Chronobiology International, 28(1): 70–75, (2011)

ISSN 0742-0528 print/1525-6073 online
DOI: 10.3109/07420528.2010.525674

informa
healthcare

Light Masking in the Field: An Experiment with Nocturnal and Diurnal Spiny Mice Under Semi-natural Field Conditions

Shay Rotics, Tamar Dayan, Ofir Levy, and Noga Kronfeld-Schor

Department of Zoology, Tel Aviv University, Tel Aviv, Israel

Light masking has been studied almost exclusively in the laboratory. The authors populated four field enclosures with locally coexisting nocturnal *Acomys cahirinus* and diurnal *A. russatus*, and monitored their body temperatures (T_b) using implanted temperature-sensitive radio transmitters. A 3-h light pulse was initiated at the beginning of two consecutive nights; preceding nights were controls. *A. cahirinus* T_b and calculated activity levels decreased significantly during the light pulse, demonstrating a negative light masking response (light effect on T_b: −0.32°C ± 0.15°C; average calculated activity records during the light pulse: 7 ± 1.53, control: 9.8 ± 1.62). Diurnal *A. russatus* did not respond to the light pulse. We conclude that light masking is not an artifact of laboratory conditions but represents a natural adaptive response in free-living populations. (Author correspondence: Shayroti@post.tau.ac.il)

Keywords: *Acomys*, Activity patterns, Body temperature, Field study, Light masking, Spiny mice, adaptive response

INTRODUCTION

The term "masking" (Aschoff, 1960) describes an immediate effect of a stimulus that overrides an animal's endogenous clock. The masking effect of light is very different in nocturnal and diurnal species: light increases activity in diurnal mammals (positive masking) and suppresses it in nocturnal ones (negative masking), whereas darkness acts in the opposite way (Aschoff & Vongoetz, 1988, 1989; Redlin & Mrosovsky, 1999a; Redlin et al., 2005). Under natural conditions, masking has the adaptive value of confining animals to their appropriate temporal niche, and may complement the circadian clock in fine-tuning activity patterns in response to environmental stimuli (Redlin, 2001).

Mrosovsky (1999) pointed out that masking had been generally neglected by circadian biologists. In the ensuing decade, however, interest in this phenomenon has increased, and masking has been described in additional species (e.g., Cohen et al., 2010; Erkert et al., 2006), masking effects of stimuli other than the classic light/dark pulses have been studied (reviewed in Kronfeld-Schor & Dayan, 2008), and the neural basis of this phenomenon has been examined (e.g., Doi et al., 2006; Mrosovsky & Thompson, 2008).

Most studies addressing masking, including the above-mentioned ones, were conducted in the laboratory, with very little research explicitly addressing masking in the field. Many nocturnal rodents are known to reduce their activity in the field during full-moon nights (reviewed in Beier, 2006) or under artificial illumination (Abramsky et al., 2004; Kotler et al., 1991; Mandelik et al., 2003). However, although masking is presumably involved, we cannot rigorously differentiate its contribution from that of other mechanisms that might be involved, such as circadian clock entrainment or a circa-lunar rhythm. Furthermore, most descriptions of this phenomenon address its ecological aspects of foraging and habitat use, but neglecting its underlying mechanisms.

We studied masking responses in two rodent species, by applying a 3-h light pulse for two consecutive nights in open-field enclosures. The enclosures, located in a rocky desert, were populated with two locally coexisting congeners: the nocturnal common spiny mouse (*Acomys cahirinus*) and the diurnal golden spiny mouse (*A. russatus*). Over the course of two decades of research, we have acquired a thorough knowledge of the ecology (see Kronfeld-Schor & Dayan, 2003; Shargal et al., 2000), physiology (e.g., Kronfeld-Schor et al., 2000), and activity rhythms (see Cohen et al., 2009; Elvert et al., 1999; Kronfeld-Schor et al., 2001; Levy et al., 2007) of these species.

