



## Social Environment and Agonistic Interactions: Strategies in a Small Social Mammal

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Received: February 16, 2011

Initial acceptance: May 21, 2011

Final acceptance: July 3, 2011

(D. Zeh)

doi: 10.1111/j.1439-0310.2011.01956.x

### Abstract

In group-living species, the development of agonistic interactions among conspecifics may be affected by socio-ecological factors, such as size and composition of social group, and availability of nests and food. We analysed the importance of size and composition of social groups on agonistic interactions among males in the Southern mountain cavy (*Microcavia australis*). We made behavioural observations in four social groups of different size and composition. We recorded two types of agonistic interactions: agonistic displays and direct agonistic behaviours; both types increased in the breeding season. A social group composed of a high number of males was associated with high frequency of agonistic displays. Direct agonistic behaviours were also influenced by the interaction of season and number of males per social group and number of females per social group. Agonistic interactions were also recorded among males of different social groups in the breeding season. Agonistic displays were most frequent among males of the same social group, whereas direct agonistic behaviours were most common among males of different social groups. These results suggest that social factors affect agonistic interactions among males of Southern mountain cavy and that in a conflict situation, males develop different strategies, such as increased frequency of agonistic behaviours in breeding season and intragroup cooperation for defence of oestrous females.

### Introduction

Social groups can be described as a network of individuals connected by interactions (Wasserman & Faust 1994) that facilitate both cooperation and competition among conspecifics (Kutsukake 2009). Competitive interactions arise due to competition for limited resources, such as food and reproductive opportunities (Kutsukake 2009). Competitive interactions include agonistic encounters among conspecifics, which are inevitable in group-living species (Emlen 1982). Agonistic encounters occur both in males (Benson & Basolo 2006; Gromov 2007) and in females (Giovenardi et al. 2000; Barley & Coleman

2010) in different conflict situations where the individuals display physical contact between them.

In a social group, agonistic interactions can be influenced by socio-ecological factors, such as size and composition of the social group and availability of nests and food (Ebensperger 2001). Several studies have shown the effects of environmental conditions on the size and composition of social groups and the influence of these factors on agonistic interactions (Barash 1973; Cassini 1989; Schwarz-Weig & Sachser 1996; Ebensperger 2001, 2003; Taraborelli & Moreno 2009). In mammals, particularly in rodents, these factors can cause adaptive changes in behaviour and, when acting together, they can influence

the complexity of interactions among individuals (Gromov 2007).

For males, the access to reproductive females is an important factor that affects inclusive fitness (Emlen & Oring 1977). In males living in social group, the number of females present in that group strongly affects male–male agonistic interactions (Lacey 2000). Agonistic interactions always involve high energy and time costs (Hoogland 1995), and in harsh environments, such as deserts, these costs are increased (Nevo 1995; Ebensperger 2001, 2003). Thus, any mechanism to reduce these costs would be beneficial. One strategy for males to reduce costs is to be aggressive only when the defence of females or other scarce resources (e.g. territory) is beneficial (Schneider 2005). Among males, another strategy is deciding whether to be alone or with others in a conflict situation by assessing the energy costs of aggression (Olson 2009; Olson & Blumstein 2009). For example, some mammals show seasonal changes in agonistic interactions in response to the presence or absence of females in oestrus (Schneider 2005). Other species, such as Barnacle goose (*Branta leucopsis*), show agonistic interactions between different intensities and duration in which individuals are involved to different degrees (Black & Owen 1989). In other species, males show coalitions, i.e. cooperation between two or more individuals against a third one during an aggressive or competitive encounter (Harcourt 1992). Coalitions may be formed to increase protection from predators (*Xerus inauris*; Waterman 1997) to increase hunting success (*Lutra canadensis*; Blundell et al. 2004) or to defend a territory or increase access to reproductive females (*Marmota flaviventris*; Olson & Blumstein 2009, 2010). The latter are reproductive coalitions that may drive indirect fitness benefits in multimale groups (Olson & Blumstein 2010). Thus, the strategy of each group member is selected in terms of a complex feedback system that is affected by the social strategies of the other group members (Kutsukake 2009).

