

HOSTED BY



ELSEVIER

Contents lists available at ScienceDirect

Sleep Science

journal homepage: www.elsevier.com/locate/ssci

Case report

Social modulation of the daily activity rhythm in a solitary subterranean rodent, the tuco-tuco (*Ctenomys* sp)^{☆, ☆}Barbara Mizumo Tomotani^{a,1}, Juan Pablo Amaya^b, Gisele Akemi Oda^a,
Veronica Sandra Valentinuzzi^{b,*}^a Departamento de Fisiologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, São Paulo, Brazil^b Centro Regional de Investigaciones Científicas y Transferencia Tecnológica de La Rioja, CRILAR-CONICET, Entre Rios y Mendoza s/n, 5301 Anillaco, La Rioja, Argentina

ARTICLE INFO

Keywords:

Ctenomyidae
Tuco-tuco
Social synchronization
Around-the-clock activity
Circadian rhythm

ABSTRACT

South American subterranean rodents are mainly described as solitary and mutual synchronization was never observed among individuals maintained together in laboratory. We report that a single birth event was capable of disrupting the robust nocturnal activity rhythm of singly housed tuco-tucos from north-west Argentina. “Around-the-clock activity” was displayed by 8 out of 13 animals whose cages were closer to the newborn pups. However, experimental exposure to a pup vocalization did not produce a similar effect on the rhythms of adult animals. Our results indicate an effect of social interaction in the expression of biological rhythms even in solitary animals.

1. Introduction

Social modulation of circadian rhythms [1–3] has been reported in several species, such as birds [4–6], rodents [7–12], bats [13], primates [14–16] and invertebrates [17–20]. For a review, see [2,21]. Although several examples involve social animals, social modulation of activity rhythms could be particularly relevant in solitary species, such as hamsters [11,12], since encounters for reproduction and/or the need of intraspecific avoidance during non-breeding seasons require timing and synchronization among individuals. This synchronization could be mediated by non-photocic social cues, such as pheromones, sound and sight of conspecifics.

Tuco-tucos (genus *Ctenomys*) are herbivorous subterranean rodents endemic to South America. The genus is very speciose, with circa 60 described species, and can be found in a great variety of habitats [22]. Despite evidence of sociality in some species (*C. sociabilis* [23]), most tuco-tucos are deemed strictly solitary [24]. Among non-social species, reports of more than one animal found together are rare and restricted to mating couples or females with young [25,26]. In this

context, we report that a single birth event unexpectedly disrupted the robust nocturnal wheel-running activity rhythm of a group of 13 singly housed tuco-tucos (*Ctenomys* sp) captured in La Rioja province in Argentina. This peculiar response of the other captive animals, which lasted one entire day on average for females and longer for males, revealed that circadian rhythms can be modulated by social cues, in this solitary subterranean rodent. An experiment was performed to test if this social modulation was intermediated by acoustic cues using playbacks of a pup vocalization.

2. Study species and ethical aspects

The animals used in this study were captured in the province of La Rioja, Argentina, in the locality of Anillaco (28° 48' S; 66° 56' W; 1445 m). The population of *Ctenomys* found in the area is called the Anillaco tuco-tuco however, species determination has not been completed yet. Morphological, molecular and genetic analysis for this purpose are ongoing.

During the time of this case report, tuco tucos were caught year-

Peer review under responsibility of Brazilian Association of Sleep.

[☆] **Grant Sponsors:** This work was supported by the Argentinean Agencies: Agencia Nacional de Promoción Científica y Tecnológica-FONCyT (Grants PICT 2011-1979 and PICT 2013-2753) and Consejo Nacional de Investigaciones Científicas y Técnicas-CONICET (Grants PIP-11420090100252 and PIP-11220120100415). Also by the Brazilian Agencies: Fundação de Amparo à Pesquisa do Estado de São Paulo-FAPESP, Grant # 2008/55035-5, 10/50222-1 and Conselho Nacional de Desenvolvimento Científico e Tecnológico-CNPq, 130021/2009-1 to BMT.

* Corresponding author.

E-mail addresses: babi.mt@gmail.com (B.M. Tomotani), jamaya@crilar-conicet.gov.ar (J.P. Amaya), gaoda@ib.usp.br (G.A. Oda), valentinuzzi@crilar-conicet.gov.ar (V.S. Valentinuzzi).

