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# Activity, range areas, and nesting patterns in the viscacha rat, Octomys mimax

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#### Abstract

Several rodent species engage in group living, meaning that individuals share nests, resting places, and range areas. Establishing how group living varies across species is critical for comparative studies to examine the origin and the adaptive value of this behavior. Comparative approaches are more powerful when a diverse array of taxonomic groups is included. We used telemetry techniques to monitor patterns of activity, resting places, and range areas at night to examine the extent of sociality of the scarcely known viscacha rats, *Octomys mimax*. Seven individuals were live trapped and fitted with radio-collars. Viscacha rat activity, as measured from distance moved between consecutive telemetry scans, took place mostly during the nighttime. During day, animals used from 2 to 6 putative nest places, but one was used more frequently. The sharing of resting locations by two or more radio-collared animals was never recorded. Viscacha rats showed relatively large range areas and low-to-moderate spatial overlap with neighbors. Male rats had larger range areas than females, but spatial overlap with neighbors was similar. Results suggest that viscacha rats are solitary living animals. This study supported a solitary-to-social trend from basal to more derivate forms across Octodontidae.

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Keywords: Group-living; Nesting site; Octomys; Range area; Range overlap; Space use

#### 1. Introduction

Social systems of rodents range from solitary living species to social and highly gregarious forms, in which individuals interact frequently, share feeding areas and a burrow system or a den (Armitage, 1999; Bennett and Faulkes, 2000; Lacey, 2000; Solomon, 2003). While evolutionary explanations for rodent sociality have focused on fitness benefits and ecological constraints (Ebensperger, 2001; Lacey, 2000), establishing how sociality varies across species is essential for comparative approaches aimed at examining its current utility

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(i.e., current fitness benefits) to face current (and past) social and ecological conditions (Blumstein and Armitage, 1998; Ebensperger and Blumstein, 2006; Ebensperger and Cofré, 2001).

Most available field data and theory developed from social rodents come from the study of a limited number of taxonomic groups, typically from African mole-rats (Bathyergidae) and North American squirrels and marmots (Sciuridae). This is particularly the case of species from desert and arid areas, where most information comes from semifossorial kangaroo rats (family Heteromyidae) and gerbils (family Muridae) (Jarvis et al., 1994; Randall, 1994, 2007). Studies on the social behavior of desert dwelling species are particularly useful given that both physiological and ecological restrictions can prevent individuals from living in stable social groups (Randall, 2007). Indeed, most species of kangaroo rats and gerbils exhibit rather solitary living habits (Randall, 1994, 2007). Data from other taxonomic groups are needed to examine the generality of this pattern (Ebensperger, 1998, 2001).

One such group is the New World hystricognathi (guinea pigs, degus, viscacha rats). Interestingly, these rodents include species that vary morphologically and physiologically, and use a great variety of habitats, including deserts (Contreras et al., 1987; Mares and Ojeda, 1982; Redford and Eisenberg, 1992). More importantly, patterns of morphological, physiological, and ecological diversity seem to covary with patterns of social organization and behavior (Ebensperger and Blumstein, 2006; Ebensperger and Cofré, 2001; Lacey and Ebensperger, 2007; Lacher, 1981; Trillmich et al., 2004).

Within the New World hystricognaths, the octodontids (Octodontidae) comprise a potentially informative group for studies aimed at examining how social behavior varies across species. The Octodontidae consists of 13 currently recognized species (Woods and Kilpatrick, 2005), that are ecologically diverse, including surface-, rock-dwelling, semi-subterranean and truly subterranean forms (Lacey and Ebensperger, 2007). These animals occur in a wide array of habitats including open grasslands, dense forests, and extremely arid salt flats (Contreras et al., 1987; Mares and Ojeda, 1982; Redford and Eisenberg, 1992). Although data for many octodontids are largely anecdotal, comparisons of the behavior of poorly known species with better studied taxa suggest that group living occurs in members of this family, including Octodon deaus (Ebensperger et al., 2004; Fulk, 1976), Spalacopus cyanus (Lacey and Ebensperger, 2007; Reig, 1970) and probably Aconaemys fuscus (Reise and Gallardo, 1989), which collectively represent the most derived forms according to the latest phylogenetic reconstructions of Octodontidae (Gallardo and Kirsch, 2001; Honeycutt et al., 2003). In contrast, data on the most basal forms is mostly anecdotal. At present the only species identified as solitary is the red viscacha rat, Tympanoctomys barrerae (Mares et al., 1997), a finding that, if confirmed, opens the possibility for an independent evolution of sociality within the octodontids. Besides T. barrerae, basal forms of Octodontidae include two other less known species, namely Octodontomys gliroides (soco) and Octomys mimax (viscacha rat). While virtually nothing is known of the behavior of O. mimax (Mares and Ojeda, 1982; Redford and Eisenberg, 1992), recent phylogenetic reconstructions place it as a sister species of T. barrerae (Gallardo and Kirsch, 2001; Honeycutt et al., 2003). Given that all three basal octodontids inhabit desert and very arid habitats (Contreras et al., 1987), studies on the social behavior of these species may provide evidence of social convergence.

