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INTER AND INTRASPECIFIC RELATIONSHIPS IN *AKODON AZARAE* AND *CALOMYS LAUCHA* (RODENTIA, SIGMODONTINAE) IN PAMPEAN AGROECOSYSTEMS

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ABSTRACT. We studied social relationships in *Akodon azarae* and *Calomys laucha* (Rodentia, Sigmodontinae), species that inhabit agroecosystems of Central Argentina. They show spatial segregation under field conditions, being *C. laucha* more abundant in the cropfields and *A. azarae* in their weedy margins (borders). In order to assess whether this spatial segregation was related to behavioral patterns, we conducted experimental encounters between individuals of the same and different species, under three different conditions: simulating borders, simulating fields and with a neutral substrate. The first two types of experiments were conducted in enclosures (4 x 2 x 1 m) located at the site of capture of rodents, while in laboratory trials we used glass boxes of 51 x 51 x 30 cm. Observations were conducted between 21 and 02 hours, corresponding to the activity period of animals. According to our results, *A. azarae* individuals were dominant over *C. laucha*, but there was a low frequency of agonistic interactions. *A. azarae* was more aggressive both intra and interspecifically. There was not a significant effect of sex or substrate on the results of the encounters, although we found differences in the frequencies of many behaviors.

RESUMEN. Relaciones inter e intraespecíficas entre Akodon azarae y Calomys laucha (Rodentia: Sigmodontinae) en agroedosistemas pampeanos. Se estudiaron las relaciones sociales entre *Akodon azarae* y *Calomys laucha* (Rodentia: Sigmodontinae), especies que habitan los agroecosistemas en la Región Central de Argentina. Estas especies muestran una distribución espacial determinada, siendo *A. azarae* más abundante en los bordes de los campos y *C. laucha* en los campos de cultivo. Para conocer si esta segregación espacial está relacionada con patrones comportamentales se realizaron encuentros experimentales entre individuos de la misma o distintas especies bajo tres tipos de condiciones experimentales: simulando el borde de los campos, simulando los campos y en un sustrato neutro (laboratorio). Los dos primeros tipos de experimentos fueron realizados en clausuras (4 x 2 x 1 m), localizadas en el sitio donde se capturaron los roedores, mientras que en los enfrentamientos de laboratorio se utilizó una caja de plástico (51 x 51 x 30 cm). Las observaciones se realizaron entre las 21 y 2 hs, correspondiendo con el período de actividad de los animales. De acuerdo con nuestros resultados, los individuos de *A. azarae* fueron dominantes sobre los de *C. laucha*, pero hubo una baja frecuencia de interacciones agonísticas. *A. azarae* fue más agresivo tanto en los enfrentamientos intra como interespecíficos. No hubo un efecto significativo del sexo o el sustrato sobre el resultado de los encuentros, sin embargo variaron las frecuencias de algunos comportamientos.

Key words: social interactions, behavior, competition, rodents, agroecosystems.

Palabras clave: interacciones sociales, comportamiento, competencia, roedores, agroecosistemas.

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INTRODUCTION

Several authors have stressed the importance of interspecific competition in determining the distribution and abundance of small mammals, not only at a geographic scale but also at smaller spatial scales (Grant, 1969; Brown, 1970; Grant, 1970, 1971, 1972; Stoecker, 1972; Connell, 1983; Schoener, 1983; Brown and Munger, 1985; Hansson, 1997; Monamy, 1999). The role of negative interactions on spatial distribution has been addressed on a wide variety of small mammal species and habitats (Andrzejewski and Olszewski, 1963; Sheppe, 1967; Getz, 1969; Brown, 1971; Murie, 1971; Grant, 1972; Morris and Grant, 1972; Hoffmeyer, 1973), using both field and laboratory data.

The pattern of spatial distribution is often used as evidence of interactions between species, but it is not generally enough to determine the processes that lead to these patterns. Agonistic interactions can be more adequately detected through inter and intraspecific encounters in controlled conditions (Grant, 1970, 1972; Schoener, 1983). Under laboratory conditions, agonistic behavior is considered as evidence of interference competition. Agonistic behavior is stereotyped in rats and mice, and it is not usually the product of learning experiences, but several authors assert that previous experiences affect the result of agonistic encounters both during development as well as at adulthood (Martínez et al., 1994; McElman and Morris, 1977).

Studies have shown that the result of interactions depend on the species, the habitat where they occur, population density, accessibility to resources, as well as on individual characteristics: sex, age and reproductive conditions. (Grant, 1970, 1972; Stoecker, 1972; McElman and Morris, 1977; Schoener, 1983; McGuire and Getz, 1998). Some authors have observed that heavier individuals are often dominant over lighter ones, both in intra and interspecific encounters (McEelman and Morris, 1977; Grant, 1980; Brown and Murger, 1985); however, they did not find a consistent relation between body mass and dominance.

