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THE RELATIONSHIP BETWEEN THE GOLDEN SPINY MOUSE CIRCADIAN SYSTEM AND ITS DIURNAL ACTIVITY: AN EXPERIMENTAL FIELD ENCLOSURES AND LABORATORY STUDY

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Examples of animals that switch activity times between nocturnality and diurnality in nature are relatively infrequent. Furthermore, the mechanism for switching activity time is not clear: does a complete inversion of the circadian system occur in conjunction with activity pattern? Are there switching centers downstream from the internal clock that interpret the clock differently? Or does the switch reflect a masking effect? Answering these key questions may shed light on the mechanisms regulating activity patterns and their evolution. The golden spiny mouse (*Acomys russatus*) can switch between nocturnal and diurnal activity. This study investigated the relationship between its internal circadian clock and its diurnal activity pattern observed in the field. The goal is to understand the mechanisms underlying species rhythm shifts in order to gain insight into the evolution of activity patterns. All golden spiny mice had opposite activity patterns in the field than those under controlled continuous dark conditions in the laboratory. Activity and body temperature patterns in the field were diurnal, while in the laboratory all individuals immediately showed a free-running rhythm starting with a nocturnal pattern. No phase transients were found toward the preferred nocturnal activity pattern, as would be expected in the case of true entrainment. Moreover, the fact that the free-running activity patterns began from the individuals' subjective night suggests that golden spiny mice are nocturnal and that their diurnality in their natural habitat in the field results from a change that is downstream to the internal clock or reflects a masking effect.

Keywords Diurnality, Masking, Golden spiny mice, Activity pattern, Circadian rhythms

INTRODUCTION

Most animal species can be defined as nocturnal, diurnal, or crepuscular based on their activity rhythms as well as their physiological, morphological, and behavioral characteristics designed to cope with

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environmental challenges posed by the different parts of the diel cycle (Daan, 1981; Enright, 1970). Being active during a defined time frame enables an adaptive interaction with the biotic and abiotic environmental changes at the diel scale and promotes the adaptive anticipation of these changes, as well as the synchronization with conspecifics, anticipation of fitness-related events such as expectation of predators or prey, and timing of physiological changes such as daily cortisol levels (Daan, 1981; DeCoursey, 2004; Enright, 1970; Gerkema, 1992).

These activity patterns result from an interaction between the environment and an internal clock, which in mammals is located in the suprachiasmatic nucleus (SCN). The mechanism by which this internal clock determines activity patterns is not clear, and the differences in SCN anatomy or function that may account for the opposite activity patterns of nocturnal and diurnal animals remain unclear (Smale et al., 2003). Nevertheless, there are definitely some characteristics of the circadian system outputs that differ between diurnal and nocturnal species (e.g., the starting phase of the free-running rhythm; see Roenneberg et al., 2003), some more marked than others.

Evolutionary transitions between nocturnality and diurnality have been relatively infrequent, probably because they involve changes in the temporal organization of a wide range of behavioral patterns and physiological processes (DeCoursey, 2004). Moreover, it was suggested that because the common ancestor of mammals was nocturnal, and because diurnality evolved several times independently (Roll et al., 2006), one may expect considerable variability in circadian mechanisms among diurnal mammals, contrary to the case for nocturnal mammals (Smale et al., 2003).

Over the years, several cases of species that change activity patterns between nocturnal and diurnal in nature have been described (for a review, see Kronfeld-Schor & Dayan, 2003; Mrosovsky, 2003; Smale et al., 2003). These species are of particular interest with respect to the relationship between overt activity patterns and internal rhythmicity. Does the circadian system change in conjunction with activity pattern (see Bloch et al., 2004)? Are there switching centers downstream from the internal clock that interpret the clock differently (Smale et al., 2003)? Or does the switch reflect a masking effect? Answering these key questions may shed light on the mechanisms regulating activity patterns and their evolution (see Mrosovsky & Hattar, 2005).