Our experimental settings enabled us to focus on light masking under semi-natural conditions and to gain insight into its occurrence and its adaptive value in the wild. We hypothesized that changes in activity levels in response to elevated light intensities are mediated by

Submitted April 8, 2010, Returned for revision May 4, 2010, Accepted September 6, 2010

Address correspondence to Shay Rotics, Department of Zoology, Tel Aviv University, Tel Aviv 69978, Israel. Tel.: 972-36409024; E-mail: Shayroti@post.tau.ac.il

masking response. Therefore, we predicted that (a) a light pulse would induce a negative masking response in the nocturnal *A. cahirinus*, i.e., a reduction in activity as was described for this species in the laboratory (Cohen et al., 2010); and (b) a light pulse may induce a positive masking response in the diurnally active *A. russatus*. However, since this latter species is not a typically diurnal one (it has some nocturnal traits and preferences [reviewed by Kronfeld-Schor & Dayan, 2003; Levy et al., 2007]), and since previous studies have failed to detect such a response in the laboratory (Cohen et al., 2010), we had less confidence in this prediction.

METHODS

Field Enclosures

Research took place at four 20 × 50-m open-field enclosures located on the eastern slopes of the Judean Desert, near the Ein Gedi nature reserve (31°28′N, 35° 23′E, 300 m below sea level). The enclosures were constructed of 70 cm high 10-mm wire mesh buried 3 cm into the ground. The top 40 cm of both sides of the mesh were covered with aluminum flashing to prevent the mice from escaping. The wire mesh fence was permeable to spiny mouse predators (raptors, foxes, and snakes; Jones & Dayan, 2000; Jones et al., 2001) and prey (vertebrates, seeds, and vegetation; Kronfeld-Schor & Dayan, 1999). Thus, the enclosure structure provided seminatural conditions for our experiment. Sixteen individuals of *A. cahirinus* and 16 of *A. russatus* were captured in the area around the enclosures, using Sherman live traps, and introduced into them (four individuals of each species in each enclosure) 1 month prior to onset of the experiment. Water was available in the enclosures at all times (see Gutman & Dayan, 2005, for technical description).

Monitoring Body Temperature (T_b)

T_b radio transmitters (Epx76 single stage transmitters to the nearest 0.1°C, weight 3.8 g; Sirtrack) were implanted in the abdominal cavity of 28 individuals: 13 common and 15 golden spiny mice (for surgical details see Levy et al., 2007), of which we managed to effectively track 11 and 13 individuals, respectively. One *A. cahirinus* that showed a completely diurnal T_b rhythm, which is extremely uncommon in this species (during two decades of research on spiny mice in that area, we had not encountered a single diurnal *A. cahirinus*), was omitted from the analysis. Signals from each implanted transmitter were logged once every 18 min by a scanner-receiver (RX-900; Televilt) connected to two dipole antennas (for more technical details see Levy et al., 2007). The receiver was connected to a battery (450A; Schnapp) charged during the day by a solar panel (SQ80; Shell). Body temperature of spiny mice was also used as a surrogate measure for activity level; body temperature is affected by activity in many mammals (including spiny mice), and is usually highly correlated with it (Cohen & Kronfeld-Schor, 2006; Decoursey et al., 1998; Elvert et al., 1999; Levy et al., 2007). In addition, we measured ambient ground temperature (using DS1921 Thermochron iButton, ±1°C accuracy; Dallas Semiconductor).

Experimental Protocol

The experiment lasted 4 days, during new-moon nights. During the first 2 days, mice were held under a natural light regime (control), whereas during the last 2 days, the enclosures were illuminated for the first 3 h of the night (ca. 17:15–20:15 h). The experiment was conducted with legal permits from the Israel Nature and Parks Authority (2007/28812) and complied with international ethical standards (Portaluppi et al., 2010).

Illumination

During the light pulse, illumination levels were quite constant throughout the enclosures with average intensity of 2 lux (measured on the ground with a TES-1337 photometer to the nearest 0.01 lux); such intensity is slightly stronger than full-moon light. Enclosures were illuminated by 70-W yellow metal halide lamps (Osram) on top of six, 3-m high poles, activated by a "super quiet" generator (E20; Honda). The generator was placed 150 m from the enclosures, in a gulley inside an insulated acoustic box that rendered it noiseless at this distance.