In rodents, behaviour has been repeatedly studied under laboratory conditions (Ruffer 1968; Schneider 2005; Pan et al. 2010; Zenuto 2010) or seminatural conditions (Rood 1970, 1972; Lacher 1981; Zenuto et al. 2002; Ensminger & Meikle 2005). Behavioural studies under natural conditions, however, are scarce because many rodent species are small, cryptic and/or nocturnal, making behavioural observations difficult (Wolff 1989).

The Southern mountain cavy (*M. australis*) is a rodent species suitable for behavioural studies in its

natural habitat, because its diurnal habits and medium-size body (200 g) facilitate behavioural observations. Southern mountain cavies live in burrow systems but are active aboveground during the day; hence, trapping, marking and observation of individuals are relatively easy. This group-living species (Rood 1967, 1972; Taraborelli & Moreno 2009) is widely distributed in Argentina, from Jujuy south to Santa Cruz (Redford & Eisenberg 1992), specifically in dry shrubland areas and sandy scrublands (Tognelli et al. 2001). The earliest studies on the social behaviour of Southern mountain cavy in seminatural conditions involved a population located in a semiarid habitat (Monte-Espinal ecotone) (Rood 1967, 1970, 1972). According to that author, Southern mountain cavy exhibits a group social structure with low-to-moderate levels of aggressiveness. Females generally display amicable social interactions; they may share home bushes and nurse other females' offspring indiscriminately. Males exhibit agonistic behaviours among adults to establish hierarchies; this behaviour is more frequent when females are in oestrus. In this rodent species, agonistic behaviour is the principal intraspecific force tending to reduce density by promoting dispersal (Rood 1972). In a population of Southern mountain cavy located in an arid scrubland with very harsh climatic conditions, low frequency of agonistic interactions was observed among the members of the same and different social groups (Taraborelli & Moreno 2009). These authors suggest that low aggressiveness among individuals of this population may be explained by ecological factors, such as risk of predation and harsh climate. Behavioural studies conducted on Southern mountain cavy both under seminatural (Rood 1967, 1970, 1972) and free-living conditions (Taraborelli & Moreno 2009) described social interactions among individuals in relation to environmental conditions, without evaluating agonistic interactions among males and how these interactions are influenced by the social environment.

Here we analysed the importance of social factors, such as size and composition of social groups, in agonistic interactions among Southern mountain cavy males. Specifically, the following questions were addressed: Do agonistic interactions between males change in the breeding and non-breeding seasons? How does group size affect agonistic interactions between males? How does the number of males and females in a social group affect male–male agonistic interactions? Do males show the same agonistic behaviour in intragroup and intergroup interactions?

## Materials and Methods

### Subjects

We studied agonistic interactions using live trapping, tagging and recapture. We captured a total of 83 individuals (47 females and 38 males) and recaptured 60% of females and 83% of males. Southern mountain cavy individuals were captured using double-door Havahart-type traps (18 × 18 × 76 cm; Havahart, Lititz, PA, USA) baited with pieces of apple. Traps were placed in active runways, usually under the canopy of creosotebush (*Larrea nitida*) and near burrow entrances for 5–10 consecutive days. Traps were opened in morning and evening hours, when these mostly diurnal animals were typically active aboveground (Rood 1970). We avoided trapping animals around noon and during early afternoon hours to minimize the chance of trapped individuals dying of overheating. Traps were checked approximately every 60 minutes. The study was conducted in the breeding and non-breeding seasons from 2006 to 2009 (2006: Mar., June, Aug., Dec.; 2007: Mar., Apr., June, July, Sep., Dec.; 2008: Apr., May, Aug., Dec.; 2009: May). In the Southern mountain cavy reproduction occurs from Aug. to Mar. (breeding season) and the non-breeding season lasts from Apr. to July (Rood 1970, 1972; Taraborelli & Moreno 2009; own unpublished data). We recorded sex, age and body weight of all individuals captured, and we determined reproductive activity based on the appearance of external genitalia. We classified the reproductive condition in males (active or inactive) based on the position of testes (scrotal and abdominal, respectively). In females, we assessed the reproductive condition by checking whether they were pregnant, whether they were nursing (based on the presence of milk in mammary glands), whether they had experienced previous parturitions (based on long nipples), whether they had a vaginal plug and whether the vagina was perforated or semi-perforated. Individuals were identified with metal ear tags (0.6 cm × 0.2 cm × 0.05 cm) and with different drawings made by staining their hair with gentian violet on different body parts according to sex, e.g. circles, squares, vertical or horizontal lines, letters, etc. (Cassini 1989; Branch 1993; Meserve et al. 1993; Hoogland 1995).