The major objective of our study was to use radio-telemetry techniques to conduct a preliminary examination of the social behavior of *O. mimax*. Based on the general pattern reported from previous studies on desert gerbils and kangaroo rats, and from what is known about the social behavior of the sister species *T. barrerae*, we predicted viscacha rats to exhibit rather solitary living habits.

#### 2. Methods

#### 2.1. Study area and animals

Observations were conducted during 23 days, from 15 November to 8 December 2006. The study population was located at the Los Rastros area (30°05′S; 67°56′W; 1,260 m of altitude), within the Parque Provincial Ischigualasto, San Juan Province, Argentina (Fig. 1). The study site was characterized by an arid climate (cold and dry) where mean annual precipitation does not exceed 100–200 mm; most rain falls during summer months (November–December). Ambient temperature averages 18 °C, and is characterized by considerable day/night variations (Abraham and Rodriguez, 2000). The area was characterized by open

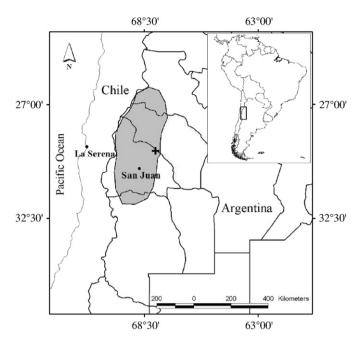


Fig. 1. Known distribution of viscacha rats (*Octomys mimax*) (gray shading) according to Mares and Ojeda (1982); the "cross" symbol indicates the location of the study area "Los Rastros" 30°05′S, 67°56′W at Parque Provincial Ischigualasto, San Juan Province, Argentina.

scrublands dominated by shrubs (*Larrea cuneifolia*, *Zuccagnia punctata*, *Prosopis torquata*), cacti (*Trichocereus terschesckii*), and bromeliads such as *Deutherocohnia longipetala*, and *Tillandsia* spp. (Márquez et al., 2005). Overall plant cover was nearly 15% (Márquez et al., 2005).

Members of the study population were captured using a combination of locally produced medium  $(28 \times 9 \times 8 \text{ cm}^3)$  and large  $(30 \times 10 \times 9.5 \text{ cm}^3)$  sized metal live-traps (similar to Sherman traps). Two previous trapping campaigns (21-26 June 2006 and 10-15 November 2006) served as pilot studies and revealed that animals were captured inside ravines and rock crevices exclusively. Thus, we placed a total of 116 traps near rock crevices and in runways (identified from the presence of fresh droppings), inside five ravines and a total of 15 capture places on an area of approximately 14 ha. Traps were distributed similarly by size and total number between ravines and baited with a mix rolled oats and tuna fish. We opened traps during early morning hours and checked them every 24 h, for a total of 10 days during late November 2006. Previous trapping indicated that viscacha rats entered the traps during morning hours exclusively.

For all animals captured, we recorded the individual's body weight and apparent reproductive status. Females were regarded as breeding when perforate, pregnant or lactating. Males were considered to be breeding when they had descended testes.

To characterize temporal and spatial relationships among adult individuals, all adult sized individuals caught during this trapping period were fitted with 4–5 g radio-collars (Wildlife Materials, Inc., Murphysboro, Illinois, USA). Weight of radio-collars represented about 4–5% of study subjects' body weight (see below). At the end of data collection (see below) radio-collared animals were recaptured and the transmitters were removed.

#### 2.2. Temporal activity

Viscacha rats are presumed to be nocturnal rodents (Bozinovic and Contreras, 1990; Mares and Ojeda, 1982), and, hence, we first needed to confirm this assumption and examine patterns of temporal activity. Daily patterns of activity were monitored using radio-telemetry. Following their release, collared animals were located using LA 12-Q receivers and 3-element hand-held Yagi antennas (AVM Instrument Company, Colfax, California, USA). We recorded locations of collared animals multiple times per day, once every 2 h.

