

Vigilance and foraging behaviour in a social desert rodent, *Microcavia australis* (Rodentia Caviidae)

PAULA TARABORELLI

Grupo de Investigaciones de la Biodiversidad, Instituto Argentino de Investigaciones de Zonas Áridas, CONICET, Av. Ruiz Leal s/n, Parque General San Martín, Mendoza, CC 507, CP 5500 Mendoza, Argentina
(E-mail: paulataraborelli@gmail.com)

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Microcavia australis is a social species, diurnal and native to South America. This rodent provides an opportunity for analyzing the relationship between group size and the vigilance and foraging behaviour of the lesser cavy in two populations inhabiting two risky sites (El Leoncito and Ñacuñán). The study should reveal the mechanisms used by *M. australis* to reduce predation risk (many-eyes effect, cooperative vigilance or/and simple dilution of per capita risk). Continuous focal sampling was conducted at times of food shortage, food abundance and reproduction, from 2003-2005. A negative correlation was found between number of individuals per group and frequency of individual vigilance, and a positive correlation between rate and proportion of total group vigilance and the number of individuals per group of both sites. There was no correlation between the number of individuals per group and group foraging at either site. A benefit of social grouping in caviés is an increased probability of survival with group vigilance, although this implies no favourable impact on foraging activity. This should reveal an effect of group in the antipredator response, i.e. groups of larger size show lower levels of individual vigilance and improved efficiency in their vigilance behaviour. That is to say that a predator would be detected earlier when approaching a group than when approaching a solitary individual and could thus be avoided (many-eyes effect and cooperative vigilance).

KEY WORDS: vigilance, foraging, effect of group, predation risk, social rodent, *Microcavia australis*.

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INTRODUCTION

One of the most important consequences of group-living is a reduction in predation risk (ALEXANDER 1974, EBENSPERGER 2001). Social foragers could experience reduced risk of predation through several mechanisms, including (a) many-eyes effect (HOOGLAND 1981); (b) cooperative vigilance (HOOGLAND 1981, CASSINI 1989); (c) simple dilution of per capita risk (DEVENPORT 1989); (d) the selfish herd effect (HAMILTON 1971, HOOGLAND 1981, YÁBER & HERRERA 1994, ROMÉY 1997, KINLAW 1999); or (e) active group defence (BERTRAM 1978, PULLIAM & CARACO 1984, MANNING et al. 1995).

(a) The many-eyes effect enhances the ability of individuals to detect predators (HOOGLAND 1981). Individuals benefit from group vigilance, which reduces per capita vigilance time and increases per capita foraging time (LIMA 1995, VASQUEZ 1997). The many eyes effect is an important benefit of social foraging in some North and South American semi-fossorial rodents. In *Cavia* sp. (Caviidae) the percentage of time that each individual spent in vigilance was lower when the group size was larger (CASSINI 1989), a result that has also been found for other semifossorial rodents such as *Cynomys ludovicianus* (Sciuridae) and *Octodon degus* (Octodontidae; HOOGLAND 1995, EBENSPERGER & WALLÉN 2002).

(b) Cooperative vigilance implies the shared monitoring by emitting alert calls and adopting alarm postures that trigger responses in the other individuals (HOOGLAND 1981, CASSINI 1989). CASSINI (1989) described for *Cavia* sp. the formation of feeding groups of 7-8 individuals; where the rate of alert calls and postures indicates that attention increases with the number of group members, these responses increase efficiency in predator detection.

(c) Simple dilution of per capita risk is suggested by the behaviour of prairie dogs which forage farther from the nearest burrow entrance when the density of above-ground individuals increases (DEVENPORT 1989).

