

ORIGINAL INVESTIGATION

Comparing composition of social groups, mating system and social behaviour in two populations of *Microcavia australis*

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Received 10 September 2007; accepted 28 August 2008

Abstract

Microcavia australis is a semifossorial, diurnal and social rodent, native to South America. The objective was to determine and compare the composition of social groups, mating system and social behaviours of cavies in two populations of the Monte (El Leoncito and Ñacuñán). The two sites differ in climate conditions and plant resource availability. Trapping was carried out on 7–11 consecutive days at three times of the year (food abundance, food shortage, reproduction), from 2003 to 2005. Individuals were identified with metal ear tags. Continuous focal samplings were performed during 4 days. The female/male proportion per group was 1/1 at both sites which, together with the absence of sexual dimorphism in body size (0.94), the accomplishment of oestrus synchronization, the large size of scrotal testes during the reproductive season and sexual patterns, suggests a promiscuous mating system. Social groups were larger and with more adults at the site with more severe climate conditions (El Leoncito). The index of association among individuals was higher at El Leoncito. Cavies could use seismic communication to avoid encounters ending in fights at El Leoncito, and the agonistic behaviour was significantly lower in this population.

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Keywords: Group composition; Mating system; *Microcavia australis*; Monte; Social

Introduction

Among the factors that would be affecting group size in rodents are extreme climate conditions (Madison 1984; Arnold 1988; Hoogland 1995; Lacey 2000; Ebensperger 2001, 2003; Ebensperger and Cofré 2001). In many homeotherms heat loss is reduced by huddling in groups, in fact all the more effectively the colder the environment and the more animals involved (Madison 1984). Populations of *Marmota* sp. located at higher altitude, in a more rigorous environment, exhibit a larger group size with more tolerance between

individuals, and the greater number of marmots per group would reduce the loss of heat (Barash 1973, 1974; Arnold 1988, 1990). Females of *Octodon degus* share a communal nest, which, among other things, allow them to improve thermoregulation (Ebensperger and Wallen 2002; Ebensperger et al. 2004) because loss of body warmth is reduced by their crowding together in groups, and which becomes more efficient the larger the group size (Arnold 1988). The degree of behavioural specialization among individuals appears to increase with group size (Lacey 2000) and the total time and energy that animals allocate to specific activities, e.g. the agonistic behaviour, are affected by physiological and morphological factors related to environment factors (Branch 1993; Ebensperger 2001, 2003). In harsh environments,

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aggression among individuals would be reduced to prevent loss of water, energy and time (Hoogland 1995; Nevo 1995; Ganem 1998; Ebensperger 2001, 2003).

The system of pairs contains a strong environment component; for example, the distribution of the food resource (uniform or accumulated) and the quality of such resource (high or low) will lead to a certain temporary inclination of sexually receptive females to be, for instance, dispersed and solitary (Barlow 1988) or aggregated around the food, favouring monogamy or polygamy, respectively (Lacher 1981; Mares and Lacher 1987; Ascher 2004).

Lacher (1981) suggests that environment variables would be a major factor in determining trends of social organization in the family Caviidae. This family belongs to the group of hystricognath rodents native to the New World (Woods 1984; Cassini 1989; Galliari et al. 1996), its individuals are middle-sized, diurnal, herbivorous, semifossorial, terrestrial with arboreal tendencies in some genera, they dwell in all kinds of soils but preferably in those not wet or swampy (Cabrera 1953; Rood 1972). It includes two subfamilies: Dolichotinae and Caviinae (Galliari et al. 1996). The latter is distributed from Venezuela south to Argentina (Rood 1972), and includes the cavies of the genera *Kerodon*, *Microcavia* sp., *Galea* sp. and *Cavia* sp. *Microcavia australis*, or lesser cavy, is one of the smallest cavies, widely distributed across Argentina, from Jujuy south to Santa Cruz (Nowak and Paradiso 1983; Redford and Eisenberg 1992; Tognelli et al. 2001; Parera 2002), specifically in dry shrub areas and sandy scrublands (Olrog and Lucero 1986; Canevari and Fernández Balboa 2003). They exhibit diurnal habits and a group social structure with low to moderate levels of aggressiveness (Rood 1967; Tognelli et al. 1995). These cavies regularly dig to build and maintain a burrow system, which they use for a long time (Contreras and Roig 1979; Taraborelli accepted). Groups are formed by several females that have a friendly relationship with one another, one or a few males, in addition to the young and juveniles (Rood 1967, 1972). Rood (1972) asserts that the mating system in this species is promiscuous, that females mate indiscriminately with any male. In the Monte they are associated with a microhabitat that includes plants with arched branches extending to the ground on the edges, and soils with herbaceous vegetation (Rood 1967; Tognelli et al. 1995). With reference to diet, they consume a wide variety of plant material, such as stems, leaves and fruits, adjusted to environmental food availability (Nowak and Paradiso 1983; Monge et al. 1994; Campos et al. 2001).