Data Analysis

The radio transmitter tracking system provided T_b data for each individual at 18-min intervals. In order to test light masking effects on T_b rhythms, we compared individuals' T_b rhythms for both species under illumination and control conditions using a generalized additive mixed model (GAMM) technique with the gamm function from the R statistical software language (version 2.9.0; R Development Core Team, 2009) mgcv package (version 1.52; Wood 2008). We used individuals as the random factor, and incorporated residuals' auto-regressive structure of order 1 (AR[1]) to account for temporal autocorrelation (Dobbie & Welsh, 2001; Zuur et al., 2009). Using the Akaike information criterion (AIC), we found the GAMM adequacy to be higher when assuming the same time-T_b relationship in both treatments. Therefore, we modeled the difference in temperature (°C) between the T_b rhythms during the two light treatments.

Activity Level and T_b Threshold

In order to determine the T_b threshold for activity, we used data from Rotics et al. (in press), where in parallel to T_b monitoring, automonitored foraging trays, recording the exact time of each individual foraging, were used (see Rotics et al., in press, for detailed description). The parallel recording of T_b and foraging time enabled us to calculate each individual's average T_b while foraging in the trays. To be conservative, this average minus 1 standard deviation was defined as the individual's activity T_b threshold, above which the animal was considered active. The average activity T_b threshold for *A. cahirinus*

was 37.14°C ± 0.14°C, and for *A. russatus* 36.28°C ± 0.17°C (mean ± SE). Since activity bursts were accompanied by a sharp elevation of T_b (see Elvert et al., 1999; Levy et al., 2007), and since the thresholds were far above the mouse average or basal T_bs (average for *A. cahirinus*: 34.78°C ± 0.17°C, *A. russatus*: 32.57°C ± 0.14°C), it is highly unlikely that a nonactive animal could have crossed this threshold. For each individual, we summed the number of T_b records above its individual calculated threshold as a measure of its activity level. This parameter was compared between experimental conditions using a paired *t* test (for each species separately).

RESULTS

The light pulse had no significant effect on T_b of *A. cahirinus* (light effect: –0.21°C ± 0.16°C; $t = -1.27$, $p = .206$). However, since the effect of light on body temperature is not expected to be immediate (unlike its effect on activity), we also tested the effect of light on T_b starting 20 min after the onset of the light pulse and found a significant decrease in body temperature during the light pulse (light effect: –0.32°C ± 0.15°C, $t = -2.10$, $p = .037$; Figures 1a, 2a, b). The effect was even stronger when we tested it starting 40 min after onset of the light pulse (light effect: –0.39°C ± 0.16°C; $t = -2.48$, $p = .014$).

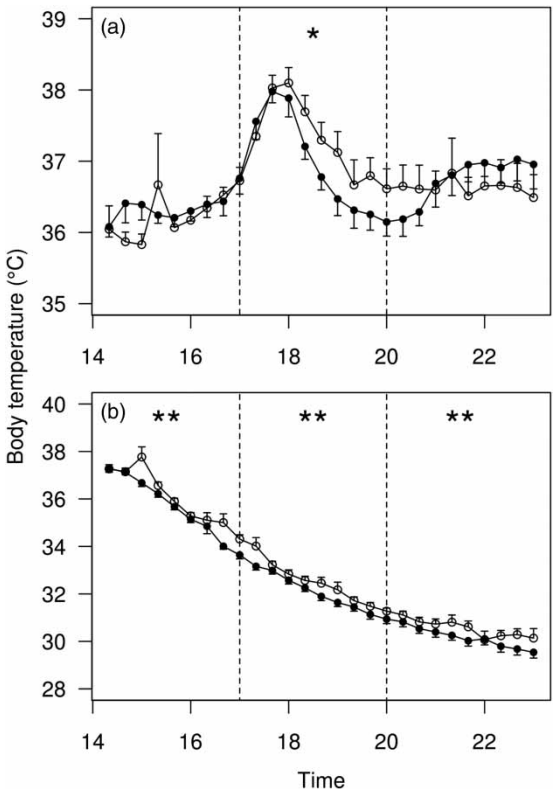

FIGURE 1. Body temperatures (T_b) of *A. cahirinus* (a) and *A. russatus* (b) during light-pulse (•) and control (○) treatments (mean ± SE). Three time periods are displayed, separated by dashed lines: the 3 h before, during, and after light manipulation. * ($p < .05$) and ** ($p < .001$) denotes significant differences between T_b rhythms (GAMM statistical analysis). The significant difference presented in panel a relates to a comparison starting 20 min after lights-on. Note that the panels are not on the same T_b scale.