¹ Current address: Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), P.O. Box 50, 6700 AB Wageningen, The Netherlands

<http://dx.doi.org/10.1016/j.slsci.2016.06.001>

Received 28 January 2016; Received in revised form 12 May 2016; Accepted 20 June 2016

Available online 01 October 2016

1984-0063/ © 2016 Brazilian Association of Sleep. Production and hosting by Elsevier B.V.

This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

round for various experiments using PVC tube traps placed at fresh surface mounds inside natural burrows. Capture techniques and laboratory experimentation protocols were approved and authorized by the Legal Technical Board (Oficina de Técnica Legal) of the Environmental Department of La Rioja (Secretaría de Ambiente, Ministerio de Producción y Desarrollo Local), Argentina (permission no 062-08). Every procedure followed the guidelines of the American Society of Mammalogists for animal care and handling [27].

3. Case report: effect of a birth event on activity rhythms

In the animal facility (410×300 cm), 13 adult animals (10 females and 3 males) were kept individually in acrylic cages (53×27 cm and 29 cm high) equipped with wire mesh lids and stainless steel running wheels. Cages were distanced from each other by 9 cm and animals were kept in 12 h light:12 h dark cycles (LD12:12) and 23 ± 2 °C. Food (fresh vegetables, seeds and rabbit pellets) was offered daily at random times. Because tuco-tucos obtain water from food, water was not provided. Wheel-running activity data was continuously recorded with

the ArChron Data Acquisition System (Simonetta System, Universidad Nacional de Quilmes, Buenos Aires) at 5-minute intervals. Graphical output (actograms) and rhythm analysis were carried out using the *El Temps* software (A. Díez-Noguera, Universitat de Barcelona, 1999).

Under light/dark cycles, all tuco-tucos displayed very robust 24 h rhythms, with wheel-running activity concentrated in the dark phase (Fig. 1A). An unusual event of rhythm disruption was registered in several individuals: On October 22th 2008, one of the females (captured in July of the same year) gave birth to two pups in the animal facility. The female abandoned the pups, which wandered around the cage for two days until perishing. This event caused an unusual response in several other animals present in the room: out of 13 animals, seven females ran during the whole day and night (animals # 9, 19, 21, 23, 27, 29 and 24, the female with pups), displaying “around-the-clock” activity for one entire day. One male (# 10) also displayed this continuous 24 h activity but then totally interrupted activity for three continuous days. Two other males displayed long-term arrhythmicity that lasted for at least 14 days (# 20 and 26) and rhythmicity was then restored without an observable phase shift (data