When habitat preferences of the competing species are different, each of them can be more efficient (both in the use of resources and in excluding the individuals of the other species) in its preferred habitat, and dominance will depend on the habitat in which interactions are taking place. On the contrary, if both species prefer the same type of habitat, spatial segregation comes through exclusion of the subordinate species from the preferred habitat, so that which species is dominant will not change according to the habitat type (Abramsky et al., 1991; Rosenzweig, 1981). Intermediate situations are also possible, in which relative competitive advantages change according to the habitat, but they do not reverse.

The role of the sex of the opponents in determining the results of interspecific encounters has been studied for many rodent species: Livoreil et al. (1993) observed that males of *Spermophylus spylosoma* and *S. mexicanus* are more aggressive than females, while McElman and Morris (1977) reported that between *Microtus pennsylvanicus* and *Clethrionomys gapperi* there is not a fixed pattern of aggression but results depend on the sex of the opponents. They also observed that previous experiences influenced the result of the encounters. Busch and Kravetz (1992a) observed negative numerical and spatial relationships between females of *A. azarae* and *C. laucha* juveniles in spite of the absence of significant relations between populations as a whole.

In the pampean agroecosystems of Central Argentina, *Akodon azarae* and *Calomys laucha* (Muridae: Sigmodontinae) are found in a variety of habitats, including native grasslands, pastures, cropfields and their borders (marginal areas below wire fences, where a weed community is found during most of the year). The composition of the rodent community varies according to the habitat, being *C. laucha* the most abundant species in cropfields and *A. azarae* in their borders (Kravetz et al., 1981; Kravetz and Polop, 1983; Busch et al., 1984; Zuleta et al., 1988; Mills et al., 1991; Busch et al., 1997; Ellis et al., 1997).

Habitat segregation between *A. azarae* and *C. laucha* was attributed to interspecific competition (Busch and Kravetz 1992a, Busch et al., 1997), and results of preliminary experimental encounters between them, simulating border conditions, suggest that behavioral dominance may contribute to maintain spatial segregation (Busch and Kravetz., 1992b). A later experiment under laboratory conditions on a neutral substrate confirmed the dominance of *A. azarae* over *C. laucha* (Cueto et al., 1995). These behavioral patterns might affect the access to food resources, as evidenced by a food supplementation experiment under field conditions during winter (Cittadino et al., 1994).

The aim of this study was to study dominance-subordination relationships in *A. azarae* and *C. laucha* under semi-captivity (simulating field and border conditions) and under laboratory conditions.

According to previous studies about the ecology and the competitive relationships between *A. azarae* y *C. laucha*, our working hypotheses were:

1. *A. azarae* will show behavioral dominance over *C. laucha* in experimental encounters.
2. *A. azarae* will display agonistic behaviors more frequently than *C. laucha* both in intraspecific and interspecific encounters.
3. Interspecific dominance will vary according to the habitat where the encounter occurs, being more intense the dominance of *A.azarae* in borders than in field or neutral substrates
4. The frequencies of the different kind of behaviors displayed by each individual depend on its species, sex, the substrate and its particular opponent.

MATERIALS AND METHODS

Two different types of experiments were performed: in open enclosures, simulating cropfields or borders, and on a neutral substrate, under laboratory conditions. The experimental animals were adult individuals live-trapped in Diego Gaynor locality (34°08'S, 59°14'W), Exaltación de la Cruz Department, Buenos Aires Province, Argentina.

We studied the effect of species, substrate and sex on the result of interactions, no residence condition was assigned, and only adult individuals of similar weight were considered. In interspecific encounters, however, *A. azarae* individuals were slightly heavier than *C. laucha*, because of species differences in body mass (mean body mass 24 and 14 g respectively). Animals were not in reproductive condition. The substrate were sods of vegetation from fields or borders for open enclosures and sawdust for laboratory experiments.

Outdoor experiments

Rodents were live-trapped during June, July and August 1993, in corn fields and stubbles. For each individual we registered sex, species, reproductive state and weight. Individuals were kept inside the traps with food (potatoes or apples) until the encounters.

Under border conditions we used a total of 18 *A. azarae* and 12 *C. laucha* in 6 interspecific and 9 intraspecific (6 *A. azarae* and 3 *C. laucha*) encounters. Under field conditions, we used a total of 32 *A. azarae* and 28 *C. laucha* in 22 interspecific and 8 intraspecific (5 *A. azarae* and 3 *C. laucha*) encounters. Each individual was used only once. In the intraspecific encounters we identified each individual by doing a white mark in the head of one of them.

Encounters were performed on an enclosure of 4 x 2 x 1 meters, where the corresponding vegetation (field or border) was placed. It was built outdoors, surrounded by a metallic wire, with a zinc sheet in the upper side to prevent rodents to jump out.

Encounters were made the day of capture of animals, from 21 to 02 hrs, corresponding to the daily activity period of both species. Red light (12 v) was used in order to avoid interfering with the nocturnal activity of animals. Individuals were placed, in pairs, one at each end of the enclosure. The observation period began after an acclimatization period of 5 minutes.