The golden spiny mouse (*Acomys russatus*) is a diurnal rodent, but it switches to nocturnal activity when environmental conditions allow it (i.e., a lack of competition; see Shkolnik 1971). Under controlled laboratory conditions, most (~86%) golden spiny mice are nocturnal (Cohen & Kronfeld-Schor, 2006), but some are diurnal, and activity patterns show high variability both at the individual and at the population scale

(Cohen & Kronfeld-Schor, 2006). Moreover, spontaneous changes in activity patterns from nocturnal to diurnal and vice versa have also been observed (Cohen & Kronfeld-Schor, 2006; Gutman & Dayan, 2005; Gutman et al., 2007).

This study investigates the relationship between the circadian system of *A. russatus* and the diurnal activity pattern observed in the field. Based on Kronfeld-Schor et al. (2001a), it is hypothesized that the circadian system of *A. russatus* remains nocturnal and that the diurnal activity of *A. russatus* in the field merely reflects a masking effect. In order to test this hypothesis, the temperature and activity rhythms of *A. russatus* individuals were studied under semi-natural conditions in the field. Then, the same individuals were transferred to constant dark laboratory conditions to reveal their free-running rhythms, then to the natural LD cycle under controlled laboratory conditions, and finally back to the field enclosures. This experimental protocol allowed for an opportunity to gain insight into whether the diurnal activity pattern observed in the field results from entrainment of the circadian system or from changes that are downstream to the core pacemaker. In the case of re-entrainment, phase transients are expected when the animals are switched from one environment to the other; otherwise, an immediate change to the new LD cycle is expected (Mrosovsky, 1999). This experiment also enabled an examination of whether the internal clock of golden spiny mice in the field is nocturnal or diurnal. If each individual's activity during the free-running period (under constant dark conditions, immediately after removal from the field) will start at its subjective night, then one can conclude that the internal clock is of a nocturnal mammal and that activity patterns in the field represent a change that is downstream to the clock or is a masking effect. However, if during the free-running session individuals will be active during their subjective day, then the activity in the field reflects the phase of the circadian system (Roenneberg et al., 2003).

METHODS

Experimental Protocol

The activity patterns (A_c) and core body temperature (T_b) rhythms of *A. russatus* individuals were studied in a semi-natural environment and in the laboratory under controlled conditions. The experiments took place between February and April 2004. Body temperature and activity of mice were first monitored under semi-natural conditions in two field enclosures for a week. At the end of the week, all *A. russatus* individuals were trapped using Sherman live traps that were set 1 h before sunrise and collected until 2 h after sunrise. The trapped mice were immediately

transferred to the laboratory (within 2 h). The mice were individually housed in 38 × 24 × 13 cm plastic cages in an isolated sound-proof room, with an ambient temperature of 29°C, which is just below the low critical temperature of the thermoneutral zone of the golden spiny mouse (Shkolnik & Borut, 1969), under constant dark (DD) conditions, and with food (standard rodent chow) and water ad lib. Once every 2–3 weeks, at random hours, food and water were changed. After 43 days, the semi-natural light dark cycle (LD 12:12, lights on at 06:00 h) was reinstated for another 21 days. Finally, all individuals were returned to their original enclosures, and their A_c and T_b were measured for another three days (until no signals were recorded due to exhaustion of the batteries).

The study was approved by the local sanctioning board (permit no. 15570) and met the ethical standards of the journal (Touitou et al., 2006).

The Experimental Enclosures

The field experiment was conducted at the Ein Gedi nature reserve, in the Judean desert, near the Dead Sea (31° 28' N, 35° 23' E, 300 m below sea level) in two established 1,000 m^2 enclosures containing *A. russatus* individuals (half males half females). The enclosures are about 50 m^2 from each other. The mice are descendants of mice that were trapped in the area in 2001 and bred in the enclosures (see Gutman & Dayan, 2005, for a detailed description of the enclosures and population care). For identification, each individual was implanted with a PIT (Passive Integrated Transponder, Boise, Idaho, USA) tag.

Each enclosure contained 7–8 individuals. Body temperature and locomotor activity transmitters were implanted in 14 ($n = 7$ in each enclosure).

Animal Surgery

All mice from the enclosures were trapped, anesthetized with isoflorane in medical grade oxygen using an anesthetic machine (Ohmeda), and implanted with single stage implanted transmitters (ca. 2 g, Sirtrack LTD, Havelock North, New Zealand) in the abdominal cavity. Both the abdominal wall and the skin were sutured with absorbable surgical suture with a 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. Mice were returned to their enclosures 48 h after capture. After a one-week recovery, body temperature and locomotor activity were monitored continuously during all experiments.