There are no studies relating the environment with the characteristics of the natural history of *M. australis*, therefore the objective was to determine and compare the composition of social groups, aspects of the mating

system and social behaviours in cavies of two populations located on sites (El Leoncito and Ñacuñán) differing in altitude, climate conditions, and plant resource availability. The general hypothesis states that environment factors such as higher altitude, climate harshness, shortage and quality of food resources, have an influence on group formation and social behaviour in *M. australis*. Proposed predictions would be that, at the site with harsher climate and markedly wide temperature ranges (El Leoncito), the social group will have greater number of individuals, and will show low records of aggressiveness and a high index of association. The mating system will be promiscuous at both sites, with a strong phylogenetic component.

Materials and methods

Study areas

The study was conducted in two populations of the Monte desert. One of them is located in the Man and Biosphere Reserve of Ñacuñán (34°2'S, 67°58'W), in the centre-east of Mendoza, which belongs to the Monte desert and receives influence from the Chaco desert (Ojeda et al. 1998). This reserve covers an area of 12,300 ha, with a mean altitude of 540 m asl (Tognelli and Boshoven 2001). The climate is semiarid (warm-dry), mean annual temperature is 15.6 °C, the maximum annual mean is 23.8 °C, and the minimum annual mean 7.6 °C. Mean annual rainfall is 329.4 mm, concentrated in the summer months from November through March; nearly 50% of rains occur in this season (Cabrera 1976; Estrella et al. 2001). The mesquite community is the habitat preferred by *M. australis*, because of its structural complexity and the food supply it provides (Campos et al. 2001), total plant cover is 54.3% (Taraborelli 2006). This community is composed of three plant layers: the tree layer dominated by *Prosopis flexuosa*, the shrub layer, and the herbaceous layer (Roig 1971). At Ñacuñán predators are raptors with 0.45 ± 0.14 raptors/cavy (mean \pm standard error); and mammalian carnivores with 0.09 ± 0.05 carnivores/cavy (Taraborelli 2006).

The second population is located in El Leoncito National Park (31°47'S, 69°17'W), in the southwest of San Juan province, which comprises 76,000 ha, with altitudes ranging from 1990 to 4390 m asl (Haene 1996; Márquez 1999). The study site, within the Park, was Ciénaga del Medio (2484 m asl), located in a sector of the Monte desert that receives influence from the Puna desert. The climate is arid, cold-dry, mean annual temperature is always below 22 °C, with marked diurnal, nocturnal as well as seasonal temperature ranges; in winter, temperature oscillates between -4 and 20 °C and in summer from 8 to 32 °C (Bracco and Contreras 2000; Márquez and Dalmasso 2003). Mean annual rainfall does not exceed 100 mm, winter precipitation in April–August reaches 75 mm, in the form of snow and hail; summer precipitation in November–March is lower than 10 mm, primarily in the form of rain (Le Houérou 1999; Márquez et al. 2000; Márquez and Dalmasso 2003). At Ciénaga del Medio occurs a creosotebush

community (*Larrea nitida*) with low cover (10%), the herbaceous layer is lower than 10 cm in height (Haene 1996; Márquez et al. 2000; Márquez and Dalmaso 2003). Total plant cover is 21.9% and there exist vast open areas (Taraborelli 2006). At El Leoncito predators are mammalian carnivores with 0.21 ± 0.05 carnivores/cavy; and raptors with 0.20 ± 0.09 raptors/cavy (Taraborelli 2006).

Population and group characterization

Live trapping, tagging and recapture was the method used, setting Havahart traps ($25 \times 30 \times 91$ cm and $18 \times 18 \times 76$ cm; Havahart, Lititz, Pennsylvania) and Tomahawk traps ($15 \times 15 \times 60$ cm; Tomahawk live trap No 202/203, Tomahawk, USA). The traps were set up on activity paths and around burrows (Rood 1970, 1972; Hoogland 1995), they were baited with apple and vanilla extract over 7–11 consecutive days at three times of the year (time of food abundance: November–February, food shortage: April–August, and reproduction: September–March) at each study site from 2003 to 2005. We included an area of 2.1 ha in El Leoncito and another one of 2.7 ha in Ñacuñán.