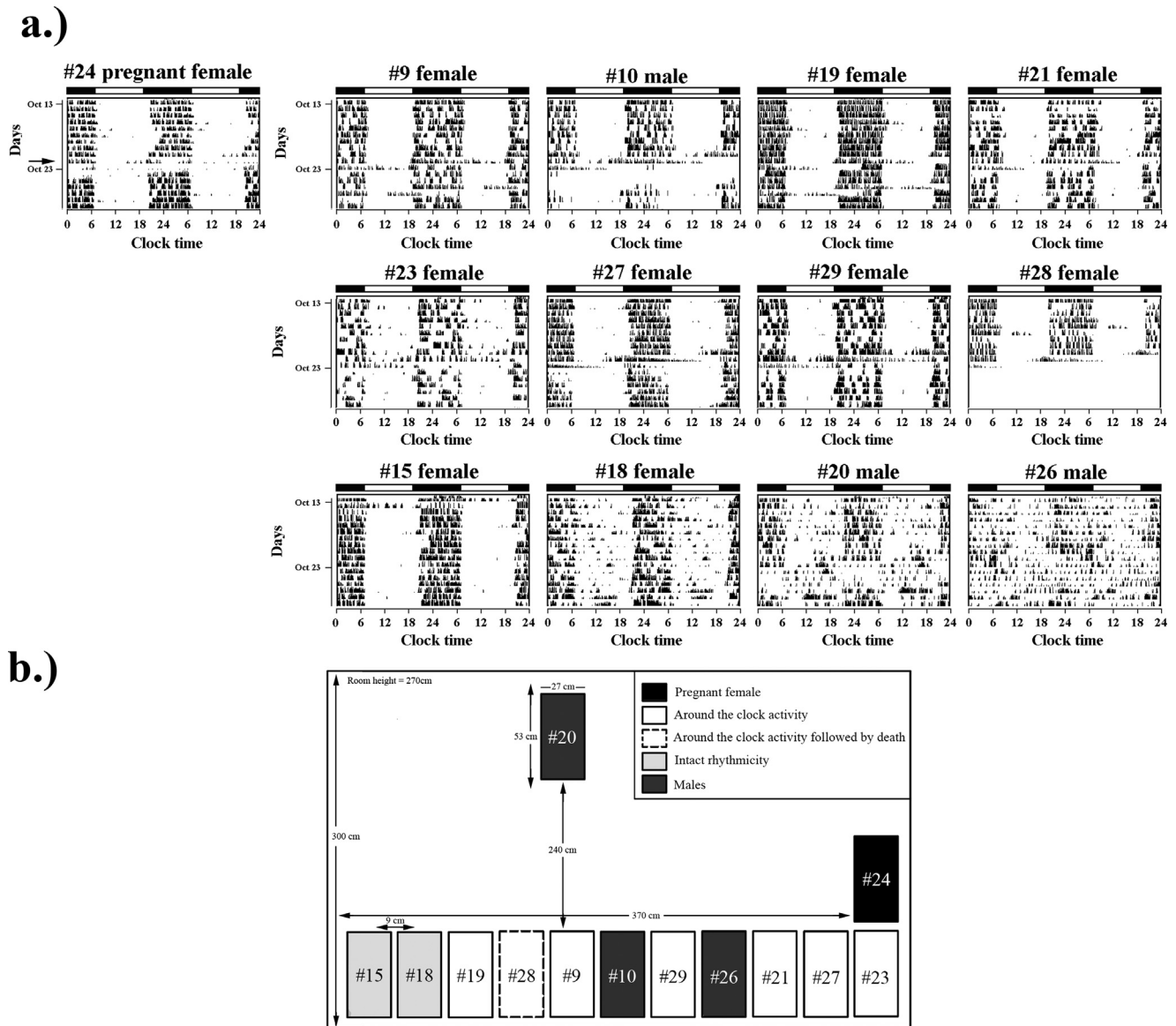


Fig. 1. Daily activity rhythms and spatial distribution of 13 individuals. A) Wheel-running activity rhythms depicted in double-plotted actograms. Each line represents two consecutive days and black marks denote activity. Black and white bars denote times of darkness and light, respectively, of an LD 12:12 cycle. On October 22, animal # 24 gave birth to two pups (shown with an arrow). B. Distribution of the animals within the animal facility. Animals # 15 and # 18 were farther away from the mom/pups and did not show any change in their rhythmic pattern.

not presented). One female died after running all day and night (# 28). Only two females maintained intact nocturnal rhythmicity (# 15 and 18 Fig. 1A) and these were notably those whose cages were farthest (340–300 cm away) from the pups (see Fig. 1B).

4. Experiment: effect of acoustic cues on activity rhythms

4.1. Playback tests

To test if acoustic stimuli emitted by the pups can cause the observed rhythmic disruption, another new set of 10 adult animals (5 females and 5 males) were exposed to playbacks of vocalizations from a new pup. The recorded vocalization consisted of calls emitted by a pup captured with the approximate age of 15 days. This estimation was based on its weight (29 g), size of incisive and time during which care-eliciting calls were recorded. Upon capture the pup was placed in a lab terrarium (60 cm×100 cm and 50 cm high), filled with wood shavings and diverse plastic and cardboard tubes used as burrows and nest. The terrarium was set by and open window and ambient temperature remained at $24 \pm ^\circ\text{C}$. Ad lib feeding included sweet potatoes, carrots, sunflower seeds, oatmeal, rabbit pellets as well as items of its natural diet collected weekly from the field (*Larrea* sp, *Opuntia* sp, *Parkinsonia praecox*). Vocalizations were recorded using a Zoom H4n digital hand recorder system with built-in microphones (frequency range 30–22,050 Hz) placed on the top of the terrarium. Sounds were recorded at a sample rate of 44.1 kHz and at 16 bit depth and then transferred to a personal computer for posterior playback-section mounting. The care-elicitation vocalization recorded in this specimen is very similar to those recorded for *Ctenomys talarum* [28], however determination of the details of this similarity is an ongoing study (Amaya et al., unpublished [44]).