On average, two teams (two observers per team) needed 20–40 min to track all radio-collared animals during the night, and 15–30 min during daylight. Once located, the position of each animal was marked with flagging material coded for individual animals. Each radio fix location was then referenced twice with a Garmin portable GPS (Garmin International Inc., Olathe, Kansas, USA). GPS readings were taken so as precision never was larger than 10 m. This procedure was precise enough as range areas of viscacha rats may cover dozens of squared meters (see Results). To characterize daily patterns of activity (and space use, see below), we recorded locations of all radio-collared animals for a total of 6 nights and 3 days. These data were collected from 23:00 to 05:00 h on night, and from 07:00 to 19:00 h on daylight hours. Sunrise occurred at approximately 06:00 h whereas sunset occurred around 20:30 h.

#### 2.3. Resting (nest) patterns

Since our activity data revealed that viscacha rats concentrate their locomotor activity during the night (see Results), we used the daylight locations of radio-collared animals to quantify the location of resting (putative nest) places and the extent of communal nesting by members of the study population (e.g., Ebensperger et al., 2004, 2006). Putative nests were locations we found two or more times during daylight telemetry near fresh droppings. Thus we recorded the number of putative nesting sites used by each viscacha rat. In addition, we measured communal nesting as the percentage of nights two or more radio-collared viscacha rats occurred at the same location during the night (Ebensperger et al., 2004; Hayes et al., 2007). To quantify nest use of all radio-collared animals, we used a total of 6 days of data during which we monitored activity twice at 2 h intervals during daylight.

## 2.4. Habitat of resting locations

Given the paucity of data available, we quantified potentially relevant ecological variables to describe the habitat used by these animals during periods of inactivity. To do so, we selected the two locations most frequently used by each viscacha rat as revealed from daylight telemetry. At each resting site we used the line intercept method (Canfield, 1941). We established four 5 m length transects in a crossed design where each resting site corresponded to the intersection point. Since resting sites were always located inside rock crevices in ravines, two transects were located parallel (upwards and downwards), whereas two others were located perpendicular (across) to the ravines. We used each transect to quantify the percentage of ground that was covered with grasses, shrubs, trees, or bare. For bare ground, we recorded its composition of either soil or rock (including pebbles and small stones). At the point of intersection between all four transects we also recorded maximum vegetation height.

#### 2.5. Range areas and overlap

Given that our data confirmed the mostly nocturnal activity of *O. mimax* (see Results), we used night radiolocations to quantify range areas during activity. While triangulation is thought to interfere less with the activity of radio-collared animals compared with homing (Ebensperger et al., 2006; Kenward, 2001), the rugged micro-topography of our study site precluded the use of long-range radio-fixings because of signal bounce. Thus, although we used the homing technique, we previously trained ourselves to locate animals quickly to minimize disrupting their behavior. In particular, we avoided stepping loudly when near each radio-collared subject and left quickly once its location was confirmed. Location data points for each individual were then mapped using the 95% minimum convex polygon algorithm of the software Ranges VI (Ebensperger et al., 2006; Hayes et al., 2007; Kenward et al., 2003). Pairwise estimates of % range overlap among individuals and nesting associations were also calculated using Ranges VI (Ebensperger et al., 2006; Kenward et al., 2003).

#### 2.6. Data analysis

We calculated distance between successive scans as a measure of viscacha rat activity. For each animal we calculated distance moved (in meters), between each pair of successive scans. Given that the same individuals

were monitored throughout consecutive days and nights, locations recorded at 24h intervals were not independent of one another. Preliminary inspection of data revealed that patterns of activity differed substantially between day and night. Consequently, we divided the data collection period into 3 day and 6 night periods, defined on the basis of sunrise and sunset at each study site. For the daytime periods, we calculated the mean for the distance between successive scans for each radio-collared individual in the population. The same procedure was applied to data from the night periods. Then, we calculated a single mean for day and other for night for each animal, yielding a total of two data points per individual for our measure of activity. Day and night activities of male and female rats were compared using separate Wilcoxon-matched pairs tests (Siegel and Castellan, 1988). We ran chi-square tests to examine the null hypothesis of equal use of resting places under random expectations by each animal subject. For description of habitat used by these animals during periods of inactivity, plant cover and ground characteristics were averaged per radio-collared animal, and the means quantified were considered as independent replicates.

