MALE-FEMALE INTERACTION DURING BREEDING AND NON-BREEDING SEASONS IN *AKODON AZARAE* (RODENTIA, MURIDAE)

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ABSTRACT

Dyad encounters between male and female adults of *Akodon azarae* (Fischer, 1829) were analyzed by means of observational techniques in a natural closure during the breeding and non-breeding seasons. The animals were held in observation during 21 days, with daily 15-minute recordings of interindividual separation distance, relative displacements, characteristics of the male-female interaction, copulation, and construction and exclusive or shared use of nests by each pair. The couples, which bred successfully, showed, on average, the longest separation distance between male and female allowed by the closure. During the first two weeks of gestation the females exhibited more displacements than their respective mates did. The male-pregnant female encounters were significantly more aggressive than those recorded between pairs which did not breed successfully. During the non-breeding season a shorter average distance between individuals and a frequent use of nests shared by the pair were recorded. The results obtained are discussed within the framework of the social system of *A. azarae*.

KEYWORDS. *Akodon*, breeding, behavior, Muridae.

INTRODUCTION

The spacing pattern, behavioral interactions and social system are the main manifestations of breeding strategies of individuals within the population. Some of the relationships between mating systems and individual behavior have already been studied in microtine rodents (GETZ & CARTER, 1980; JANNETT, 1980; MADISON, 1980a, b; SHAPIRO *et al*., 1986; MCGUIRE & GETZ, 1998), but it is still not well known in sigmodontins.

Direct observation of *Akodon azarae* (Fischer, 1829) is difficult to carry out in its natural habitat due to its small size and its crepuscular and nocturnal habits. Therefore, most studies of its social structure and use of space necessarily come from indirect records (DALBY, 1975; ZULETA *et al*., 1988; BONAVENTURA *et al*., 1992; BUSCH & KRAVETZ, 1992a, b). Few studies have measured interindividual interactions directly and described their importance for the definition of a social pattern. SUÁREZ (1998a) showed that females of *A. azarae* coming from natural populations and immediately mated in the laboratory develop strategies for care of the offspring resembling those described for wild populations. *A. azarae* presents seasonal breeding, with polygynous mating system and with offspring exclusively care by females (ZULETA *et al*., 1988; SUÁREZ & KRAVETZ, 1998a, b). Following the preceding studies, the goal of the present work is to compare the social behavior of *A. azarae* during the breeding and non-breeding seasons through direct observations of dyads of adult animals of different sex in a natural closure.

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MATERIAL AND METHODS

A total of 60 adult individuals, 30 males and 30 females of *Akodon azarae*, were captured alive from September 1992 to August 1993 in Diego Gaynor (34° 08' S, 59° 14' W, Buenos Aires Province, Argentina). The animals were placed in randomly chosen pairs into individual closures built in an outdoor area of the main bioterium of the Universidad de Buenos Aires. Temperature, photoperiod, and humidity varied seasonally according to the conditions of the environment. Each closure was consisted of 4 glass boxes of 0.30 by 0.30 by 0.20 m and interconnected by wire frame tubes 0.5 m in diameter and 2.85 m in length, with a total linear length of 12.6 m. A substrate 0.10 m thick of unsieved soil was placed in each box. Food (sunflower seeds, maize and oat), water and nesting material (plant remains) were provided *ad libitum*. The observations were carried out starting two days after placement of each pair into the closure and during 21 consecutive days. During the breeding season (September to March) the females were weighed every 5 days to detect weight changes due to pregnancy. Pairs including pregnant females (n=10) formed the P group and those which did not copulate or underwent an unsuccessful mating (n=10) constituted the NP group. During the non-breeding season (NB) (April to August) one third group formed 10 pairs were observed but only 7 survived by the end of the experiment.

Male-female spacing: daily 15-minute observations were made during the period of activity of the animals. For each observation, the distance between male and female (in meters) was recorded, identifying the individual performing the displacement (male and/or female) and the distance covered.

Male-female interaction: during the breeding season a pair from both groups (P and NP) was randomly selected daily. The observations were made by taking instantaneous samples of the interindividual behavior during the period of activity. The behaviors were characterized according to the classification by GAVISH *et al*. (1983) as: agonistic (negative interaction); recognition (positive interaction) or indifferent. Use of nests: a daily record was made of the number of nests built and during the period of activity, its occupation by one individual or by the pair.

Male-female spacing: for each experimental group (P pairs; NP pairs and NB pairs) weekly the male-female distance mean and standard deviation was calculated. A two-way analysis of variance with repeated measures on one factor (ZAR, 1996) was performed to compare the male-female spacing pattern (factor with repeated measures) between experimental groups. We used the Cox-Stuart test for trend (DANIEL, 1978) to analyze male and female daily displacements. Male and female individual average daily displacement in each couple was compared with Wilcoxon paired-sample test. The weekly pattern of displacement was analyzed with the Mann Whitney test for independent samples (SIEGEL, 1989).