### Study Area

The study population was located in El Leoncito National Park (31°47' S, 69°17' W, San Juan Prov-

ince, Argentina), a protected area belonging to the Argentine National System of Protected Zones. The climate is arid (cold and dry), with mean annual precipitation not exceeding 100 mm; winter precipitation (Apr.–Aug.) reaches 75 mm in the form of snow and hail and summer rainfall (Nov.–Dec.) is below 10 mm (Le Houerou 1999). Within the park, the study site was Ciénaga del Medio (2484 m asl), an area located in a sector of the Monte desert that is influenced by the Puna desert. The site is characterized by a flat area surrounded by low hills and dominated by scattered thorn bush associations, mostly of creosotebush with low cover (Taraborelli 2007). The herbaceous layer is lower than 10 cm in height (Márquez et al. 2000; Márquez & Dalmaso 2003), and total plant cover is 21.9%, with vast open areas (Taraborelli 2007).

### Composition of Social Groups

The composition of social groups was determined with capture–recapture data and by direct observation (which provided information on spatial location of the groups). We defined a social group as a group of individuals that remained together and interacted more with each other than with other conspecifics (Sobodchikoff & Shields 1988; Bowyer et al. 2001). Thus, we counted the number of males and females in each social group on each sampling occasion. In the breeding season, we considered marked and unmarked animals for direct observations because sex could be recognized with the naked eye (i.e. males developed easily observable large scrotal testes). In the non-breeding season, we considered only marked individuals because we could not distinguish sex of individuals with the naked eye.

The home range size was estimated with capture–recapture data of individuals of each social group between 2006 and 2009 using the minimum convex polygon method (Jennrich & Turner 1969).

### Behavioural Observations

We made behavioural observations of 32 Southern mountain cavy adult males from 800 to 1300 h and from 1600 to 2000 h over 4 consecutive days in the breeding and non-breeding seasons during each sampling month from 2006 to 2009. We used binoculars (10 × 50) and tape recorder from a 2-m-high observation tower that was 10–30 m away from the animals to minimize disturbance. Behaviours were described using focal sampling (continuous focal sampling, Martin & Bateson 1993; Lehner 1996) for

5 min at 60-min intervals to give independence to the data; only adult animals were considered. Behavioural observations included animals of the same social group and of different social groups (intragroup and intergroup interaction, respectively). We recorded the frequency of agonistic behaviours following the classification used by Rood (1972) and Taraborelli (2007) for this species. Agonistic behaviours were recorded as push the head, attack, chase, fight, bite, and withdraw.

### Statistical analysis

We used a non-parametric Kruskal–Wallis test to analyse the size and composition of social groups (Sokal & Rohlf 1995). For the behavioural data, we obtained rates of agonistic behaviour (frequency of behaviour/minutes; Martin & Bateson 1993), and a generalized linear mixed model (GLMM), with Poisson distribution, provided in R 2.10.0 (R Development Core Team 2009) software was used to identify the factors that affect agonistic behaviour in Southern mountain cavy males. We used number of males and females in each social group (covariates) and season (fixed factor with two levels: breeding and non-breeding seasons). We also considered the interactions among these fixed factors. We included group as a random factor and male identity as nested in group. Individuals were not considered as repeated measures, because there were not observations of the same individual in all months during the study period. Several models were compared considering all combinations of the predictors mentioned earlier. Akaike information criterion (AIC) was used as a measure of the fit of a model (Burnham & Anderson 2002). The comparison between models was based on the values  $\Delta$ AIC (difference between the model with the minimum AIC value and the model *i*) starting with the model with the lowest value of AIC. The models with a  $\Delta$ AIC value between 0 and 2 are the ones that best fit the response variable (Burnham & Anderson 2002). For interactions among males of different groups, we used a general linear model (GLM), and the significance of each fixed effect was assessed using Wald statistics test (Sokal & Rohlf 1995). Results are expressed as mean  $\pm$  standard error.