We compared the mean size (in hectares) of range areas and % overlap by male and female viscacha rats with other male and female rats with the use of Mann–Whitney U tests. The extent to which ranges of radio-collared subjects overlapped other neighbors was also examined with the Wilcoxon-matched pairs test. Given the reduced number of subjects of our study population, we provide power  $(1-\beta)$  estimates when reporting statistically non-significant results.

Statistical tests were two-tailed and were performed using Statistica 6.0 (StatSoft Inc., Tulsa, Oklahoma, USA). We used S-Plus 2000 professional release to compute power of tests (Copyright © 1988–1999, MathSoft, Inc.). Data are presented as  $\bar{x} \pm SE$ .

#### 3. Results

#### 3.1. Characteristics of radio-collared animals and trapping effort

A total of seven individuals (four females and three males) were live trapped and fitted with radio-collars during the study. Of these, four were females that weighed  $120\pm2\,\mathrm{g}$ , and three were males that weighed  $109\pm9\,\mathrm{g}$ . Among the females, one was pregnant, and three others exhibited a vaginal plug, suggesting breeding activity. Of the three males, one had descended testes. The trapping effort was adequate to catch and identify most, if not all individuals in our study population. No new individuals were caught after 7 days of continuous trapping, confirming that the abundance of *O. mimax* populations is low. In addition, all captured animals were recaptures from previous pilot trapping and all were radio-collared.

#### 3.2. Temporal activity

Animals in the study population displayed temporal variation in activity. Viscacha rat activity was markedly higher after sunset, and decreased substantially after sunrise (Fig. 2). There was a significant effect of time of day on mean distance moved between successive scans. The distance moved between any two consecutive radio fixes during the night averaged  $86 \pm 8$  m (n = 7, range: 0–361 m), and was 21.5 times larger than distance moved during day ( $4 \pm 1$  m, range: 0–65 m; Wilcoxon-matched pairs test, z = 2.37; P < 0.018).

#### 3.3. Resting (nest) patterns

A total of 21 radio-telemetry scan sessions were completed during daylight hours. Animals used from 2 to 6 different resting places (n=7, mean  $\pm$  SE =  $4.1\pm0.5$ ), namely locations where an animal was found repeatedly during two or more scans. When considered individually, two radio-collared females (one of which was pregnant) used some day resting places disproportionately more than expected as revealed from chisquare analyses (Table 1). In contrast, five other subjects used their day resting places similarly (Table 1,  $1-\beta$  ranged between 0.1 and 0.58, mean = 0.24). Males ( $5.0\pm1$ ) and females ( $3.5\pm1$ ) used a statistically similar number of resting places (Kolmogorov–Smirnov two-sample test,  $D_{\text{max}}=0.50$ , P>0.10,  $1-\beta=0.50$ ). We recorded no cases of two or more radio-collared animals sharing a resting location simultaneously.

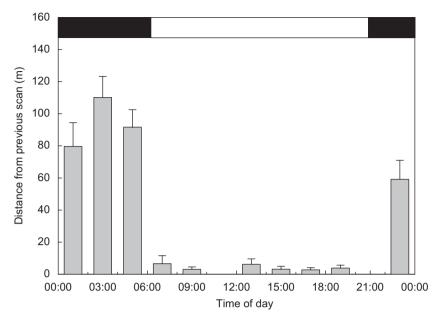


Fig. 2. Mean ( $\pm 1$  SE) distance moved (m) since previous scan for viscacha rats (Octomys mimax) monitored every 2h for 3 days and 6 nights at Parque Provincial Ischigualasto, Argentina (n = 7 animals). Black bars at the top of graphs indicate night hours.

Table 1
Sex and identity of female and male viscacha rats that were radio-collared, number of daytime radio-fixings used to identify resting sites, total number of resting (putative nest) sites identified, and chi-square and associated *P*-values (df in parentheses) used to test the null hypothesis of equal use

Sex and identity of radio-collared rat	Number of day telemetry scans	Number of resting sites	Chi-square, (df), and associated <i>P</i> -values
♀0010	21	4	$\chi^2 = 6.80 (3), P = 0.079$
♀0011	21	2	$\chi^2 = 7.58 (1), P = 0.006*$
♀0012	19	5	$\chi^2 = 3.38$ (4), $P = 0.496$
♀0013	21	3	$\chi^2 = 6.54$ (2), $P = 0.038*$
♂ 0015	21	5	$\chi^2 = 6.53$ (4), $P = 0.163$
♂ 0022	21	4	$\chi^2 = 0.65$ (3), $P = 0.885$
♂ 0023	21	6	$\chi^2 = 3.40 (5), P = 0.639$

The number of different resting locations included places where an animal was recorded on at least two separate occasions. Asterisks are used to highlight statistically significant differences.