Monitoring Body and Ambient Temperatures

Body temperature is easier to measure and more precise under field conditions and is accepted as a surrogate for measuring activity rhythms (Decoursey et al., 1998). Each implanted radio-transmitter uses a unique frequency that enables its identification. The transmitter uses a comparison circuit against which to reference the pulse period being determined by the temperature. An RX-900 scanner-receiver (Televilt LTD) was connected to two dipole antennas for data logging. The receiver scans each frequency for a period of 45 sec, and whenever a signal is received, the time, frequency, pulse parameters, active antenna, and signal strength are logged. Data for each transmitter were logged once every 20 min. For each transmitter, the pulse period was converted to a temperature using a calibration curve produced in the laboratory using five different temperatures.

An antenna was located in front of each enclosure to efficiently receive the transmission from all individuals. The receiver unit was located in the middle of the enclosure complex and covered with thermally isolating bricks for the prevention of over-heating by the sun and of animal damage. During the laboratory session, one antenna was placed in the room containing the experimental subjects, and the scanner-receiver was located in a nearby room.

Ambient temperatures were measured every 30 min using three data logger thermometers (iButton ds1921 thermochrom). The thermometers were placed in one enclosure, under boulders, in the open, and between boulders, all in the shade.

Data Analysis

Body Temperature

During the experimental period, more than 400,000 body-temperature logs were recorded. In order to analyze the data efficiently, a computer program was developed that ascertains the log files as an input, computes T_b according to the transmitter-specific calibration curve, and enters the log records into Access SQL database (Microsoft). A filter algorithm was included in the program to mark any unreasonable T_b logs that should be ignored during data analysis: the criteria for omitting a log was if it was below 25°C or above 42°C, and if it differed from the previous and subsequent logs from the same individual by more than 7°C. The filter algorithm excluded ~22% of the logs from the field sessions and ~7% from the laboratory session.

When the database development was completed, SQL queries were made that calculated mean T_b and mean activity level of each 20 min interval for each individual on each session. The SQL database was used to

calculate mean night (from last light to first light) and day (from first light to last light) body temperatures for each individual during the three days before and the three days after each change in treatment then took place.

Ambient temperature measurements from each microhabitat were also inserted into the SQL database. Using SQL query, seasonal mean ambient temperatures were calculated.

Activity

Activity was monitored as described in Elvert et al. (1999). Differences in signal strength between two successive logs were calculated, and signal strength differences that were less than two units (units varied between 0–10) were regarded as noise (0 units). From these data, the relative fraction of activity from total daily activity was calculated for each 20 min interval. Diurnal and nocturnal activity fractions were calculated as the sum of the activity during the daytime and during the night, respectively, divided by total activity during the entire 24 h.

Statistical Analysis

In order to test statistically the effect of transferring golden spiny mice from the enclosures into the laboratory and vice versa, the results were compared using one-way analysis of variance (ANOVA) with repeated measures, with individuals as the repeated factor. Actograms were plotted and tau was calculated; onsets of temperature rise above the daily average were determined using Clocklab^{TM} Actimetrics Software, Wilmette, Illinois, USA. In order to test the difference in daily activity and body temperature rhythms, a two-way ANOVA was used, with time (in 20 min intervals) and treatment (in field enclosures, DD in the laboratory, LD in the laboratory and again in the field enclosures) as the categorical factors.

RESULTS

A total of 14 *A. russatus* individuals were implanted with transmitters and released back into the enclosures. Of these, data were logged during both the daytime (from first light until no light is visible after sunset) and nighttime (no light is visible) every day from 8 individuals in the field and 10 individuals in the laboratory.

