

Artículo



DAILY PATTERNS OF ACTIVITY IN FREE-LIVING RIO NEGRO TUCO-TUCOS (*Ctenomys rionegrensis*)

Ignacio Estevan¹, Eileen. A. Lacey², and Bettina Tassino¹

¹ Sección Etología, Facultad de Ciencias, Universidad de la República, Iguá 4225 Esq. Mataojo, 11400 Montevideo, Uruguay. [Correspondence: Bettina Tassino <tassino@fcien.edu.uy>]

² Museum of Vertebrate Zoology and Department of Integrative Biology, University of California, 1005 Valley Life Sciences Bldg #3140, 94720-3140 Berkeley, USA.

ABSTRACT. Activity patterns are a fundamental aspect of the biology of many species, with important implications for survival and reproduction. Typically, such patterns of activity are thought to be entrained by light cues, raising intriguing questions about the nature of circadian rhythms in subterranean species, members of which spend virtually their entire lives in dark, underground burrows. As part of ongoing studies of the behavioural biology of the Rio Negro tuco-tuco (*Ctenomys rionegrensis*), we used data from free-living animals to characterize daily patterns of activity in this subterranean species of rodent. The locations of 5 radiocollared adults were recorded hourly for 72 consecutive hours during November, 2005. Analyses of 5 measures of activity based on these data revealed that individuals changed locations more often and moved greater distances between successive radio fixes during daylight hours. These data are consistent with studies of other ctenomyid rodents in suggesting that *C. rionegrensis* tends toward diurnality. Comparisons with other lineages of subterranean rodents indicate that activity patterns vary markedly among these burrow-dwelling mammals, with substantial intra- as well as inter-specific differences in activity reported.

RESUMEN. Patrones de actividad diaria en libertad de los tuco-tucos de Río Negro (*Ctenomys rionegrensis*). Los patrones de actividad son un aspecto fundamental de la biología de muchas especies, con gran impacto en su sobrevivencia y reproducción. Típicamente, se considera que los patrones de actividad, aun siendo endógenos, se sincronizan con la luz, lo cual plantea interrogantes sobre la expresión de los ritmos circadianos en las especies subterráneas, cuyos miembros pasan virtualmente toda su vida en oscuras cuevas subterráneas. Como parte del estudio de la biología del comportamiento del tuco-tuco de Río Negro (*Ctenomys rionegrensis*), colectamos datos de animales en condiciones naturales para caracterizar el patrón diario de actividad en esta especie de roedor subterráneo. Se registró la localización de 5 individuos cada hora durante 72 horas consecutivas en noviembre 2005. El análisis de 5 medidas de actividad calculadas a partir de los datos mostró que los individuos cambian de localización más frecuentemente y se mueven mayores distancias durante el día. Esta tendencia a mayor actividad diurna es consistente con estudios realizados en otras especies de ctenómidos. Las comparaciones con otros roedores subterráneos muestran que el patrón de actividad diario es un rasgo muy variable, con importantes variaciones tanto dentro como entre especies.

Key words: Activity patterns. Circadian rhythms. *Ctenomys*. Tuco-tucos.

Palabras clave: *Ctenomys*. Patrones de actividad. Ritmos circadianos. Tuco-tucos.

INTRODUCTION

Circadian patterns of activity are a critical component of the biology of many organisms (Horton, 2001). Circadian rhythms fulfill a wide range of functions, from mediating predation pressures to synchronizing reproductive activities (Sharma, 2003; Paranjpe and Sharma, 2005). Endogenous circadian clocks are typically entrained to a 24-hour cycle by external cues, one of the most important of which is ambient light (Ben-Shlomo and Kyriacou, 2002; Cermakian and Sassone-Corsi, 2002; Sharma and Chandrashekar, 2005; Golombek and Rosenstein, 2010). Depending upon how individuals respond to light cues, members of a species will be diurnal, nocturnal, crepuscular, or arrhythmic with regard to circadian patterns of activity (Doyle and Menaker, 2007). The diversity of patterns of activity evident among mammals suggests they are adaptive and may be influenced by the ecological conditions under which a species lives (Halle, 2000).

Because subterranean rodents spend virtually their entire lives in underground burrows (Nevo, 1979; Lacey et al., 2000), it has been suggested that these animals are less subject to entrainment by light cues and thus should display less pronounced circadian patterns of activity than surface-dwelling rodents (Ben-Shlomo et al., 1995; Buffenstein, 2000). Subterranean rodents are challenging to study in the field, with the result that analyses of activity patterns in some species have been conducted primarily under laboratory conditions (e.g., Begall et al., 2002; Oosthuizen et al., 2003; Hart et al., 2004). Those studies that have examined natural populations of subterranean rodents have revealed a variety of diel patterns of activity, including species that are primarily diurnal (e.g., *Thomomys bottae*: Gettinger, 1984; *Spalacopus cyanus*: Urrejola et al., 2005; *Ctenomys talarum*: Cutrera et al., 2006; *Fukomys anselli*: Šklíba et al., 2014), species that are primarily nocturnal (e.g., *Georychus capensis*: Lovegrove and Papenfus, 1995; *Fukomys mechowii*: Lövy et al., 2013), and species in which activity occurs in bouts throughout the 24-hour cycle (e.g., *Cryptomys hottentotus*: Hickman, 1980;

Fukomys damarensis: Lovegrove, 1988). In addition, pronounced individual variation in circadian activity has been reported within some species (Kushnirov et al., 2000), thus adding a level of complexity to efforts to identify the adaptive bases for differences in circadian behavior. Collectively, these findings suggest that there is no consistent effect of a subterranean lifestyle on activity patterns (Buffenstein, 2000).