(d) The selfish herd effect: individuals locating themselves such that other group members become more vulnerable to attacks (HAMILTON 1971, HOOGLAND 1981, YÁBER & HERRERA 1994, ROMÉY 1997, KINLAW 1999). The occurrence of the selfish herd effects seems to be supported by the behaviour of *Marmota flaviventris* (Sciuridae) and *Hydrochaeris hydrochaeris* (Hydrochaeridae). In these rodents, individuals located at the periphery of a group devote more time to vigilance than individuals in more central positions (ARMITAGE 1962, YÁBER & HERRERA 1994).

(e) Active group defence as seen when grouped individuals repel predators more efficiently than solitary-living animals (BERTRAM 1978, PULLIAM & CARACO 1984, MANNING et al. 1995). Other rodents use active group defence to decrease their per capita risk. Belding's ground squirrels *Spermophilus beldingi* (Sciuridae) chase weasels inside their colony (ROBINSON 1980), and the mobbing of reptile predators has been detected in *Cynomys ludovicianus* (Sciuridae, LOUGHRY 1987).

Vigilance behaviour responses are affected by biotic factors, such as plant structure and predation risk (LIMA 1987, EBENSPERGER & HURTADO 2005). Predation risk increases significantly in open areas (LIMA 1987). LIMA (1987) described that when the distance to the plant cover increases, the like-

likelihood of escaping decreases since predators prefer to attack in open areas. Therefore, the area of danger increases with distance from a refuge (TAYLOR 1998), because predation risk per time unit is higher in open places than near or under shrubs (DJAWDAN & GARLAND 1988, HUGHES & WARD 1993). Some authors report that an increase in the rate of predator attacks results in an increase in individual vigilance levels (LIMA 1987, ELGAR 1989, SUNDELL & YLÖNEN 2004). However, the relationship between predation risk and group vigilance has not yet been studied.

The South American semi-fossorial social rodent *Microcavia australis* is an interesting species for the analysis of group vigilance. Little is known about the behaviour and ecology of this cavy. ROOD (1967) and TOGNETTI et al. (1995) have described it as a diurnal herbivore and a burrowing rodent that exhibits a group social structure with low levels of aggressiveness. It dwells specifically in arid shrubland areas and sandy scrublands (OLROG & LUCERO 1986, CANEVARI & FERNÁNDEZ BALBOA 2003). Groups are composed of several females, one or a few males, plus the young and juveniles (ROOD 1967, 1972). Each group is associated with a burrow and the groups are permanent, i.e. they are not transitory groups (TARABORELLI 2006). This cavy, alone or in a group, displays its behavioural patterns (e.g. foraging, resting) in the burrow area, under the cover afforded by trees and/or shrubs where predation risk is lower (ROOD 1967, TOGNETTI et al. 1995). When cavies are in groups they carry out several activities, such as resting, foraging, social grooming, huddling, chin-rump follow, vigilance, among others, which means that foraging together is not the sole reason for forming groups. Consequently this paper will address the issues of social groups and not foraging groups. In *M. australis*, individuals did not occupy organised locations within the groups (pers. obs.). When confronted with predators, the cavies reacted with a higher frequency of vigilance behaviour, and by fleeing towards the burrow and/or by hiding in the galleries, but not by repelling the predators (TARABORELLI et al. in press). Therefore, there is no evidence to support the above-mentioned mechanisms of the selfish herd effect nor active group defence in *M. australis*. The cavies never emitted alarm calls in response to the presence of a predator but simply responded with an alert posture (TARABORELLI 2006, TARABORELLI et al. in press).

The objective of this study was to analyze the relationship between group size and the vigilance and foraging behaviour of *M. australis* in two populations located on two risky sites (El Leoncito and Ñacuñán). The study should reveal the mechanisms used by *M. australis* to reduce predation risk (many-eyes effect, cooperative vigilance or/and simple dilution of per capita risk). The many eyes hypothesis predicts that detection ability increases with increasing group size. In this case, individuals should spend less time in vigilance and more time in foraging behaviours. To support the many eyes hypothesis, cavies in larger groups should exhibit less per capita vigilance and more per capita feeding time than cavies in small groups at both sites. The cooperative vigilance hypothesis predicts that cavies will adopt alarm postures that trigger responses in the other individuals at both sites. And the simple dilution effect predicts that predation risk will decrease with increasing group size when alertness (vigilance) and spatial location are controlled, and that the cavies will forage farther from the nearest burrow entrance when the density

of the above-ground individuals increases. The simple dilution effect will be more evident at El Leoncito, which is a site with wide open areas where the predation risk is high.