#### 3.4. Habitat of putative nest locations

We quantified ecological characteristics of the two resting places most frequently used during daylight by each of the seven viscacha rats studied. These sites were located at places with relatively low plant cover  $(19.1\pm6.7\%)$  and bare substrate  $(80.9\pm6.7\%)$ . The bare ground of sites was composed similarly of soil  $(39.0\pm6.1\%)$  and rocks  $(41.9\pm8.5\%)$ . The average height of vegetation at these sites was  $83.1\pm8.9$  cm. Males and females used individual resting places with similar characteristics of plant cover (Kolmogorov–Smirnov two-sample test,  $D_{\text{max}} = 0.42$ , P > 0.10,  $1 - \beta = 1$ ).

#### 3.5. Range areas and overlap

Seven individuals were radio-tracked during the night, which provided an average of  $25 \pm 3$  radio fixes per animal. If data for all radio-collared male and female rats are combined, the size of range areas averaged

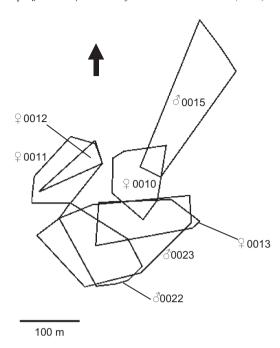


Fig. 3. Range areas (95% minimum convex polygons) of seven viscacha rats (*Octomys mimax*) during the night. Individual labels for each polygon correspond to labels in Table 1. The black arrow signals the geographic north. Ranges were obtained by means of radio-tracking four adult female and three adult male viscacha rats during November 2006 at Parque Provincial Ischigualasto, Argentina.

 $12,370 \pm 2975 \,\mathrm{m}^2$  (n=7). When sex was examined, males exhibited larger range areas ( $18,595 \pm 4708 \,\mathrm{m}^2$ , n=3) than females ( $7702 \pm 1717 \,\mathrm{m}^2$ , n=4), a significant difference (Mann–Whitney U test, z=2.12, P=0.034).

While radio-collared viscacha rats revealed a relatively low mean spatial overlap  $(11.5\pm2.7\%)$  with other viscacha rats, overlap ranged from 0% to 98% (Fig. 3). Range overlap of males with any other radio-collared subject  $(10.7\pm4.7\%)$  was similar to that recorded in the females  $(12.1\pm3.6\%)$  (Mann–Whitney U test,  $z=0.35, P=0.724; 1-\beta=0.45$ ). We recorded on only two occasions two animals located in the same place during the night. Male ranges overlapped those of other males  $(21.8\pm13.5\%)$  similarly compared with those of females  $(5.2\pm2.5\%)$  (Wilcoxon-matched pairs test,  $z=1.07, P=0.285; 1-\beta=1$ ). Likewise, the ranges of female radio-collared viscacha rats overlapped with those of other females  $(12.4\pm6.9\%)$  and males  $(11.8\pm8.6\%)$  similarly (Wilcoxon-matched pairs test,  $z=0.53, P=0.593; 1-\beta=0.14$ ).

#### 4. Discussion

Our study yields insights into the previously unknown behavior and ecology of *O. mimax*. We found that adult males and females restrict locomotor activity mostly to the night. During the day, male and females rest individually in places with similar ecological characteristics. The sharing of resting locations by two or more radio-collared animals was never recorded. When active at night, these animals range over large areas and exhibit relatively low (albeit variable) spatial overlap. Taken together, and based on this short-term study, the data suggest that male and female viscacha rats exhibit solitary living habits, a finding that fits the general pattern of social behavior across species in desert habitats (Randall, 1994, 2007).

While rather the small number of subjects studied seems to reflect a natural characteristic of wild populations of *O. mimax* populations, future long-term studies are clearly needed to confirm these findings. In particular, the social behavior of *O. mimax* may exhibit changes with varying density conditions, as described in other rodents (Cooper and Randall, 2007; Pilastro et al., 1996; Randall et al., 2005; Wolff, 1994). Populations of desert rodents in particular are well known for drastic changes in density in response to interannual fluctuations in precipitation and food availability (Jiménez et al., 1992; Meserve et al., 1995). Given the

relatively low power of our sex-linked contrasts, further efforts also are needed to examine the potential influence of sex differences on the spatial and social behavior of viscacha rats.