Body and Ambient Temperatures in the Field

All successfully logged individuals in the field enclosures ($n = 8$) had higher body temperatures during the daytime (see Figures 1A, 1B, and 2). Average core body temperature and activity were significantly

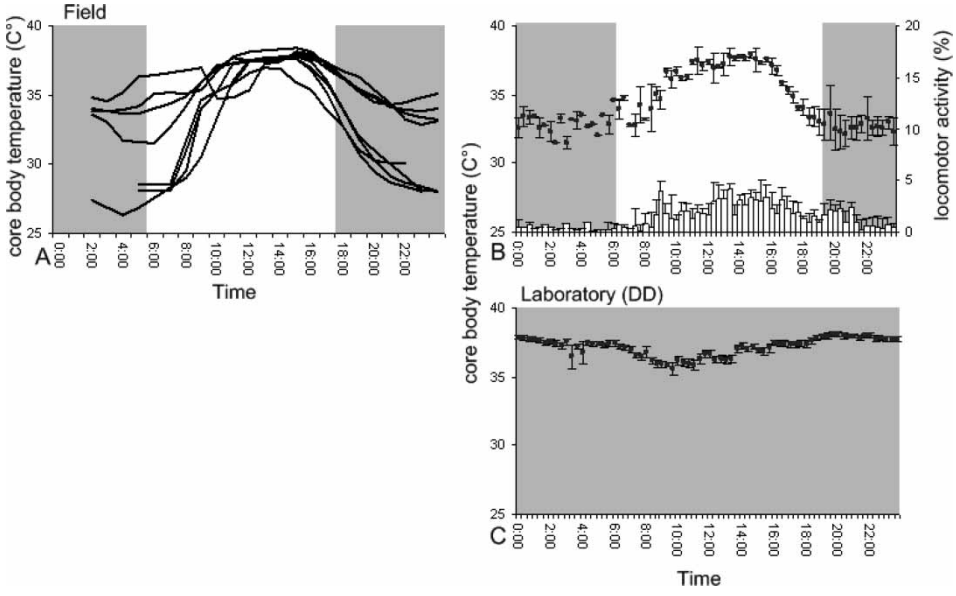

FIGURE 1 (A) Individual and (B) mean (±SEM) core body temperature (■) and locomotor activity (bars) of *A. russatus* in field enclosures, and (C) mean core body temperature one day after removal to laboratory DD conditions. Grey area represents the scotophase.

higher during the daytime than nighttime (core body temperature: $F = 31.44$, $df = 1$, $p < 0.001$, see Figure 3; activity: $F = 35.77$, $df = 1$, $p < 0.001$, see Figure 4). Some individuals decreased their core body temperatures during the nighttime to ~28°C (see Figure 1A), which may indicate the use of torpor.

Ambient temperatures showed pronounced daily variations in the study area at all habitats (see Table 1). However, the daily variation was greater in the open microhabitat compared to the boulder microhabitat. Maximal temperatures were recorded under the boulders, where temperature reached approximately 20°C. Minimal temperatures were recorded in the open habitat, where temperatures decreased to approximately 11°C. Minimal temperatures were always recorded at sunrise (about 07:00 h), while maximal temperatures were recorded around noon (about 13:00 h).

From the Field Enclosures to the Laboratory

Immediately after the transfer to DD conditions in the laboratory, all captured individuals ($n = 10$) had higher body temperatures during their subjective nights (defined as dark hours the day before) than during their subjective days (defined as light hours the day before; see Figures 1B and 2). The onset of temperature rise in the individuals