MATERIALS AND METHODS

Study areas

The study took place at two sites. Research was conducted in a population of *M. australis* in the Monte semiarid desert, in the Man and Biosphere Reserve of Ñacuñán (34°2'S, 67°58'W, 12,300 ha, 540 m a.s.l.) in the centre-west of Mendoza (OJEDA et al. 1998). The climate is warm, dry and semiarid; the mean annual precipitation is 329.4 mm, with 50% of rainfall occurring in the summer months (CABRERA 1976, ESTRELLA et al. 2001). The mesquite plant community is the most extensive and complex at Ñacuñán, composed of three plant layers, the tree layer, the shrub layer and the very species-rich herb layer (ROIG 1971); the total plant cover is 54.3% (TARABORELLI 2006). The density of cavies at Ñacuñán is 1.91 ± 0.22 adults ha⁻¹ (TARABORELLI 2006). Potential predators are diurnal raptors (*Buteo polyosoma*, *Milvago chimango*), diurnal and crepuscular mammalian carnivores (*Lycalopex gymnocercus*, *Galictis cuja*, *Conepatus chinga*, *Felis catus*) and snakes (*Bothrops ammodytoides*, CONTRERAS & ROIG 1979, OJEDA et al. 1998, TARABORELLI 2006). At Ñacuñán, raptors are the most frequently recorded predators (TARABORELLI 2006). The second population dwells in the arid Monte of El Leoncito National Park (31°47'S, 69°17'W; 76,000 ha, 2484 m a.s.l.), in the southeast of San Juan province (MÁRQUEZ 1999). The climate is cold, dry and arid, with large diurnal, nocturnal and seasonal temperature ranges (BRACCO & CONTRERAS 2000, MÁRQUEZ & DALMASSO 2003). The mean annual precipitation does not exceed 100 mm. Precipitation is in the form of snow and hail in winter (reaching 75 mm), and in the form of rain and less than 10 mm in summer (LE HOUÉROU 1999, MÁRQUEZ et al. 2000, MÁRQUEZ & DALMASSO 2003). In the Monte of El Leoncito there is a shrubland of *Larrea nitida* with low cover (10%) and the herb layer is less than 10 cm in height (MÁRQUEZ et al. 2000, MÁRQUEZ & DALMASSO 2003). The total plant cover is only 21.9% and there exist vast open areas (TARABORELLI 2006). The density of cavies at El Leoncito is 7.22 ± 0.5 adults ha⁻¹ (TARABORELLI 2006). Potential predators are crepuscular and nocturnal mammalian carnivores (*Lycalopex culpaeus* and *Puma concolor*), diurnal raptors (*Geranoaetus melanoleucus*, *Buteo polyosoma*, *Falco femoralis*, *Falco sparverius*, *Circus cinereus*), and snakes (*Phyllorhynchus trilineatus*, MÁRQUEZ 1999, TARABORELLI 2006). At El Leoncito the predation risk is lower than at Ñacuñán (fewer records, TARABORELLI 2006).

Behaviour sampling

A description of individual and social vigilance and foraging behaviour was achieved through focal samplings (focal-continuous sampling, ALTMANN 1974, MARTIN & BATESON 1993, LEHNER 1996). Observations were made with binoculars (8 × 40, Hoken, Wald S.A., China), vocal tape recording and video taping from an observation tower 2 m high and 30-50 m away from the burrows. They were made from 8:00-12:30 and 15:00-20:30 hr on 3-4 days per week at 3 times of the year: the time of food abundance and peak of population (November-February), food shortage and population decline (April-August), and reproduction and the peak of cavy movement among plant patches (September-March). This procedure was used at each study site from 2003 to 2005.