A three-min interval of these recordings in the terrarium was selected, based on its long duration, frequent and clear vocalizations, as well as free of background noise, to be used to assemble the 10-h playback section used in this experiment. Two different sequences were mounted for the playback sections. In the first (non-continuous calls) the selected three-min interval was repeated during 30 min followed by a 30-min interval of silence; this continued for the remaining 9 h. In the second sequence (continuous calls), 30 min interval of silence was eliminated and vocalizations were played throughout the 10-h pulse. Intensity was the same in both sequences. Two loudspeakers were placed in the animal facility orientated towards the 10 experimental animal cages in such a way that the distance between them and the cages was always within 1–2 m. Playback sections occurred in two times along the light-dark cycle, one along the light-phase, from 09:00 to 19:00 h, and the second along the dark-phase, from 21:00 to 09:00. However only the 5-h middle section was used for analysis to avoid potential effects due to the presence of the experimenters in the limits of the playback interval.

4.2. Statistical analysis

Activity levels during the 5 h interval with playback and during the corresponding time in the previous day were compared using paired *T*-test with significance when $P < 0.05$, in R 2.12.1 [29], as done in similar test protocols for acute effects on rhythmicity [30]. Activity levels during the 5 h intervals were quantified as the total number of 5-minute bins displaying a detected wheel-running revolution. The experiment was then repeated using the continuous calls and the same comparison was done in the expression of running-wheel revolutions. Additionally, in this second experiment, general activity levels were also registered using infrared sensors located in the middle-top of each cage, which are sensible to subtle movements.

In the first experiment, using non-continuous calls, we observed only a slight increase in nocturnal, and not in diurnal wheel-running levels (diurnal: $t(9)=1.32$, $p=0.22$; nocturnal: $t(9)=-3.70$, $p < 0.01$)

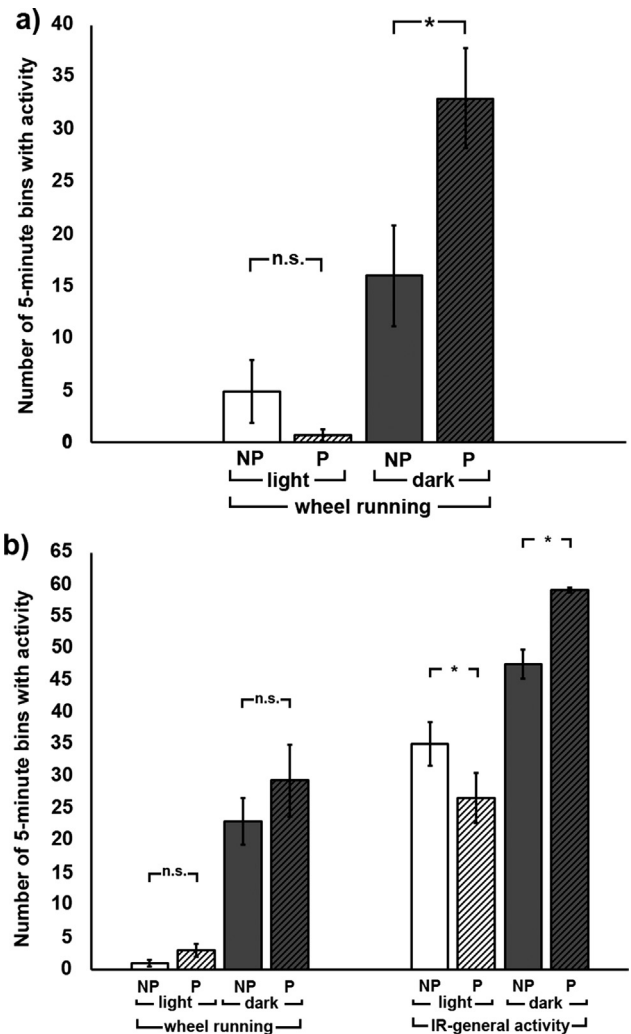


Fig. 2. Activity levels of captive tuco-tucos measured with running wheels and infrared detectors during the playback experiment 1 (a) and 2 (b) (mean number of activity bouts \pm SE). White bars represent activity levels during the light phase (11:00 to 16:00) at the day without the playback (No Playback: NP) (plain white) and the correspondent time at the day with the playback (Playback: P) (hatched white; P). Dark grey bars represent activity levels during the dark phase (23:00 to 04:00) at the night without the playback (No playback: NP) (plain grey) and the correspondent time at the night with the playback (Playback: P) (hatched grey). * $P < 0.05$ in the respective paired *T*-test analysis.