Tuco-tucos (genus *Ctenomys*) are subterranean rodents that occur throughout much of sub-Amazonian South America, where they occupy habitats ranging from arid coastal sand dunes to mesic montane meadows. Although the behavioral biology of most tuco-tucos remains poorly known, the genus includes both solitary and social species (Lacey, 2000). With regard to daily rhythms, the few studies that have monitored the activity of free-living ctenomyids, indicate that the solitary *C. talarum* tends to be most active during daylight hours (Cutrera et al., 2006) and that the group-living *C. sociabilis* is strictly diurnal (Lacey et al., 1997). Similarly, observational studies of *C. knightii* housed under semi-natural conditions have revealed that members of this solitary species are active at the soil surface (e.g., foraging, burrow excavation) during daylight hours (Tomotani et al., 2012). Although all three of these species are active during the daytime, interspecific variation is evident in their daily patterns of activity, raising intriguing questions regarding the role of factors such as social structure and ecology in shaping circadian rhythms in these animals.

The Rio Negro tuco-tuco (*C. rionegrensis*) is endemic to western Uruguay, where it occurs at high densities (40 adults/ha) in sandy dune habitats (Tassinio, 2006). This species is unusual among ctenomyids in that it exhibits an apparently intermediate form of social structure characterized by occasional spatial overlap among adults resident in different burrow systems (Tassinio et al., 2011). The aim of this study was to characterize daily patterns of activity in a natural population of this species. In particular, we sought to compare patterns of activity in *C. rionegrensis* to those reported for other species of tuco-tucos.

MATERIALS AND METHODS

Study population

The population of *C. rionegrensis* studied was located at El Rincón, Departamento de Río Negro, Uruguay (33° 20' 43 S, 58° 17' 45 W). The study site consisted of old sand dunes located between the Río Negro and the Río Uruguay. The climate at this site was temperate and rainfall was evenly distributed throughout the year, with an average annual precipitation of 1130 mm and a mean monthly temperature of 21.8 °C. Vegetation at the site consisted of a mixture of patchily distributed annual grasses and woody shrubs. The estimated density of tuco-tucos in the 60 x 60 m study area was 64 individuals per hectare (Tassino, 2006).

Members of the study population were captured using Oneida-Victor live-traps. Burrow entrances containing fresh (moist) soil plugs were opened and a trap was placed inside the adjoining tunnel. Traps were checked every 2 hours; captured animals were removed as soon as they were detected. Although traps were set at all burrow entrances characterized by fresh soil plugs or mounds, we did not systematically attempt to capture all animals in the study population (e.g., individuals were not held in captivity to determine if additional animals were resident in the same burrow system; Lacey et al., 1997). As a result, it is possible that not all adults resident within the focal study area were included in our analyses.

The locality at which each animal was captured was recorded to the nearest meter using a reference grid established on the study site (see below). The weight and sex of each individual captured were recorded. The age (juvenile or adult) of each individual was determined on the basis of body weight (Tassino and Passos, 2010). For adult females, reproductive status (e.g., pregnant, lactating) was assessed via visual inspection of the external genitalia, palpation of the abdomen, and vaginal lavage (Tassino and Passos, 2010). Due to the limited number of radiocollars, only a subset of the adults captured were fitted with them (see below). Upon completion of these procedures, each individual was released into the burrow in which it was captured. All procedures were approved by institutional and national agencies (Exp 240011-002308-14, Comisión Honoraria de Experimentación Animal, Universidad de la República, Uruguay) and conformed to the guidelines for research established by the American Society of Mammalogists (Sikes et al., 2011).

Radiotelemetry studies

Ten animals were fitted with radiocollars (G3-1V transmitters; AVM Instruments, Colfax, California) on September 2005 as part of a study of spatial relationships among members of the study population (Tassino et al., 2011). Each radiocollar weighed approximately 5 g, which represented ~ 3% of the body weight of an adult *C. rionegrensis*. Due to transmitter failures and apparent predation, only 4 females (weight 146.5 ± 13.4 g) and 1 male (weight 210 g) were available for this study; these individuals were radiotracked for 72 consecutive hours from 9 November (19:00 h) until 12 November (19:00 h). During this period (the late austral spring), sunrise occurred at 06:30 and sunset occurred at 20:30.