The vigilance and foraging behaviours of each animal, their duration and frequency were recorded on each sampling date. The individual or individuals were recognized by being identified with coded metal tags (0.6 cm long), staining the hair of different body parts with gentian violet, making diverse drawings on them, for example circles, squares, vertical or horizontal lines, letters, etc. (65 animals at El Leoncito and 12 at Ñacuñán; TARABORELLI 2006). Vigilance was defined as alert posture, typically the animal 'freezes' with its front legs extended; the eyes directed toward the stimulus (ROOD 1972, TARABORELLI 2006). Foraging behaviour was defined as one or more individuals searching for food, moving slowly in a crouching posture with the head lowered to ground level, smelling the soil or stretching up on their hind limbs to reach a branch (ROOD 1972, TARABORELLI 2006).

Group size was also measured. From direct observations, group size was taken as two or more individuals jointly displaying their activities and interacting in or near the burrow area. To quantify grouping, I considered a cavy as part of a given group when it was at a distance of 4 m or less from any other individual (similar to EBENSPERGER & WALLEN 2002). The use of such a criterion ensured that all group members were in visual contact with each other, particularly when in covered areas (EBENSPERGER & WALLEN 2002). Observations were switched among individuals and among several groups formed by different individuals (2 to 5 individuals in each group), and not repeated for the same individual or group. I used only the first observation of each individual or group. The sample size at El Leoncito included: solitary individuals (29), groups with 2 members (20), groups with 3 members (12), groups with 4 members (4), groups with 5 members (4). The sample size at Ñacuñán was composed of: solitary individuals (12), groups with 2 members (10), groups with 3 members (6), groups with 4 members (3), groups with 5 members (3).

I utilized the concepts of rate and proportion as defined by MARTÍN & BATESON (1993). Frequency is the total number of occurrences of behavioural events. Rates (frequency of behaviour/observation period in minutes) and proportions (duration of behaviour in minutes/observation period in minutes) were obtained for each site. Total group vigilance rate and proportion were achieved by summing the frequencies and durations of vigilance behaviour in each individual within the group.

Statistical analysis

ANOVA was used to compare the mean rates and proportions of behaviours (group vigilance and foraging) between sites (El Leoncito and Ñacuñán), among times of the year (November-February, April-August and September-March) and group sizes. Posthoc tests (Tukey test, $P < 0.05$ and $\alpha = 0.05$) were performed among the variables considered. Log (x) transformations of the data were used to conform to the ANOVA assumptions. Since the data were not normally distributed, Spearman's rank correlation procedure was used for further analyses. The results are displayed as mean \pm one standard error (SE).

RESULTS

Many cavies (solitary individuals or in social groups) remained vigilant, foraged or rested near the burrow opening. The cavies did not forage farther from the nearest burrow when the density of individuals increased; they always foraged near the burrow (less than 2 m) or beneath the plant

cover. Different individuals within a group were frequently observed to stand in an alert posture when apparently detecting a threat, or perhaps they were possibly scanning the environment. Most members of a group were alerted once danger was detected by one group member, then they responded with flight towards a burrow. Large-sized groups were rarely recorded at either site.