(Fig. 2A). We then increased only the frequency of calls in the second experiment. No significant changes were observed in wheel-running activity (diurnal: $t(9)=-2.07$, $p=0.06$; nocturnal: $t(9)=-1.26$, $p=0.23$), but a significant decrease in diurnal ($t(4)=6.16$, $p < 0.01$) and increase in nocturnal ($t(4)=-4.96$, $p < 0.01$) general activity was detected (Fig. 2B).

5. Discussion

5.1. Around-the-clock activity caused by a birth event

Because light/dark cycles are strong synchronizers of circadian rhythms, social modulation of rhythmic parameters have better been revealed in rodents under constant lighting conditions and after long-term cohabitation [8,11,12]. In this context, it's notable that several experiments had already been conducted with tuco-tucos under constant darkness conditions [31, see this work also for more details on laboratory conditions; 32–34], but never before had any mutual synchronization among individuals been detected. The animals cannot see each other and we also know that they do not react to the sight of

others, even when two translucent cages are placed side-by-side. Their cages were not, however, isolated in terms of sound or smell, suggesting that these factors could have mediated the observed rhythmic changes.

Changes in rhythmic patterns intermediated by chemical cues have been shown, for instance, in social interactions between two rodent *Acomys* species [35] and among socially interacting *Octodon degus* individuals [36]. It has been reported that through close inspection of urine, feces or dirt, tuco-tucos can discriminate chemical cues and use them to assess the reproductive condition of conspecifics [37,38]. In this sense, social modulation of rhythmicity could potentially be mediated by chemical factors in tuco-tucos, although such phenomenon has not been described before.

Acoustic signals in tuco-tucos seem to be particularly important in social interactions, as they extensively use vocalizations to communicate between individuals in the same burrow as well as in different burrows [26,28,39–43]. This genus displays complex vocalization patterns, which have been described for *C. talarum* [28,42,43], *C. pearsoni* [26,39–41] as well as for the Anillaco species referred to here [44]. One of the vocalizations described is the high frequency distress call emitted by newborn pups when far from their mother [40,42,43]. We hypothesize that either calls and/or chemical cues emitted by pups could have triggered the around-the-clock activity displayed by most of the animals.

Surprisingly, males were also affected by the social event however, the response was different and longer-lasting. They displayed at least 14 days of arrhythmicity before resuming normal rhythmicity. Another possibility is that the mother emitted signal that affected the males. The fact that the female abandoned the pups is an indication that this female was stressed maybe because the captivity conditions were not ideal for rearing pups or because she detected the presence of other animals. The presence of other animals during parturition in a solitary species may be a strong threatening stimulus.

It is also interesting to note that, unlike most reports of social synchronization in long-cohabiting rodent species [8,12], the around-the-clock activity of tuco-tucos was immediately triggered by unpredictable social stimuli.

5.2. Playback tests

Results of the playback tests were not consistent with the observed around-the-clock phenomenon, which could not be reproduced by merely imposing the pup sound. It could be that the vocalization that was recorded did not correspond to the particular newborn pattern that triggered the rhythmic disruption of tucos. In *C. talarum*, a care eliciting vocalization pattern has been registered from birth to 5 weeks of life [42,43] but there is a possibility of age changes, and our recorded pup was aged around 2 weeks. Besides this, our results can indicate that the vocalization alone, if any, was not the triggering stimulus, rescuing the role of the olfactory and perhaps other sensory components. We could be sure, however, with these results, that the activity rhythm of tuco-tucos is not easily modulated by sound.

Around-the-clock activity has emerged in a variety of biological contexts and has been recognized as a special, “extreme form of chronobiological plasticity” [45]. Because day/night segregation is displayed by most physiological and behavioral variables, the emergence of around-the-clock activity in some species, under particular contexts should possess a strong functional value. This seems the case, for instance, of nocturnal flight displayed by diurnal birds during migration [46], nursing eusocial insects caring day and night for developing larvae [20], frequent day and night feeding of small herbivore mammals [47–49] and around-the-clock vigilance of aquatic mammals [50]. The around-the-clock activity displayed by closely caged female tuco-tucos was clearly associated in time with the birth of pups and seemingly lasted the two days of their unattended life. After a long 3-month gestation, females give birth to relatively