Individuals were identified with metal ear tags $0.6 \times 0.2 \times 0.05$ cm and coded with numbers (National Band and Tag Co. Newport, USA) and/or plastic tags $0.8 \times 0.5 \times 0.1$ cm of different colours (Mini-Rototag, Dalton Continental, Bocholt, Germany), and their hair was stained with gentian violet on different body parts according to sex and age, making diverse drawings on them, for example circles, squares, vertical or horizontal lines, letters, etc. (Cassini 1989; Branch 1993; Meserve et al. 1993; Hoogland 1995). Sex, age, body weight and reproductive condition were determined for each individual. Reproductive condition was assessed in females by checking whether or not they were pregnant, whether they were lactating based on the presence of milk in mammary glands, whether they had experienced previous parturitions on account of greater nipple development (long nipples), presence or absence of vaginal plug, perforated or semi-perforated vagina. And testis development, abdominal or scrotal testes, was assessed in males.

Behaviour samplings

Behaviours were described by using focal samplings (continuous focal, Altman 1974; Martin and Bateson 1993; Lehner 1996). Observations were made with binoculars (40×80), tape-recorded (using voice) from an observation tower 2 m high and 30–50 m away from the burrows. They were taken from 8:00 to 12:30 h and from 15:00 to 20:30 h over 3–4 days at the three times of the year for each study site. Observations were shifted among cavies that were alone or accompanied by only one more individual of the group (combination between individuals of a same group).

Agonistic behaviour, seismic communication and sexual patterns were recorded. These behaviours were defined as follows: agonistic behaviour: an individual chased another individual; the attacker would usually thrust and jump on the chased individual, and the latter would run away (Rood 1972; Taraborelli 2006). Seismic communication: it consisted of 2–6

foot thumps per series, with 1–2 series repeated one after the other and lasting 3–21 s (Randall 1984; Taraborelli 2006). Sexual patterns: an adult male, with its flanks raised, approached an adult or juvenile female, then he followed her in a pattern of circles or eights, he also gave her small knocks on the anal region (Rood 1972; Taraborelli 2006). For comparing behaviours between sites, rates (frequency of behaviour/observation period in minutes) and proportions (duration of behaviour in minutes/observation period in minutes) were obtained (Martin and Bateson 1993). Frequency is the total number of occurrences of a given behaviour. The Index of Association (Martin and Bateson 1993) was calculated as well:

$$N_{AB}/(N_A + N_B + N_{AB})$$

N_{AB} is the number of occasions when individual A and individual B were seen together;

N_A is the number of occasions when A was observed without B;

N_B is the number of occasions when B was observed without A.

Statistical analysis

ANOVA was used to compare the mean number of adult cavies/ha and the total cavies/ha between sites, and also to test for the existence of differences in body weight between sexes at both sites. Post-ANOVA (Test de Tukey, $P < 0.05$) tests were carried out among the variables considered. The Kruskal–Wallis test was employed to search for differences in the number of individuals per group and in the number of young, juveniles and adults per group at both study sites. This same test was also used to search for differences in the mean female/male proportion per group between sites and periods of the year and in the number of young per female in each group at both study sites. ANOVA was used to compare the index of association between sites, sexes and age categories. The t -test was applied to check for differences between sites in the rate of agonistic behaviour. Results are expressed as sampling mean \pm standard error.

Results

Population

Total trapping effort was calculated as trap-hours, at El Leoncito it was 23,480 trap-hours with a total of 65 individuals captured (35 adults, 22 juveniles and 8 young) and 54 recaptures; at Ñacuñán it was 22,128 trap-hours, with 12 individuals captured (7 adults, 4 juveniles and 1 young) and 7 recaptures. There were significant differences between sites in the density of cavies captured, with the number of cavies per hectare being higher at El Leoncito (7.22 ± 0.5 adults/ha; Ñacuñán 1.91 ± 0.22 adults/ha; $F = 86.99$, $df = 1$, $P = 0.0001$, $N = 12$). Significant differences also appeared between both study sites when estimating the

number of total cavies, including the young and juveniles, with the number of cavies per hectare being higher for El Leoncito ($F = 52.72$, $df = 1$, $P = 0.0003$, $N = 12$; Table 1).

