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Circadian locomotor activity and response to different light conditions in the Volcano mouse, *Neotomodon alstoni* (Merriam, 1898)

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The volcano mouse, *Neotomodon alstoni*, was studied in order to describe basic circadian behavior during free running and entrainment to parametric and non-parametric photoperiods. Responses to short and long days were also tested to ascertain any potential photoperiodic response. This species is endemic to the high grasslands of central Mexico. Its breeding peaks during summer, indicating a possible circannual regulation of reproduction. Our results indicate that locomotor activity in *Neotomodon alstoni* is typical of a nocturnal rodent when studied using running wheels, however, when activity was observed in freely moving recordings with no running wheel, locomotor activity shifts to a semidiurnal architecture when exposed to long day photoperiods. When gonadal activity was studied in males exposed to short and long days, significant differences were observed in testis size, nevertheless levels of testosterone and seminiferous tubuli indicated that day length does not inhibit sexual maturity in this species. The results indicated that *N. alstoni* may not be photoperiodic with regard to gonadal activity, however it does display photoperiodic differences with regard to behavior, body weight and testis size.

Keywords: circadian; volcano mouse; locomotor activity; *Neotomodon alstoni*

Introduction

Circadian rhythms allow an organism to fit its physiology and behavior to natural cycles, in such way that they enable the organism to modify its physiology and biochemistry in anticipation of changes in the environment (Morgan 2004). As a consequence, phase preferences exist between organisms and the environment in such a way that there are times when it is optimal to perform certain activities, and times when performing the same activity may be disadvantageous. Therefore most animals have a distinct activity pattern confined to a certain part of the day, and to which they are adapted behaviorally, anatomically, and physiologically (Daan 1981; DeCoursey 2004).

In mammals, the main circadian oscillator is located in the hypothalamic suprachiasmatic nucleus (SCN) (Moore and Leak 2000) and it regulates the phase

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and amplitude of peripheral oscillators (Yamazaki et al. 2000; Stokkan et al. 2000). Circadian rhythms in mammals are phase shifted or entrained by light–dark cycles through retino-hypothalamic pathways that terminate on the SCN (Meijer 2000). Similarly, seasonal changes in day length can be discriminated by animals and day length is an important cue which precipitates physiological and behavioral changes related to the seasons, traits known as photoperiodic responses (Gorman et al. 2000; Boden and Kenaway 2006).

Different murine models have been used in order to increase our knowledge about circadian organization and photoperiodism, however, using inbred species maintained in laboratory conditions reduces our ability to understand how circadian organization varies among wild animals and what significance for fitness this variation may have. The volcano mouse, *Neotomodon alstoni*, is endemic to the mountain ridges of central México (Chávez 2005). This species has been an interesting and useful model for investigating physiological, behavioral, molecular and ecological questions (Fa et al. 1996; Granados et al. 1996; Martínez Merlos et al. 1997; Ayala-Guerrero et al. 1998; Villapando et al. 2000, 2005; Macías et al. 2004; Luis et al. 2000, 2004). The importance of documenting the basic biology of endemic species, and the importance of studying non-traditional animal models, will provide better insight into the evolution of circadian rhythms. Our aim here is to describe basic circadian patterns of activity in the volcano mouse by comparing two different recording methods, freely moving, as detected with infrared sensors (FM), and running wheel activity (WR). We tested the gonadal responses of volcano mice to short and long days in FM conditions in order to reduce the possibility of an inhibitory effect by WR, as described in hamsters (Van Reeth et al. 1994; Menet et al. 2005). Our results indicate that *N. alstoni* displays bimodal nocturnal locomotor activity in WR and entrains to different photoperiods in parametric and non-parametric manners. When exposed to different photoperiods, their circadian rhythms are patterned differently, such that diurnal bouts of activity are more frequent during long days. Changes in testis size indicates a differential response to photoperiod, however the associated hormonal profiles demonstrates that this species does not display the typical photoperiodic response as observed in hamsters.

Materials and methods

Animals and housing

Male adult *Neotomodon alstoni* were collected in the forests of the Ajusco mountain ridges (above 2500 m) at Parres, D.F. Animals were collected in April and May and kept in vivarium facilities for quarantine at the Facultad de Ciencias (FC) UNAM in individual cages containing woodchips. Food (Rodent Lab Chow 5001, Purina Inc.) and tap water was provided *ad libitum*, environmental temperature was between 18 and 23°C and lighting was set at 12:12 (0600–1800, 200–250 lux). After four weeks of acclimation, animals (body weight average 47.3g) were transferred to cages for long-term recordings.