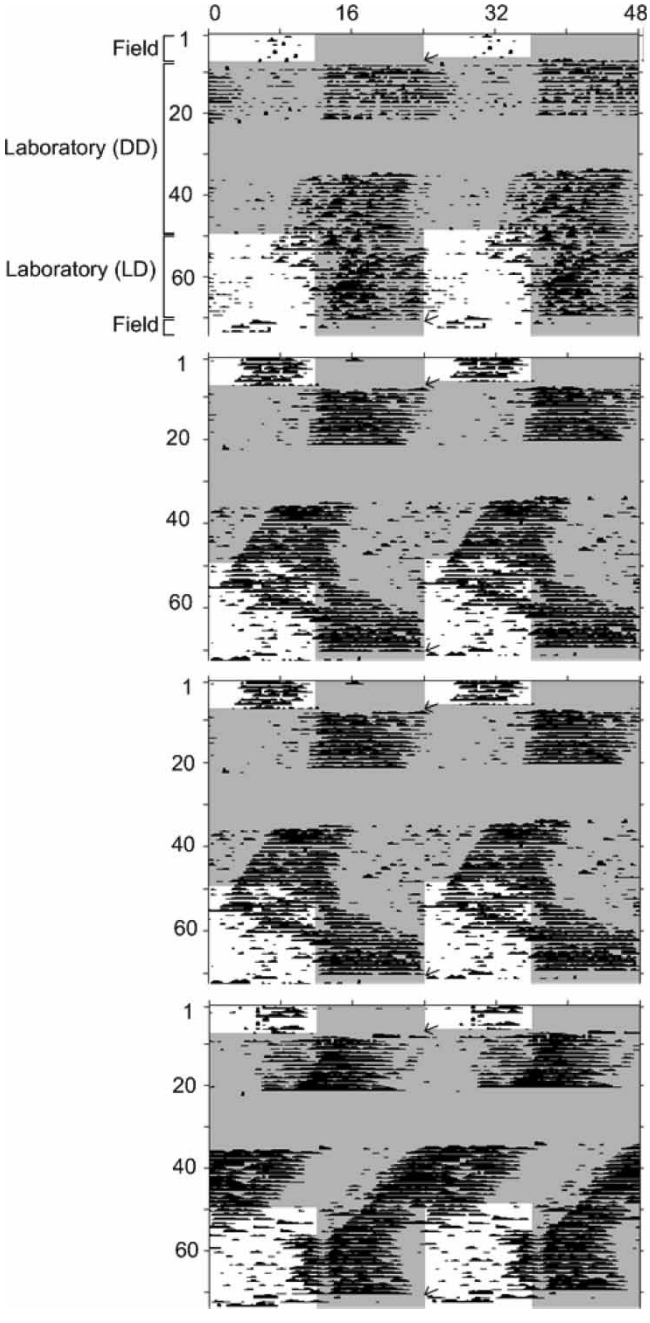

FIGURE 2 Actograms of core body temperature of four individuals during the experiment. The black bars represent temperatures that are above average for that day. White area represents the photophase, and the grey area represents the scotophase. The x-axis represents Zeitgeber time. Arrows show the time and day when the transfers to and from the field were made. The scanner-receiver malfunctioned for a few days during the laboratory DD session; therefore, no data are presented for these days.

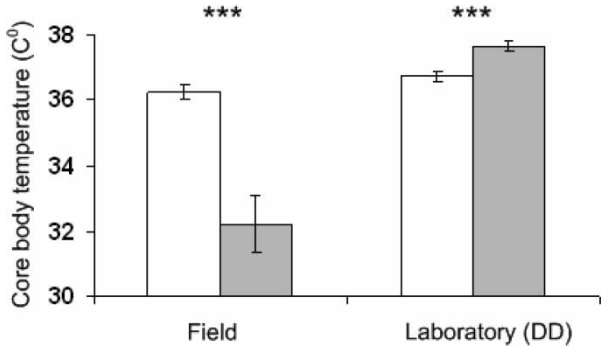

FIGURE 3 Mean (±SEM) day (white bars) and night (grey bars) T_b during the week before and a day after removal to the laboratory. $^{***}p < 0.001$.

shifted within a day, from the beginning of the day (10:40 h ± 65 min [clock time ± SEM]) at the field enclosures to the beginning of the night (19:35 h ± 16 min [clock time ± SEM]) in the laboratory (see Figure 5). Under DD conditions, the mean subjective night body temperatures were significantly higher than the mean subjective day body temperatures ($F = 47.28$, $df = 1$, $p < 0.001$, see Figure 3).

All individuals ($n = 7$, as three transmitters ceased working at this stage) displayed free-running rhythms under DD conditions with a tau shorter than 24 h (23.8 ± 0.04 [hour ± SEM]), as shown in Figure 2.

DD/LD (12:12) in the Laboratory

Upon returning to LD from DD in the laboratory, all individuals displayed re-entrainment to nocturnal rhythm (see Figures 2 and 5). At the

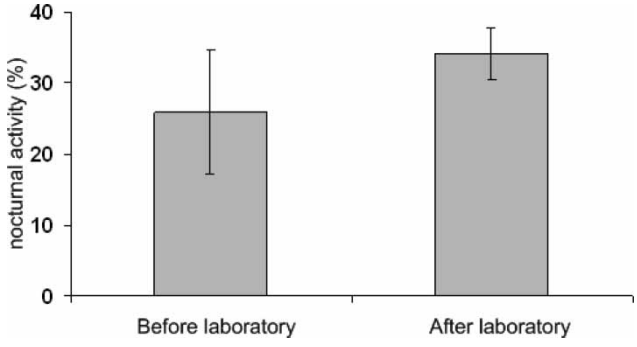

FIGURE 4 Mean (±SEM) nocturnal activity fraction during the week before removal to laboratory conditions and three days after returning to field enclosures.