Group vigilance showed no differences between sites (rate: $F = 0.04$, $P = 0.834$, $df = 1$; $n = 103$; Ñacuñán 0.44 ± 0.03 frequency/min, El Leoncito 0.42 ± 0.04 frequency/min; proportion: $F = 4.62$, $P = 0.36$, $df = 1$, $n = 103$; Ñacuñán 0.14 ± 0.02 min/min, El Leoncito 0.13 ± 0.01 min/min). Nor did group vigilance show any differences among times of the year (rate: $F = 0.21$, $P = 0.8075$, $df = 2$; $n = 103$; proportion: $F = 0.42$, $P = 0.6556$, $df = 2$, $n = 103$). Hence, the data collected across the year for both sites were combined for the further analysis. The rate of vigilance in solitary individuals was greater than in groups of 2-3 animals (34%, 0.6 ± 0.04 frequency/min for a solitary individual and 0.4 ± 0.03 frequency/min for groups of 2-3 animals). And the rate of vigilance in groups of 2-3 animals was greater than in groups of 4-5 animals (32.67 %, 0.4 ± 0.03 frequency/min for groups of 2-3 animals and 0.2 ± 0.02 frequency/min for groups of 4-5 animals, $F = 4.52$, $P = 0.0014$, $df = 4$, $n = 103$; Fig. 1a). But the test did not show significant differences in the duration of vigilance between solitary animals and individuals in groups with 2-5 members ($F = 1.47$, $P = 0.2106$, $df = 4$, $n = 103$; Fig. 1b). Total group vigilance (rate and proportion) in solitary individuals was lower than in groups of 3-4 animals, and total group vigilance in groups of 3-4 animals was lower than in groups of 5 animals (rate: $F = 14.13$, $P < 0.0001$, $df = 4$, $n = 103$, Fig. 1a; proportion: $F = 16.94$, $P < 0.0001$, $df = 4$, $n = 103$, Fig. 1b).

In relating vigilance rate to group size, at both sites there was a negative correlation throughout the year, individual vigilance decreased with increasing group size ($r_s = -0.13$, $P = 0.02$, $n = 103$; Fig. 1a). There was no correlation between number of individuals per group and vigilance proportion at either site across the year ($r_s = -0.05$, $P = 0.40$, $n = 103$; Fig. 1b). There were positive correlations of total group vigilance rate and proportion with the number of individuals per group for both sites across the year (rate: $r_s = 0.54$, $P < 0.0001$; $n = 103$, Fig. 1a; proportion: $r_s = 0.51$, $P < 0.0001$; $n = 103$; Fig. 1b). Total group vigilance (rate and proportion) increased with increasing group size.

The foraging behaviour showed no differences between sites (rate: $F = 7.77$, $P = 0.097$, $df = 1$; $n = 103$; Ñacuñán 0.81 ± 0.1 frequency/min, El Leoncito 0.72 ± 0.06 frequency/min; proportion: $F = 11.07$, $P = 0.108$, $df = 1$, $n = 103$; Ñacuñán 0.17 ± 0.02 min/min, El Leoncito 0.16 ± 0.01 min/min). Foraging showed no differences among times of the year (rate: $F = 4.75$, $P = 0.492$, $df = 2$; $n = 103$; proportion: $F = 11.89$, $P = 0.211$, $df = 2$, $n = 103$). Therefore, the data collected over the year at each site were combined for the correlation analysis. Foraging showed no differences between solitary animals and individuals in groups of 2-5 members (rate: $F = 14.07$, $P = 0.31$, $df = 4$, $n = 103$, Fig. 1a; proportion: $F = 3.14$, $P = 0.147$, $df = 4$, $n = 103$, Fig. 1b). There was no correlation between the number of individuals per group and foraging (rate: $r_s = 0.006$, $P = 0.29$, $n = 103$, Fig. 1a; proportion: $r_s = 0.001$, $P = 0.35$, $n = 103$, Fig. 1b) at either site across the year.