Observations lasted twenty minutes, subdivided in one-minute intervals. We recorded all activities performed during those intervals. We calculated the frecuency of each behavior per encounter as: Number of time intervals in which the behavior was observed at least one time in any of the opponents/ total number of time intervals (20).

The list of observable behaviors was modified, according to preliminary observations of the studied species, from Grant (1970) and Stoecker (1972). Behaviors were grouped, for statistical analyses, under five categories (**Table 1**).

Indoor experiments

The individuals used in these experiments were trapped during August and September 1994, in cropfields and borders of the same area where individuals for the outdoor experiments were trapped. We recorded sex, reproductive condition and body mass of each individual. They were maintained in laboratory for at least 4 weeks for acclimatization,

Table 1

Behaviors observed in *Akodon azarae* and *Calomys laucha* during outdoor and laboratory conditions (*behavior observed only in laboratory conditions).

BEHAVIORS	DESCRIPTION
a) Dominance	Pursuit: Individual following another * Attack: One member of the pair is bitten and chased by its opponent
b) Subordination	Flight without contact: An individual flees without actually contacting its opponent Flight after contact: An individual flees after making contact with its opponent * Motionless without encounter: Individual remains quiet in one place without meeting its opponent * Motionless after encounter: An individual remains quiet after meeting its partner
c) Alertness	Attitude of alertness: Individuals remain quiet, with their ears pricked and doing constant head movements, with frequent sniffing
d) Exploratory	Vertical and horizontal exploration: Movements in both directions, along the floor or climbing the lateral fences Sniffing: Constant movement of the nose
e) Amicable	Nasal Contacts: A member of the pair touches the other individual's nose Closeness without contact: An individual approaches its head towards the other's without actually touching it Encounter: Both individuals in contact Closeness and space sharing: Opponents stay close and share a common space within the enclosure
f) Defensive	* Boxing position: An individual with a bipedal posture, with upper members lifted as if doing a boxing attack, frequently with their mouth open. Stoecker, R.E. 1972.

in individual cages provided with sawdust, water and food ad libitum, under natural photoperiod.

We conducted 23 interspecific (*A. azarae-C. laucha*) and 31 intraspecific encounters (18 *A. azarae-A. azarae* and 13 *C. laucha-C. laucha*). In order to have more replicates, we used more than one time each individual, but each of them participated only in three or less encounters (one intraspecific and one or two interspecific), with at least a three-day interval between them. Pairs were not repeated in order to avoid the potential influence of previous experience (McElman and Morris, 1977; Martínez et al., 1994).

Encounters were performed in a 51 x 51 x 30 cm glass box, with a metallic wire lid, and a mobile acrylic division in the middle. The substrate was sawdust that was replaced after each encounter. Observations took place from 21 to 24 hs. Red light was used, in order to avoid interfering with the nocturnal habits of rodents. Fifteen minutes before each encounter, both individuals were placed inside the box with the acrylic division between them. Time zero was marked when the division was removed. Observations lasted twenty minutes, subdivided in one-minute intervals.

The observational protocol, as well as the behaviors considered, were the same as for the field trials.

Data analysis

We conducted two levels of analysis: 1) Considering the proportions of encounters with agonistic behaviors, and 2) Considering the frequencies of the different kind of behaviors per encounter.

Proportion of agonistic encounters

Encounters were scored as with or without agonistic behavior, according to the observation of dominance, subordinate or defensive behaviors

(**Table 1**) in one or both opponents in any of the intervals. The opponent who more frequently displayed dominant behaviors was considered dominant in the encounter. The opponent who more frequently displayed subordinate behavior was considered subordinate**.** The defensive behavior was only observed in laboratory encounters between *A. azarae*. These encounters were considered agonistic.

The proportion of agonistic results (Number of encounters with agonistic result/ Total Number of encounters) was compared among encounters with different combination of sexes or according to the substrate by means of the Fisher Exact test. We compared the proportion of agonistic encounters among inter- and both types of intraspecific encounters, between intraspecific *A. azarae* and *C. laucha* trials, and opposing different sex combinations in both intra- and interspecific encounters.

The proportion of agonistic encounters in which *A. azarae* was dominant over *C. laucha* was compared with that expected according to the binomial distribution considering equal probability for loose or win (p= q= 0.5).

Frequencies of the different kind of behaviors according to the opponent in different type of encounters

Species differences in the frequencies of the different kind of behaviors (Number of time intervals in which the behavior was present/ Total number of time intervals= 20) were compared with a Wilcoxon rank signed paired test, considering significant differences when P<0.05 (Daniels, 1978; Lehner 1979).