A. russatus T_bs were also significantly lower during the illuminated hours in comparison to the same control hours (light effect: –0.41°C ± 0.06°C; $t = -7.26$, $p < .001$; Figures 1b, 2c, d). However, ambient temperatures too were lower during the light pulse hours (mean values; light pulse: 24.75°C, control: 25.31°C), as well as throughout the entire days of lighting treatment (mean values; illumination: 24.06°C, control: 24.64°C). In order to account for the ambient temperature effect, we also examined the 3 h preceding and following the illuminated hours. We found no significant difference in *A. cahirinus* T_{bs} between control and light-pulse days during the 3 h preceding the light pulse (light effect: 0.11°C ± 0.11°C; $t = 1.0$, $p = .321$; Figure 1a) or the 3 h following it (light effect: 0.03°C ± 0.23°C; $t = 0.14$, $p = .886$; Figure 1a). In contrast, *A. russatus* showed significantly lower T_b values also during the 3 h preceding (light effect: –0.43°C ± 0.11°C; $t = -3.87$, $p < .001$; Figures 1b, 2c, d), and following the light pulse (light effect: –0.42° C ± 0.09°C; $t = -4.48$, $p < .001$; Figures 1b, 2c, d).

A. cahirinus's average number of "activity" T_b records (i.e., records above the individual's activity T_b threshold) was significantly lower during the light-pulse hours in comparison to control conditions ($t_9 = 2.81$, $p = .021$, means ± SE; light pulse: 9.8 ± 1.6, control: 7 ± 1.5; Figure 3). *A. russatus* individuals were not recorded above their individual activity T_b threshold, neither during the light pulse nor during the control hours, although their average threshold was much lower than that of *A. cahirinus*.

DISCUSSION

We examined light masking responses of a nocturnal and a diurnal rodent under semi-natural conditions in field enclosures. As expected, the nocturnal *A. cahirinus* showed a decrease in T_b and in the calculated activity levels during the light-pulse period. This reduction was exclusive to this period. The experimental design precluded the possibility of clock entrainment or a circalunar rhythm, which together with the nature of the response suggests that negative light masking was responsible for the observed pattern. A similar masking response was described in this species in a recent laboratory study (Cohen et al., 2010).

The experimental light pulse was applied during the beginning of the night. Redlin and Mrosovsky (1999b) found that during this time hamsters were particularly susceptible to light masking. They suggested that when activity is expected to start, it is of greatest adaptive value to be sensitive to light changes, compensating for possible minor inaccuracies of the endogenous clock. Indeed, in our study, a low-intensity light pulse (2 lux) triggered a negative masking response (Mrosovsky et al., 1999; Redlin & Mrosovsky, 1999b).