Group living seems common within Octodontide, particularly in the most derived forms (Ebensperger et al., 2004; Fulk, 1976; Lacey and Ebensperger, 2007; Reig 1970; Reise and Gallardo, 1989), according to recent phylogenetic reconstructions of Octodontidae (Gallardo and Kirsch, 2001; Honeycutt et al., 2003). Data on the only basal form that has been studied suggest a solitary living habit in *T. barrerae* (Mares et al., 1997). Our study on *O. mimax* adds to this evidence, supporting the hypothesis that basal octodontids may be solitary. Given that group living is also common within hystricognath families, basal to Octodontidae (Ebensperger and Blumstein, 2006; Opazo et al., 2005), our data are also consistent with the hypothesis of an independent origin of sociality within Octodontidae. Additional, long-term studies on the social behavior of *Octomys* and on the remaining basal octodontids (e.g., *Octodontomys*, *Pipanoctomys*, Woods and Kilpatrick, 2005) are strongly needed to further explore this hypothesis.

During the day resting places consisted typically of rock crevices, located inside ravines, and relatively with low vegetation cover. The sites were sometimes associated with the presence of thorny shrubs. We found no signs (e.g., mounds of fresh dirt or rocks) that *O. mimax* in our study population use digging to modify these resting places. Although we did not break into these locations to confirm the presence of bedding, food remnants, or other items indicative of a nest, the tendency for animals to co-occur at a rather limited number of sites is consistent with these signs recorded in other rodents (e.g., Armitage and Gurri-Glass, 1994; Lacey et al., 1997; Solomon et al., 1998; Tristiani et al., 2003; Wilkinson and Baker, 1988; Wolton, 1985) and is suggestive that these localities function as nests in viscacha rats. Overall then, these results are in agreement with Mares (1980) who labelled *O. mimax* as a rock-dwelling species based on the presence of indirect signs of these animals.

Similar to most small desert rodents (Degen, 1997), *O. mimax* restricted most of its locomotor activity to night, an observation that confirms previous suggestions (Bozinovic and Contreras, 1990; Mares and Ojeda, 1982). The nocturnal activity of viscacha rats fits well with the fact that these rodents are relatively good thermoregulators, able to endure the colder ambient temperatures during the night (Bozinovic and Contreras, 1990). However, whether nocturnal activity of *O. mimax* evolved as a strategy to avoid heat during the day, as frequently suggested, remains debatable. Other desert rodents that have adopted diurnality adjust their temporal use of burrows or shade during day to cope with warm conditions (Degen, 1997), implying that nocturnality is not required in small rodents to inhabit warm arid environments.

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#### References

Abraham, M.E., Rodríguez, F., 2000. Argentina, recursos y problemas ambientales de la zona árida. Primera parte: Provincia de Mendoza, San Juan y la Rioja. Argentina. Junta de Gobierno de Andalucía, Tomo I, Universidades y Centros de Investigación de la Región Andina Argentina.

Armitage, K.B., 1999. Evolution of sociality in marmots. Journal of Mammalogy 80, 1-10.