Additionally, eight male hamsters (4 months old, about 90 g body weight) obtained from our colony at FC were used as a positive control to gauge photoperiodic response. Cleaning of cages occurred once a week. When in constant darkness, animals were checked on twice a week using dim red light (1–2 lux) provided by a small red bulb lamp. Animals were maintained and treated according to the official Mexican regulation for experimentation in animals.

Locomotor activity recordings

Locomotor activity was recorded using infrared light beams, coupled to an acquisition data board (NAFRI, México) in a PC. Four light beams were located 4 cm above the bottom of a glass cage (18 × 20 × 30 cm), for free moving activity, or in the top of the cage to record running wheel movements. Recordings from freely moving animals were performed in cages without a running wheel. Each beam interruption was considered as a single event. Data were summarized every 10 minutes (10 min bin cell) and stored in a PC until further analysis.

Each cage was placed in a light-tight wooden box (70 × 40 × 30 cm), equipped with a fluorescent lamp (150–200 lux) controlled by a timer. Ventilation was kept constant using a small fan and temperature was maintained at $24 \pm 2^\circ\text{C}$.

Protocols

Wheel running activity recordings were performed in eight adult mice for a minimum of 10 days under each light condition: 12:12 light dark cycles (LD), constant darkness (DD), skeleton photoperiod (SP11:1, 11:1), DD and constant light (LL).

In order to reduce the possible influence of running wheel usage upon the photoperiodic response, free moving recordings were only used when testing photoperiodic responses. A group of animals were exposed to long days (LD 16:8, $n = 10$) or short days (LD 8:16, $n = 10$). Simultaneously, a group of male hamsters were set under either short ($n = 4$) or long days protocol ($n = 4$) to be used as a positive control for photoperiodic response. By the end of three months, mice and hamsters were anesthetized with Atropine sulfate (0.1 ml), Ketamine-Xylazine (40 and 7 mg/kg b.w., respectively) and Pentobarbital (20 mg/kg b.w.), a blood sample taken through the periorbital sinus, and testis were removed, measured and fixed in 10% formaldehyde for subsequent histological examination. Body weights were recorded at the beginning and the end of each experiment. Blood samples were taken in heparinized-capillary tubes, centrifuged and plasma was separated and frozen until analyzed for testosterone using a radioimmunoassay (RIA; Coat-A-Count kit; Siemens Medical Solutions Diagnostics, Los Angeles CA, USA) at the Hospital General in Mexico City.

Histology

Testes were dehydrated and embedded in paraffin. Seven μm thick sections were obtained using a microtome (Leica mod. RM2165). Sections were placed in glass slides stained with hemtoxilin-eosin (Estrada et al. 1982), mounted in synthetic resin, photographed using a photomicroscope (Olympus Provis. AX 70, Japan) and digitalized in order to quantify the longest and shortest diameter of the seminiferous tubules ($n = 67$ for each group).

Data analysis

Locomotor activity data were organized into double plotted actograms; a minimum of 10 days of recording were used to calculate X^2 periodogram and waveforms with DISPAC software (Aguilar-Roblero et al. 1997). Waveforms were fit to the dominant period and analyzed in free running rhythms, in order to obtain the α/ρ

ratio as well as the average activity level. Data were compared among groups by means of a Student's t test (Statistica, Handel Scientific, USA); significant differences were considered when $p < 0.05$. Data are expressed as the mean value with corresponding standard error, unless indicated otherwise.

Results

Wheel running locomotor activity rhythm

Figure 1 shows a representative example of wheel running locomotor activity rhythm from a mouse kept at different light conditions. On the left (A), 12:12 LD and DD showed a typical nocturnal behavior. Onset of activity is shortly after lights off, and a bimodal pattern is observed at the beginning and at the end of night. When exposed to a symmetrical skeleton photoperiod (B), locomotor activity onset entrains by a series of phase advances until the phase of activity corresponds to the afternoon pulse of light. A mechanical failure deactivated the timer controlling SP, and further reactivation was shifted slightly earlier during these days. This event confirmed true entrainment to the evening pulse, as the phase of the resulting free-running rhythm of activity began during the subjective night. When exposed to constant light (C) of the same intensity as in the previous photoperiods, a lengthening of the period of free running activity and a shortening of alpha is observed. When released again into DD, a robust bimodal free running rhythm was present. Period values obtained from Chi-square periodograms are indicated above each average waveform.