Male-female interactions: for each type of interaction recorded (positive; negative and/or indifferent) a weekly frequency was calculated and its time variation was analyzed using a best- fitness test. For each group (P pairs and NP pairs) a comparison was made between the frequency of recognition (positive) and agonistic (negative) behaviors using Fisher's exact test. The hypothesis that there are not differences in the frequency of behaviors of interaction (positive and negative) and indifference (do not exist) was tested by means of a χ^2 analysis. Use of nests: a χ^2 analysis of frequencies was applied to analyze the frequency of use of nests during the non-breeding season. The male and female nest use frequency was contrasted with the records of individual use and of cohabitation of the pair. Temporal variations in the frequency of cohabitation of males and females was tested by means of Cochran's test (SIEGEL, 1989) under the null hypothesis that the probability to find the mate inhabiting the same nest does not vary for the lapse of along the experiment.

RESULTS

Male-female spacing: the average distance (spacing) between sex was longer in the breeding season between P pairs than between NP pairs and shorter during the non-breeding season (tab. I). The variation range between shortest and longest distances was longer during the breeding season than non-breeding season (tab. I). The two-way Anova with repeated measures performed on average distance between male and female revealed a significant ($F=17.17$; $df=17.34$; $P<0.05$) difference between experimental groups. No significant difference ($F=0.21$; $df=34.34$; $P>0.05$) was found in the average distance between sex during the experiment and there were not significant interaction between factors ($F=0.75$; $df=34$; $P>0.05$).

Table I. Mean weekly and standard deviation of the spacing distance (in meters) between male and female adults of *Akodon azarae* during three weeks with daily 15-minutes observations. Pairs including male and pregnant females (P); those which did not copulate or underwent an unsuccessful mating (NP) and pairs during the non-breeding season (NB).

Pairs	Average distance	Minimum	Maximum
P	5.73±1.06	4.22	7.29
NP	3.96±1.61	1.54	6.02
NB	1.61±0.31	1.25	2.20

Table II. Frequency daily of interactive (agonistic and recognition) and non interactive behaviors between male and female adults of *Akodon azarae*. (P pairs, including male and pregnant females; NP pairs, not copulate or underwent an unsuccessful mating, NB pairs, during non breeding season).

Behaviors		P Pairs	NP Pairs
Interactive	Agonistic	8	1
	Recognition	1	6
No interactive		12	14
Frequency total		21	21

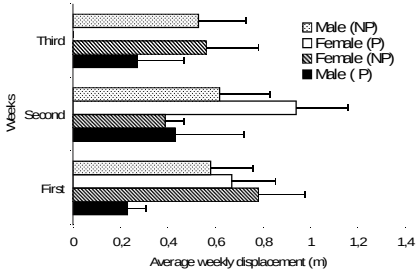

Fig. 1. Average weekly displacement and standard deviation (in meters) between male and female adults of *Akodon azarae* during three weeks with daily 15-minutes observations. Pairs including male and pregnant females formed the P group and those which did not copulate or underwent an unsuccessful mating constituted the NP group.

Pregnant females presented greater displacement during the first two weeks of gestation than during the third week (Wilcoxon $P<0.05$) (fig. 1). The weekly comparison with males showed that during the first two weeks the females moved significantly more than males (n=10 pairs; Wilcoxon $P<0.05$); instead during the third week there were no significant differences (Wilcoxon $P>0.05$). For NP male-female pairs, no differences were recorded between sexes in average weekly displacement during the three weeks that the experiment lasted (n=10; Wilcoxon $P>0.05$) (fig. 1). Comparison between the displacements made by pregnant and non-pregnant females showed that only in the third week did the non-pregnant females move more frequently than the pregnant ones (Mann-Whitney U test, $P<0.01$). Males from non-pregnant pairs presented greater displacements throughout the experiment than males from pregnant pairs (Mann Whitney U test, $P<0.01$) (fig. 1).

Male-female interaction: the frequency between interactive behaviors (both agonistic and recognition) and no interactive was not different between both groups ($x^2=0.4$; $P>0.05$). The agonistic behaviors were more frequently in the P than in the NP in which the recognition behaviors were observed more frequently (Fisher's exact test, $P<0.008$) (tab. II).

Use of nests: during the breeding season, each mate built and occupied its own nest. During the non-reproductive season cohabitation by both mates was frequently observed, even though most mates of NB pairs (n=8) were still building their own nests. The time spent within the same nest for both mates of a pair was significantly longer [50 of 69 observations (72.5%)] than the individual or exclusive use of the nest of each mate (of the pair) ($x^2=16.2$; $P<0.05$). There were not change in the weekly average frequency of cohabitation along the three weeks of observation (Cochran=23.48; $P>0.05$).