Age categories could be established from morphological measures (Taraborelli 2006) and reproductive condition, the young are less than 5 months of age, juveniles are 5–10 months old, and adults are more than 10 months of age. There were no significant differences in body weight between sexes (females 253.57 ± 6.98 g; males 238.18 ± 9.13 g; $F = 0.47$, $df = 1$, $P = 0.4962$, $N = 77$), pregnant females reached 345 ± 11.25 g in body weight. Sexual dimorphism, calculated as male body weight/female body weight, was 0.94 for both populations (Table 1).

Social group

Groups at El Leoncito were formed by a higher number of individuals than groups at Ñacuñán (Table 1; Kruskal–Wallis test, $H = 6.62$, $df = 1$, $P = 0.0093$, $N = 10$) and there were no differences among the times sampled (Kruskal–Wallis test, $H = 2.3$, $df = 5$, $P = 0.7706$, $N = 10$). On analysing group composition throughout the year, differences were found in the number of adults between sites, but not in juveniles or young (Kruskal–Wallis test, $H = 49.6$, $df = 5$, $P < 0.0001$, $N = 10$; Fig. 1). At El Leoncito the group was composed of an average number of 3.52 ± 0.34 adults (3–6); 1.04 ± 0.22 juveniles (1–4); and 0.44 ± 0.27 young (1–6). At Ñacuñán there were 1.72 ± 0.23 adults (2–3), 0.94 ± 0.3 juveniles (1–4) and 0.67 ± 0.36 young (1–6). A total of 4 social groups were defined for Ñacuñán and 6 for El Leoncito.

There were no differences in the female/male proportion per group between both study sites (El Leoncito 0.99 ± 0.16 H/M; Ñacuñán 1.39 ± 0.27 H/M; Kruskal–Wallis test, $H = 1.73$, $df = 1$, $P = 0.1826$, $N = 10$; Table 1). Nor were differences found between sites in the number of young per female within each group (Kruskal–Wallis test, $H = 0.0$, $df = 1$, $P > 0.9999$, $N = 9$). At El Leoncito the proportion was 2.19 ± 1.30 young/female, and at Ñacuñán 1.70 ± 0.54 young/female (Table 1).

By means of captures and direct observation at Ñacuñán, litters were observed in October 2004 and June 2003 and 2004, and pregnant females and males with scrotal testes as from October (Table 2). At El Leoncito the young were observed from November through March, in the time of food abundance; already by September pregnant females with vaginal plug could be found, as well as females with perforated or semi-perforated vagina and males with scrotal testes, that is to say that this would already be the start of the reproductive season. Males continued to show

Table 1. Characteristics of populations, social grouping and social behaviours at El Leoncito and Ñacuñán

Sites	Population		Social group			Social behaviours				
	Density (cavies/ha)	Sexual di-morph.	Number of individuals	Nbr. of females/male	Nbr. of young/female	Index of association	Agonistic behaviour Rate (freq/min)	Pro-portion (min/min)	Seismic comm.	Sexual patterns IM to +1F (%) 1F by +1M (%)
El Leoncito	9.92 ± 0.53	0.94	5 ± 0.42	1	2	0.15 ± 0.03	0.17 ± 0.02	0.05 ± 0.03	Yes	30–31
Ñacuñán	3.70 ± 0.68		3.33 ± 0.47			0.04 ± 0.01	0.36 ± 0.08	0.33 ± 0.08	No	

Mean \pm standard error. Freq = frequency; min = min; comm = communication; M = male, F = female, + 1 = more than one individual.

developed scrotal testes in February, but no longer in April–May when they had abdominal testes (time of resource shortage, Table 2).

