Individual variability and photic entrainment of circadian rhythms in golden spiny mice

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Received 15 September 2005; received in revised form 4 December 2005; accepted 6 December 2005

Abstract

Golden spiny mice are diurnally active in most of their natural habitat. Their diurnal activity is ascribed to non-photic cues: competitive exclusion from the nocturnal niche, or thermoregulatory considerations. Here we studied the entrainment of golden spiny mice to light.

In the laboratory, golden spiny mice were primarily nocturnal and displayed an unusual variety of rhythm patterns, with activity bursts occurring during both activity and rest periods. Spontaneous shifts of activity rhythms between light phases were sometimes recorded. In all cases but one, body temperature shifted in parallel with activity. Under DD conditions, the free running period (tau) of all individuals but one was shorter than 24 h, and in all individuals but the same one it was shorter than tau under LL conditions.

In response to a 6 h phase delay, all individuals entrained to the new LD cycle in a relatively uniform way. During phase advance four out of the twelve individuals further delayed their activity and body temperature rhythms, and eight individuals advanced their activity rhythm, but the re-entrainment took them over twice as long as to re-entrain to the phase delay.

We suggest that the golden spiny mouse is a nocturnal rodent whose circadian system developed the flexibility to be nocturnal or diurnal according to environmental conditions, or a nocturnal rodent in the process of turning diurnal, and that it has low sensitivity to the immediate masking effect of light on activity.

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Keywords: Circadian rhythms; Acomys russatus; Diurnal activity; Masking

1. Introduction

Mammalian diurnality has attracted considerable attention lately [e.g., 1–5]. It was suggested that since the common ancestors to all mammals were nocturnal, the circadian system of present-day nocturnal mammals is relatively uniform, while that of diurnal mammals, which evolved independently at various times [1,6,7] may be diverse [1,6]. To date, however, circadian rhythms have only been studied in a limited number of closely related species [2,3,8], and this is especially true for diurnal species [1,9,10], so relatively little information exists on their circadian system. Consequently, research into the circadian system of diverse species, and especially diurnal ones, is needed [1–3,6].

The golden spiny mouse (Acomys russatus) offers an interesting rodent model for the study of activity patterns and diurnality. This species has a limited distribution in rocky deserts in northeastern Egypt, southern Israel and Jordan [11]. In most of its natural habitat, the golden spiny mouse is diurnal [12–17]; it is active in winter during the warmer hours of midday, and in the cooler mornings and afternoons during summer [12–17]. However, in northeast Jordan, golden spiny mice were trapped during the night [18]. Furthermore, field experiments at Ein Gedi near the Dead Sea, have shown that when its nocturnal congener, the common spiny mouse (A. cahirinus), is removed from the shared habitat, the golden spiny mouse shifts from a diurnal to a more nocturnal activity pattern [12,13,19,20]. This may explain why golden spiny mice in northeast Jordan were trapped during the night, since no common spiny mice were trapped during that study [18]. These results suggest that interspecific competition with common spiny mice results in exclusion of the golden spiny mice from the nocturnal niche into the diurnal one. Nevertheless, in another habitat, the high mountains of the Sinai desert in southern Egypt, golden spiny mice are diurnal even though the common spiny mice are absent from that area [14]. Ambient
temperatures in this habitat during winter may drop below 0 °C, and the authors ascribed the diurnal activity of the golden spiny mouse in this area to thermoregulatory considerations [21]. In sum, golden spiny mice are diurnally active in most of their natural habitat (except from one record from Jordan), and their diurnal activity is ascribed to competitive exclusion from the nocturnal niche, or to thermoregulatory considerations.