### Results

The study covered a 1.8-ha area and included a total of 1095 minutes of behavioural observation of four social groups of the Southern mountain cavy

indicated as A, B, C and D, made in the breeding and non-breeding seasons from 2006 to 2009. The home ranges of each social group were different (Kruskal–Wallis test;  $H = 23.17$ ,  $df = 3$ ,  $p < 0.0001$ ; Table 1). Social group D differed in size (Kruskal–Wallis test;  $H = 28.48$ ,  $df = 3$ ,  $p < 0.01$ ) and composition: number of males (Kruskal–Wallis test;  $H = 35.52$ ,  $df = 3$ ,  $p < 0.001$ ) and number of females (Kruskal–Wallis test;  $H = 11.33$ ,  $df = 3$ ;  $p < 0.01$ ; Table 1). Group C had the highest number of males, and group A had the highest number of females (Table 1).

In the four social groups, we recorded a total of 120 agonistic interactions among males, which we classified into two types: agonistic displays and direct agonistic behaviour. Agonistic displays, which included threat (push the head) and withdraw, did not involve contact between individuals. On the other hand, direct agonistic behaviours were more aggressive and involved contact between males. In this category, we recorded attack, chase, fight and sometimes bites. We found agonistic interactions among males in the breeding and non-breeding seasons. We recorded a total of 54 agonistic displays (35 and 19 in the breeding and non-breeding seasons, respectively) and 66 direct agonistic displays (43 and 23 in the breeding and non-breeding seasons, respectively).

We built 10 models to evaluate the effect of size and composition of social group on agonistic display and direct agonistic behaviour of Southern mountain cavy males (Tables 2 and 3). GLMM analysis based on  $\Delta$ AIC revealed that season and males per social group were the most important factors affecting agonistic display in males of Southern mountain cavy in El Leoncito National Park (Table 2). The interaction between number of males per social group and season significantly explained agonistic displays in the Southern mountain cavy. Agonistic displays were recorded in the breeding and non-breeding seasons in all social groups but were less frequent in the

**Table 1:** Mean ( $\pm$ SE) of number of individuals per social group, number of males and females of each social group and size of the home range of each social group

Social group	Size of social group	Number of males	Number of females	Home range (m <sup>2</sup> )
A	13.10 $\pm$ 0.60	5.64 $\pm$ 0.30	7.10 $\pm$ 0.40	1515.77 $\pm$ 30.04
B	10.00 $\pm$ 0.23	4.28 $\pm$ 0.23	5.23 $\pm$ 0.32	1103.46 $\pm$ 43.30
C	14.87 $\pm$ 0.67	8.56 $\pm$ 0.44	6.12 $\pm$ 0.49	931.22 $\pm$ 39.98
D	11.76 $\pm$ 0.65	6.53 $\pm$ 0.62	4.92 $\pm$ 0.38	1010.25 $\pm$ 45.78

**Table 2:** Model selection, based on AIC comparison, of a generalized linear mixed model (GLMM) describing the agonistic display in Southern mountain cavy males

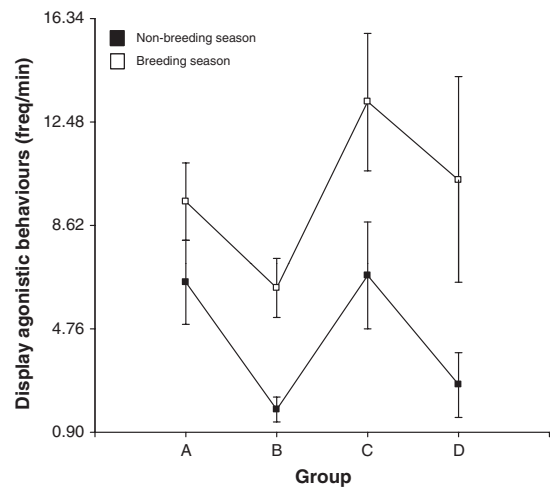
Models	AIC	ΔAIC
Season × number males/social group	<b>123.40</b>	<b>0</b>
Season + number males/social group	126.50	3.10
Season + number females/social group	128.27	4.87
Season + number males/social group + number females/social group	128.49	5.09
Number males/social group + number females/social group	133.59	10.19
Number males/social group	133.91	10.51
Season	139.80	16.4
Season × number females/social group	140.74	17.34
Number females/social group	175.46	52.06