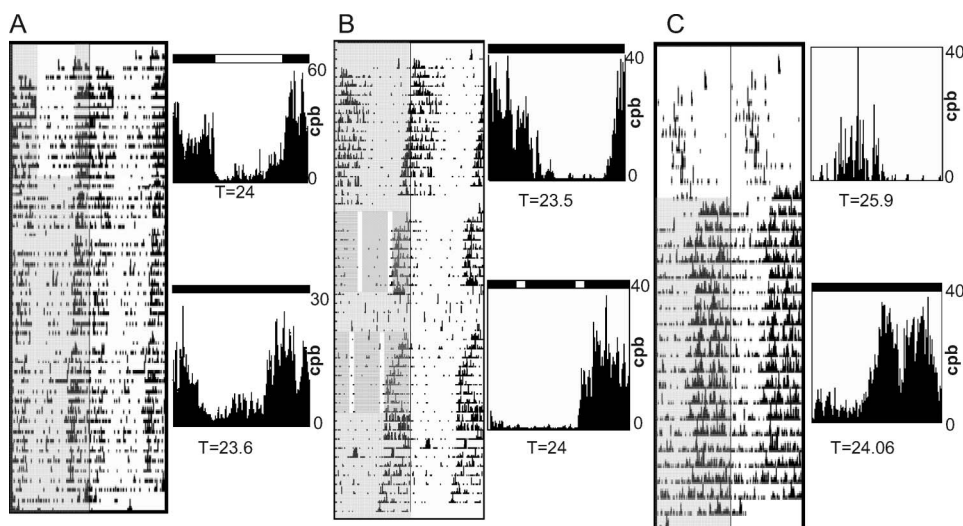


Figure 1. Entrained and free running circadian rhythms of locomotor activity in wheel running obtained under different lighting conditions in a male mouse, *Neotomodon alstoni*. Both parametric and non-parametric entrainment confirms its nocturnal behavior, however diurnal activity bouts are spread throughout the recordings. In A, LD and then DD; in B, SP is indicated with clear bars on left side actogram; in C, LL and then DD. Gray areas indicate darkness (cpb = counts per bin).

All mice tested under these conditions showed similar responses, however individual variability in free running periods was observed, as well as after effects following each light condition, as shown in Table 1. Variability in the α/ρ ratio and maximum average activity is dependent upon photoperiod.

Short and long day response

Figure 2 shows a representative example of freely moving locomotor activity from two mice in short and long day photoperiods, respectively. When locomotor activity is recorded without a running wheel, disperse bouts of activity are observed throughout the day, however the bulk of activity is distributed close to lights off during the first month of the recording. After approximately one month, different responses are observed: in long day photoperiods locomotor activity is not as robust as in short days, and more frequent diurnal bouts appear.

All animals exposed to short days exhibited a large number of transient cycles (10–20 days) before assuming a stable phase relationship with the light/dark cycle. In long days diurnal and nocturnal bouts of activity waxed and waned, without any clear circadian organization until finally reorganizing and entraining after approximately one month.

Testicular size at the end of the third month of exposure to both conditions is compared in Figure 3. A statistical difference was observed in our control hamsters maintained under the same parameters as *Neotomodon*, which indicates that our protocol for short and long day photoperiods is effective in a known photoperiodic species (Figure 3A). Significant differences ($p < 0.05$) in testis size were also noted in *Neotomodon* (Figure 3B), but tubular diameter and blood testosterone levels did not change (Table 2). A particularly interesting observation is that mice increased body weight in either photoperiod, with a greater increase observed in short days, while the body weight of hamsters decreased under the same protocol.

Discussion

During the last 15 years, our knowledge about the physiology and molecular biology of circadian rhythms has made significant progress. This information must be utilized to translate behavioral rhythms, so that the adaptive values of the described mechanisms can be fully comprehended. In order to achieve this, the study of circadian rhythms in diverse animal species is required. Studying rodent activity patterns and seasonal phase shifting might provide useful insight for further ecophysiological studies, perhaps relating to the strength of coupling between central and peripheral oscillators (Kronfeld-Schor and Tamar 2008).