precocious pups that are poorly furred and, consequently, have probably deficient thermoregulatory capability. These characteristics imply strong dependency on the maternal-pup bond for survival. In fact, in another solitary species of *Ctenomys*, Pereira [51] described a clear dependency on maternal care reflected in high daily maternal investment; mothers spend 90% of their time in the nest in close contact with the pups during the first week postpartum. During the second week, pups open their eyes, start wondering around, self-groom and eat solid food. The incidence and duration of maternal activities decreases gradually until nutritional weaning between 30 and 50 days postpartum while social weaning occurs later on. Considering this strong mother-pup bond and the known fact that lactating females accept and nurse not only their own pups but also alien ones, despite recognizing they are not their own [51], adult females should be sensitive to pups and this may explain the hyperactive response observed in these data. Despite being an unexpected laboratory artifact, it nevertheless reveals that tuco-tucos might display social modulation of activity rhythms.

It is also interesting that the birth event caused a long-lasting effect (arrhythmicity) in two of the males and a 24 h continuous activity followed by three days of activity suppression in a third one. This suggests the existence of individual variation in responses to social stimuli, reinforcing the need to better understand such social effects on activity rhythms in this and other species. In natural conditions males have no contact with offspring's whatsoever so that sensitivity to pups signal would not be expected unless it served to restrain approximation. On the other hand, males have contact with adult females for reproduction purposes so that female's signals would be expected to affect males in some way. We cannot rule out that all the animals were affected by signals from the female instead of the pups.

In general, little is known about social contacts that occur during breeding seasons in *Ctenomys* species considered solitary, and there is much to be known about trends in sociality [52].

6. Concluding remarks

Although solitary, the tuco-tucos found in Anillaco might be susceptible to activity rhythm modulation by social cues and offer an intriguing example of immediately evoked around-the-clock activity related to maternal care. Possible social cues that trigger this phenomenon are of chemical and/or acoustic nature, but this remains speculative for the moment. Nevertheless, these results open a novel path for investigation on the social interaction of subterranean rodents and emphasize the importance of considering social interactions in future studies with this and other subterranean species considered solitary.

Acknowledgements

The authors thank technician Jose. D. Paliza for assistance in animal capture and maintenance, P. Tachinardi and D. Flores for constant support and R. Salvador for revision of an early version of the manuscript. We also thank two anonymous referees for the constructive comments to improve this manuscript.

References

- [1] Mistlberger RE, Skene DJ. Social influences on mammalian circadian rhythms: animal and human studies. *Biol Rev Camb Philos Soc* 2004;79:533–56.
- [2] Castillo-Ruiz A, Paul MJ, Schwartz WJ. In search of a temporal niche: social interactions. In: Kalsbeek A, Merrow M, Roenneberg T, Foster RG, editors. *Progress in brain research*, 199. London: University College London; 2012. p. 267–80.
- [3] Bloch G, Herzog ED, Levine JD, Schwartz WJ. Socially synchronized circadian oscillators. *Proc R Soc B* 2013;280:20130035.
- [4] Menaker M, Eskin A. Entrainment of circadian rhythms by sound in *Passer domesticus*. *Science* 1966;154:1579–81.
- [5] Gwinner E. Periodicity of a circadian rhythm in birds by species-specific song cycles (*Aves*, Fringillidae: *Carduelis spinus*, *Serinus serinus*). *Experientia* 1966;22:765–6.