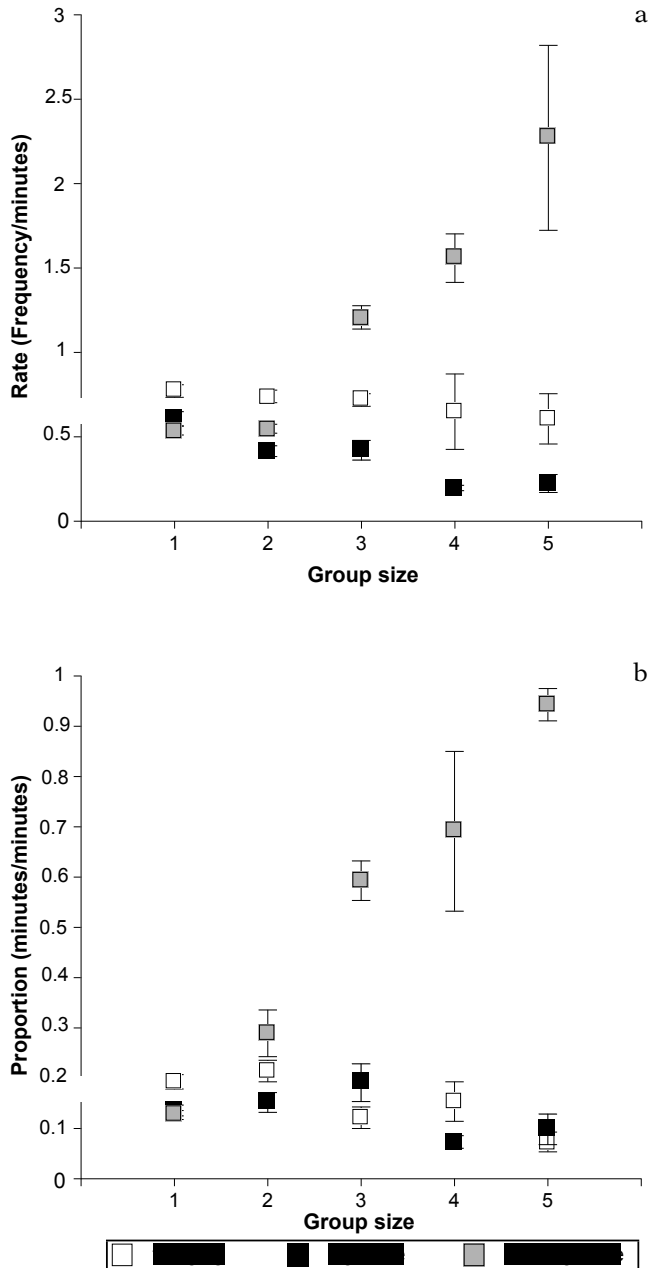


Fig. 1. — (a) Relationship between different rates (frequency of behaviour/minutes of observation) and group size at both sites. (b) Relationship between different proportions (minutes of behaviour/minutes of observation) and group size at both sites. White squares show foraging behaviour, black squares indicate vigilance per individual, and grey squares total vigilance per group. (Mean \pm SE).

DISCUSSION

Among the benefits of group living would be an increased efficiency in antipredator strategy through group vigilance or defence (ARMITAGE 1988, GIRALDEAU 1988, LOVEGROVE & WISSEL 1988, LACEY 2000). The occurrence of the many-eyes effect seems to be supported in part by the behaviour of *Microcavia australis*. In this rodent, the rate of individual vigilance diminishes but total group vigilance rate and proportion increase when group size increases. For example, the individual vigilance frequency decreases from solitary individuals to groups of 2-3 animals by 34%, and from groups of 2-3 animals to groups of 4-5 animals by 33%. Yet both frequency and duration increase in total group vigilance from solitary individuals to groups of 3-4 animals, and again there is a large increase in total group vigilance from groups of 3-4 animals to groups of 5 animals. Hence there is an effect of group on the antipredator response, since cavies forming larger groups show lower frequencies of individual vigilance while the other individuals forage, groom, rest or move inside the burrow, but total vigilance increases with group size. VASQUEZ (1997), EBENSPERGER (2001), EBENSPERGER & COFRE (2001) and EBENSPERGER & WALLEN (2002) found that diurnal rodents like *Octodon degus* can live in groups, thereby reducing individual risk of predation, increasing their ability to detect and escape from predators, and that total vigilance increases with group size, consequently harsh habitats with poor vegetation exhibit larger sized groups.