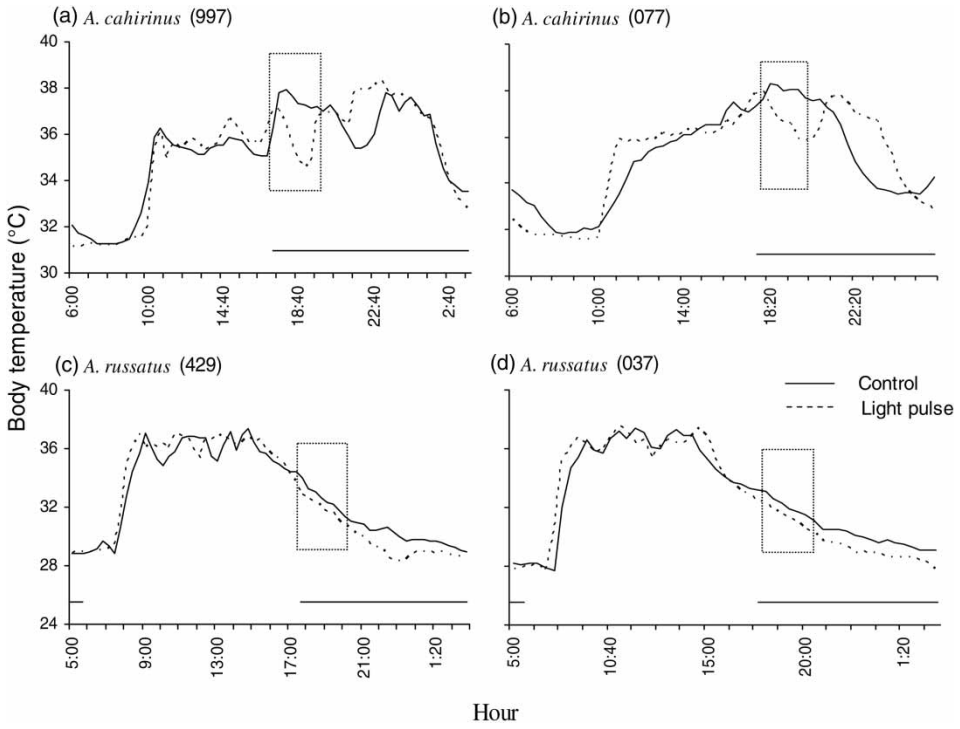

FIGURE 2. Body temperatures of two *A. cahirinus* individuals (a, b) and two *A. russatus* individuals (c, d) during a control and a light-pulse day (solid and dashed lines, respectively). Dashed rectangles mark the compared hours of the light manipulation. Horizontal thick line indicates the darkness hours.

Negative light masking has an obvious adaptive value for *A. cahirinus*, since elevated light intensities are known to facilitate predation by nocturnal visual raptors (Brown et al., 1988; Clarke, 1983; Lima & Dill, 1990), such as Hume's tawny owl (*Strix butleri*) in the study area (Jones et al., 2001; Mandelik et al., 2003). The masking mechanism enables the flexibility of immediate adjustment to the light pulse, thus reducing predation risk. The negative masking response of nocturnal rodents to light in the laboratory may possibly also reflect an adaptive response to predation risk.

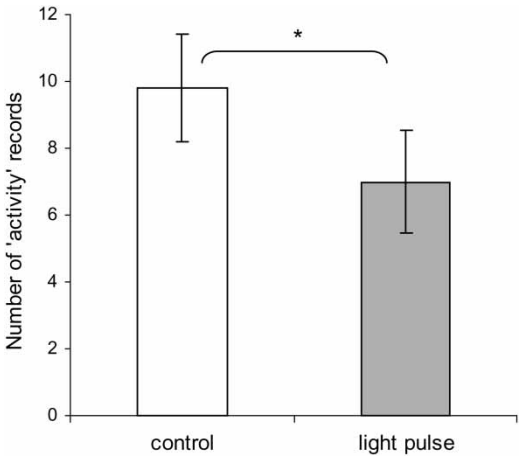

FIGURE 3. *A. cahirinus*'s number of "activity" records (body temperature records above the individual's calculated activity T_b threshold) under control versus light-pulse conditions (mean ± SE). An asterisk denotes significant difference ($p = .021$; paired t test). N = 10. *Note: A. russatus* had no "activity" records during both treatments.

A. russatus T_b was also significantly lower during the light-pulse hours. However, this pattern was found also prior to and after the light pulse (Figure 1b), and, therefore, it did not result from the light pulse, itself. Moreover, *A. russatus* T_bs were far below their activity thresholds, suggesting that mice were actually inactive during the hours of light manipulation. Hence, we can confidently say that the observed decrease was not caused by a behavioral light masking response. The body temperature of spiny mice, as well as of other rodents that enter daily torpor, is affected by ambient temperatures when they are inactive (Geiser, 2004; Levy et al., accepted). *A. russatus*, in contrast to *A. cahirinus*, was inactive during the examined time periods, and ambient temperature was lower during the light-pulse days. Therefore we assume that the difference in its T_b between the light treatments was due to the drop in ambient temperature.