The differences in the frequencies of the different behaviors among encounters in which were opposed different pairs of opponents (individuals of the same species and of the same sex, same species, different sex, different species, same sex or different species and different sex) were compared by means of the one-way Kruskal-Wallis non parametric test, considering significant differences when P<0.05 (Daniels, 1978; Lehner, 1979). We conducted a posteriori multiple comparisons of Dunn (Siegel 1998) in order to assess which groups differed significantly, considering significant differences when P<0.15.

RESULTS

Proportions of agonistic encounters

A 26% of the total encounters had agonistic results (26/99). Agonistic encounters between *A. azarae* individuals were more frequent than those between individuals of *C. laucha* and for interspecific encounters in the three substrates (**Fig. 1**), but differences were statistically significant only for the laboratory trials (Fisher Exact test, P= 0.0094 and P= 0.0031, for differences between encounters of *A. azarae* with respect to encounters between *C. laucha* individuals and interspecific encounters, respectively). *A. azarae* dominated over *C. laucha* in all interspecific encounters were agonism was detected (7/7, P= 0.004). The proportion of agonistic encounters between *A. azarae* and between *A .azarae* and *C. laucha* individuals did not differ among fields, border, and laboratory (Fisher Exact Test, P>0.05 in all cases).

The proportion of agonistic results did not differ according to the sex combination neither for intraspecific nor for interspecific encounters (Fisher Exact test, P>0.05 in all cases; **Fig. 2**).

Frequencies of the different kind of behaviors according to the opponent in different type of encounters

Dominant behaviors were only displayed by *A. azarae* individuals independently of the type of substrate and encounter. Intraspecific encounters in *A. azarae* and *C. laucha* under laboratory conditions showed differences in the frequencies of dominance, subordination, alertness and defensive behavior (**Table 2**). *C. laucha* showed subordination and alertness in more time intervals than *A. azarae*, while the latter displayed defensive and dominance behaviors on a greater number of intervals than *C. laucha*. This analysis was not conducted for field and border conditions because of the lack of sufficient replicates.

In the interspecific encounters (**Tabla 3**), *C. laucha* showed alertness in a greater number of intervals than *A. azarae* for the three substrates (Z= 3.127, P= 0.002; Z= 2.020, P= 0.043; and Z= 2.111, P= 0.035 for field, border and laboratory, respectively). In field conditions, *C. laucha* explored more frequently than *A .azarae* (Z= 3.023, P= 0.003). Under laboratory conditions, *A. azarae* exhibited dominant behaviors, while *C. laucha* did not (Z= 2.121, P= 0.034).

The analysis of the frequency of the different behaviors according to the sex of the indi-

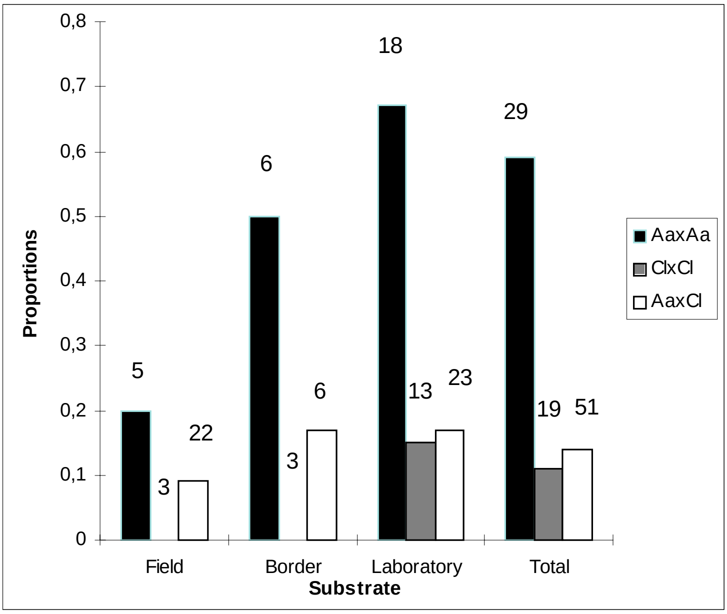


Fig. 1. Proportion of agonistic intra and interspecific encounters for the field, border and laboratory substrates. The observed frequencies were compared with those expected under the null hypothesis of equal probability of agonistic and non-agonistic results according to the Binomial test. The numbers above the bars show the number of encounters. The observed frequencies of agonistic and non-agonistic results according to the type of encounter were compared by the Fisher Exact test. Significant differences were only found for laboratory conditions.