- [6] Gwinner E. Circannual rhythms: their dependence on circadian systems. In: Follet BK, Follet DE, editors, *Biological clocks in seasonal reproductive cycles*. Proceedings of the thirty second symposium of the colston research society. Bristol; 1981. pp. 153–169.
- [7] Mrosovsky N. Phase response curves for social entrainment. *J Comp Physiol A* 1988;162:35–46.
- [8] Crowley M, Bovet J. Social synchronization of circadian rhythms in deer mice (*Peromyscus maniculatus*). *Behav Ecol Sociobiol* 1980;7:99–105.
- [9] Goel N, Lee TM. Social cues modulate free-running circadian rhythms in the diurnal rodent *Octodon degus*. *Am J Physiol* 1997;42:R797–R804.
- [10] Scheibler E, Wollnik F. Interspecific contact affects phase response and activity in Desert hamsters. *Physiol Behav* 2009;98:288–95.
- [11] Paul MJ, Schwartz WJ. On the chronobiology of cohabitation. *Cold Spring Harb Symp Quant Biol* 2007;72:615–21.
- [12] Paul MJ, Indic P, Schwartz WJ. Social forces can impact the circadian clocks of cohabiting Hamsters. *Proc R Soc B* 2014;281:2535.
- [13] Marimuthu G, Rajan S, Chandrashekar MK. Social entrainment of the circadian rhythm in the flight activity of the microchiropteran bat *Hipposideros speoris*. *Behav Ecol Sociobiol* 1981;8:147–50.
- [14] Erkert HG, Schardt U. Social entrainment of circadian activity rhythms in common marmosets, *Callithrix j. jacchus* (Primates). *Ethology* 1991;87:189–202.
- [15] Melo PR, Gonçalves BSB, Menezes AAL, Azevedo CVM. Socially adjusted synchrony in the activity profiles of common marmosets in light-dark conditions. *Chronobiol Int* 2013;30:818–27.
- [16] Silva CA, Pontes ALB, Cavalcante JS, Azevedo CVM. Conspecific vocalizations modulate the circadian activity rhythm of marmosets. *Biol Rhythm Res* 2014;45:1–14.
- [17] Loher W. The effect of male calling on female locomotor activity of *Teleogrillus comodus*. *Behav Ecol Sociobiol* 1979;5:383–90.
- [18] Moritz RFA, Sakofski F. The role of the queen in circadian rhythms of honeybees (*Apis mellifera* L.). *Behav Ecol Sociobiol* 1991;29:361–5.
- [19] Oda GA, Belluscio S, Marques MD. Daily rhythms related to distinct social tasks inside an eusocial bee colony. *Chronobiol Int* 2007;24:845–58.
- [20] Eban-Rothschild A, Bellucci S, Bloch G. Maternity-related plasticity in circadian rhythms of bumble-bee queens. *Proc R Soc B* 2011;278:3510–6.
- [21] Favreau A, Richard-Yris MA, Bertin A, Houdelier C, Lumineau S. Social influences on circadian behavioural rhythms in vertebrates. *Anim Behav* 2009;77:983–9.
- [22] Bidau C. Familia Ctenomyidae. In: Barquez RM, Díaz MM, Ojeda RA, editors. *Mamíferos DE Argentina, sistemática y distribución*. Tucumán: Sarem; 2006. p. 219–31.
- [23] Lacey EA, Braude SH, Wieczorek JR. Burrow sharing by colonial tuco-tucos (*Ctenomys sociabilis*). *J Mamm* 1997;78:556–62.
- [24] Lacey EA, Ebensperger LA. Social structure in octodontid and ctenomyid rodents. In: Wolff JO, Sherman PW, editors. *Rodent societies: an ecological and evolutionary perspective*. Chicago, Illinois: University of Chicago Press; 2007. p. 403–15.
- [25] Lacey EA, Braude SH, Wieczorek JR. Solitary burrow use by adult patagonian tuco-tucos (*Ctenomys haigi*). *J Mamm* 1998;79:986–91.
- [26] Francescoli G. Tuco-tucos' vocalization output varies seasonally (*Ctenomys pearsoni*; Rodentia, Ctenomyidae): implications for reproductive signaling. *Acta Ethol* 2001;14:1–6.
- [27] Sikes RS, Gannon WL. The animal care and use committee of the American Society of Mammalogists, Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *J Mamm* 2011;92(1):235–53.
- [28] Schleich CE, Busch C. Acoustic signals of a solitary subterranean rodent *Ctenomys talarum* (Rodentia: Ctenomyidae): physical characteristics and behavioural correlates. *J Ethol* 2002;20:123–31.
- [29] R Core Team, R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria; 2014. URL: (<http://www.R-project.org/>).