Throughout the sampling period, the location of each radiocollared individual was recorded hourly. Locations were determined using a handheld 3-element Yagi directional antenna and an LA12-Q receiver (AVM Instruments, Livermore, California). To minimize potential disturbance of the study animals, we approached each burrow system occupied by a radiocollared animal slowly and carefully. To facilitate data collection, the study site was gridded into 4 x 4 m squares. Using this grid, we recorded the location of each radio fix to the nearest meter. Fixes of radiotransmitters placed at known locations revealed this procedure to be accurate to within 0.5 m (Lacey et al., 1997; Urrejola et al., 2005). Radio fixes were converted to Cartesian coordinates for analysis. In addition, we recorded the occurrence of all tuco-tuco vocalizations heard during each hourly scan. After all data had been collected, the study animals were recaptured and their radiocollars were removed.

Measuring animal activity

Five behavioural measures were used to characterize patterns of activity in the study population. Four of these measures were employed by Urrejola et al. (2005) to document activity in cururos (*Spalacopus cyanus*). Based upon observations of our study animals, we added an additional measure that recorded whether an individual moved between radio fixes. Thus, the following measures used to characterize activity in our study population:

(1) *Percentage of fixes outside of nest*. Telemetry data revealed a single most-frequently used locality per individual that was identified as that animal's putative nest site. Animals were located at putative nest sites in 42.1 ± 17.9 % of radiofixes (range 23.2–62.5%). Given the accuracy of our telemetry data, all fixes located within a 0.7 m radius of this

locality were considered to be in the putative nest. Once the location of each putative nest had been determined, the percentage of fixes occurring outside of the nest was calculated for each individual.

(2) *Distance to putative nest.* For each radio fix, the distance to that individual's putative nest was calculated. To account for potential differences in burrow system size, we divided each distance by the maximum distance from the nest recorded for that animal.

(3) *Change in location between successive scans.* For each radio fix, we determined whether an individual had changed locations since the previous fix. For each individual, we then determined the percentage of interfix intervals during which that animal had moved.

(4) *Distance between successive scans.* For each location identified via telemetry, we calculated the distance that the individual had moved since the previous fix. These values were standardized by dividing each distance by the maximum distance that the individual moved between successive fixes.

(5) *Vocalizations.* For each fix, we recorded whether spontaneous vocalizations in the study population were detected. Because the identity of the animal(s) calling was difficult to determine, we quantified only the occurrence of vocalizations and not the number of individuals or number of distinct calls detected.

Statistical analyses

Because daylight is thought to be an important entrainment cue for circadian patterns of activity (Ben-Shlomo and Kyriacou, 2002) and because previous studies of subterranean rodents have contrasted diurnal and nocturnal patterns of activity (e.g., Urrejola et al., 2005; Cutrera et al., 2006), we partitioned our data into those radiofixes collected during the night (21:00 to 06:00) versus those collected during the day (07:00 to 20:00). Accordingly, the 72-hr data collection period was divided into 3 night-day cycles. For each sampling period, we then calculated either the sum (categorical variables) or the mean (continuous variables) for each measure of activity for each animal monitored. Because the number of radiofixes per individual sometimes varied within a given day- or night-time sampling period, data for each individual were standardized by dividing by the total number of fixes (or interfix intervals) for that animal during the sampling period in question.

Because the same individuals were monitored throughout the study, locations recorded during different day- and night-time sampling periods were not independent of one another. Thus, measures of

day- and night-time activity were compared using Friedman's ANOVAs, with individuals as blocks and day and night as treatments (Urrejola et al., 2005). Post-hoc analyses were completed using Wilcoxon Signed-Rank tests, with a Bonferroni correction applied when multiple post-hoc tests were conducted. Frequencies of day- and night-time vocalizations were compared using Fisher's exact test. Throughout the text, means are reported ± 1 SD. Statistical analyses were performed using Statistica 6.0 (StatSoft 2008).

RESULTS

The mean distance between adjacent capture locations was 8.9 ± 5.3 m ($N=5$; range: 4.1–17.0 m) and the mean distance between adjacent putative nests was 11.9 ± 4.2 m ($N=5$; range 8.3–16.6 m). Although all data were collected over the same 72-hr period, the number of fixes per individual varied due to difficulties detecting the signals for two animals during some radiofixes. As a result, the mean total number of fixes per individual was 68.4 ± 4.3 (range 61–71). When fixes were partitioned into daytime versus nighttime sampling periods, the means per individual were 39.2 ± 3.0 and 29.2 ± 1.3 , respectively. The mean total number of interfix intervals per animal was 65.6 ± 7.0 (range 54–70), with 36.6 ± 5.6 diurnal and 29.0 ± 1.4 nocturnal interfix intervals per individual (**Table 1**).