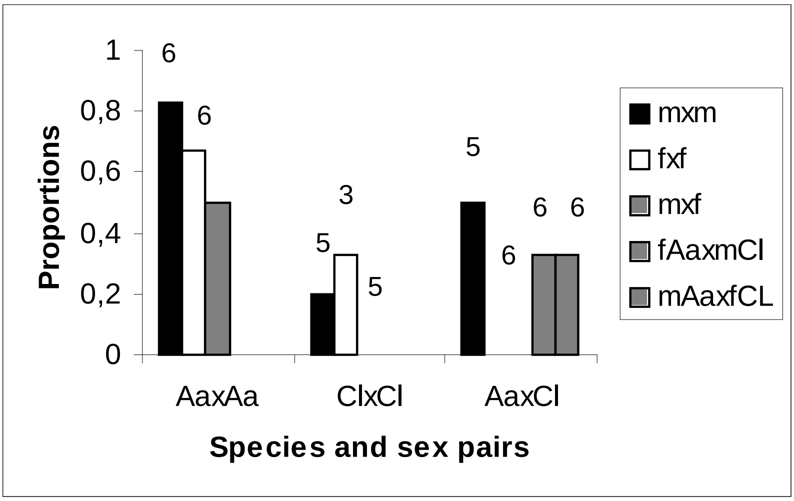


Fig. 2. Proportion of agonistic encounters according to the species and sex pair, under laboratory conditions. The numbers above the bars show the number of encounters The observed frequencies of agonistic and non agonistic results according to the type of encounter were compared by the Fisher Exact test. Result were not statistically significant for all combinations.

Table 2

Median values of the frequencies (number of time intervals in which the behavior was present/ total number of time intervals) of the different behaviors in intraspecific encounters for ***A. azarae*** (n= 18) and ***C. laucha*** (n= 13) under laboratory conditions. Between brackets are shown the quartiles. We compared the frequencies of each type of behavior between species by means of the Wilcoxon signed paired rank test*: P< 0.05, NS: P> 0.05.

Behavior	***A. azarae vs A. azarae***	***C. laucha vs C. laucha***	**P**
Dominance	0 (0 - 1,5)	0 (0 - 0)	0.007* Z=2.697
Subordination	3.5 (1,5 - 8,0)	8 (4 - 11)	0.007* Z=2.683
Alertness	0 (0 - 2)	3,5 (1 -5)	0.007* Z=2.697
Exploratory	6,5 (3,5 – 10,5)	5 (2 - 9)	0.761 NS
Defensive	1 (0 - 2)	0 (0 - 0)	0.038* Z=3.089

Table 3

Median values for the frequencies of *A. azarae* and *C. laucha* behaviors for interspecific encounters under outdoor and indoor conditions. Differences between species were assessed by means of the Mann-Whitney non-parametric U test. * = p< 0.05, NS= p>0.05.

Substrate	**Pair**	**Dominance**	**Subordination**	**Alertness**	**Exploratory**	**Amicable**
Field	*A. azarae* x *C. laucha*	0 (0-0) Ba (-)	3 (0-6) 2 (1-6)	0 (0-0) 1 (0-2)	4 (5-10) 10 (8-15)	Ba Ba
	Significance	NS	NS	*	*	NS
Border	*A. azarae* x *C. laucha*	0 (0-0) 0 (0-0)	0 (0-0) 1.5 (0-3)	4 (2-7) 7 (5-17)	15.8 (11-17) 8.5 (3-16)	0.5 (0-2) 0 (0-2)
	Significance	#	NS	*	NS	#
Laboratory	*A. azarae* x *C. laucha*	0 (0-0) Ba (0-0)	4 (2-9) 10 (2-12)	0 (0-2) 2 (0-4)	10 (4-13) 9 (4-10)	0 (0-0) 0 (0-0)
	Significance	*	NS	*	NS	#

Ba: Behavior absent
#: we did not conduct the analysis because one species did not present the behavior.