Daily rhythms in mammalian physiology, hormone concentrations, biochemistry, and behavior are all driven by an internal circadian clock that is entrained by environmental cues or zeitgebers [e.g., 22–24]. In mammals, the primary circadian clock is located in the suprachiasmatic nucleus (SCN) [25]. In the absence of external zeitgebers, the internal clock free runs, with a period (τ) of about 24 h. External cues can either entrain the circadian clock or mask its effect on behavior. It is still unclear whether the effect of temperature, as well as that of the common spiny mouse on the golden spiny mouse activity and body temperature rhythms, results from a difference in the way that the clock is entrained to the light dark cycle, a difference in the way that the clock is coupled to the behavioral rhythm (and other rhythms that it controls), or masking. Previous studies suggest that the golden spiny mouse has underlying nocturnal activity and temperature rhythms [17]: immediately upon removal from its natural habitat at Ein Gedi to the laboratory, golden spiny mice displayed nocturnal activity rhythms, or were active both during the light and dark periods, but did not show a diurnal activity pattern [17]. We concluded that this immediate inversion of phase preference, without evidence of a phase shift that would be expected in the case of true entrainment [26–28], indicates that the diurnal activity of golden spiny mice in the field, coupled with the overt temperature rhythms, is probably not a result of an entrainment process [17]. Furthermore, laboratory experiments on captive golden spiny mice found that under controlled conditions, this species is nocturnally active [29]. However, in both experiments described above, wheel running was used to measure activity pattern, which in itself can sometimes change and even invert activity rhythms [5,27,30,31].

Based on the results described above, we hypothesized that the diurnal activity of the golden spiny mouse under controlled LD conditions will show high variability, and that their circadian system will be less responsive than normal to photic inputs. We studied for the first time the general activity and body temperature rhythms under controlled LD conditions, and the effect of photic input on the circadian system of animals from a golden spiny mouse colony, originating from individuals trapped at Ein Gedi and bred in our laboratory. We examined entrainment to light dark (LD) cycle, its free running rhythms under constant light (LL) and dark (DD) conditions, and responsiveness to phase shifts of the LD cycle.

2. Methods

2.1. Animals and housing

29 golden spiny mice (12 males and 17 females) from our breeding colony at the I. Meir Segals Zoological Garden at Tel Aviv University were used in this study. The source of the breeding colony (funded in 1995) is Ein Gedi, near the Dead Sea, where the two species (common and golden spiny mice) coexist. The mice were individually housed in 38×24×13 cm plastic cages, under controlled laboratory conditions of LD 12:12 (unless specified differently) in an isolated sound proof room, with ambient temperature of 29 °C, and food (standard rodent chow) and water ad lib. Once every 2–3 weeks, at random times, we entered the controlled chambers in order to change food and water.

2.2. Body temperature and activity

Body temperature and activity were continuously recorded using one of two different systems: an integrated telemetry and data acquisition system (Dataquest III, Data Sciences Inc., St. Paul, MN, USA, n=17) with a temperature-sensing transmitter (TA10TA-F20, Data Sciences, Inc., St. Paul, MN, USA); or a self-combined system including temperature sensitive single stage implanted transmitters (Sirtrack, New Zealand) and RX-900 scanner–receiver (Televilt, Sweden) for the measurement of core body temperature, and infra-red detectors

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![Fig. 1. The distribution of average percentage activity at night of naïve golden spiny mice during 15 days under 12:12 LD conditions. N=29.](image1)

![Fig. 2. Average body temperature (±SE) during the light (white) and dark (gray) phase of naïve golden spiny mice during 15 days under 12:12 LD conditions. N=29.](image2)
Fig. 3. Double daily plots of activity (a1–f1) and body temperature (a2–f2) of naïve golden spiny mice during 15 days under 12:12 LD conditions. a — Representative actogram of an individual which was continuously active during the dark phase. b — Representative actogram of an individual that showed bimodal activity pattern, with activity peak occurring either at the beginning and end of the dark phase. c — Representative actogram of an individual that showed bimodal activity pattern with one dominant peak towards the end of the light phase and one towards the dark phase. d — Representative actogram of an individual that showed one peak of activity, at or around the beginning of the dark phase. e — Representative actogram of an individual that was active both during the night and during the day and could not be assigned to any one of the above groups. f — Representative actogram of a diurnal individual that displayed most of its activity during the day, with another peak towards the end of the night. Black bars at top of plot represent the light schedule.
(Intrusion detector model MH10, Crow group, Israel) connected to a PC. Data were collected using Strawberry tree software \((n=12)\). The DSI system allowed continuous measurement of activity level and body temperature. However, it demands operating the animals and implanting them with the transmitters, a procedure that by itself may affect activity rhythms. Furthermore, the number of animals we can test simultaneously in this system is limited to 12. The infra-red detectors system is

Fig. 3 (continued).
noninvasive, and allows monitoring of a larger sample size. Nevertheless, it does not provide us with information regarding body temperature of the experimental animals. Therefore, the two systems were used in the study. Comparing the results obtained by the two systems, no differences were detected. Therefore, we analyzed the results collected using the two systems together.