Graphic representation of the data shown that members of the study population were active in irregular bursts throughout each 24-hr cycle, with no clearly discernible daily pattern of activity (**Fig. 1**). Analyses of the 5 quantitative measures of activity considered revealed the following:

(1) *Percentage of fixes outside of nest.* When all data points were considered, a mean of 44.0 ± 9.5 % of fixes per individual were located outside of the putative nest site. When these data were partitioned into day- versus night-time fixes, the mean percentages of fixes located outside of the nest were 59.1 ± 16.9 % and 57.7 ± 22.4 %, respectively (**Fig. 2a**). The percentage of fixes located outside of the nest did not differ significantly between day- and night-time sampling periods (Friedman's ANOVA $\chi^2=1.6$, d.f. 5, $p=0.91$).

Table 1

Summary of attributes of the adult *C. rionegrensis* monitored during this study. For each animal, sex, home-range size, maximum distance moved between fixes, and number radio fixes and interscan intervals monitored are provided. Data on home range size are from Tassinio et al. (2011).

Sex	Home-range (m ²)	Maximum distance moved between successive scans (m)	Maximum distance located away from nest (m)	Number of fixes						Number of 1 h interscans									
				Night-1		Day-1		Night-2		Day-2		Night-3		Day-3		Night-3		Day-3	
♀	34.9	12.0	11	10	14	14	10	14	10	10	14	10	14	10	14	10	14	10	12
♂	96.3	13.2	11	7	12	10	9	10	13	7	10	10	5	10	10	10	12	10	12
♀	132.0	19.6	20	10	14	10	14	10	13	10	14	10	14	10	14	10	14	10	12
♀	89.8	9.0	9.8	10	13	9	13	10	13	10	13	10	12	8	12	10	12	10	12
♀	106.6	14.6	14	10	14	10	14	10	13	10	14	10	14	10	14	10	14	10	12

(2) *Distance to nest.* Overall, the mean percentage of an individual's maximum distance to its nest was $19.5 \pm 11.2\%$, which corresponds to a linear distance of 2.5 ± 1.5 m. When these data were partitioned into day- versus night-time fixes, the mean percentages were $20.3 \pm 11.7\%$ and $18.4 \pm 11.0\%$, respectively (Fig. 2b). As with the percentage of fixes outside of the nest, the percentage of maximum distance from the nest did not differ significantly between day- and night-time sampling periods (Friedman's ANOVA $\chi^2 = 4.9$, d.f. 5, $p = 0.43$).

(3) *Changes in locations.* When all data points were considered, a mean of $89.4 \pm 6.4\%$ of interfix intervals per individual ($N = 54-70$ intervals) included a change in location (Fig. 3a). For daytime fixes, a mean of $93.8 \pm 3.8\%$ of intervals ($N = 40$ intervals) included a change in location versus $83.7 \pm 10.7\%$ of intervals ($N = 30$ intervals) between nighttime fixes (Fig. 3a). This difference was significant (Friedman's ANOVA $\chi^2 = 11.8$, d.f. 5, $p = 0.037$), although subsequent post-hoc tests failed to reveal significant contrasts between specific day- and night-time sampling periods (all n.s., Bonferroni corrected $\alpha = 0.0083$).

(4) *Distance between successive scans.* Overall, the mean distance moved between successive fixes was 2.9 ± 1.2 m ($N = 54-70$ intervals), which represents $21.9 \pm 8.0\%$ of the maximum distance moved between scans (Fig. 3b). When day- and night-time fixes were considered separately, the mean distances moved were $25.0 \pm 8.4\%$ ($N = 41$ intervals) and $18.1 \pm 8.0\%$ ($N = 30$ intervals), respectively, of the maximum distances moved (Fig. 3b). This difference was significant (Friedman's ANOVA $\chi^2 = 17.0$, d.f. 5, $p = 0.004$), although subsequent post-hoc tests revealed no significant contrasts between specific day- and night-time sampling periods.

(5) *Vocalizations.* Vocalizations were detected during 34 (47.9%) of hourly scans; 46.3% of daytime scans included vocalizations versus 50.0% of nighttime scans; this difference was not significant ($\chi^2 = 0.093$, d.f. 1, $p = 0.76$).

DISCUSSION

This study is the first to provide quantitative data regarding daily patterns of activity