TABLE 1 Minimum, Maximum, and Mean (±SD) Ambient Temperatures in Three Different Microhabitats (Open, Between boulders, and Under boulders) at the Field Enclosures

	Min (C°)	Max (C°)	Average night (C°)	Average day (C°)
T_{open}	9.9 ± 1.6	16.5 ± 4.2	11.2 ± 1.3	14.1 ± 2.9
$T_{between\ boulders}$	15.3 ± 1.7	22.2 ± 3.4	16.9 ± 1.5	19.6 ± 2.6
$T_{under\ boulders}$	15.9 ± 1.7	23.7 ± 5.7	17.4 ± 1.5	19.8 ± 2.6

end of the entrainment process, which took 9–12 days, core body temperatures of all individuals were significantly higher during the dark than during the light phase ($F = 176.62$, $df = 1$, $p < 0.001$, see Figures 6A and 7).

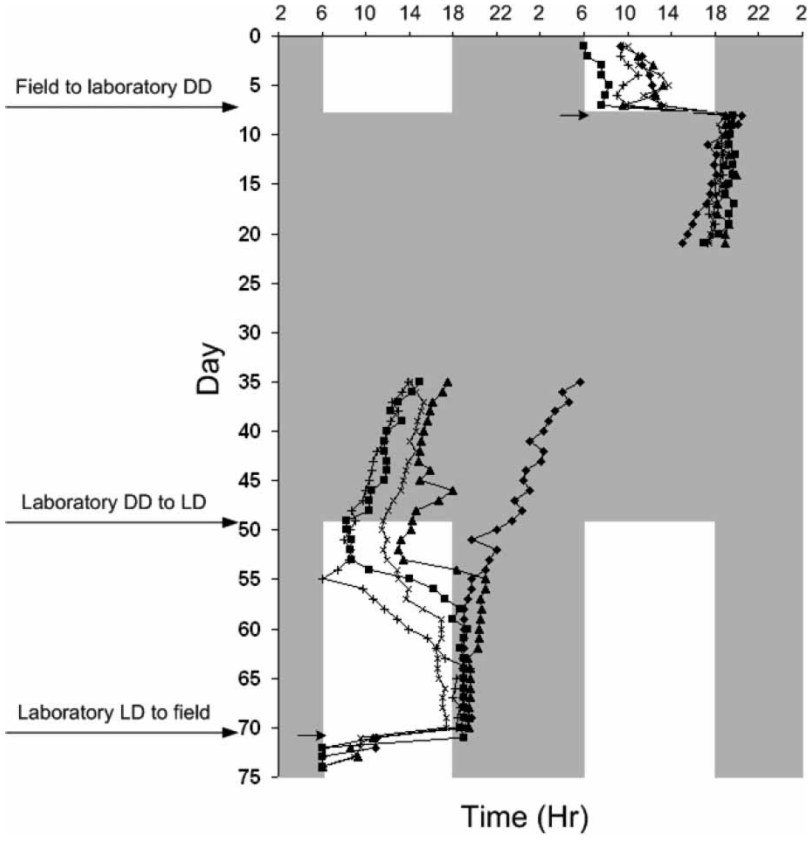

FIGURE 5 Individual daily onsets of temperature above individual daily mean temperature during the experiment. Grey area represents the scotophase. Arrows show the time and the day when the transfers to and from the field were made. The scanner-receiver malfunctioned for a few days during the laboratory DD session; therefore, no data are presented for these days.

