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Original investigation

Diurnal surface activity of the Ciscaucasian hamster (*Mesocricetus raddei*) in the field

Peter Fritzsche[a,*], Magomed M. Chunkov[b], Maria V. Ushakova[c], Kamil Z. Omarov[b], Dietmar Weinert[a], Alexey V. Surov[c]

[a] *Institute of Biology/Zoology, Martin Luther University Halle-Wittenberg, Domplatz 4, 06108 Halle, Germany*
[b] *Precaspian Institute of Biological Resources of Dagestan Scientific Center of Russian Academy of Sciences, M. Gadzhiev St., 45, 36700 Makhachkala, Russia*
[c] *Severtsov Institute of Animal Ecology & Evolution Russian Academy of Sciences, Leninsky pr., 33, Moscow 119071, Russia*

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ABSTRACT

Monitoring daily activity patterns of animals in the field and in captivity often revealed different results. For example, Syrian hamsters *Mesocricetus auratus* showed diurnal surface activity in the field, but nocturnal patterns in the laboratory. The aim of our study was to monitor the field activity of a close relative of this species, the Ciscaucasian hamster *Mesocricetus raddei* from Dagestan. Using the radio-frequency identification (RFID) technique we were able to obtain field data from 20 Ciscaucasian hamsters. In contrast to the data obtained in captivity where the Ciscaucasian hamsters were active mainly at night, they showed a diurnal activity pattern in the field, i.e. animals were observed on surface between sunrise and sunset. Discussing the putative causes of the different activity patterns, we are focusing especially on ecological constraints and advantages. Also, we stress the necessity of more field observations.

Introduction

Rhythmic changes in behavioural and physiological processes and especially circadian rhythms are an inherent property of living systems. They enable organisms to anticipate predictable periodic changes in their environment, which is essential for their survival (DeCoursey et al., 2000; Vaze and Sharma, 2013; Spoelstra et al., 2016). Circadian rhythms are generated by an endogenous pacemaker located within the SCN (Weaver, 1998; Dibner et al., 2010). As the period length (τ) of these rhythms is different from 24 h a correction is necessary, and a proper phase relationship with the environment must be established (Aschoff, 1989; Johnson et al., 2003). This is an inevitable prerequisite for proper adaptation to regular external alterations not only on a daily but also on a seasonal basis (Goldman, 2001). Environmental periodicities that are able to realize such a phase relationship are called zeitgeber (Aschoff, 1960; Sharma and Chandrashekaran, 2005). The main zeitgeber for most if not all animals is the light-dark (LD) cycle. However, there is a number of other environmental cycles which are of great ecological relevance and important for fine tuning of circadian rhythms. This includes abiotic and biotic environmental factors like temperature or humidity changes, cycles of food availability, behavioural rhythms of prey, predators and conspecifics, e.g. mates (Mistlberger and Skene, 2004; Sharma and Chandrashekaran, 2005).

Animals can be active during the light phase (diurnal), at night (nocturnal), during dusk and dawn (crepuscular) or throughout the whole day (cathemeral) (Smale et al., 2003; Marques and Waterhouse, 2004; Roll et al., 2006). The earliest mammals were nocturnal insectivores (Roll et al., 2006). Menaker and coworkers postulated a nocturnal bottleneck hypothesis (Menaker et al., 1997; Gerkema et al., 2013). During the Mesozoic era, early eutherian mammals faced competition with diurnal reptiles, which were ectothermic and restricted their activity to the daytime. The development of endothermia allowed mammals to occupy the nocturnal niche and thus avoid predation pressure and competition (Crompton et al., 1978). Most of the modern mammals are still active at night, though a certain number shows a diurnal pattern, which probably evolved through secondary evolution (Roll et al., 2006).

There is increasing evidence that activity patterns of the same animal might be completely different in the laboratory compared to field conditions (for review, see (Calisi and Bentley, 2009; Hut et al., 2012)). Our own studies on golden and common hamsters revealed bimodal daily patterns with maximum activity around dawn and dusk. The percentage of total 24-h activity was significantly higher during light time than during night time (Gattermann

* Corresponding author.
E-mail address: peter.fritzsche@zoologie.uni-halle.de (P. Fritzsche).

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et al., 2008; Mundt, 2008; Larimer et al., 2011). Such patterns have never been found under laboratory conditions where hamsters of both species are active only during the night (Wollnik et al., 1991; Weinert et al., 2001; Monecke and Wollnik, 2005). A switch from diurnality in the field to nocturnality in the laboratory was also observed in tuco-tuco (*Ctenomys* aff. *knighti*), a South American subterranean rodent (Valentinuzzi et al., 2009; Tomotani et al., 2012; Tachinardi et al., 2014), the golden spiny mouse (*Acomys russatus*) (Levy et al., 2007), the fat sand rat (*Psamomys obesus*) (Barak and Kronfeld-Schor, 2013), the unstriped Nile rats (*Arvicanthis niloticus*, Blanchong and Smale, 2000) and other species. The reasons for these differences are unknown, and it is necessary to find out which (environmental) factors determine the expression of a certain rhythmic phenotype (Mrosovsky, 2003; Marques and Waterhouse, 2004; Weinert et al., 2007; Hut et al., 2012). To find out, more comparative field and laboratory studies are necessary.