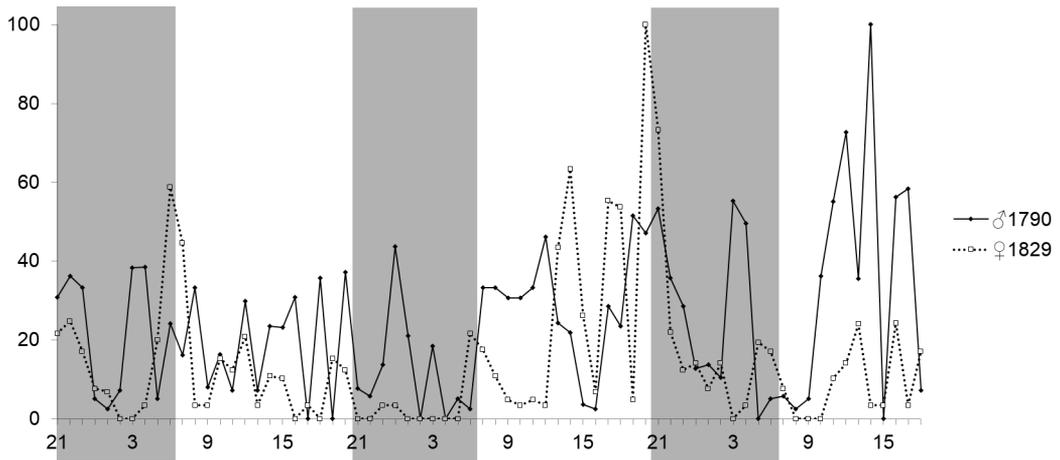


Fig. 1. Distance moved between successive radiofixes as a percentage of maximum distance moved between fixes during the 72 hour study period. Data are from a subset of two individuals, one male and one female. Gray bar indicates night periods.

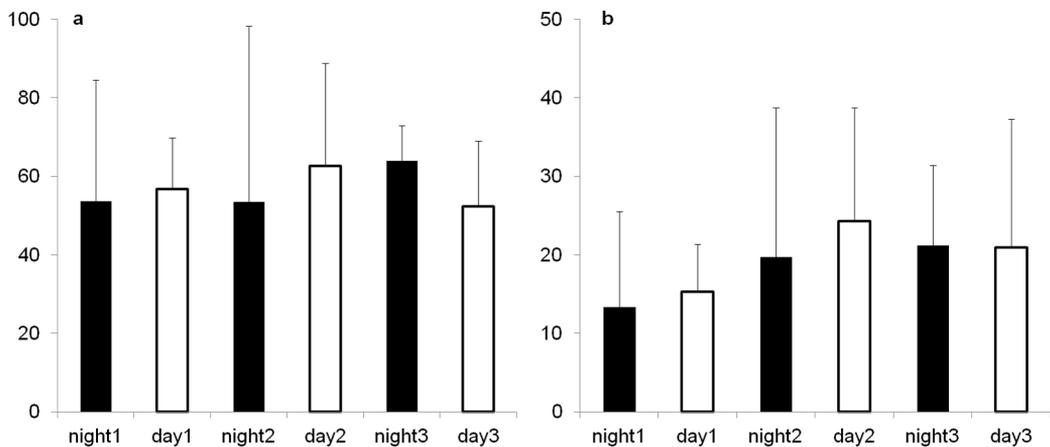


Fig. 2. Measurements of activity relative to the putative nest. (a) mean (± 1 SD) percentage of fixes in which individuals ($N=5$) were located outside of their putative nest. (b) mean (± 1 SD) percentage of maximum distance from the nest. In both panels, daytime (white bars) and nighttime (black bars) sampling periods are denoted. No significant differences were found between daytime and nighttime values for either of these measures of activity (both $p > 0.05$).

in *C. rionengrensis*. Our results indicate that members of the study population were active throughout the 24-hr cycle. However, two of the measures employed—frequency of changes in location between fixes and distance between fixes—suggested that the animals were more active during the daytime. Interestingly, measures of activity based on the location of an individual's nest did not differ between day-

and night-time fixes, suggesting that although movement was greater during daylight hours, proximity to the nest did not vary across the 24-hr cycle.

Our finding that members of the study population tended to move more during the daytime is generally consistent with data from other species of ctenomyids for which patterns of activity have been documented in free-living

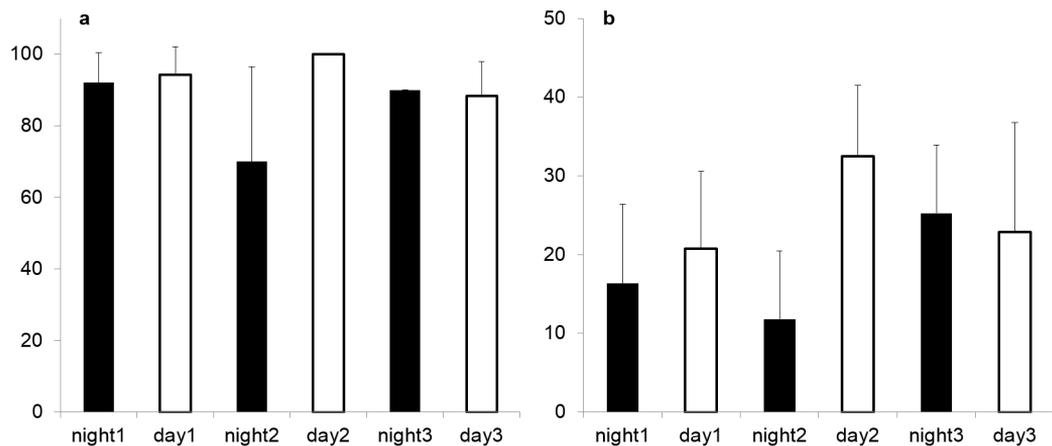


Fig. 3. Measurements of movements between radio fixes. (a) mean (± 1 SD) percentage of interfix intervals during which an individual changed locations. (b) mean (± 1 SD) percentage of the maximum distance moved by an individual between fixes. In both panels, daytime (white bars) and nighttime (black bars) sampling periods are denoted. For both measures, activity was significantly greater ($p < 0.05$) during daytime sampling periods.