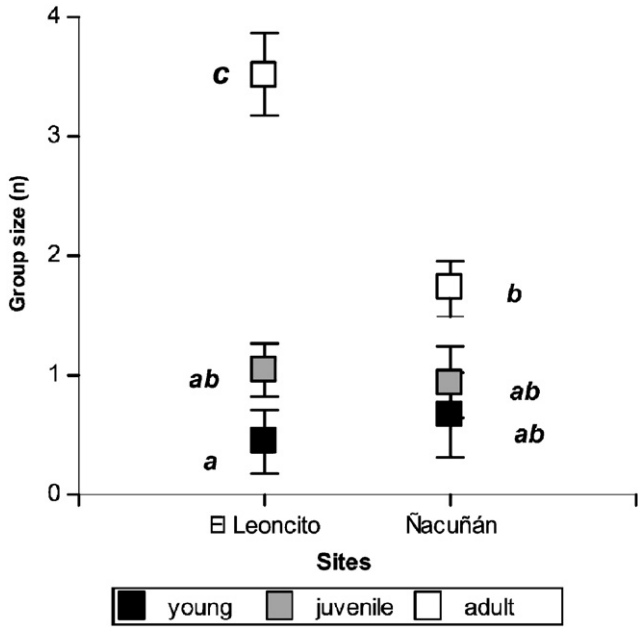


Fig. 1. Average number of young, juveniles and adults per group across the year for both study sites. Mean \pm standard error. a, b, c indicate significant differences (Tukey test, $p < 0.05$)

Behaviour

The index of association among individuals was significantly higher at El Leoncito (maximum of 0.64, at Ñacuñán maximum of 0.11; $F = 6.74$, $p = 0.0122$, $df = 1$, $N = 61$; Table 1). Moreover, the index of association at both sites was higher among the young than among adults ($F = 8.5$, $p = 0.0006$, $df = 2$, $N = 61$), for example the index of association among the young was 0.2 ± 0.05 (0.2–0.64), between adults and young it was 0.09 ± 0.02 (0.09–0.52), and among adults 0.04 ± 0.01 (0.04–0.13). There were no differences in index of association between adult males and young, or between adult females and young ($F = 1.01$, $p = 0.3262$, $df = 1$, $N = 25$) at either site. No differences in association index were found between sexes (male with male, female with female, and male with female; $F = 0.01$, $p = 0.989$, $df = 2$, $N = 56$).

Rate and proportion of agonistic behaviour were significantly higher at Ñacuñán (rate $T = -2.81$; $p = 0.018$, $N = 14$; proportion $T = -2.92$; $p = 0.015$; $N = 14$; Table 1). At El Leoncito this behaviour was observed in the reproductive season, from one male to another male from a different burrow; at Ñacuñán records correspond to times of food shortage and abundance, also between males from different burrows. With respect to seismic communication, it was only recorded at El Leoncito at the time of food abundance for solitary male and female adults, juveniles and young (Table 1).

Table 2. Time of abundance of cavies (with litters; gray line); of reproduction (dotted line); of food abundance (long-dashed line), and of food shortage (black line) at both sites

Sites	Jan	Febr	Mar	Apr	May	Jun	Jul	Aug	Sept	Oct	Nov	Dec
El Leoncito	[Gray line: abundance of cavies (with litters)]											
	[Dotted line: reproduction]											
	[Long-dashed line: food abundance]											
	[Black line: food shortage]											
Ñacuñán	[Gray line: abundance of cavies (with litters)]											
	[Dotted line: reproduction]											
	[Long-dashed line: food abundance]											
	[Black line: food shortage]											

Sexual patterns on both sites occurred between adult males and females, or between adult males and juvenile females. About 30–31% of the sexual pursuit involved one male and more than one female of the social group, and 30–31% of the females were sexually chased by different males from the same social group to which they belonged (Table 1).

Discussion

The number of adults sharing a burrow system is a fundamental feature of group living which is thought to be causally linked to numerous other aspects of social behaviour (Sherman et al. 1995). In particular, the degree of reproductive and behavioural specialization among individuals appears to increase with group size, leading to the general perception that species with larger groups are more socially “complex” (Lacey 2000). Ecological limitations would be affecting various aspects of caviés. For example, El Leoncito is an arid scrubland with higher climate harshness, marked temperature ranges for its being at 2484 masl, with longer periods of low temperatures, lower plant availability (cover and richness) for refuge and foraging (Taraborelli 2006), less amount of food because *Larrea nitida* (75–85% in the diet) has a low nitrogen percentage and a high fibre percentage compared to the diet of the population at Ñacuñán where animals select *Prosopis flexuosa*, which contains a high nitrogen percentage, less fibre and a higher amount of soluble carbohydrates (Sassi et al. 2007). On this harsh site of the arid Monte desert we found caviés of smaller body size than those of the population at Ñacuñán (semiarid scrubland), with social groups formed by a higher number of individuals than at Ñacuñán (5–6 and 3–4, respectively, with more adults at the former site). The fact that caviés congregate underground during the night and maintain stable associations confirmed that this species nests communally, and suggested that nesting associations represent distinct social units (Ebensperger et al. 2006). Extreme climate conditions could be influencing toward a higher number of individuals per social group, to be able to keep body temperature constant through group nesting (social thermoregulation) throughout the year. Physical contact would allow individuals to diminish the energetic cost of maintaining body temperature constant, so that the area/volume ratio for each individual diminishes. This would account for the larger size of social groups in the population located in the coldest habitat, where individuals exhibit smaller body size (Taraborelli 2006). Madison (1984) considered that group huddling is more efficient in a colder environment and when the number of individuals per group is high.