The genus *Mesocricetus* consists of four species: *M. auratus*, *M. brandti*, *M. newtoni*, *M. raddei* (Wilson and Reeder, 2005; Neumann et al., 2006). In contrast to the well-studied Syrian or golden hamster (*M. auratus*) nothing is known on the behaviour of *M. brandtii, M. newtoni* and particularly the Ciscaucasian hamster (*M. raddei*) in the wild. The distribution of *M. raddei* is restricted to mountain regions of the Caucasus and Ciscaucasia in Dagestan and North Azerbaijan (Yigit et al., 2006). Originally, it inhabited grasslands and steppe areas but nowadays can be found mainly in agricultural areas (fields and their boundaries) on mountain terraces up to 2300 m. The Ciscaucasian hamster lives solitary in self-dug burrows. Since ages they prefer agriculture used land to live. These fields provided them with storable food for the winter time. Starting about 1990 in the last century *M. raddei* experienced a dramatic decline because of the intensified use of land and the changes in crop cultivation from grain to less energetic valuable potatoes (Ushakova et al., 2010).

The aim of the present field study was to gain more insights into the activity behaviour of this rare hamster species. In addition to recording its actual distribution, we monitored the surface activity of wild Ciscaucasian hamsters in their natural habitat. We compared the activity patterns of hamsters living in the wild with those obtained in captivity and discuss putative factors causing the switch from diurnality in the field to nocturnality in the laboratory.

Material and methods

Field studies

Investigations were performed in Dagestan around the village of Mochoh (42°40′30″N, 46°37′55″E) at an altitude of 1670 m. We monitored the surface activity of a total of 20 Ciscaucasian hamsters during the years 2012–2014 in June and July. The mean temperatures during these months were 13.6 and 16.1 °C with minima of 5.8 and 9.5 °C and maxima of 28.0 and 25.8 °C. During the observation the mean time sunset was at around 18:40 h and the mean sunrise at around 03:20 h. On sunny days, the light intensities could reach 100,000 lx.

All hamsters were monitored using our self-developed Field-Animal-Identification- System (FAIS; Gattermann et al., 2008; Larimer et al., 2011). We caught the animals by means of live traps and marked them with passive integrated transponder (PIT) tags injected subcutaneously. Then, we fitted plastic rings with integrated antennas and two light barriers (one above the other) to the entrances of occupied burrows. The antenna of each ring was connected to a PIT tag reader and a data logger. Thereby it was possible to identify animals individually and to distinguish between exits and entries, i.e. whether a hamster went into the burrow or left it. The date and the time of day of these events were stored together with the animal ID. Using these data, the duration an individual was out of its burrow was calculated. To create mean daily activity patterns from each animal, only individuals with continuous data of at least five days were used. Thus, 10 each male and female hamsters monitored on average over 10 or 12 days respectively were considered for further analyses. From these individual patterns of the animals the mean daily pattern of the males and females were calculated.

Studies in captivity

Eight adult male hamsters (three in 2009 and five in 2010) were caught in June in Dagestan and immediately transferred to the Biological Station of the Severtsov Institute of Ecology and Evolution (Russian Academy of Sciences) in Chernogolovka (56°2′11″N, 38°25′25″E). They were kept solitarily in cages (100 × 100 × 60 cm) under natural temperature (mean 18.0 °C) and light conditions (mean sunset at 20:17, mean sunrise at 02:42 h). The cages were provided with a wooden box as shelter. From June, 22nd until July, 2nd (10 days) we continuously monitored the locomotor activity of each individual using passive infrared detectors. These were mounted above the cage roof to track motions of the animal in all sectors of the cage. We recorded and analyzed activity counts per minute using the Chronobiology Kit (Stanford Software Systems, Santa Cruz, CA, USA).

Data analysis

To compare the data from the field with the results obtained in captivity, the percentage of the 24-h activity accounted for each hour was calculated for each individual. Hourly mean values and standard errors both from hamsters in the field and in captivity were depicted. A Cosinor analysis was applied to estimate the acrophases of the daily activity rhythms (Bingham et al., 1982). As the daily patterns do not have a cosine shape, the acrophases were taken not as the daily maximum but as an estimate of the gravity centre of activity. Also, cross correlations between field data from males and females and the data from captivity were calculated to estimate the phase relations between the corresponding daily patterns as this approach does not presume a definite shape of the daily patterns. To test for significant differences of the means after test for normal distribution (Kolmogorov-Smirnov-test) the Studentís *t*-test was applied. For further details, see Results.

Results

Activity in the field

A representative actogram for one male hamster each from the field and the laboratory is shown in the upper panel of Fig. 1. Mean patterns for male and female animals from the field are depicted in Fig. 2A and B. The hamsters of both sexes left their burrows after sunrise and were active nearly exclusively during day time. After sunset, they reduced their surface activity and stayed in their burrows over night until next sunrise. In females, the acrophase of the activity rhythm, i.e. the centre of gravity was at 13.30 h during bright sunlight. Males also left their burrows after sunrise, their acrophase was about three hours later at 16.42 h. This time difference of three hours was confirmed by cross-correlation analysis (highest correlation between males and females at 3 h, $r = 0.92$, $p < 0.001$).

The hamsters of both sexes left their burrows daily for nearly the same duration (Fig. 3, left panel). Males were found outside their burrows for 105.8 ± 17.5 min and females for 96.6 ± 13.1 min per day ($t = 0.41$, $p = 0.68$). Most of this surface activity occurred during the light time, i.e. from sunrise to sunset (84.3 ± 4.1%