**Table 3:** Model selection, based on AIC comparison, of a generalized linear mixed model (GLMM) describing the direct agonistic behaviour in Southern mountain cavy males

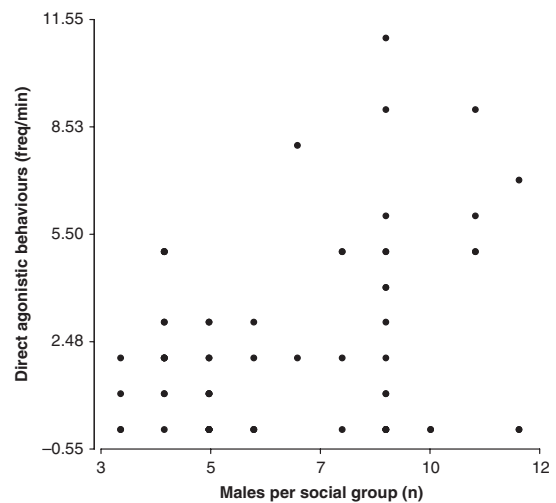
Models	AIC	ΔAIC
Season × number males/social group	<b>151.20</b>	<b>0</b>
Season × number females/social group	<b>151.98</b>	<b>0.78</b>
Season + number males/social group + number females/social group	153.35	2.15
Season	153.70	2.50
Season + number females/social group	153.98	2.70
Season + number males/social group	155.69	4.49
Number males/social group + number females/social group	165.29	14.09
Number females/social group	166.33	15.13
Number males/social group	178.33	27.13

non-breeding season. We recorded 35 interactions of agonistic display between males in the breeding season and 19 interactions in the non-breeding season. The highest frequency of agonistic displays was observed in the breeding season in social groups with a high number of males (Fig. 1). In the social groups with high number of individuals, males showed a higher frequency of agonistic displays in the breeding season.

Generalized linear mixed model analysis based on ΔAIC of direct agonistic behaviour revealed that season, males per social group, females per social group were the factors affecting direct agonistic behaviour in males of Southern mountain cavy (Table 3). Thus, direct agonistic behaviours were influenced by seasons and the interaction of season with number of males per social group and the interaction with



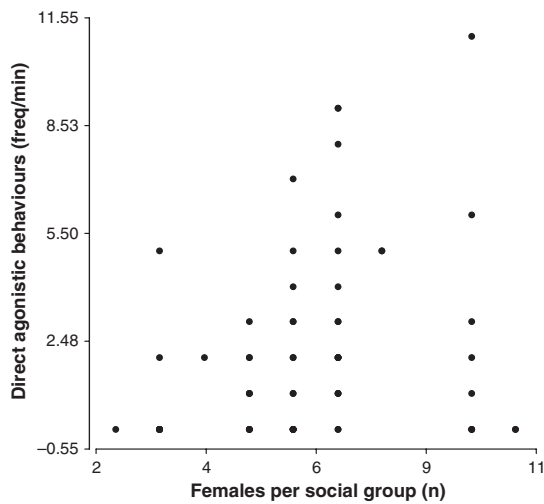
**Fig. 1:** Frequency of agonistic displays (freq/min) in Southern mountain cavy males considering only males in the four social groups in The Leoncito National Park.



**Fig. 2:** Relation between frequency of agonistic behaviours (freq/min) and Southern mountain cavy males per social group.

number of females per social group (Table 3). In the breeding season, a high number of males in a social group were associated with a high frequency of direct agonistic behaviours (Fig. 2). In the same season, a high number of females in a social group were associated with a high frequency of these behaviours (Fig. 3).