At both study sites the female/male proportion per social group was 1/1, with absence of sexual dimorphism

(0.94), and the sexual patterns would be indicating that the mating system is promiscuous (random mating of males and females) but not polygamous. Rood (1972) asserts that the mating system in this species, in the Monte-Espinal ecotone, is promiscuous, that females mate indiscriminately with any male. At each study site, oestrus periods in *M. australis* would be synchronized, therefore polygamy would not be favoured, as happens in *Kerodon rupestres* and *Galea spixii* (Lacher 1981; Mares and Lacher 1987). Besides, Ebensperger et al. (2006) suggest for this species that females would have multiple parturitions during the reproductive season. Scrotal testis size would also be indicating that this is a promiscuous species, because in this mating system the male, lacking exclusive access to females, develops larger testes, which allows it to increase sperm production due to sperm competition (Dewsbury and Sawrey 1984; Parker 1984; Agren 1990; Sachser et al. 1999). In a population of *M. australis* located in the Monte-Cardonal ecotone of the Villavicencio Natural Reserve (Mendoza province), Vélez (2006) found significant variations in testis weight across the year, with minimum values from March through July, a period that coincides with the time of food shortage, and with maximum values from September through January, a period that is warmer, moister and shows food abundance. Another characteristic, but this time behavioural, that would be corroborating that the mating system is promiscuous, is the sexual pursuit of more than one female of the social group by the males, and the records of females that were sexually chased by several males of the same social group. Then the mating system in *M. australis* is promiscuous in the Monte-Espinal ecotone (Rood 1972), in the Monte desert area with influence from the Puna desert (El Leoncito), in the Monte desert area with influence from the Chaco desert (Ñacuñán) and in the Monte-Cardonal ecotone (Vélez 2006). That is to say that random mating could exist in the small cavy, and that the mating system could have a strong phylogenetic component. Other additional methodologies that can be used to characterize the social and mating systems of caviés are molecular genetic surveys. Molecular genetic studies provide valuable insights into patterns of parentage, kinship within social groups and reproductive success, as well as estimates of dispersal (measured as gene flow) among populations (Lacey 2000). Such data should allow us to address many of the questions that currently drive mating systems research.

The number of young per female in each social group was the same for El Leoncito (2–4 young/female) as for Ñacuñán (2–3 young/female). But at Ñacuñán the reproductive season lasts 9 months (September–October to May) with at least two litters, and at El Leoncito 7 months (September to February–March) with more than two litters. The population peak at Ñacuñán would begin in October–November with the first litters, and

would extend until June; the young would develop while there is food abundance (primarily herbs and *Prosopis flexuosa* fruits). At El Leoncito the first litters were observed in November and the last ones in March, with the population peak also coinciding with the time of food abundance (fundamentally herbs and fruits of *Larrea nitida* and *Hoffmannseggia eremophylla*). In the reproductive period pregnant females with vaginal plug or with perforated or semi-perforated vagina were observed at both sites, as well as males with scrotal testes. At the Villavicencio Natural Reserve the male of *M. australis* shows a regression period of 5 months (disruption of spermatogenesis) that usually starts when temperature decreases and rains become scarce, in coincidence with the winter period and/or the dry season, and shows a 7-month period of activity (spermatogenesis in seminiferous tubules) from July through January, in adaptation to the time of higher food availability and lower climatic harshness, that is, spring and summer (Vélez 2006). Rood (1970, 1972) described five litters a year for the lesser cavy, with two or more young per litter, and duration of 9 months, from August to April, for the reproductive season in the south of Buenos Aires province. That is to say that, similarly to other rodent species, reproduction would be primarily seasonal and would occur in the season when temperatures are appropriate, rainfall augments, and food availability and abundance increase (Gutierrez et al. 1995; Portales et al. 2004).