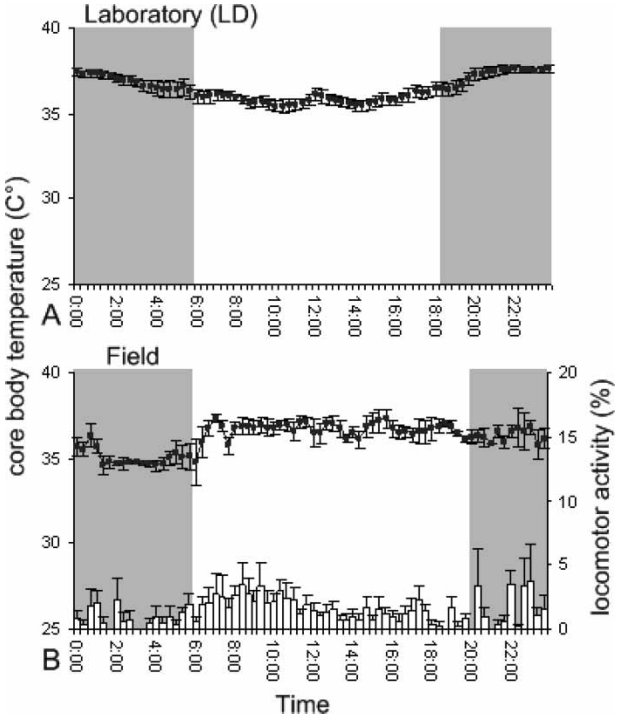

FIGURE 6 Mean core body temperature (■) and locomotor activity (bars) of *A. russatus* (A) under laboratory LD conditions and (B) two days after they were transferred back to the original field enclosures. Grey area represents the scotophase.

Back from the Laboratory to the Field Enclosures

Immediately upon returning to the field enclosures, all successfully logged individuals (n = 5) inverted their activity patterns and body temperature rhythm back to a diurnal pattern (see Figures 2 and 6B). The onset

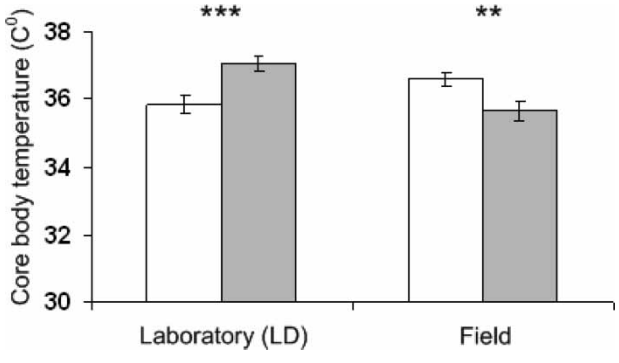

FIGURE 7 Mean (±SEM) day (white bars) and night (grey bars) T_b during the day before and the day after returning to the field enclosures. $^{**}p < 0.01$, $^{***}p < 0.001$.

of the temperature rise in the individuals shifted within a day, from the beginning of the night (18:36 h ± 22 min [clock time ± SEM]) in the laboratory to the day (09:30 h ± 65 min [clock time ± SEM]) in the field enclosures (see Figure 5). Daytime average body temperatures were again significantly higher than nighttime body temperatures ($F = 8.13$, $df = 1$, $p < 0.01$, see Figure 7). Activity in the field enclosures at this stage was higher during the day ($p = 0.14$, probably due to small sample size), as shown in Figure 4. Individual body temperatures at the 20 min intervals were significantly different between the last three days in the laboratory and the first three days in the field enclosures (two-way ANOVA, $p < 0.001$). Fisher LSD post–hoc test revealed that core body temperatures were significantly lower in the field enclosures compared to the laboratory during the second half of the night.

DISCUSSION

In their natural habitat, animal species may be active in contrast to their internal nature, whenever conditions compel it (Kronfeld-Schor & Dayan, 2003); therefore, the internal rhythmicity and preferences of species may be revealed only under controlled conditions, and these are not always similar to activity rhythms under natural conditions (e.g., Blanchong et al., 1999; Challet et al., 2002). Thus, to study evolutionary processes leading to nocturnal and diurnal ways of life, it is essential to study species both in their natural habitat and under controlled conditions.