- [30] Cohen R, Smale L, Kronfeld-Schor N. Masking and temporal niche switches in spiny mice. *J Biol Rhythm* 2010;25:47–52.
- [31] Valentinuzzi VS, Oda GA, Araújo JF, Ralph MR. Circadian pattern of wheel-running activity of a south american subterranean rodent (*Ctenomys cf knightii*). *Chronobiol Int* 2009;26:14–27.
- [32] Tomotani BM, Flóres DEFL, Tachinardi P, Paliza JD, Oda GA, Valentinuzzi VS. Field and laboratory studies provide insights into the meaning of day-time activity in a subterranean rodent (*Ctenomys aff. knightii*), the tuco-tuco. *PLOS One* 2012;7:e37918.
- [33] Flóres DEFL, Tomotani BM, Tachinardi P, Oda GA, Valentinuzzi VS. Modeling natural photic entrainment in a subterranean rodent (*Ctenomys aff. knightii*), the tuco-tuco. *PLoS One* 2013;8:e68243.
- [34] Tachinardi P, Bicudo EWJ, Oda AG, Valentinuzzi VS. Rhythmic 24h variation of core body temperature and locomotor activity in a subterranean rodent (*Ctenomys aff. knightii*), the tuco-tuco. *PLoS One* 2014;9:e85674.
- [35] Fluxman S, Haim A. Daily rhythms of body temperature in *Acomys russatus*: the response to chemical signals released by *Acomys cahirinus*. *Chronobiol Int* 1993;10:159–64.
- [36] Jechura TJ, Mahoney MM, Stimpson CD, Lee TM. Odor-specific effects on reentrainment following phase advances in the diurnal rodent *Octodon degus*. *Am J Physiol* 2006;291:R1806–R1808.
- [37] Zenuto RR, Fanjul MS. Olfactory discrimination of individual scents in the subterranean rodent *Ctenomys talarum* (tuco-tuco). *Ethology* 2002;108:629–41.
- [38] Zenuto RR, Fanjul MS, Busch C. Use of chemical communication by the subterranean rodent *Ctenomys talarum* (tuco-tuco) during the breeding season. *J Chem Ecol* 2004;30:2111–26.
- [39] Francescoli G. A preliminary report on the acoustic communication in Uruguayan *Ctenomys* (Rodentia, Octodontidae): basic sounds types. *Bioacoustics* 1999;10:203–18.
- [40] Francescoli G. Vocal signals from *Ctenomys pearsoni* pups. *Acta Theriol* 2001;46:327–30.
- [41] Francescoli G. Geographic variation in vocal signals of *Ctenomys pearsoni*. *Acta Theriol* 2002;47(1):35–44.
- [42] Schleich CE, Busch C. Juvenile vocalizations of *Ctenomys talarum* (Rodentia: Octodontidae). *Acta Theriol* 2002;47(1):25–33.
- [43] Schleich CE, Busch C. Energetic expenditure during vocalization in pups of the subterranean rodent *Ctenomys talarum*. *Naturwissenschaften* 2004;91:548–51.
- [44] J.P. Amaya, J.I. Areta, V.S. Valentinuzzi, E. Zufiaurre. Form and function of long-range vocalizations in a Neotropical fossorial rodent: the Anillaco Tuco-Tuco (*Ctenomys* sp.). 2016, *PeerJ* 4:e2559; <http://dx.doi.org/10.7717/peerj.2559>
- [45] Bloch G, Robinson GE. Chronobiology: Reversal of honeybee behavioural rhythms. *Nature* 2001;410:1048.
- [46] Helm B. Zugunruhe of migratory and nonmigratory birds in a circannual context. *J Avian Biol* 2006;37:533–40.
- [47] Daan S, Slopsema S. Short-Term Rhythms in foraging behavior of the common vole, *Microtus arvalis*. *J Comp Physiol* 1978;127:215–27.
- [48] Gerkema MP, Groos GA, Daan S. Differential elimination of circadian and ultradian rhythmicity by hypothalamic lesions in the common vole, *Microtus arvalis*. *J Biol Rhythm* 1990;5:81–95.
- [49] Merritt JF, Vessey SH. Shrews – small insectivores with polyphasic patterns. In: Halle S, Stenseth NC, editors. *Activity patterns in small mammals*. Berlin, Heidelberg: Springer-Verlag; 2000. p. 235–51.
- [50] Rattenborg NC, Amlaner CJ, Lima SL. Behavioral, neurophysiological and evolutionary perspectives on unihemispheric sleep. *Neurosci Biobehav R* 2000;24:817–42.
- [51] Pereira M. Nonselective maternal bonding but pup recognition in the subterranean rodent *Ctenomys pearsoni*. *J. Comp. Physiol.* 2006;120(4):411–5.
- [52] Lacey EA. Spatial and social systems of subterranean rodents. In: Lacey EA, Cameron G, Patton JL, editors. *Life underground: the biology of subterranean rodents*. Chicago: University of Chicago Press; 2000. p. 257–96.