As in our present study, previous laboratory studies too found no positive light masking response in *A. russatus* (Cohen & Kronfeld-Schor, 2006; Cohen et al., 2010). As mentioned earlier, *A. russatus* is not a typical diurnal species; it has shown nocturnal activity rhythms in the laboratory (Cohen et al., 2009; Levy et al., 2007), and it possesses some nocturnal physiological characteristics (Kronfeld-Schor & Dayan, 2008). Thus, it is not surprising that it did not respond to the light pulse as would be expected from a typical diurnal species, i.e., enhancing its

activity during the light pulse. It is also possible that the cool ambient temperatures during the first 3 h of the night (24.75°C) were less favorable for this heat-adapted species (Haim & Borut, 1976; Shkolnik, 1971), overriding the influence of the light pulse. This hypothesis is in accord with previous findings showing that in the absence of *A. cahirinus*, *A. russatus* shifted to nocturnal activity only after ca. 6 months, following a very hot day (Shkolnik, 1971); and in another study conducted in the same field enclosure, in the absence of *A. cahirinus*, *A. russatus* remained active mainly during the day, although some activity shifted to the night (Gutman & Dayan, 2005). Furthermore, in the high mountains of the Sinai desert, golden spiny mice are diurnal in the absence of the common spiny mice, and their diurnal activity in that habitat has been ascribed to the unfavorable cold conditions during the night (Haim & Borut, 1976). An interactive effect of light and temperature in the wild was reported by Fernandez-Duque (2003), who found that the cathemeral owl monkey (*Aotus azarai*) increased its nocturnal activity as moonlight increased; however, this increase was also dependent on suitable ambient temperatures. More possible explanations for the lack of *A. russatus*'s positive masking response include the low intensity of the light pulse or competition from its congener, *A. cahirinus* (see Gutman & Dayan, 2005; Shkolnik, 1971). In summary, *A. russatus* possibly did not respond to the experimental light pulse, because it had no effect on it, or because any such effect was masked by other environmental factors.

Among the few studies that have addressed light masking in the field are those by Fernandez-Duque (2003) and Kappeler and Erkert (2003) on primates (owl monkeys and red-fronted lemurs), showing increased nocturnal activity with increased intensities of moonlight. Erkert (2008) emphasized light masking as responsible for these observed patterns. In addition, although reduction of rodent activity on full-moon nights is probably also mediated by masking, the available studies (e.g., Daly et al., 1992; Mandelik et al., 2003; Topping et al., 1999) were not conducted in a way that enables us to verify this mechanism. Our present study, on the other hand, controlled for lighting and enabled the elimination of possible influencing factors; we can, thus, attribute the *A. cahirinus* response to the masking mechanism. As far as we know, this is the first study to use light-masking laboratory procedures under field conditions.

In summary, to date light masking has been studied almost exclusively in the laboratory. Here, we applied a controlled light-pulse procedure in open enclosures, and describe explicitly a negative masking response in *A. cahirinus* under semi-natural conditions. This study of the masking response provides evolutionary insight into its adaptive value in the field. We conclude that light masking is not an artifact of laboratory conditions, but represents a natural adaptive response in free-living populations.

ACKNOWLEDGMENTS

We thank G. Sterzer for her devoted assistance in conducting the field experiments, J. Kazes for his dedicated help in many field logistics issues, R. Cohen for her excellent help in animal surgery, other lab members, family, and friends who helped to construct the experimental set-up, the Israel Nature and Parks Authority for their help and friendship, and the Ein Gedi Field School of the Society for the Protection of Nature in Israel for their hospitality.

Declaration of Interest: The authors report no conflicts of interest. The authors alone are responsible for the content and writing of the paper.

REFERENCES

Abramsky Z, Rosenzweig ML, Belmaker J, Bar A. (2004). The impact of long-term continuous risk of predation on two species of gerbils. *Can. J. Zool.* 82:464–474.

Aschoff J. (1960). Exogenous and endogenous components in circadian rhythms. *Cold Spring Harb. Symp. Quant. Biol.* 25:11–28.

Aschoff J, Vongoetz C. (1988). Masking of circadian activity rhythms in hamsters by darkness. *J. Comp. Physiol. A Sens. Neural Behav. Physiol.* 162:559–562.

Aschoff J, Vongoetz C. (1989). Masking of circadian activity rhythms in canaries by light and dark. *J. Biol. Rhythms* 4:29–38.