- Armitage, K.B., Gurri-Glass, G.E., 1994. Communal nesting in yellow-bellied marmots. In: Rumiantsev, V. (Ed.), Actual Problems of Marmots Investigation. ABF Publishing House, Moscow, Russia, pp. 14–26.
- Bennett, N.C., Faulkes, C.G., 2000. African Mole-Rats: Ecology and Eusociality. Cambridge University Press, Cambridge, UK.
- Blumstein, D.T., Armitage, K.B., 1998. Life history consequences of social complexity: a comparative study of ground-dwelling sciurids. Behavioral Ecology 9, 8–19.
- Bozinovic, F., Contreras, L.C., 1990. Basal rate of metabolism and temperature regulation of two desert herbivorous octodontid rodents: *Octomys mimax* and *Tympanoctomys barrerae*. Oecologia 84, 567–570.
- Canfield, R.H., 1941. Application of the line interception method in sampling range vegetation. Journal of Forestry 39, 388–394.
- Contreras, L.C., Torres-Mura, J.C., Yáñez, J.L., 1987. Biogeography of octodontid rodents: an eco-evolutionary hypothesis. Fieldiana Zoology 39, 401–411.
- Cooper, L.D., Randall, J.A., 2007. Seasonal changes in home ranges of the giant kangaroo rat (*Dipodomys ingens*): a study of flexible social structure. Journal of Mammalogy 88, 1000–1008.
- Degen, A.A., 1997. Ecophysiology of Small Desert Mammals. Springer, Berlin, Germany.
- Ebensperger, L.A., 1998. Sociality in rodents: the New World fossorial hystricognaths as study models. Revista Chilena de Historia Natural 71, 65–77.
- Ebensperger, L.A., 2001. A review of the evolutionary causes of rodent group-living. Acta Theriologica 46, 115–144.
- Ebensperger, L.A., Blumstein, D.T., 2006. Sociality in New World hystricognath rodents is linked to predators and burrow digging. Behavioral Ecology 17, 410–418.
- Ebensperger, L.A., Cofré, H., 2001. On the evolution of group-living in the New World cursorial hystricognath rodents. Behavioral Ecology 12, 227–236.
- Ebensperger, L.A., Hurtado, M.J., Soto-Gamboa, M., Lacey, E.A., Chang, A.T., 2004. Communal nesting and kinship in degus (*Octodon degus*). Naturwissenschaften 91, 391–395.
- Ebensperger, L.A., Taraborelli, P., Giannoni, S.M., Hurtado, M.J., León, C., Bozinovic, F., 2006. Nest and space use in a highland population of the lesser cavy. *Microcavia australis*. Journal of Mammalogy 87, 834–840.
- Fulk, G.W., 1976. Notes on the activity, reproduction, and social behavior of *Octodon degus*. Journal of Mammalogy 57, 495–505.
- Gallardo, M.H., Kirsch, J.A.W., 2001. Molecular relationships among Octodontidae (Mammalia: Rodentia: Caviomorpha). Journal of Mammalian Evolution 8, 73–89.
- Hayes, L.D., Chesh, A., Ebensperger, L.A., 2007. Ecological predictors of range areas and use of burrow systems in the diurnal rodent, *Octodon degus*. Ethology 113, 155–165.
- Honeycutt, R.L., Rowe, D.L., Gallardo, M.H., 2003. Molecular systematics of the South American relationships among species and genera in the family Octodontidae. Molecular Phylogenetics and Evolution 26, 476–489.
- Jarvis, J.U.M., O'Riain, M.J., Bennett, N.C., Sherman, P.W., 1994. Mammalian eusociality: a family affair. Trends in Ecology and Evolution 9, 47-51.
- Jiménez, J.E., Feinsinger, P., Jaksic, F.M., 1992. Spatiotemporal patterns of an irruption and decline of small mammals in northcentral Chile. Journal of Mammalogy 76, 580–595.
- Kenward, R.E., 2001. A Manual for Wildlife Radio Tagging. Academic Press, San Diego, CA, USA.
- Kenward, R.E., South, A.B., Walls, S.S., 2003. Ranges 6, Version 1.2: For the Analysis of Tracking and Location Data. Online Manual. Anatrack Ltd., Wareham, United Kingdom.
- Lacey, E.A., 2000. Spatial and social systems of subterranean rodents. In: Lacey, E.A., Patton, J.L., Cameron, G.N. (Eds.), Life Underground: The Biology of Subterranean Rodents. University of Chicago Press, Chicago, IL, pp. 257–296.
- Lacey, E.A., Ebensperger, L.A., 2007. Social structure in Octodontid and Ctenomyid rodents. In: Wolff, J.O., Sherman, PW. (Eds.), Rodent Societies: An Ecological and Evolutionary Perspective. University of Chicago Press, Chicago, IL, USA, pp. 257–296.
- Lacey, E.A., Braude, S.H., Wieczorek, J.R., 1997. Burrow sharing by colonial tuco-tucos (*Ctenomys sociabilis*). Journal of Mammalogy 78, 556–562.
- Lacher, T.E., 1981. The comparative social behavior of *Kerodon rupestris* and *Galea spixii* and the evolution of behavior in the Caviidae. Bulletin of the Carnegie Museum of Natural History 17, 1–71.
- Mares, M.A., 1980. Convergent evolution among desert rodents: a global perspective. Bulletin of the Carnegie Museum of Natural History 16, 1–51.
- Mares, M.A., Ojeda, R.A., 1982. Patterns of diversity and adaptation in South American hystricognath rodents. Pymatuning Laboratory of Ecology, Special Publication Series 6, pp. 393–431.
- Mares, M.A., Braun, J.K., Channell, R., 1997. Ecological observations on the octodontid rodent, *Tympanoctomys barrerae*, in Argentina. Southwestern Naturalist 42, 488–504.
- Márquez, J., Martinez Carretero, E., Dalmasso, A., Pastran, G., Ortiz, S., 2005. Las áreas protegidas de la provincia de San Juan (Argentina) II La vegetación del Parque Provincial Ischigualasto. Multequina 14, 1–27.
- Meserve, P.L., Yunger, J.A., Gutiérrez, J.R., Contreras, L.C., Milstead, W.B., Lang, B.K., Cramer, K.L., Herrera, S., Lagos, V.O., Silva, S.I., Tabilo, E.L., Torrealba, M.A., Jaksic, F.M., 1995. Heterogeneous responses of small mammals to an El Niño (ENSO) event in north-central semiarid Chile and the importance of ecological scale. Journal of Mammalogy 76, 133–148.
- Opazo, J.C., Palma, R.A., Melo, F., Lessa, E., 2005. Adaptive evolution of the insulin gene in caviomorph rodents. Molecular Biology and Evolution 22, 1290–1298.
- Pilastro, A., Missiaglia, E., Marin, G., 1996. Age-related reproductive success in solitarily and communally nesting female dormice (*Glis glis*). Journal of Zoology, London 239, 601–608.

