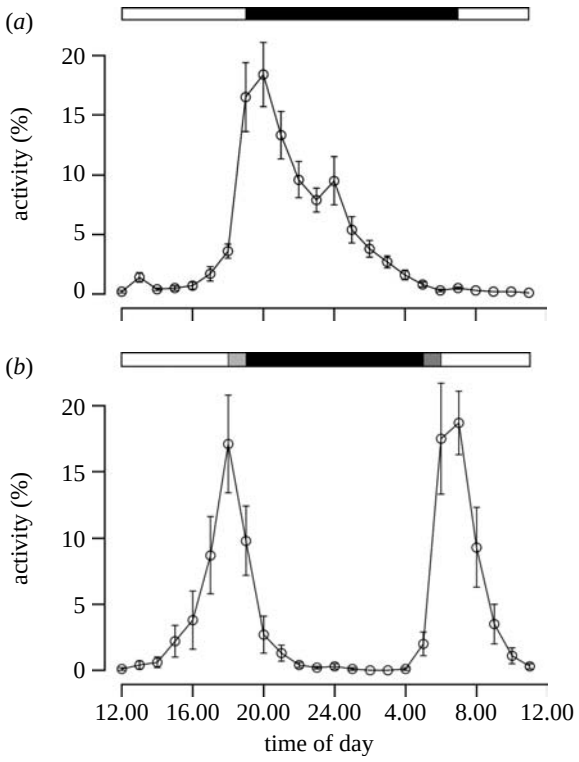

Figure 1. Percentage of time active per hour during a 24-hour period: data collected in (*a*) the German laboratory and (*b*) the field (Turkey). The bars are 95% CIs; the dark period is indicated by the black bar above the graph and the grey bar indicates dawn and dusk.

10 cm in diameter) that was closed on both ends; at one end was a 5 cm diameter entrance. Standardized food (Altromin) and drinking water were available ad libitum.

The locomotor activity outside the sleeping box was monitored continuously using a passive infrared detector. A single beam ran through the centre of the cage and the activity was counted as the number of times the beam was broken; the activity counts were recorded using the Chronobiology Kit (Stanford Software Systems, Santa Cruz, CA, USA). As with the field data, these data were used to calculate the number of minutes per hour an animal was active.

(b) *Wild populations*

In the wild, golden hamsters are solitary, widely dispersed and do not engage in much social activity. We observed the behaviour and daily activity patterns for 12 female hamsters in southern Turkey for 9–28 days during April and May 2005 and 2006. The temperature in April ranged from 5 to 25°C and in May from 6 to 36°C. The mean temperature for 2005 and 2006 was 17 ± 1.2°C and 18 ± 1.6°C, respectively. On a sunny day, the light intensities could reach 100 000 lx.

To record activity, an individually coded passive integrated transponder (PIT) tag was injected subcutaneously into each individual. Burrow entrances of occupied burrows were fitted with a plastic ring containing a PIT tag reader that recorded which individuals were moving in and out of the burrow. The rings also projected two infrared beams, one above the other, across the burrow entrance; the sequence of the beam interruption indicated whether the animal was entering or exiting the burrow. These data were recorded and used to calculate the number of minutes per hour the animal was out of the burrow.

3. RESULTS

(a) *Activity in the laboratory*

The activity patterns for the laboratory population were sharply nocturnal, with activity peaking at the start of the dark period; virtually no activity occurred when lights were on (figure 1*a*). The amount of activity varied across the females' 4-day oestrous cycle, but there were no differences in the onset of activity across the cycle and thus no differences in the overall activity pattern.

(b) *Activity in nature*

In the wild, female golden hamsters were out of their burrows almost exclusively during daylight hours (figure 1*b*). There were two periods of activity: between 06.00 and 08.00 and 16.00 and 19.30. Almost no activity occurred during the middle of the day (10.00–16.00) or at night (after 20.00 hours). The average total time spent in surface activity over 24 hours was 87 min; almost all of this time was spent foraging. The overall patterns did not change with temperature.

While all females were active during the morning and afternoon periods, there were differences in the onset of timing of activity across individuals. Some females displayed more activity in the morning, while others preferred the afternoon; one female tended to start and end her activity later in the morning than any of the others. Sometimes a female skipped a morning or afternoon period of activity. However, we do not know how much or when the females were active inside their burrow. Attempts to obtain these data were unsuccessful due to technical problems.

4. DISCUSSION

These findings for females differ from all reports on this species in captivity, both in the timing and the total duration of activity, including studies in which the animals lived in burrows (Pratt & Goldman 1986*a*). Although bimodal circadian rhythms have been produced in captivity under special lighting conditions (Shibuya *et al.* 1980), these patterns are quite different from the regular bimodal patterns we observed in nature.

The activity patterns we observed cannot necessarily be attributed to genetic changes in laboratory strains. The patterns shown by the fifth generation wild-type stock tested in Germany are not different from similar data collected from domestic stock tested at Cornell University (Larimer 2007). In addition, 10 wild-caught male hamsters were observed in captivity in Germany four weeks after their capture and transfer to standard laboratory conditions. Although these hamsters showed the strictly nocturnal pattern shown in figure 1*a*, males in the wild show activity throughout the 24-hour period (R. E. Johnston 2005, 2006, unpublished data; Weinert *et al.* 2001).

What factors account for differences between activity patterns in nature and in captivity? Levy *et al.* (2007) found that laboratory golden spiny mice (*Acomys russatus*) are nocturnal while wild mice are diurnal. They suggested that environmental cues in the field mask internal rhythms, resulting in activity patterns that differ between the field and laboratory (Levy *et al.* 2007).

A variety of factors are known to influence (or mask) activity rhythms, including predation, temperature, humidity, rainfall and food availability (for a discussion of masking, see Mrosovsky (1999) and Dunlap *et al.* (2004)). We propose that the diurnal pattern observed in female hamsters may be a

mechanism to avoid nocturnal predators. Owl (*Tylo alba*, *Athene noctua*) pellets collected around our field site contained hamster teeth, while fox (*V. vulpes*) were observed in the area at dawn and dusk and feral dogs were observed at all times. Potential diurnal predators include migrating and resident raptors (e.g. *Buteo rufinus*, *Circus pygargus*, *Falco tinnunculus*) and white storks (*Ciconia ciconia*) but all of these were rare. A number of snakes were recorded in the general area (e.g. *Vipera lebetina*, *Coluber jugularis*, *Spalerosophis diadema*) but none were seen around hamster burrows.

In addition, we suggest that hamsters in the field constrain their activity to avoid high mid-day surface temperatures. The short duration of the daily activity suggests that females balance foraging needs, predator avoidance and potential heat stress.

Our observations indicate that the control of activity rhythms in hamsters is much more complex and more sensitive to environmental factors than previously realized, thus suggesting new questions for investigation. We do not know how hamster activity patterns vary throughout the year, but our findings raise the question of whether the activity patterns described in laboratories ever occur in nature. To obtain a thorough understanding of biological rhythms and their plasticity, we must expand the range of experiments carried out in captivity and conduct more research in natural and laboratory settings (Smale *et al.* 2003).

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