2.3. Animal surgery

Mice were anesthetized with isoflurane in medical grade oxygen using an anesthetic machine (Ohmeda, 1.5% vol, 1 L/min) and implanted with either DSI biotelemetry transmitters or the single stage implanted transmitters in the abdominal cavity. Both the abdominal wall and the skin were sutured with absorbable surgical suture, with cutting needle (5-0 Dexon) and the incision was treated with topical antibiotic (silver sulfadiazine 1%; Silverol Cream). Prophylactic antibiotics (Baytril 5% 24 mg/kg) and artificial tear ointment (to prevent desiccation) were administered preoperatively. At least two weeks of recovery from surgery was allowed before initiation of data collection.

All procedures were conducted in accordance with and approved by the Institutional Animal Ethics Committee (L-02-45).

2.4. Experimental protocol

Body temperature and activity were monitored continuously during all the experiments. First, all 29 mice were monitored for 15 (using the self-build system) or 24 (using the DSI system) days under a 12:12 LD regime. Twelve individuals (6 males and 6 females) of the 17 that were monitored for 24 days using the DSI system, were then placed under constant light (LL) conditions for 20 days. At the end of this period, a 12:12 LD cycle was reinstated. After 40 days, the animals were placed in constant darkness (DD) for another 60 days. A 12:12 LD cycle was then reinstated for another 30 days. This was followed by a 6 h phase advance and, 24 days later, a 6 h phase delay of the LD cycle.

2.5. Data analysis

Data were collected at 6-min intervals in all experiments, and were analyzed using the Clocklab program (Actimetrics Wilmette, IL). We attempted to define activity onset and offset on both the Clocklab program using various settings according to published papers (e.g., onset — the first active bout that was preceded by at least 20 min of inactivity, offset — the last bin of activity that was followed by at least 20 min of inactivity [32], onset — 30 min of activity, subsequent to 3 h of inactivity [33]), and by visual inspection, but could not determine either onset or offset in most individuals. Therefore, response to phase shifts (phase delay and phase advance) was analyzed, using clear peak of activity in each individual (e.g., Fig. 4). The day of re-entrainment after a phase advance was defined as the day after the onset of the activity peak no longer advanced, and the day of re-entrainment after a phase delay was defined as the day after which the onset of the activity peak no longer delayed. Chi-square periodogram was used to calculate the periods of free running rhythms. The Clocklab program was also used to generate all actograms. Microsoft Excel was used to generate the figures. Data are presented as means±SEM; statistical tests used include paired t-test, repeated measures, one-way and two-way ANOVA, and Scheffe post hoc test (Statistica).

3. Results

3.1. 12:12 LD cycle

During the first LD period, all individuals (N=29) displayed daily activity and temperature rhythms that were entrained to the 24 h LD cycle. FFT (Fast Fourier Transformation, Clocklab) analysis showed that in addition to a significant 24 h rhythm, some individuals displayed other significant rhythms with periods such as 12, 6, 8 and 4 h. Activity rhythms were very diverse, and we therefore classified individuals for which over 50% of their activity occurred during the dark phase as nocturnal, and individuals for which 50% of their activity occurred during the light phase as diurnal. Based on this classification, 25 out of the 29 individuals tested were nocturnal, and 4 were diurnal (Fig. 1). Average body temperature of all individuals was significantly higher (t(26)=−5.16, P<0.01) during the dark phase (Fig. 2), and increased activity and body
temperature were coincident (Fig. 3). No significant differences in body temperatures between sexes were found, and no interaction between sex and light phase (2-way ANOVA). Therefore, the results for males and females were combined.

Golden spiny mice showed extremely diverse activity patterns. Eight out of the 29 individuals were continuously active during the dark phase (e.g., Fig. 3a). Eight showed a bimodal activity pattern, with activity peak occurring either at the beginning and end of the dark phase (e.g., Fig. 3b), or one peak towards the end of the light phase and one towards the dark phase (e.g., Fig. 3c). Seven individuals had one peak of activity, at or around the beginning of the dark phase (e.g., Fig. 3d), and another two were active both during the night and during the day and could not be assigned to any one of the above groups (e.g., Fig. 3e). The four diurnal individuals displayed most of their activity during the day, with another peak towards the end of the night (e.g., Fig. 3f).