Agonistic interactions were also recorded among males of different social groups: 67% corresponded to intragroup interactions and 33% to intergroup interactions. Of a total of 38 intergroup interactions recorded in the breeding season, 25 involved three

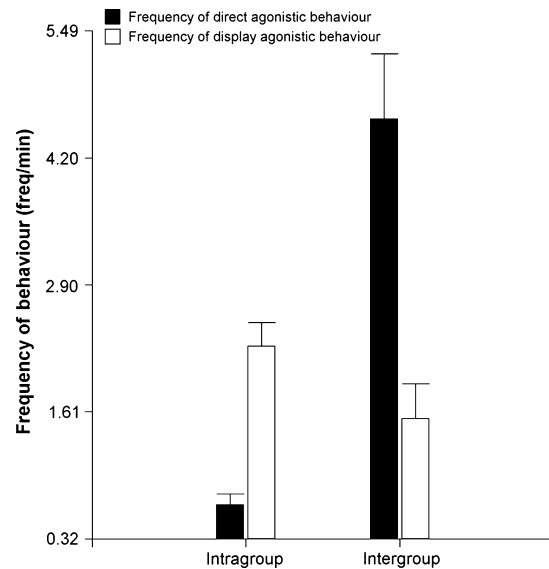


**Fig. 3:** Relation between frequency of agonistic behaviours (freq/min) and Southern mountain cavy females per social group.

males (two males of one social group versus one male of another social group). We found that frequency of direct agonistic behaviours was different between intragroup and intergroup interactions (0.66 freq/min and 4.59 freq/min, respectively; Wald test = 208.67;  $p < 0.01$ ). Frequency of agonistic displays was also different between intragroup and intergroup interactions (2.28 and 1.54 freq/min, respectively; Wald test = 7.30;  $p < 0.01$ ). Agonistic displays were most frequent among males of the same social group, whereas direct agonistic behaviours were most common among males of different social groups (Fig. 4).

## Discussion

Among males, agonistic interactions arise due to competition for resources e.g. territory, food and receptive females (Clutton-Brock 1989; Schneider 2005). In an agonistic interaction, the energy expended depends on the value of the resource and the probability of an individual winning it (Riechert 1988). Agonistic behaviours are particularly expensive in terms of energy costs and missed courtship opportunities, and risky in terms of injury and predation (Jakobsson et al. 1995; Hack 1997; Kelly & Godin 2001). Thus, the high costs of these interactions could determine an individual's strategies, and any mechanism to reduce these costs will be beneficial. In males, a strategy to reduce costs is to increase agonistic interactions only during the period when the defence of a resource is a benefit. In many species, males have agonistic behaviours only in the



**Fig. 4:** Frequency of displays and direct agonistic behaviours (freq/min) among males in intragroup and intergroup interactions.

breeding season, when females are receptive, and reduce these behaviours during the non-breeding season to save energy (Schneider 2005). In our study, agonistic behaviours in males of Southern mountain cavy occurred in both seasons and were more frequent during the breeding season. Males of South African striped mouse (*Rhabdomys pumilio*) were also more aggressive during the breeding season, and this behaviour was interpreted as a strategy to defend access to fertile females (Schneider 2005). In Southern mountain cavy, Rood (1967, 1970, 1972) and Taraborelli (2007) also found agonistic interactions among males but only in the breeding season. The presence of oestrous females may account for agonistic interactions among males in the breeding season but not outside it. Our results on agonistic interactions in both seasons could be explaining inevitable competitive relations in group-living species (Emlen 1982). In high-density populations, agonistic interactions are also expected to arise due to competition for access to resources. We found a higher population density than those reported by Rood (1970) and Taraborelli (2007); indeed, the population studied in the present work was about five times greater than that evaluated by Taraborelli (2007) in a site close to the present study area (Rood 1970: 24.4 cavies/ha, Taraborelli 2007: 9.9 and 47.8 cavies/ha in this study).