Social foragers frequently show diminishing levels of per capita vigilance as the group size increases (CASSINI 1989, VASQUEZ 1997). The foraging time of group members was longer with increasing group size in *O. degus* (VASQUEZ 1997). Therefore, group foraging may confer antipredator as well as short-term feeding advantages to *O. degus* (VASQUEZ 1997). *M. australis* does not generally form cohesive groups when foraging, and its foraging behaviour does not increase with group size, the time saved from vigilance is not allocated to foraging. But the social group operates like a vigilance group, thus increasing survival. Therefore, the many-eyes effect appears not to benefit foraging in this rodent. Many cavies (either solitary individuals or social groups) remained vigilant, foraged or rested near the burrow opening. The cavies did not forage farther from the nearest burrow when the density of individuals increased; they always foraged near the burrow (less than 2 m) or beneath the plant cover. Therefore, the simple dilution mechanism does not exist in *M. australis*.

The occurrence of cooperative vigilance seems to be supported by the behaviour of *M. australis*. When cavies are vigilant they stop other activities to engage in a more static alert posture which allows visual scanning of the surroundings, and hence visual detection of dangerous events that occur unpredictably in the environment. Most members of a group are alerted once danger is detected by one group member, then they respond with flight toward the burrow. Cavies can discriminate between threat and non-threat events, and vigilance behaviour may contribute to distinguishing these events. This antipredator adaptation may have played an important role in the social evolution of cavies. At neither site did the cavies emit alarm calls in response to preda-

tor presence. Other species such as *Cavia* sp. (Caviidae) exhibit alert calls and postures; and the rate of alert postures is higher when animals are alone than in groups, also increased group size results in increased efficiency in predator detection (CASSINI 1989). *Cynomys leucurus* and *C. Ludovicianus*, on detecting a predator, alert nearby individuals with a loud cry (antipredator call) or by visual alarms (running to the burrow or adopting alert postures); and the number of antipredator calls varies directly with the number of vigilant animals (HOGLAND 1981, 1995). Therefore visualization of a predator and the antipredator call are faster when the group size is larger, and the percentage of time each individual spends on vigilance is lower when the degree of vigilance is higher (HOGLAND 1981, 1995; LIMA 1987). In cavies, the latency until the first antipredator response is lower with larger group size, so the efficiency is higher and the response is faster (TARABORELLI et al. in press). Many factors are associated with sociality and risk of predation could be one of them, at least in murid, caviid and sciurid rodents (CASSINI 1989, LIMA & DILL 1990, EBENSPERGER & WALLEN 2002).

Group vigilance is a benefit of group-living in cavies, and it is an antipredator behaviour of *M. australis* that does not change between sites with different plant structure or availability or under predation risk. Although the study sites have different predation risks, at Ñacuñán the number of records of predators is higher and the greatest risk of predation comes from raptors, as these are predators that overlap with the period of activity of cavies (TARABORELLI 2006). Besides, at Ñacuñán the cover provided by shrubs and trees would give vertical protection from raptors, but herbaceous plants would obstruct visual detection of terrestrial mammalian predators and of the shadow of raptors on the ground (EBENSPERGER & HURTADO 2005, TARABORELLI 2006, TARABORELLI et al. in press). At El Leoncito there are wide open areas where predation risk increases because predators prefer to attack in these areas, decreasing the likelihood of escaping (LIMA 1987). But in open areas the prey's vision would be less impaired by shrubs and herbaceous plants (EBENSPERGER & HURTADO 2005, TARABORELLI et al. in press). These biotic characteristics have no influence on group vigilance, but if these they do affect other antipredator responses, like intermittent locomotion in open areas, latency until the first antipredator response, distance between cavy or cavies and predator at the moment of the response (distance of reaction), speed of escape (distance of travel until hiding in meters/time of travel in seconds) (TARABORELLI 2006, TARABORELLI et al. in press).

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