The photoperiod-dependent changes in locomotor activity; seem to be related to regionally specific circadian oscillations. It has been demonstrated that of the separate oscillating cell groups in the mouse suprachiasmatic nucleus (SCN), at least two sub-populations are involved in the photoperiodic response of behavioral rhythms in mice (Inagaki et al. 2007).

Neotomodon alstoni is an endemic species of mouse that inhabits the mountain ridges of central Mexico, also known as the transversal neo volcanic axis. The volcano mouse shares its habitat with other species of rodents and lagomorphs which compete for similar resources in these high grasslands (Chávez 2005). This species has proven to be important for physiological studies, however until now little

Table 1. Parameters evaluated while free running and during entrainment. Changes in maximum amplitude as well as in α/ρ ratio were noted. Values are mean \pm SE. Same letters indicate differences between respective groups (t -test* $p < 0.05$).

	LD 12:12	DD	SP	DD	LL	DD
Period (h)	24.09 \pm 0.2	23.9 \pm 0.07 ^b	23.8 \pm 0.08 ^a	23.9 \pm 0.2	24.47 \pm 0.14 ^a	23.54 \pm 0.13 ^b
Amplitude (mov/bin)	127.85 \pm 26.7 ^a	70.9 \pm 17.7	115.5 \pm 10.9 ^b	160.7 \pm 46.6 ^c	45.26 \pm 13.9 ^{abc}	79.8 \pm 17.7
α/ρ ratio	0.97 \pm 0.06	1.36 \pm 0.19	1.12 \pm 0.35	1.08 \pm 0.125	0.8 \pm 0.07	1.18 \pm 0.24

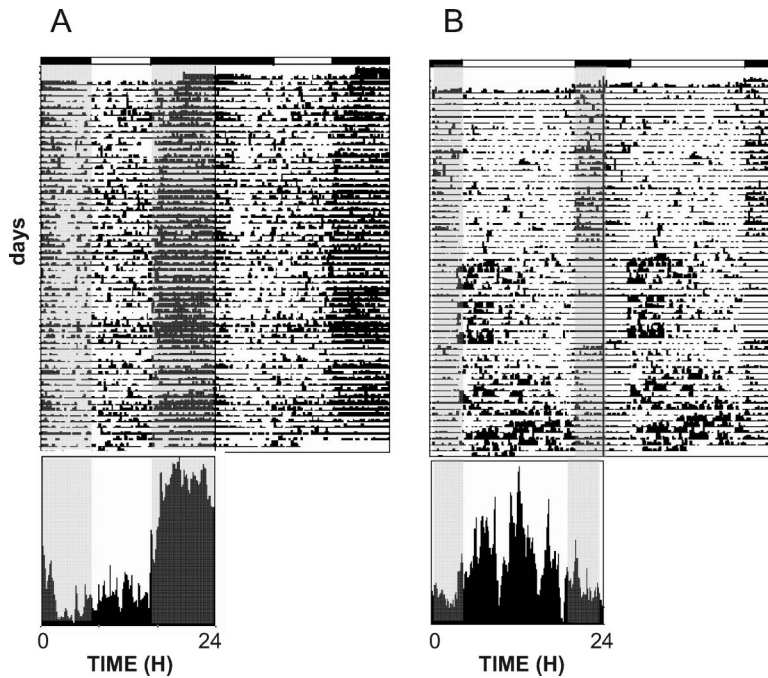


Figure 2. Actograms of two mice exposed to short day (A) and long day (B) photoperiod. Note a shift in diurnal activity phase by the second half of the long day protocol. Average waveforms are displayed; shaded areas represent darkness during each LD cycle.

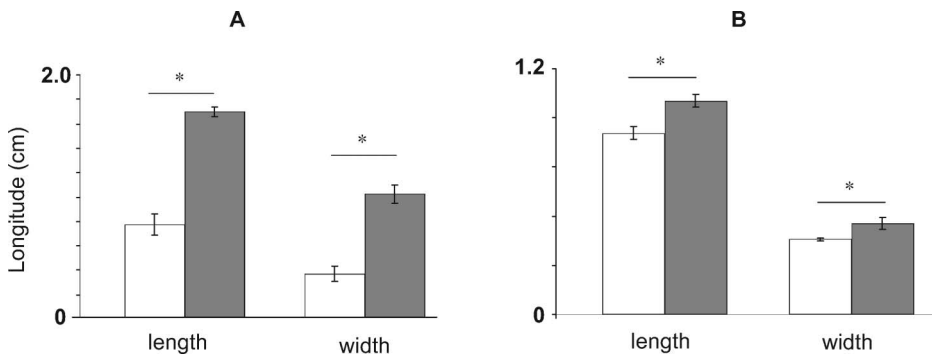


Figure 3. Maximum length and width of testis from animals held in short (8:16, white bars) and long photoperiods (16:8, gray bars). Average size values \pm SE of left testis are shown. (A) hamsters, (B) volcano mice; differences are noted $*p < 0.05$.