Beier P. (2006). Effects of artificial night lighting on terrestrial mammals. In Rich C, Longcore T (eds.), *Ecological consequences of artificial night lighting*. Washington, DC: Island Press, 19–42.

Brown JS, Kotler BP, Smith RJ, Wirtz WO. (1988). The effects of owl predation on the foraging behavior of heteromyid rodents. *Oecologia* 76:408–415.

Clarke JA. (1983). Moonlight's influence on predator/prey interactions between short-eared owls (*Asio flammeus*) and deermice (*Peromyscus maniculatus*). *Behav. Ecol. Sociobiol.* 13:205–209.

Cohen R, Kronfeld-Schor N. (2006). Individual variability and photic entrainment of circadian rhythms in golden spiny mice. *Physiol. Behav.* 87:563–574.

Cohen R, Smale L, Kronfeld-Schor N. (2009). Plasticity of circadian activity and body temperature rhythms in golden spiny mice. *Chronobiol. Int.* 26:430–446.

Cohen R, Smale L, Kronfeld-Schor N. (2010). Masking and temporal niche switches in spiny mice. *J. Biol. Rhythms* 25:47–52.

Daly M, Behrends PR, Wilson MI, Jacobs LF. (1992). Behavioural modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*. *Anim. Behav.* 44:1–9.

Decoursey PJ, Pius S, Sandlin C, Wethey D, Schull J. (1998). Relationship of circadian temperature and activity rhythms in two rodent species. *Physiol. Behav.* 65:457–463.

Dobbie MJ, Welsh AH. (2001). Modelling correlated zero-inflated count data. *Aust. N. Z. J. Stat.* 43:431–444.

Doi M, Yujnovsky I, Hirayama J, Malerba M, Tirotta E, Sassone-Corsi P, Borrelli E. (2006). Impaired light masking in dopamine D2 receptor-null mice. *Nat. Neurosci.* 9:732–734.

Elvert R, Kronfeld N, Dayan T, Haim A, Zisapel N, Heldmaier G. (1999). Telemetric field studies of body temperature and activity rhythms of *Acomys russatus* and *A. cahirinus* in the Judean Desert of Israel. *Oecologia* 119:484–492.

Erkert HG. (2008). Diurnality and nocturnality in nonhuman primates: comparative chronobiological studies in laboratory and nature. *Biol. Rhythm Res.* 39:229–267.

Erkert HG, Gburek V, Scheideler A. (2006). Photic entrainment and masking of prosimian circadian rhythms (*Otolemur garnettii*, Primates). *Physiol. Behav.* 88:39–46.

Fernandez-Duque E. (2003). Influences of moonlight, ambient temperature, and food availability on the diurnal and nocturnal activity of owl monkeys (*Aotus azarai*). *Behav. Ecol. Sociobiol.* 54:431–440.

Geiser F. (2004). Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annu. Rev. Physiol.* 66:239–274.

Gutman R, Dayan T, (2005). Temporal partitioning: an experiment with two species of spiny mice. *Ecology* 86:164–173.

Haim A, Borut A. (1976). Thermoregulation and nonshivering thermogenesis as factors limiting distribution of golden spiny mouse (Acomys-Russatus). *Isr. J. Med. Sci.* 12:896–896.

Jones M, Dayan T. (2000). Foraging behavior and microhabitat use by spiny mice, *Acomys cahirinus* and *A. russatus*, in the presence of blanford's fox (*Vulpes cana*) odor. *J. Chem. Ecol.* 26:455–469.

Jones M, Mandelik Y, Dayan T. (2001). Coexistence of temporally partitioned spiny mice: roles of habitat structure and foraging behavior. *Ecology* 82:2164–2176.

Kappeler PM, Erkert HG. (2003). On the move around the clock: correlates and determinants of cathemeral activity in wild redfronted lemurs (*Eulemur fulvus rufus*). *Behav. Ecol. Sociobiol.* 54:359–369.

Kotler BP, Brown JS, Hasson O. (1991). Factors affecting gerbil foraging behavior and rates of owl predation. *Ecology* 72:2249–2260.

Kronfeld-Schor N, Dayan T. (1999). The dietary basis for temporal partitioning: food habits of coexisting *Acomys* species. *Oecologia* 121:123–128.