In all individuals, activity bursts were also common during the resting period, and in most of them it was impossible to pinpoint activity onset or offset, neither by visual inspection nor the Clocklab program (see Methods).

### 3.2. LL/DD

All individuals ($n = 12$) displayed free running rhythms under LL and DD conditions. Under LL conditions, the free running period (FRP) of all individuals was longer than 24 h ($24.47 \pm 0.05$, range: 24.14–24.73 h, e.g., Fig. 4). Under DD conditions, the free running rhythm period of all individuals but one (female 201) was shorter than 24 h ($23.72 \pm 0.1$, range: 23.41–24.66 h, e.g., Fig. 4), and in all individuals but the same one it was shorter than the FRP of the same individual under LL conditions ($t(11) = -5.08, P < 0.001$).

Upon returning to LD from constant light conditions (LL or DD) two different patterns were observed: 1) an abrupt shift in activity and body temperature rhythms (e.g., Fig. 5a1,2), or 2) a shift through phase transients to the entrained rhythm (e.g., Fig. 5b1,2).

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**Fig. 5.** Double daily plots of the effect of returning to LD from constant light conditions (LL or DD) on activity (a1, b1) and body temperature (a2, b2) rhythms of a representative golden spiny mouse individual that abruptly shifted its activity and body temperature rhythms (a), and a representative golden spiny mouse individual that shifted its activity and body temperature through phase transients to the entrained rhythm (b). Black bars at top of plot represent the light schedule during the LD periods.
Percentage of nocturnal activity under LD conditions significantly decreased during the course of experiments. At the first LD phase, 77.4±4.2% of activity occurred during the dark phase, while at the LD phase at the end of the LL (LD2) and DD (LD3) experiments, only 57.25±5.7% and 59.2±5.0% of activity (respectively) occurred during the dark phase (Fig. 6a, repeated measure ANOVA, $F(2,22)=5.54$, $P<0.01$, Scheffe $P<0.05$). Average body temperature during the night under LD conditions showed the same trend as activity, i.e., decreased significantly from 36.6±0.3 °C during the first LD period to 36.1±0.3 and 36.0±0.2 °C during LD2 and LD3 periods, respectively (Fig. 6b, repeated measure ANOVA, $F(2,22)=6.45$, $P<0.05$, Scheffe $P<0.05$). An opposite trend, although not significant, was observed in average body temperature during the day (Fig. 6b, repeated measure ANOVA, $F(2,22)=1.22$, NS). Nevertheless, average body temperature during the night during LD1 and LD3 was significantly higher than during the day (LD1: $t(11)=6.35$, $P<0.05$, LD2: $t(11)=0.85$, NS, LD3: $t(11)=2.21$, $P<0.05$). During LD2 there was no significant difference between average body temperature during the day and during the night, although the latter was a bit higher (Fig. 6b).

During LD2 (after LL), one individual (440) who was nocturnally active during LD1, turned diurnal when LD was reinserted after LL, and its body temperature was higher during the day. After two weeks, it spontaneously shifted its activity rhythms ca 10 h to a more nocturnal activity (Fig. 7a1). Body temperature, that was high during the night during LD1, was higher during the day in LD2, remained high during the day when the shift in activity occurred, together with another peak in body temperature which paralleled the shifting activity (Fig. 7a2).

During LD3, two individuals were diurnally active, but shifted their activity to a more nocturnal activity after ca 40 days under LD (e.g., Fig. 7b1). In this case, body temperature was coupled with activity and shifted in parallel (Fig. 7b2). One individual was nocturnal and entrained to the photoperiod during the first 40 days of LD3, but then started free running again ($tau=24.98$). After ca 25 days, when activity onset coincided lights off, it entrained its rhythm once again with the daily photoperiod (Fig. 7c1,2). Another individual was unstable during LD3. It was nocturnally active for ca 20 days, and then shifted to being active around lights offset for about 14 days, and then turned active mainly during the light period with another component towards light onset.