In relation to the index of association among individuals, it was four times higher at El Leoncito, so association among individuals was higher at the site with higher climate harshness where social groups are composed of greater number of members. Moreover, the index of association was higher among the young than among adults, and contact interactions always occurred among individuals of the same group. Likewise, Lacey (2000) found for *Ctenomys sociabilis* that members of cohesive social groups sharing the same burrow system were more closely associated with one another than with other individuals. Also Branch (1993) registered that allogrooming occurs among all sex-age classes within a social group of plains vizcachas but not between members of different social groups. Ebensperger (2001) described that the number of social interactions in rodents increased with the number of group members.

At El Leoncito, there was a higher index of association and less agonistic behaviour among the members of the group. Only during the time of reproduction was such behaviour observed from one male to another male from a different burrow. This could be due to the fact that social tolerance, and therefore sociality, in harsh environments would be the result of a reduction of aggressiveness among individuals, which would in turn reduce the loss of water, energy and time (Hoogland 1995; Nevo 1995; Ganem

1998; Ebensperger 2001, 2003). The Olympic marmot (*Marmota olympus*) at high elevations has high sociality and tolerance in comparison with the woodchuck (*M. monax*) who is basically solitary and aggressive (Barash 1973). At Ñacuñán, records were taken at the times of food shortage and abundance (which overlap with the reproductive season), also between males from different burrows. The time of the year at which this behaviour was observed could be indicating the existence of a territorial defence and a defence of females of the same group, as it occurs at the time when individuals are sexually active. Rood (1967, 1970, 1972) asserted that aggressiveness in *M. australis* would be the major intraspecific interaction among adult males, which increases when females are in heat, and also among adult females, to put one of them away from a male, and that it could contribute to reduce population density by promoting dispersal. In this study the main interactions among individuals were peaceful, and no cavies with scars from a fight were captured, therefore no marked hierarchies in males and females were found either. Actually, in agreement with descriptions by Cassini (1989), the lesser cavy was found to have low levels of aggressiveness, which is interpreted as an adaptation to harsher environments. In contrast, *Galea* sp. and *Cavia* sp., which occupy more productive, more diverse, and less climatically severe environments (forests, scrublands, pampas), exhibit lower social tolerance within their populations (Cassini 1989). In the plains vizcacha, agonistic interactions occur more often between members of different social groups than within a group (Branch 1993).

A behaviour that would be indicating higher social complexity associated with large group size in *M. australis* at El Leoncito would be seismic communication through hind foot thumps on the ground, although their intended purpose could not be assured without enough records, and this issue would need further study. Randall (1984) asserted that this behaviour in social animals determines higher communication complexity. Considering the distances separating the burrows used by a same social group, and the time at which this behaviour was observed, i.e. the time of food abundance (coincident with the time of reproduction and population peak), displayed by solitary male or female adults, juveniles and young, this type of communication could be a sign of sexual availability and a signal of warning and territorial defence for conspecifics. Randall (1984, 1989, 2001), and Randall and Stevens (1987) hold that these seismic vibrations, produced by adult and juvenile males and females of *Dipodomys spectabilis* by foot drumming on the substrate, communicate multiple messages to their conspecifics about territoriality, competitive superiority (agonistic interactions), sexual availability or presence of predators in open areas. This rodent species

recognizes the foot thumps of neighbours and strangers. Besides, the frequency of drumming sounds is low, and low frequencies reach longer distances than do high frequencies (Gould 1983). Records of this behaviour in adults increased when population density increased and, more specifically, when the number of males in the area increased, therefore seismic communication would result in higher tolerance of neighbours and in avoidance of encounters ending in fights (Randall 1984, 1989, 2001). Most probably individuals at El Leoncito use this behaviour more than the agonistic one that entails aggressive confrontations and higher energy cost.

Sociality in *M. australis* may be influenced by ecological factors such as energy and water stress and predation risk. Future studies on social rodents need to continue to address the current selective pressures causing the formation of social groups, communal nests and mating system.

Acknowledgements

This study was partially financed by CONICET, PICT No 03281 and PIP 02884. The authors wish to express their thanks in the first place to park rangers A.J. Sandobal and M. Martinez; to A. Srur, N. Borruel, M.C. González, M.F. Carballido and V. Bauni for their cooperation in the field. To N. Horak for the English version of the manuscript. We especially want to acknowledge Dr. R. Ojeda and S.M. Giannoni for the literature provided.

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