In group-living species, social and ecological factors strongly influence agonistic interactions (Gromov 2007). In the present study, we focused on the

effect of social environment (size and composition of social group) on agonistic interactions of Southern mountain cavy males, and the development of strategies to deal with the conflict. In the study area, we found social groups of different size and composition, with a maximum of eight males and seven females plus the offspring. Total agonistic interactions among males were mainly affected by the number of males composing the social group, and the frequency of agonistic interactions was higher in groups with a higher number of males, mainly in the breeding season, than in groups with a smaller number of males. This could explain the low frequency of agonistic interactions restricted to the breeding season found by Taraborelli (2007), who recorded small social groups composed of 2–3 males and 2–3 females, with low frequency of agonistic behaviours among males. In a semicaptive small social group composed of six males, including subordinate males, and two females, Rood (1967) found a strong agonistic interaction also restricted to the breeding season. Agonistic interactions are likely to arise by competition among males for a low number of females. Rood (1967) also found that agonistic interactions among males results in a straight-line dominance hierarchy.

In the domestic guinea pig (*Cavia aperea*), a caviid species, males changed their social relationships in response to the number of females in the group. When the number of females was low, a single male was involved in defence and the groups were composed of a dominant male and two females. However, when the number of females increased, several subordinate males cooperated with the dominant male in defence of females (Sachser 1986).

The costs of agonistic interactions can be severe and may cause social stress, injury and even death (Marchant et al. 1995; Turner et al. 2006). Males could evaluate these interactions and decide whether to participate or not in such interactions (Parker & Rubenstein 1981; Briffa & Elwood 2001, 2005). Therefore, when risks of injury and energy expenditure are high, the intensity of agonistic interactions could vary with the behaviours that the individuals perform (Black & Owen 1989). Thus, two types of agonistic behaviours can be found: direct agonistic behaviours and agonistic displays. The former involve physical contact and pose a greater risk of injury than displays or those behaviours that do not involve contact (Riechert 1978; Clutton-Brock et al. 1979). In Southern mountain cavy, we found both types of agonistic behaviours, but their frequency varied between the breeding and non-breeding sea-

sons, and in the interactions among males from a single social group and from different social groups. In intragroup interactions, males showed a greater amount (frequency) of agonistic displays and direct agonistic behaviour in the breeding season than in the non-breeding season. This variation in type of behaviours between seasons could be a response to the presence of females in oestrus and perhaps to the maintenance of dominance hierarchies outside the breeding season.

In species living in large groups, dominance hierarchies are established as a strategy to save time and energy. Energy saving is important in harsh environments, where aggression among individuals needs to be reduced to prevent loss of water, energy and time (Hoogland 1995; Nevo 1995; Ebensperger 2001, 2003). The high-elevation population of Southern mountain cavy studied lives under conditions of relatively harsh climate (extreme cold and snowy weather in winter, and warm and dry conditions during summer) and low plant availability (cover and richness) for refuge and foraging (Taraborelli 2007). The vegetation is mainly composed of creosotebush, which provides food of low nutritional quality due to its low nitrogen and high fibre content (Sassi et al. 2007). Under these conditions, the large social groups of Southern mountain cavy could be supported by the establishment of dominance hierarchies. Although in this study we were unable to determine presence of dominance hierarchies among males of a social group, increased frequency of agonistic displays in large groups could be indicative of the presence of hierarchies, as reported by Rood (1970) for another population of the same species.

On the other hand, in intergroup interactions, we found high frequency of direct agonistic behaviours. These interactions generally involved three individuals (two males of one social group versus one male of another social group), which could be indicating coalitions among individuals of the same group.

Coalitions may also be formed to defend a territory, increase access to reproductive females or defend reproductive females (Caro & Collins 1987; Doolan & Macdonald 1996; Olson & Blumstein 2009). However, coalitions are difficult to explain because the main resource generally sought by males is successful fertilization, which is non-divisible; thus, it would appear to be most beneficial for a single male to attempt to monopolize as many females as possible and to be intolerant to the presence of competitor males (van Hooff & van Schaik 1992). However, to have access to females, males depend