individuals. In *C. talarum*, the rate of movement between successive radiofixes was significantly greater during the daytime (Cutrera et al., 2006). In *C. sociabilis*, comparisons of the locations of daytime and nighttime radiofixes revealed a striking tendency for individuals to be outside of the nest only during daylight hours (Lacey et al., 1997). Finally, direct observations of members of a semi-natural population of *C. knighti* (Tomotani et al., 2012) revealed that individuals were regularly active at the soil surface during daylight; although comparable nighttime data were not obtained, this result indicates that, minimally, members of the study population were active during the day. Thus, among the ctenomyid species studied to date, there appears to be a consistent tendency for individuals to be more active during the day, with at least some measures of activity indicating that *C. rionegrensis*, *C. talarum*, and *C. sociabilis* are more active during daylight hours.

Greater activity during daylight hours has also been reported for several other taxa of subterranean rodents (*Tachyoryctes splendens*: Jarvis, 1973; *T. bottae*: Gettinger, 1984; *N. ehrenbergi*: Rado et al., 1993; *S. cyanus*: Urrejola et al., 2005; *Heliophobius argenteocinereus*: Šklíba et al., 2007; *F. anelli*: Šklíba et al., 2014). In contrast, at least one species of African mole-rat is more active at night (*F. mechowii*: Lövy et

al., 2013), while other species of subterranean rodents show no difference between diurnal and nocturnal activity (*T. talpoides*: Andersen and MacMahon, 1981; *Geomys attwateri*: Cameron et al., 1988; *F. damarensis*: Lovegrove, 1988; *Geomys bursarius*: Benedix Jr., 1994). Consequently, across the wider range of rodent taxa recognized as subterranean (Nevo, 1979; Lacey et al., 2000), there is considerable variability in patterns of circadian activity.

Because the studies of circadian activity in subterranean rodents reviewed here were conducted in field settings, interspecific variation in activity patterns cannot be attributed to contrasts between natural and laboratory conditions (eg., Begall et al., 2002; Urrejola et al., 2005) nor to associated differences in the sensitivity of the measures used to document activity in these distinct settings (eg., Zenuto et al., 2002). Instead, the interspecific variation in activity patterns revealed by these studies suggests that the selective pressures shaping circadian rhythms vary among subterranean taxa. In particular, the differences evident among African mole-rats (family Bathyergidae) suggest that this variation is adaptive, rather than solely a result of the distinct evolutionary histories of the different subterranean lineages. The selective pressures favouring diurnality (or other patterns of circadian

activity) remain poorly understood (Smale et al., 2003) but may include foraging ecology, predation pressure, physiology, and burrowing requirements. Although social structure has also been suggested as a potential correlate of differences in circadian activity (eg., Bennett, 2009), the available data reveal no conspicuous relationship between social structure and diel rhythms, with both social (e.g., *C. sociabilis*, *F. damarensis*, *F. mechowii*) and solitary (e.g., *C. talarum*, *G. attwateri*, *N. ehrenbergi*) species displaying the full range of circadian patterns identified among subterranean rodents: diurnal, nocturnal, and arrhythmic.

Despite a general tendency to be more mobile during daylight hours, members of our study population displayed considerable variation in individual patterns of daily activity. Intraspecific variability in circadian activity has been reported in for other subterranean rodents, in which activity by different individuals occurs in asynchronous bursts throughout the 24-hr cycle (*T. talpoides*: Andersen and MacMahon, 1981; *G. attwateri*: Cameron et al., 1988; *S. ehrenbergi*: Kushnirov et al., 2000; *F. mechowii*: Lövy et al., 2013). More generally, there is considerable individual variability in activity even among members of those species characterized by significant overall patterns of diurnal or nocturnal circadian activity (*C. talarum*: Cutrera et al., 2006; *H. argenteocinereus*: Šklíba et al., 2007). This variation is particularly conspicuous in laboratory studies that allow longer and more accurate measurements of individual activity and that may be free of important external constraints on activity such as diurnal patterns of predation (e.g., Oosthuizen et al., 2003; De Vries et al., 2008).

Potential correlates of variation in circadian activity require additional study. Such patterns may vary temporally (e.g., *N. ehrenbergi*: Kushnirov et al., 2000), perhaps reflecting seasonal differences in resource availability, reproductive status, or opportunities for burrow expansion (Zenuto et al., 2001). Previous studies of *C. rionegrensis* (Tassino et al., 2011) suggest that patterns of space use vary seasonally in this species, raising the possibility that activity patterns also vary over time. Future

studies will document activity by members of the study population during multiple portions of the year to explore this potential source of variation in activity rhythms. Within seasons, individual variation in activity patterns may reflect differences in sex, physical condition, or burrow quality. By monitoring larger numbers of animals per sampling period, future studies of *C. rionegrensis* will explore these potential correlates of intraspecific variation in activity patterns. Combined with data regarding the phenotypic attributes of and the environmental conditions experienced by individuals, these analyses will provide a much more comprehensive understanding of the nature and potential correlates of daily patterns of activity in this species of subterranean rodent.