Kronfeld-Schor N, Dayan T. (2003). Partitioning of time as an ecological resource. *Annu. Rev. Ecol. Evol. Syst.* 34:153–181.

Kronfeld-Schor N, Dayan T. (2008). Activity patterns of rodents: the physiological ecology of biological rhythms. *Biol. Rhythm Res.* 39:193–211.

Kronfeld-Schor N, Haim A, Dayan T, Zisapel N, Klingenspor M, Heldmaier G. (2000). Seasonal thermogenic acclimation of diurnally and nocturnally active desert spiny mice. *Physiol. Biochem. Zool.* 73:37–44.

Kronfeld-Schor N, Dayan T, Elvert R, Haim A, Zisapel N, Heldmaier G. (2001). On the use of the time axis for ecological separation: diel rhythms as an evolutionary constraint. *Am. Nat.* 158:451–457.

Levy O, Dayan T, Kronfeld-Schor N. (2007). The relationship between the golden spiny mouse circadian system and its diurnal activity: an experimental field enclosures and laboratory study. *Chronobiol. Int.* 24:599–613.

Levy O, Dayan T, Kronfeld-Schor N. (accepted). Adaptive thermoregulation in golden spiny mice: The influence of season and food availability on body temperature. *Physiol. Biochem. Zool.*

Lima SL, Dill LM. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* 68:619–640.

Mandelik Y, Jones M, Dayan T. (2003). Structurally complex habitat and sensory adaptations mediate the behavioural responses of a desert rodent to an indirect cue for increased predation risk. *Evol. Ecol. Res.* 5:501–515.

Mrosovsky N. (1999). Masking: history, definitions, and measurement. *Chronobiol. Int.* 16:415–429.

Mrosovsky N, Thompson S. (2008). Negative and positive masking responses to light in retinal degenerate slow (rds/rds) mice during aging. *Vision Res.* 48:1270–1273.

Mrosovsky N, Foster RG, Salmon PA. (1999). Thresholds for masking responses to light in three strains of retinally degenerate mice. *J. Comp. Physiol. A Sens. Neural Behav. Physiol.* 184:423–428.

Portaluppi F, Smolensky M, Touitou Y. (2010). Ethics and methods for biological rhythm research on animals and human beings. *Chronobiol. Int.* 27:1911–1929.

Redlin U. (2001). Neural basis and biological function of masking by light in mammals: suppression of melatonin and locomotor activity. *Chronobiol. Int.* 18:737–758.

Redlin U, Mrosovsky N. (1999a). Masking by light in hamsters with SCN lesions. *J. Comp. Physiol. A Sens. Neural Behav. Physiol.* 184:439–448.

Redlin U, Mrosovsky N. (1999b). Masking of locomotor activity in hamsters. *J. Comp. Physiol. A Sens. Neural Behav. Physiol.* 184:429–437.

Redlin U, Hattar S, Mrosovsky N. (2005). The circadian Clock mutant mouse: impaired masking response to light. *J. Comp. Physiol. A Neuroethol. Sens. Neural Behav. Physiol.* 191:51–59.

Rotics S, Dayan T, Kronfeld-Schor N. (In press). The effect of artificial night lighting on temporally partitioned spiny mice. *J. Mammal.*

Shargal E, Kronfeld N, Dayan T. (2000). Population biology and spatial relationships of coexisting spiny mice (*Acomys*) in Israel. *J. Mammal.* 81:1046–1052.

Shkolnik A. (1971). Diurnal activity in a small desert rodent. *Int. J. Biometeorol.* 15:115–120.

Topping MG, Millar JS, Goddard JA. (1999). The effects of moonlight on nocturnal activity in bushy-tailed wood rats (*Neotoma cinerea*). *Can. J. Zool.* 77:480–485.

Wood SN. (2008). Fast stable direct fitting and smoothness selection for generalized additive models. *J. R. Stat. Soc. Ser. B Stat. Methodol.* 70:495–518.

Zuur AF, Leno EN, Walker N, Saveliev AA, Smith GM. (2009). Mixed effects models and extensions in ecology with R. *Statistics for Biology and Health*. New York: Springer.