### 3.3. Phase shift

Since we were unable to determine activity onset and offset (see Methods), we chose a clear peak of activity, and studied its adjustment to the phase shift (e.g., Fig. 8a,b). Four individuals (e.g., Fig. 8c,d) delayed their activity as a result of both phase delay and phase advance, and were analyzed separately. In order to compare the rest of the individuals ($n=8$), average time of peak activity occurrence during the last 10 days of the LD cycle before the shift was set as 0, and the changes in the activity rhythms were described in relation to that time point (Fig. 9). In these individuals, when lights were delayed 6 h, activity peak re-entrained after 6.12±0.69 days (range=2–8). When lights were advanced 6 h, it took activity peak much longer to re-entrain ($tau(7)=−10.9$, $P<0.001$): 15.12±0.74 days (range=13–19). Re-entrainment after phase delay was not only faster, but also smoother and more uniform as compared to that after phase advance (Fig. 9).

### 4. Discussion

We found that under laboratory 12:12 LD conditions, golden spiny mice are primarily nocturnal: 25 out of 29 individuals measured in this study concentrated most of their general activity during the dark period, and their body temperature was significantly higher during this time. This result is in accord with previous laboratory experiments that used running wheels to study activity rhythms of golden spiny mice, and found that under controlled laboratory conditions, they showed activity and oxygen consumption rhythms that are typical for nocturnal mammals [17,29,34,35], even though this species is diurnally active in most of its natural habitat [13–17, but see Ref. 18]. The variety of rhythm patterns displayed by the golden spiny mice was vast. There were no two individuals with the same activity...
Fig. 7. Double daily plots of activity (a1–c1) and body temperature (a2–c2) of individuals that spontaneously shifted their activity and/or body temperature rhythms.  

a — During LD2 (after LL), individual 440 who was nocturnally active during LD1, turned diurnal when LD was reinserted (a1), and its body temperature was higher during the day. After two weeks, it spontaneously shifted its activity rhythms ca 10 h to a more nocturnal activity (a1). Body temperature (a2), that was high during the night during LD1, was higher during the day in LD2, remained high during the day when the shift in activity occurred, together with another peak in body temperature which paralleled the shifting activity.  

b — During LD3, one individual was diurnally active, but shifted its activity to a more nocturnal activity after ca 40 days under LD (b1). In this case, body temperature was coupled with activity and shifted in parallel (b2).  

c — One individual was nocturnal and entrained to the photoperiod during the first 40 days of LD3, but then started free running again (τ=24.98). After ca 25 days, when activity onset coincided lights off, it entrained its rhythm once again with the daily photoperoid (c1). In this case too, body temperature was coupled with activity and shifted in parallel (c2). Black bars at top of plot represent the light schedule during the LD periods.
pattern, and all rhythm types were displayed (nocturnal, diurnal, crepuscular, morning types, evening types, etc.). Furthermore, in most individuals, it was impossible to determine the time of activity onset or offset, either by visual inspection or by the Clocklab program, and activity bursts were also commonly displayed during the rest period. To the best of our knowledge, such extreme variation in activity rhythms in a single species is rare. Usually, even in species that exhibit both diurnal and nocturnal patterns, distinct activity patterns are described, and some features are common for the species [but see Refs. 10,36]. For example, in the Nile grass rat, *Arvicanthis niloticus,* wheel-running activity of both diurnal and nocturnal individuals had bimodal activity rhythms, with peaks of activity occurring at the beginning and end of the active phase under LD, LL and DD conditions [32]. Furthermore, without a running wheel, general activity in this species is always diurnal [30]. Even in the degu (*Octodon degus*), which displays distinct inter-individual variation in the timing and expression of circadian activity and body temperature rhythms, three chronotypes (morning, intermediate [crepuscular], and evening) were described [37]. Nocturnal activity was also observed in this species when exposed to a running wheel [27]. Furthermore, on all occasions, prominent crepuscular episodes of behavioral activity and body temperature while entrained to a LD cycle were exhibited, with clear onset and offset of activity [27,37]. Similarly high inter-individual variability in circadian activity patterns was previously observed in subterranean rodents that are subjected to relatively more constant habitat characteristics than rodents that live above ground [e.g., 38–43]. It was suggested that in these species, the circadian clock is not very strongly coupled to the photic input [42], and that non-photic cues may play an important role. Based on the high individual variation of the circadian rhythms of golden spiny mice found in the current study, and on the well documented effect of non-photic cues on their activity pattern in the field [12,13,19–21], we suggest that similar to subterranean species, non-photic cues may play an important role in the determination of activity patterns in this species.