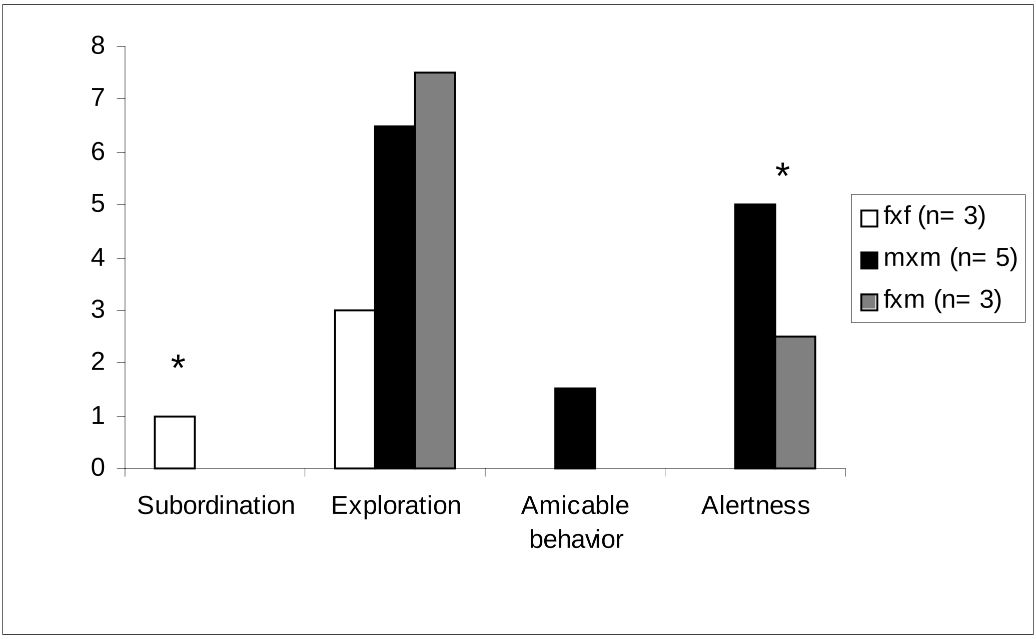
viduals opposed in intraspecific encounters could only be conducted for laboratory conditions, where we observed that for *A. azarae* (**Fig. 3a**) the frequency of subordinate and dominant behaviors differed according to the sexes of the opponents (Kruskal Wallis test statistics, Z= 13.763, P= 0.001; Z= 7.570, P= 0.023, for each behavior respectively). Both behaviors were more frequent in encounters between males with respect to the heterosexual pair (Multiple comparisons of Dunn, q= 13.16, P< 0.05 and q= 9.2, P< 0.05, respectively). Alertness also showed differences among groups (Kruskal Wallis test statistics Z= 7.654, P=0.022). It was more frequent when different sexes were opposed than in encounters between males (Multiple comparisons of Dunn, q= 10.45, P<0.05). Amicable behaviors were more frequent during female encounters than in heterosexual runs (Kruskal Wallis test statistics Z= 5.860, P= 0.053, multiple comparisons of Dunn q = 8.875, P<0.05). For *C. laucha* (**Fig. 3b**), subordination was more frequent when two females were confronted than in heterosexual encounters (Kruskal Wallis test statistics, Z= 8.221, P= 0.016, Multiple comparisons of Dunn, q= 8.67, P< 0.05), while alertness was more frequent when two males were opposed (Kruskal Wallis test statistics Z= 15.432, P= 0.000, Multiple comparisons of Dunn, q= 7.9, P< 0.05).

The analysis of the frequency of the different behaviors according to the sex of the individuals opposed in interspecific encounters in field conditions (**Fig. 4a**) showed that the frequency of exploratory behaviors differed according to the group (Kruskal-Wallis test statistics Z= 8.512, P= 0.037), being more frequent when two females were opposed than when *A. azarae* females were opposed to *C. laucha* males (Multiple comparisons of Dunn, q= 12.75, P< 0.05). Alertness was more frequent when confronting *C. laucha* females with *A. azarae* males than in any other encounter (Kruskal-Wallis test statistics Z= 11.897, P= 0.008), although differences were significant only for the pair *A. azarae* female- *C. laucha* male (Multiple comparisons of Dunn, q= 15.75, P<0.05). Under laboratory conditions (**Fig. 4b**), alertness behaviors also showed differences among sex groups (Kruskal-Wallis test statistics Z=16.337, P= 0.001). They were less frequent when two males were opposed with respect to the females pair (Multiple comparisons of Dunn, q= 19.50, P< 0.05) and with respect to the female *A. azarae*- male *C. laucha* pair (Multiple comparisons of Dunn, q= 18.4, P< 0.05). Exploratory behaviors differed between the female and the males pair (Kruskal-Wallis test statistics Z= 10.247, P= 0.017; Multiple comparisons of Dunn, q= 18.12, P< 0.05). The pair *A. azarae* male and *C. laucha* female showed amicable behaviors more frequently than the females pair (Kruskal-Wallis test statistics Z= 14.551, P= 0.002; Multiple comparisons of Dunn, q= 18.33, P< 0.05).

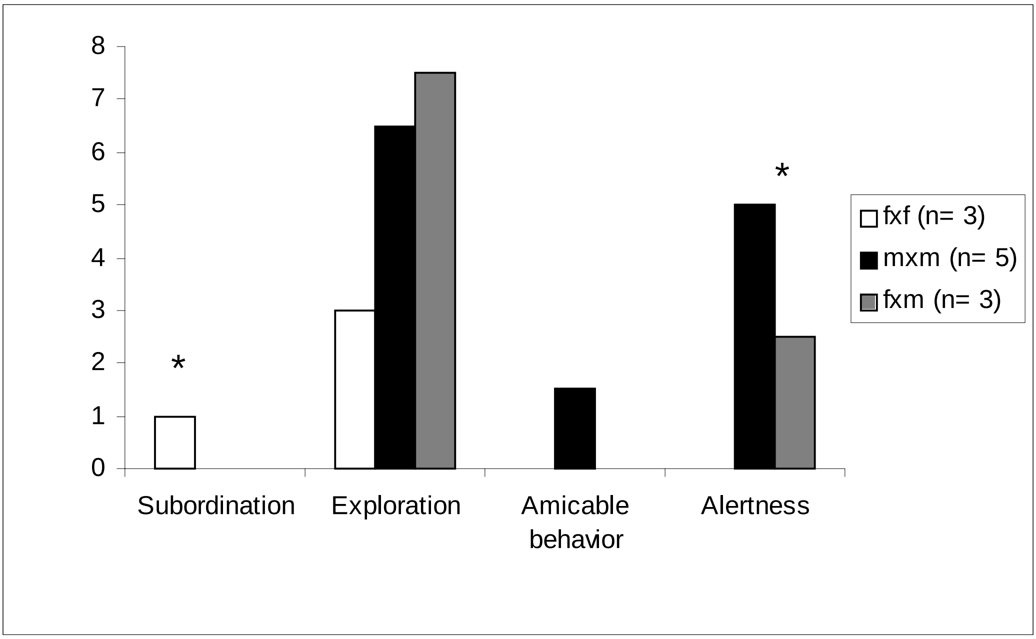
A. azarae individuals showed dominance and amicable behaviors more frequently when opposed to another *A. azarae* than when opposed to a *C. laucha* (Median= 0, Quartiles (0-1.5), Z= 0.26, P= 0.036 and Median=1, Quartiles (0-1.5), Z= 0.47, P= 0.022, respectively), while differences for the defensive behavior were only marginal (Median =1, Quartiles(0-2), Z= 0.520, P= 0.086).