ACKNOWLEDGEMENTS

We wish to thank E. Lessa for encouraging this project and for facilitating the field work required to complete the study. For assistance in the field, we thank C. Olivera, P. Altesor, R. Pereira-Garbero, V. Pereyra, A. Ligrone, M. Bozzolasco and F. Rivas. Permits to work at El Rincón were provided by S. Pereira Testa. Financial support for the project was received from Comisión Sectorial de Investigación Científica, Universidad de la República, Uruguay. Programa de Desarrollo de las Ciencias Básicas, Uruguay provided a Ph.D. research fellowship to BT.

LITERATURE CITED

- ANDERSEN DC and JA MACMAHON. 1981. Population dynamics and bioenergetics of a fossorial herbivore, *Thomomys talpoides* (Rodentia: Geomyidae), in a spruce-fir sere. *Ecological Monographs* 51:179-202.
- BEGALL S, S DAAN, H BURDA, and GJF OVERKAMP. 2002. Activity patterns in a subterranean social rodent, *Spalacopus cyanus* (Octodontidae). *Journal of Mammalogy* 83:153-158.
- BENEDIX JR. JH. 1994. A predictable pattern of daily activity by the pocket gopher *Geomys bursarius*. *Animal Behaviour* 48:501-509.
- BENNETT NC. 2009. African mole-rats (family Bathyergidae): Models for studies in animal physiology. *African Zoology* 44:263-270.
- BEN-SHLOMO R and CP KYRIACOU. 2002. Circadian rhythm entrainment in flies and mammals. *Cell biochemistry and biophysics* 37:141-156.
- BEN-SHLOMO R, U RITTE, and E NEVO. 1995. Activity pattern and rhythm in the subterranean mole rat superspecies *Spalax ehrenbergi*. *Behavior Genetics* 25:239-245.
- BUFFENSTEIN R. 2000. Ecophysiological responses of subterranean rodents to underground habitats. Pp. 62-