In this study, all golden spiny mice had opposite activity patterns in the field compared to when placed in controlled continuous dark conditions or the natural L:D cycle in the laboratory. Activity and body temperature patterns in the field were diurnal, both before and after the laboratory experiment, while in the laboratory all individuals immediately showed a free-running rhythm starting with a nocturnal pattern. During the first field session, some individuals used torpor during the night. The usage of torpor in golden spiny mice has been previously observed under laboratory conditions of low ambient temperatures or low food availability (Ehrhardt et al., 2005; Gutman et al., 2006). When the natural L:D cycle was re-instated, all individuals entrained to a nocturnal activity rhythm, a process that took 7–15 days. However, upon return to the field, they immediately returned to a diurnal activity pattern, and not gradually as would be expected in the case of an entrainment process. These results support the hypothesis of Kronfeld-Schor et al. (2001a), that in terms of their circadian system, golden spiny mice are nocturnal and their diurnality in their natural habitat results from a change that is downstream to the internal clock or reflects a masking effect.

Although masking is usually studied in relation to light (i.e., exposure of nocturnal rodents to light suppresses activity while darkness suppresses

activity in diurnal species; Mrosovsky, 1999), several non-photic cues, such as ambient temperature (Bacigalupe et al., 2003; Halle, 1995), predation (Fenn & Macdonald, 1995), wheel running (Kas & Edgar, 1999), and even cage size (Lehmann, 1976), can mask activity. These environmental cues influence the displayed activity rhythms without changing the underlying clock that times the rhythm (Mrosovsky, 2003).

It appears that *A. russatus* is not a typical diurnal or nocturnal species. This notion is supported by adaptations to both nocturnal and diurnal ways of life, which have been described in this species. It has a high ability to reduce fecal water loss (Kam & Degen, 1993) and produce highly concentrated urine (Shkolnik, 1966; Shkolnik & Borut, 1969), and no significant differences in water turnover rates were found between nocturnal *A. cahirinus* and diurnal *A. russatus* in any season, reflecting adaptations of *A. russatus* to water conservation (Kronfeld-Schor et al., 2001c). Furthermore, *A. russatus* has evolved dark skin pigmentation and a high concentration of ascorbic acid in its eyes (Koskela et al., 1989), both protective against the high ultraviolet radiation during the day (Chaplin, 2004; Diamond, 2005; Jablonski, 2004). However, it has also retained traits that would typify a nocturnal mammal. It has a similar potential for nonshivering thermogenesis (NST) as does its nocturnal congener *A. cahirinus* (Kronfeld-Schor et al., 2000), which is exposed in winter to much lower ambient temperatures and expends more energy on thermoregulation (Kronfeld-Schor et al., 2000, 2001c), suggesting that in terms of the NST, *A. russatus* still displays its legacy as a nocturnal rodent. It also retains the retinal structure of a nocturnal mammal (i.e., its retina is composed of rod photoreceptors only), and it has not evolved to meet with their needs as a diurnal species (Kronfeld-Schor et al., 2001b).

An unresolved question that arises is whether the nocturnal internal clock and the adaptations to a nocturnal way of life are the legacy of a nocturnal past: is *A. russatus* in the evolutionary process of turning diurnal? Alternatively, there may be an evolutionary advantage to the plasticity of activity rhythms and the preservation of past nocturnal characteristics while developing diurnal ones (Cohen & Kronfeld-Schor, 2006; Kronfeld-Schor & Dayan, 2003). High flexibility and variability of the circadian rhythms may enable *A. russatus* to better exploit its habitat, switching between diurnal and nocturnal activity patterns in order to optimize its use of the environment (Kronfeld-Schor & Dayan, 2003).

In summary, the classification of a species as nocturnal or diurnal may sometimes be very deceptive. Diurnality has evolved on several unrelated events; therefore, it may include many different forms of activity patterns and circadian mechanisms (Roll et al., 2006; Smale et al., 2003). Nocturnal adaptations in diurnal *A. russatus*, together with nocturnal activity that has been found in nature in previous studies (Gutman & Dayan, 2005; Haim & Fluxman, 1996; Kronfeld-Schor et al., 2000, 2001a, 2001b, 2001c;

Shkolnik, 1971), suggested to us that in its natural habitat, *A. russatus* is active diurnally despite its internal rhythmicity and whenever possible switches to the preferred nocturnal niche. The present study provides strong support for this hypothesis. The major challenge now is to understand the neural and molecular mechanisms allowing for such plasticity.

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