information existed about its biology. In the present work, these mice displayed nocturnal behavior when we used running wheels to record activity, similar to what is described for other nocturnal rodents, such as *Peromyscus leucopus* (Pittendrigh and Daan 1976). The onset of activity in freely moving conditions is quite stable and makes *Neotomodon* a suitable model for studying phase shift responses. Even though the animals used in this work were obtained from their natural environment, activity

Table 2. Parameters tested in short day and long day protocols. Only hamsters showed significant differences in seminiferous tubule dimensions and plasma testosterone levels, respectively, as indicated by asterisks.

	Hamster		Neotomodon	
	Short days	Long days	Short days	Long days
Long Tubuli diameter (μm)	120.93 ± 1.77	$260.12 \pm 5.3^*$	213.3 ± 3.26	214.5 ± 3.12
Short Tubuli diameter (μm)	108.37 ± 1.47	$215.93 \pm 4.9^*$	184.7 ± 2.04	189.1 ± 2.43
Testosterone (ng/ml)	0.18 ± 0.05	$2.7 \pm 0.46^*$	0.55 ± 0.06	0.43 ± 0.06
Initial body weight	139 ± 5	122.75 ± 11	47.33 ± 1.5	47.3 ± 1.6
Final body weight	135.75 ± 11	121 ± 8	51.63 ± 1.75	50.2 ± 2.12

recordings were clear enough to distinguish inter-individual differences in the rhythmic properties we assessed.

An observation of particular interest is that different patterns of activity are observed under short and long days (Figure 2). This finding is of particular interest, since field observations had stated that the onset of activity may occur before sunset (Davis and Follansbee 1945). *Neotomodon* is capable of breeding year round, but the majority of breeding occurs between April and September (Chávez 2005), indicating that photoperiod may influence this seasonal rhythm.

In the present study we tested whether *Neotomodon* is a photoperiodic species. Our results showed no differences when comparing the diameter of seminiferous tubules and testosterone levels. In this experiment, we used the hamster as a positive control in order to know if the number of days and light intensity was adequate for eliciting a photoperiodic response. The golden hamster naturally inhabits areas exposed to extreme changes during the year; its reproductive fitness has to be organized according to the best season for its offspring's survival. *Neotomodon* inhabits forest above 2550 m, in high grasslands in central México, therefore it is not surprising that *Neotomodon* does not show the changes in testis function that hamsters do. Indeed, it appears that photoperiodic changes may prime the reproductive axis of *Neotomodon*, however photoperiodic changes alone are not sufficient to induce full gonadal functioning. It is likely that *Neotomodon*'s seasonal breeding would be more closely associated to seasonal fluctuations of natural resources, such as changes in food quality due to changes in vegetation; temperature may also play an important factor together in addition to photoperiod (Bronson 1985).

Neotomodon exhibits parental care when held in captivity. Pup survival is favored by additional care from males, enabling females to provide higher quality care during rearing (Luis et al. 2000, 2004). When combined with the observation that reproduction peaks during longer days in the wild, a shift in the phase of activity may allow animals to find additional resources for breeding by subsuming a different temporal niche instead of being exclusively nocturnal. Examples of rodents switching activity times in nature are relatively rare; by studying the physiological mechanisms by which photic cues elicit this switching is of major interest in comprehension of the ecological significance of biological rhythms. The adaptation of consolidating activity to one phase of the day can be advantageous, however in ephemeral environments if those that actually switch phases with the seasons may find specific

advantages that correspond to temporal changes in their habitat (Erkinaro 1969; Refinetti 2008).

Studying non-traditional models allows testing variation in physiology to be typical within natural populations (Heideman 2004). *N. alstoni* presents an interesting advantage: when in captive conditions, animals increase their weight and some individuals develop symptoms equivalent to a metabolic syndrome (Carmona 2006). We observed that these weight increases were larger in animals exposed to short days, suggesting that photoperiod may influence metabolic changes in this species, a finding potentially of interest in future research regarding human health.

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