- Randall, J.A., 1994. Convergences and divergences in communication and social organization of desert rodents. Australian Journal of Zoology 42, 405–433.
- Randall, J.A., 2007. Environmental constraints and the evolution of sociality in semifossorial desert rodents. In: Wolff, J.O., Sherman, P.W. (Eds.), Rodent Societies: An Ecological and Evolutionary Perspective. University of Chicago Press, Chicago, IL, USA, pp. 368–379.
- Randall, J.A., Rogovin, K., Parker, P.G., Eimes, J.A., 2005. Flexible social structure of a desert rodent, *Rhombomys opimus*: philopatry, kinship, and ecological constraints. Behavioral Ecology 16, 961–973.
- Redford, K.H., Eisenberg, J.F., 1992. Mammals of the Neotropics: The Southern Cone. University of Chicago Press, Chicago, IL, USA. Reig, O.A., 1970. Ecological notes on the fossorial octodont rodent *Spalacopus cyanus* (Molina). Journal of Mammalogy 51, 592–601.
- Reise, D., Gallardo, M.H., 1989. An extraordinary occurrence of the tunduco *Aconaemys fuscus* (Waterhouse, 1841) (Rodentia, Octodontidae) in the central valley, Chillán, Chile. Medio Ambiente (Chile) 10, 67–69.
- Siegel, S., Castellan Jr., N.J., 1988. Nonparametric Statistics for The Behavioral Sciences. McGraw-Hill, Inc., New York, USA.
- Solomon, N.G., 2003. A reexamination of factors influencing philopatry in rodents. Journal of Mammalogy 84, 1182–1197.
- Solomon, N.G., Vandenbergh, J.G., Sullivan Jr., W.T., 1998. Social influences on intergroup transfer by pine voles (*Microtus pinetorum*). Canadian Journal of Zoology 76, 2131–2136.
- Trillmich, F., Kraus, C., Künkele, J., Asher, M., Clara, M., Dekomien, G., Epplen, J.T., Saralegui, A., Sachser, N., 2004. Species-level differentiation of two cryptic species pairs of wild cavies, genera *Cavia* and *Galea*, with a discussion of the relationship between social systems and phylogeny in the Caviinae. Canadian Journal of Zoology 82, 516–524.
- Tristiani, H., Murakami, O., Watanabe, H., 2003. Ranging and nesting behavior of the ricefield rat *Rattus argentiventer* (Rodentia: Muridae) in west Java, Indonesia. Journal of Mammalogy 84, 1228–1236.
- Wilkinson, G.S., Baker, A.E.M., 1988. Communal nesting among genetically similar house mice. Ethology 77, 103-114.
- Wolff, J.O., 1994. Reproductive success of solitarily and communally nesting white-footed mice and deer mice. Behavioral Ecology 5, 206–209.
- Wolton, R.J., 1985. The ranging and nesting behaviour of wood mice, *Apodemus sylvaticus* (Rodentia: Muridae), as revealed by radio-tracking. Journal of Zoology, London 206, 203–224.
- Woods, C.A., Kilpatrick, C.W., 2005. Infraorder hystricognathi. In: Wilson, DE., Reeder, DM. (Eds.), Mammal Species of The World: A Taxonomic And Geographic Reference. Smithsonian Institution Press, Washington, District of Columbia, USA, pp. 1538–1600.