This suggestion was further supported by other results obtained in the current study. As stated before, activity onset and offset were difficult to determine. Under LD conditions, all individuals showed activity bursts during the resting period, and were not strictly diurnal or nocturnal. During the different

**Fig. 8.** Double daily plots of activity (a1, b1) and body temperature (a2, b2) of golden spiny mice during a 6 h phase delay and a 6 h phase advance of the 12:12 LD cycle. a — A representative individual that delayed its activity and body temperature in response to phase delay and advanced its activity and body temperature rhythms in response to the phase advance. b — A representative individual that delayed its activity and body temperature in response to phase delay and responded to the phase advance by further delaying its activity and body temperature rhythms until entrained to the new LD cycle. Black bars at top of the plot represent the light schedule during the normal LD periods.
LD phases of the experiments, spontaneous shifts of activity rhythms from a more nocturnal to a more diurnal activity or vice versa were recorded in several individuals. It is impossible to say from the current results whether these shifts result from a shift in the clock, splitting, or masking, and this point deserves further study. Following constant LL, individuals significantly reduced their activity level during the dark period by 20% (from an average of 77% to 57%). Exposure to DD conditions did not change that pattern, and the activity level during the dark period upon their return to LD conditions remained 57%. The decrease in nocturnal activity during the course of the experiments was accompanied by a parallel decrease in average body temperature during the night, and an increase in body temperature during the light period.

In response to a 6 h phase delay, all individuals entrained to the new LD cycle in a relatively uniform way, and within the time frame reported for other species [e.g., 32,44]. However, during phase advance two interesting phenomena were observed: First, four out of the twelve individuals responded by further delaying their activity and body temperature rhythms until they were entrained to the new LD cycle. Second, eight out of the twelve individuals advanced their activity rhythm as expected, but the re-entrainment took them over twice as long as to re-entrain to the phase delay (6.12 vs. 15.12 days). Re-entrainment to phase advance taking much longer than to phase delay was previously observed in other species [e.g., 45,46].

Since golden spiny mice are able to be active either diurnally or nocturnally in their natural habitat, it is possible that the immediate masking effects of light or darkness on behavior [28] are not strong in this species. In accord, it was previously suggested that changes in masking responses to light might be an essential and integral component of switching between nocturnal and diurnal activity [5]. This possible change in the masking response to light or dark may partially explain the difficulty in determining activity onset and offset, the spontaneous shifts, and other observations of the current study. These results also support our notion that non-photic cues play an important role in the determination of activity rhythms in this species.

In 1960, Aschoff suggested that nocturnal animals have tau shorter than 24 h under DD conditions, and that tau will lengthen under LL conditions. Diurnal animals, he further suggested, have tau longer than 24 h under DD conditions, and tau will shorten under LL conditions. However, it is now clear that although the rules generally hold for nocturnal species, diurnal species are much more variable [1,6]. In the current study we found that golden spiny mice had tau longer than 24 h under LL conditions. Under DD conditions, tau of all individuals but one was shorter than 24 h, and in all individuals but the same one it was shorter than tau of the same individual under LL conditions. Therefore, golden spiny mice generally fit the nocturnal pattern in this respect too, and provide yet another example of the diversity of the circadian system in diurnal mammals.