- 110, in: Life underground: The biology of subterranean rodents (EA Lacey, JL Patton and GN Cameron, eds.). University Of Chicago Press, Chicago.
- CAMERON GN, SR SPENCER, BD ESHELMAN, LR WILLIAMS and MJ GREGORY. 1988. Activity and burrow structure of attwater's pocket gopher (*Geomys attwateri*). Journal of Mammalogy 69:667-677.
- CERMAKIAN N and P SASSONE-CORSI. 2002. Environmental stimulus perception and control of circadian clocks. Current Opinion in Neurobiology 12:359-365.
- CUTRERA AP, CD ANTINUCHI, MS MORA, and AI VASSALLO. 2006. Home-range and activity patterns of the South American subterranean rodent *Ctenomys talarum*. Journal of Mammalogy 87:1183-1191.
- DOYLE S and M MENAKER. 2007. Circadian photoreception in vertebrates. Cold Spring Harbor Symposia on Quantitative Biology 72:499-508.
- GETTINGER RD. 1984. A field study of activity patterns of *Thomomys bottae*. Journal of Mammalogy 65:76-84.
- GOLOMBEK DA and RE ROSENSTEIN. 2010. Physiology of Circadian Entrainment. Physiological Reviews 90:1063-1102.
- HALLE S. 2000. Ecological relevance of daily activity patterns. Pp. 67-90, in: Activity Patterns in small mammals: An ecological approach (S Halle and NC Stenseth, eds.). Springer, Berlin; New York.
- HART L, N BENNETT, B MALPAUX, C CHIMIMBA, and M OOSTHUIZEN. 2004. The chronobiology of the Natal mole-rat, *Cryptomys hottentotus natalensis*. Physiology and Behavior 82:563-569.
- HICKMAN GC. 1980. Locomotory activity of captive *Cryptomys hottentotus* (Mammalia: Bathyergidae), a fossorial rodent. Journal of Zoology 192:225-235.
- HORTON TH. 2001. Conceptual issues in the ecology and evolution of circadian rhythms. Pp. 45-57, in: Circadian Clocks (JS Takahashi, FW Turek, and RY Moore, eds.). Springer, New York, NY.
- JARVIS JUM. 1973. The structure of a population of mole-rats, *Tachyoryctes splendens*, (Rodentia: Rhizomyidae). Journal of Zoology 171:1-14.
- KUSHNIROV D, F BEOLCHINI, F LOMBARDINI, and E NEVO. 2000. Elucidating activity patterns of mole rats via radiotelemetry. Israel Journal of Zoology 46:377.
- LACEY EA. 2000. Spatial and social systems of subterranean rodents. Pp. 255-296, in: Life underground: The biology of subterranean rodents (EA Lacey, JL Patton, and GN Cameron, eds.). University Of Chicago Press, Chicago.
- LACEY EA, SH BRAUDE, and JR WIECZOREK. 1997. Burrow Sharing by Colonial Tuco-Tucos (*Ctenomys sociabilis*). Journal of Mammalogy 78:556-562.
- LACEY EA, JL PATTON, and GN CAMERON (eds.). 2000. Life underground: The biology of subterranean rodents. University of Chicago Press, Chicago.
- LOVEGROVE BG. 1988. Colony size and structure, activity patterns and foraging behaviour of a colony of the social mole-rat *Cryptomys damarensis* (Bathyergidae). Journal of Zoology 216:391-402.
- LOVEGROVE BG and ME PAPENFUS. 1995. Circadian activity rhythms in the solitary Cape mole-rat (*Georychus capensis*: Bathyergidae) with some evidence of splitting. Physiology and Behavior 58:679-685.
- LÖVY M, J ŠKLÍBA, and R ŠUMBERA. 2013. Spatial and temporal activity patterns of the free-living giant mole-rat (*Fukomys mechowii*), the largest social bathyergid. PLoS ONE 8:e55357.
- NEVO E. 1979. Adaptive convergence and divergence of subterranean mammals. Annual Review of Ecology and Systematics 10:269-308.
- OOSTHUIZEN MK, HM COOPER, and NC BENNETT. 2003. Circadian rhythms of locomotor activity in solitary and social species of african mole-rats (family: Bathyergidae). Journal of Biological Rhythms 18:481-490.
- PARANJPE DA and VK SHARMA. 2005. Evolution of temporal order in living organisms. Journal of Circadian Rhythms 3:7.
- RADO R, U SHANAS, I ZURI, and J TERKEL. 1993. Seasonal activity in the blind mole rat (*Spalax ehrenbergi*). Canadian Journal of Zoology 71:1733-1737.
- SHARMA VK. 2003. Adaptive significance of circadian clocks. Chronobiology international 20:901-919.
- SHARMA VK and MK CHANDRASHEKARAN. 2005. Zeitgebers (time cues) for biological clocks. Current Science 89:1136-1146.
- SIKES RS, WL GANNON, and THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235-253.
- ŠKLÍBA J, M LÖVY, E HROUZKOVÁ, O KOTT, J OKROUHLÍK, and R ŠUMBERA. 2014. Social and environmental influences on daily activity pattern in free-living subterranean rodents: the case of a eusocial bathyergid. Journal of Biological Rhythms 29:203-214.
- ŠKLÍBA J, R ŠUMBERA, WN CHITAUKALI, and H BURDA. 2007. Determinants of daily activity patterns in a free-living afro-tropical solitary subterranean rodent. Journal of Mammalogy 88:1009-1016.
- SMALE L, T LEE, and AA NUNEZ. 2003. Mammalian diurnality: Some facts and gaps. Journal of Biological Rhythms 18:356-366.
- TASSINO B. 2006. Estructura poblacional y biología reproductiva del tucu-tucu de Río Negro (*Ctenomys rionegrensis*): relaciones entre el comportamiento y los procesos evolutivos. Unpublished Doctoral Thesis, Universidad de la República, Montevideo, Uruguay.
- TASSINO B, I ESTEVAN, RP GARBERO, P ALTESOR, and EA LACEY. 2011. Space use by Río Negro tuco-tucos (*Ctenomys rionegrensis*): Excursions and spatial overlap. Mammalian Biology - Zeitschrift für Säugetierkunde 76:143-147.
- TASSINO B and CA PASSOS. 2010. Reproductive biology of Río Negro tuco-tuco, *Ctenomys rionegrensis* (Rodentia: Octodontidae). Mammalian Biology - Zeitschrift für Säugetierkunde 75:253-260.
- TOMOTANI BM, DEFL FLORES, P TACHINARDI, JD PALIZA, GA ODA, and VS VALENTINUZZI. 2012. Field and laboratory studies provide insights into the meaning of day-time activity in a subterranean

- rodent (*Ctenomys* aff. *knighti*), the tuco-tuco. PLoS ONE 7:e37918.
- URREJOLA D, EA LACEY, JR WIECZOREK, and LA EBENSBERGER. 2005. Daily activity patterns of free-living cururos (*Spalacopus cyanus*). Journal of Mammalogy 86:302-308.
- DE VRIES JL, MK OOSTHUIZEN, AM SICHILIMA, and NC BENNETT. 2008. Circadian rhythms of locomotor activity in Ansell's mole-rat: Are mole-rat's clocks ticking? Journal of Zoology 276:343-349.
- ZENUTO RR, AI VASSALLO, and C BUSCH. 2001. A method for studying social and reproductive behaviour of subterranean rodents in captivity. Acta Theriologica 46:161-170.
- ZENUTO RR, AI VASSALLO and C BUSCH. 2002. Comportamiento social y reproductivo del roedor subterráneo solitario *Ctenomys talarum* (Rodentia: Ctenomyidae) en condiciones de semicautiverio. Revista Chilena de Historia Natural 75:165-177.