DISCUSSION

According to our results, a behavioral dominance of *A. azarae* over *C. laucha* is not sufficient to explain the spatial segregation observed in the field, because most encounters between species were not agonistic and there were not established dominance-subordination relationships between individuals of both species. In those cases where hierarchies were observed, however, *A. azarae* was the dominant species, and *C. laucha* exhibited subordinate behaviors, as has been described in previous studies (Busch and Kravetz, 1992a, b; Cueto et al., 1995). We found a lower frequency of aggressions than those observed by Cueto et al. (1995). These differences could have been due to the particular experimental conditions, because in Cueto's study, animals competed for a food source during the encounters. Although there were some differences in the evaluation of behaviors, comparing both studies, it seems that agonistic behaviors are less frequently found under semicaptivity con-

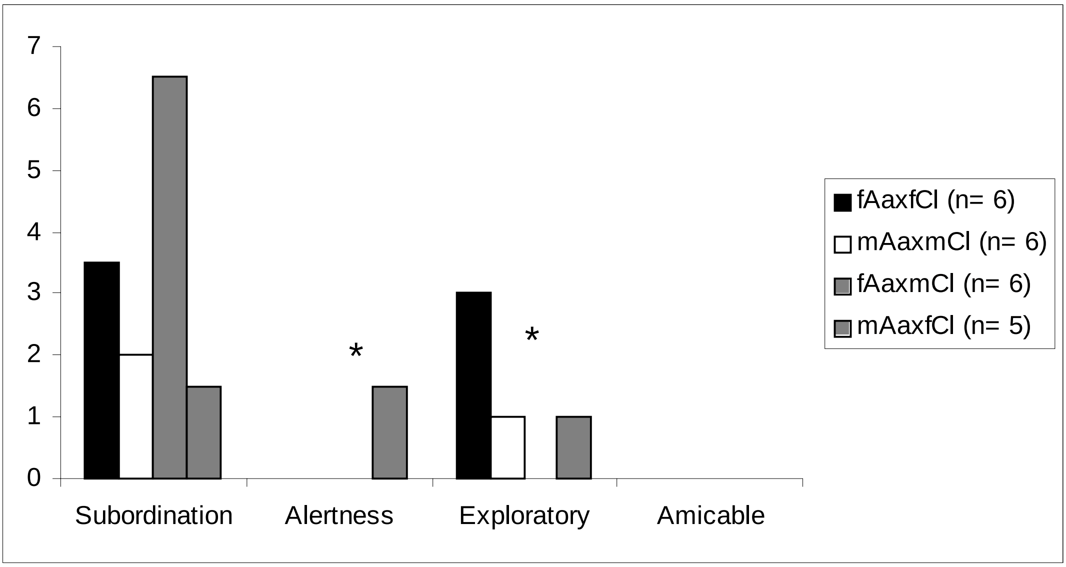


(a) *Akodon azarae*

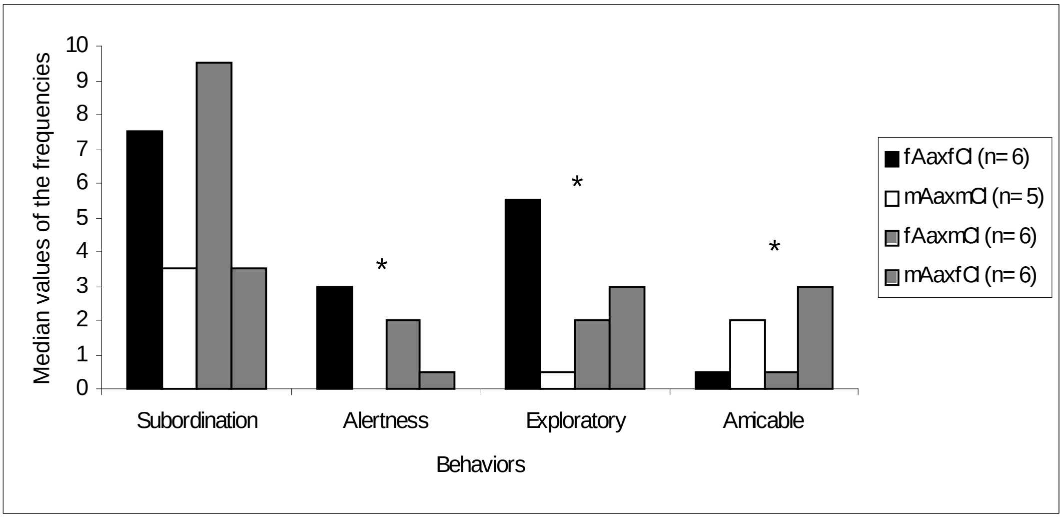


(b) *Calomys laucha*

Fig. 3. Median values of the frequencies of the behaviors according to the sex of the opponents for intraspecific encounters under laboratory conditions. Differences according to the pair opposed were assessed by means of the one-way Kruskal-Wallis non-parametric test. n = number of encounters performed for the group. f = female; m = male; *= $p<0.05$.



(a) Field



(b) Laboratory

Fig. 4. Median values for the frequencies of *A. azarae* and *C. laucha* behaviors according to the sex of the opponents for interspecific encounters under field (a) and laboratory conditions (b). Differences between species were assessed by means of the Wikoxon signed rank test. n= number of encounters performed for the group. f = female; m = male; * = $p<0.05$.

ditions, in enclosures which allow animals to move without interacting, with respect to laboratory studies in small cages, where animals could not ignore the opponent. Laboratory studies also showed differences, being less agonistic interactions when food is not supplied than when food is offered during the trial; and finally, the more clear dominance was observed in laboratory studies when food was supplied and animals were previously fasted (Cueto et al., 1995). On the other hand differences between field and laboratory encounters in the period elapsed between the capture and the experimental trials may also have influenced the results. The low frequency of aggressions described in this study agrees with field observations of Zuleta (1989) where wounds and external scars were not frequently found in *A. azarae* individuals. Even though confinement should favor aggressive behaviors in semi captivity and laboratory trials, the absence of residence conditions may have reduced them. These disagreements between results highlight the fact that agonistic behavior depends on the conditions under which the interaction occurs, and the difficulty of the extrapolation of laboratory results to field conditions. In our study we tried to minimize species differences in weight, but in the field *C. laucha* individuals probably encounter heavier *A. azarae*, and dominance-subordination interactions may be more frequent than those registered in our experiments.