Almost all species can be classified as nocturnal, diurnal or crepuscular, and each activity pattern is accompanied by physiological, behavioral and anatomical adaptations [47,48]. As a result, evolutionary transitions between nocturnal and diurnal lifestyles have been relatively infrequent, because they would involve a coordinated suite of changes not only in the temporal organization of a wide range of behavioral patterns and physiological processes, but also in other physiological and anatomical adaptations for nocturnality or diurnality [8,48]. Hence, closely related species are generally active during the same part of the diel cycle [day or night, 7,47]. All species in the genus *Acomys* except the golden spiny mouse are nocturnal. While the golden spiny mouse has evolved some adaptations to diurnal activity such as dark skin pigmentation and a high concentration of ascorbic acid in its eyes [49], both protective against the high ultraviolet radiation during the day [49–52], it has also retained traits that would typify a nocturnal mammal: it has a similar potential for non-shivering thermogenesis (NST) as does its nocturnal congener, the common spiny mouse [53], which is exposed in winter to much lower ambient temperatures, and expends more energy on thermoregulation [53,54], suggesting that in terms of NST the golden spiny mouse still displays its ancestry as a nocturnal rodent. It also retains the retinal structure of a nocturnal mammal, i.e., its retina is composed of rod photoreceptors, and has not evolved to meet with their needs as a diurnal species [55]. Moreover, our field studies suggest that in its natural habitat the golden spiny mouse has underlying nocturnal activity and temperature rhythms [8,16,54], but is also able to be diurnally active. Based on the results of this and previous studies, we suggest that the circadian system of golden spiny mice is very flexible. It is originally a nocturnal rodent that has developed the ability to be nocturnally or diurnally active, according to the environmental conditions, or a nocturnal animal during evolutionary transitions between nocturnal and diurnal lifestyles. This transition between nocturnal and diurnal ways of life, infers that the golden spiny mouse has a reduced response to the immediate masking effect of...
light and/or dark on activity. This hypothesis should be further studied.

The high flexibility and variability of the circadian rhythms of the golden spiny mice may enable it to better exploit its habitat, switching between diurnal and nocturnal activity patterns in order to optimize its niche in the temporal axis [56].

The physiological adaptations of the golden spiny mouse to both diurnal and nocturnal activity, or its ability to switch from a nocturnal to a diurnal activity pattern, can be explained in the light of its zoogeographical history. Shkolnik (1966) suggested that since the species Acomys was originally a savanna rodent of tropical Africa [57], it developed adaptations to high ambient temperatures that preceded its adaptation to water shortage. These adaptations to heat demanded high rates of evaporative water loss for thermoregulation [58]. Later on, when the species expanded its range to dry deserts, it developed adaptations to water shortage, manifested in a high ability to conserve water in the kidney [58]. We suggest that these adaptations enabled the golden spiny mouse to switch its activity to the more thermoregulatory challenging diurnal niche upon encountering unfavorable conditions during the night (i.e., low ambient temperatures in the Sinai desert, competition with the common spiny mouse in the Judean desert).

The inability to assign the golden spiny mouse to a specific activity phase was reinforced in the current study. We found a high variation in activity and body temperature rhythms, and concluded that as far as rhythm characteristics are concerned, it is unclear whether the golden spiny mouse should be categorized as diurnal or nocturnal rodent. We also suggest that this species is not very responsive to the immediate masking effect of light or dark, and that during its zoogeographical history, it also selectively developed plasticity in the mechanisms that determine daily activity patterns. This finding also reinforces the hypothesis that, since the common ancestors to all mammals were nocturnal, the circadian system of present-day nocturnal mammals expanded its range to dry deserts, it developed adaptations to heat demanded high rates of evaporative water loss for thermoregulation [58]. Later on, when the species expanded its range to dry deserts, it developed adaptations to water shortage, manifested in a high ability to conserve water in the kidney [58]. We suggest that these adaptations enabled the golden spiny mouse to switch its activity to the more thermoregulatory challenging diurnal niche upon encountering unfavorable conditions during the night (i.e., low ambient temperatures in the Sinai desert, competition with the common spiny mouse in the Judean desert).

The inability to assign the golden spiny mouse to a specific activity phase was reinforced in the current study. We found a high variation in activity and body temperature rhythms, and concluded that as far as rhythm characteristics are concerned, it is unclear whether the golden spiny mouse should be categorized as diurnal or nocturnal rodent. We also suggest that this species is not very responsive to the immediate masking effect of light or dark, and that during its zoogeographical history, it also selectively developed plasticity in the mechanisms that determine daily activity patterns. This finding also reinforces the hypothesis that, since the common ancestors to all mammals were nocturnal, the circadian system of present-day nocturnal mammals is relatively fixed, while that of diurnal mammals, which evolved independently at various times [1,6,7], is more likely to be flexible [1,6].

Acknowledgments

We wish to dedicate this paper to the late Prof. A. Shkolnik, whose insights and support keep inspiring our work. We thank Prof. Laura Smale and Prof. Tamar Dayan for their insightful comments on a previous version of this MS and Nomi Paz for editing the MS. This research was supported by a BSF grant (2003048).

References