on the spatial and temporal distribution of receptive females; in turn, female distribution depends on variation in the distribution of resources, such as vegetation (Emlen & Oring 1977). Vegetation in the study area is a creosotebush community with 90% of *L. nitida*, low vegetation cover (16%) and random spatial distribution (own unpublished data). In this area, the home range size of the Southern mountain cavy is 1166 m<sup>2</sup> for females and 1311 m<sup>2</sup> for males, and both move among an average of 17 patches of vegetation (own unpublished data). In domestic guinea pig, in south-eastern Brazil, Asher et al. (2004) found small social groups composed of one adult male and one to two adult females with small home ranges (females: 549 m<sup>2</sup> and males: 880 m<sup>2</sup>). In these social groups, males regularly marked their females with anal glands and chased intruding males when they approached one of the females. In Southern mountain cavy, the high numbers of females in the social groups, the large home range of females and the long oestrous cycle (15 d) compared to others rodents (e.g. *Ochotona curzoniae* and *Hydrochoerus hydrochaeris* with 1 and 0.63 d of oestrous duration respectively, Olson & Blumstein 2009) hinder monopolization of females by a single male. Therefore, coalitions may be a strategy to increase reproductive opportunities. In severe weather, individuals may huddle together to conserve body heat (Ebensperger et al. 2006) and they practise mutual grooming (Rood 1970), and indiscriminate nursing has been commonly observed both in wild and in captive animals (Rood 1972). Thus, reproductive coalition appears to occur in the study population of Southern mountain cavy males.

Coalitions can range from rudimentary to complex along a continuum. Olson & Blumstein (2009) propose three key traits to define coalitions: mutual tolerance, collaboration of group members (against inter- or intragroup conspecifics) and preference for certain partners over others during intragroup competition. In males of Southern mountain cavy, we found two of these key traits: mutual tolerance and collaboration. Mutual tolerance can occur whenever a social group has two or more males and when individuals coexist both spatially and temporally (Olson & Blumstein 2009, 2010). In such cases, males must tolerate each other to the point that neither is forced to leave the group. Environmental constraints might influence formation of multimale groups. Patch availability is important for protection from predators in a burrow system (Armitage 1999; Blumstein et al. 2006). Saturation of patches can occur either when a local patch is fully occupied or when

several families occupy a large habitat patch (Armitage 1996). In the Monte Desert, the Southern mountain cavy digs burrow systems in plants with low branches that offer protection from predators (Tognelli et al. 1995). In the study area, the burrow systems are associated with creosotebush patches of 23.24 m<sup>2</sup>, leaving few patches vacant (own unpublished data). Thus, the few vacant patches available may compel males to remain in social groups, leading to the formation of multimale groups.

Collaboration occurs when two or more individuals work together to increase their potential access to reproductive females (Olson & Blumstein 2009). In Southern mountain cavy, collaboration within a group can occur when individuals support one another against another group member to maintain or raise their position in a dominance hierarchy (Silk 1999), or against conspecifics of different social groups. We observed that two males of a social group expelled a male of another social group by direct agonistic behaviour. This collaboration is likely to occur in the large home range of females where a single male is not able to control access to all females. Thus, collaboration among males of the same social group would facilitate control of females. By forming multimale groups, males are expected to increase their reproductive success because they gain access to a higher number of females or are able to compete for females with the help of male group-mates (Emlen & Oring 1977; Clutton-Brock 1989). According to the key traits described by Olson & Blumstein (2009), we defined the Southern mountain cavy as moderate coalition former.

The agonistic behaviours of Southern mountain cavy males seem to be affected by both the social and ecological environments. Because of the interrelation between both factors, individuals develop complex behaviours that enable them to cope with the prevailing conditions. Under harsh environmental conditions, as in desert environments, where the Southern mountain cavy occurs, different types of strategies in a conflict situation are used. Accordingly, the highest frequency of agonistic interactions in the breeding season and cooperation between males of the same social group could allow males to save energy and increase access to oestrous females, and therefore to increase their reproductive success.

### Acknowledgements

We are indebted to the Sistema de Parques Nacionales de Argentina, particularly to park rangers of Parque Nacional El Leoncito, for providing all



the necessary facilities during fieldwork. N. Andino, L. Reus and Campos, V. received a research grant from the National Council for Science and Technology (CONICET), S.M. Giannoni is CONICET researcher. We thank an anonymous reviewer for his/her suggestions. We acknowledge and are grateful for the help received from all the members of the INTERBIODES. Jorgelina Brasca assisted us with the English translation. Funding was provided by a CICITCA-UNSJ 21/E626 Grant #1060499 (SG).

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