A. azarae exhibited dominance-subordination patterns more frequently than *C. laucha*, in coincidence with observations under natural conditions, where *A. azarae* females are territorial (Zuleta 1989), while *C. laucha* tends to form social groups (Kravetz and De Villafañe, 1981). This pattern in which the species which is more aggressive intraspecifically is also dominant interspecifically was also observed for other pairs of small mammal species, as *Spermophilus spilosoma* and *S. mexicanus* (Millan Pena, 1998) and *Clethrionomys glareolus* and *C. rutilus* (Sokolov et al., 1996).

The higher frequency of dominance-subordination behavior observed in intraspecific encounters for *A. azarae* in relation to the interspecific ones agrees with the relation between competitive coefficients estimated by Busch et al. (1997). A higher frequency of intraspecific with respect to interspecific aggressions has also been observed for other species of small rodents (Stoecker 1971; McElman and Morris, 1977), but it is not a general result.

Reported results about the effect of sex on the results of encounters are variable according to the species (Conley, 1976; Grant 1970). The higher frequency of dominant and subordinate behaviors between *A. azarae* males with respect to heterosexual pairs agrees with that expected according to its promiscuous/poliginic mating system, in which competition must be stronger within than between sexes (Zuleta, 1989). A similar pattern was observed by Gromoy and Vorob'eva (1995) in the gerbil *Meriones meridianus*.

Our experiments were conducted during the non-reproductive period of both species, and the effect of sex could have been higher if we had worked during the reproductive season, since Suárez (pers. comm.) observed that social tolerance in *A. azarae* changes according to the reproductive status of individuals.

In summary, we can conclude that this pair of species exhibited low frequency of aggressive behaviors, being more frequent between individuals of *A. azarae* than between *C. laucha* or between individuals of different species. The spatial segregation between species observed in natural conditions can not be explained by the existence of a stereotyped interspecific hierarchy, although *A. azarae* is more aggressive both intra and interspecifically than *C. laucha*. In nature the dominance of *A. azarae* over *C. laucha* may be more frequent than in experimental trials, due to species differences in body mass.

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