DISCUSSION

We observed differences in social tolerance of individuals according to their breeding condition being the male-female spacing the main manifestation of these differences. The maximum spacing was observed during the breeding season in those pairs which mated successfully (6.05 ± 0.35 m). Intermediate values were observed during this same season but in pairs where pregnancy was not detected (3.83 ± 0.55 m) and finally, the minimum separation was observed during the non-breeding season (1.61 ± 0.34 m). The shortest and longest distances recorded in each case also pointed to the existence of differences in the social tolerance between individuals according to their breeding state. During the breeding season the mean shortest distances between male and pregnant female were of 4.22 meter however, during the non-reproductive season the spacing was minimum (1.25 meter). Male and pregnant female apart each other as far as the closure allows them. Conversely NP male female distance was minimal and NB intermediate distance. ZULETA *et al.* (1988) reported a great tolerance between mates and females of *A. azarae* to share their home range during non-reproductive period, while the adult individuals of the species use their own home ranges without overlapping during the reproductive season. Behavioral differences in the use of space too were observed in *Apodemus sylvaticus* (L., 1758) (TEW & MACDONALD, 1994) being the home range of both sexes significantly longer during the breeding season than in other periods and particularly being that of the male longer than the female one during the breeding season

It was observed that during the breeding season males and females use separated nests unlike the non-breeding season when there are a high frequency of cohabitation by both mates of the pair, in spite of the fact that they build more than one nest. These results resemble those obtained by different authors for *Microtus pennsylvanicus* (Ord, 1815) (MADISON, 1980b; WEBSTER & BROOKS, 1981; MADISON *et al.*, 1984). These authors stated that during the breeding season there is less tolerance than during the non-reproductive season, when tensions relax and individuals could live together in the same nest.

The analysis of the displacements in the breeding season showed that during the first two weeks of gestation there was a bias inducing pregnant females to travel longer distances than their respective mates. Instead, the non-pregnant females traveled similar distances than the males during the three weeks of the experiment. The pregnant females did not move very much outside the nest during the third and last week of gestation. During the first two weeks, the pregnant females made displacements patrolling the neighborhood of the nest they were occupying and avoided the proximity of the males through agonistic confrontations. Encounters between males and non-pregnant females were either of the social or recognition types. These results show that aggression by the females is related not only with care of offspring but also with the defense of the nesting territory, where the offspring will be born (CROWCROFT & ROWE, 1963; ST. JOHN & CORNING, 1973; LIDICKER, 1976; LYNDS, 1976; SINGLETON & HAY, 1983; WOLFF, 1993). Territoriality for pregnant females may favor the access to the food supply, and therefore, ensuring the growth and survival of the offspring (BONAVENTURA *et al.*, 1992). For non-pregnant females the defense of an exclusive space might be more expensive than the possible benefits to be obtained from it, thus minimizing the probability of interaction with the male (HURST, 1987). Being *A. azarae* a promiscuous polygynous species (BONAVENTURA *et al.*,

1992; SUÁREZ & KRAVETZ, 1998b), males do not take part in the care of offspring and therefore, their breeding success is not limited to a single mating. In captivity, pregnant females are observed to limit the males displacements by means of aggressive confrontations, while in natural conditions the male could leave the female, looking for another potential mate. Similar results were obtained for *Microtus pennsylvanicus*, (MADISON, 1980a, b). Where the male does not take part in the care of offspring and it is even excluded from the nest by the female, behavior which is consistent with the promiscuous-polygynous mating system observed in that species.

In studies carried out in natural conditions, (Gustavo Adolfo Zuleta, personal commun.) records low rates of direct aggression among resident individuals during the breeding season, suggesting that social intolerance in this period might be maintained by means of marking with chemicals. However, the highest rates of aggression are detected in spring, particularly in October (for the Southern Hemisphere), month in which the first births take place. In the present study aggressive behavior was detected during the whole breeding season, and the disagreement may be attributed to the conditions of study. Under conditions of captivity social intolerance between individuals might leading to an increase in the level of direct aggression. The narrow line condition of experimental sands difficult bad to avoid females when they move across the cages. In contrast with the social interactions in NP couples, the aggressive interactions observed between males and pregnant females during the breeding seasons concord with the known territoriality of *A. azarae* female and favor the exclusive use of its nest areas to prevent disturbances to the nest. This study found that the social interaction developed by the male-female dyads of *A. azarae* is consistent with observations obtained in the natural state. The integration of behavioral and ecological studies let us explain the role of social behavior as an its adaptive meaning.

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