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Do polygynous males of *Akodon azarae* (Rodentia: Sigmodontinae) vary their mating tactics at low availability of females?

Abstract: We examined in *Akodon azarae* if at low availability of females (sex ratio biased toward males, 3:1), the mating tactics of males are determined by the number of receptive females to which they have access, or by the number of male competitors with which they interact. To test these hypotheses, we measured the home range size and overlap degree. At the beginning of the reproductive season, we studied spacing patterns using 57 and 30 home ranges established by reproductive males and females in three enclosure populations. We statistically compared our results with those previously obtained in enclosure populations with a sex ratio of 1:1. Male home range sizes were larger than those recorded in populations with a sex ratio of 1:1. The degree of male intra-sexual overlap increased about 3.5 times with respect to that observed under a sex ratio of 1:1. The increase in home range sizes and intra-sexual overlap degree of reproductive males reflects that *A. azarae* males may adjust their spacing strategy to increase their mating opportunities at low density of females. Our results suggest that at low breeding female availability, male mating tactics could be determined by the number of receptive females to which they have access.

Keywords: female availability; mating tactics; reproductive success; Sigmodontinae; spacing strategies.

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Introduction

Space use decisions and the resulting spacing patterns exhibited by individuals have profound ecological consequences, affecting individual fitness and population dynamics (Brown and Orians 1970, Waterman 2007). At the individual level, the way an organism uses space can influence its survival and reproductive success (Greenwood 1980, Madison 1980, Clutton-Brock 1989, Agrell et al. 1996). Space use can vary between individuals within a species owing to differences in sex, age, habitat quality, population density, and absence of conspecific adults in the area (Wolff 1985, Pusenius and Viitala 1993a,b, Bond and Wolff 1999, Steinmann et al. 2006a,b). In mammals, home range size and overlap could vary according to population density, density of females, and/or males, and both depend to a great extent on the sex and reproductive conditions of individuals (Fortier and Tamarin 1998, Ochiai and Susaki 2002). Male rodents typically have larger home ranges than females; however, the relationship among female density, male home range size, and the degree of intra-sexual overlap remains unclear (Erlinge et al. 1990, Nelson 1995a,b, Bond and Wolff 1999, Wolff et al. 2002, Wolff 2003).

Because males attempt to maximize their reproductive success by mating with as many females as possible (Emlen and Oring 1977), the two main factors that would limit their reproductive success are the number of females to which they have access and the number of male competitors with which they interact (Ostfeld et al. 1993, Pusenius and Viitala 1993a,b, Nelson 1995a,b, Ostfeld and Canham 1995, Wolff and Macdonald 2004, Steinmann et al. 2006a,b, Waterman 2007, Steinmann and Priotto 2011). Thus, variations in mating behavior are expected both within and between populations as a consequence of the adaptive adjustment of male and female behavior to differences in the social and ecological local environment (Emlen and Oring 1977, Clutton-Brock and Harvey 1978, Dunbar 1982, Clutton-Brock 1989, Loughran 2007). In the polygynous species *Microtus agrestis* (Linnaeus 1761) (Nelson 1995a,b, Agrell et al. 1996) and the promiscuous

species *Microtus canicaudus* (Miller 1897) (Bond and Wolff 1999) and *Calomys musculus* (Thomas 1913) (Steinmann and Priotto 2011), a low availability of females led to an increase in male competition.

The mating system of voles and mice reflects a variety of sex-specific mating tactics used by individuals to maximize their reproductive success (Clutton-Brock 1989, Wolff 1993, Randall et al. 2002, Wolff and Macdonald 2004, Waterman 2007). Polygyny is a mating system in which a minority of males control or gain access to multiple females (Emlen and Oring 1977, McEachern et al. 2009, Cudworth and Koprowski 2010). Typically polygynous males have larger home ranges than females with high inter-sexual and low intra-sexual overlap; however, these spatial features could vary at low density of females (Ostfeld et al. 1985, Ostfeld 1986, Ostfeld and Klosterman 1986, Wolff 2007). Many studies at the population level have revealed the impact of density and sex ratio on spacing and mating behaviors (Nelson 1995a,b, Bond and Wolff 1999, Moorhouse and Macdonald 2008, Knell 2009, Steinmann and Priotto 2011). The operational sex ratio (OSR), defined as the average ratio of sexually active males to fertilizable females at any given time, provides an empirical measure of the degree of monopolizability of mates (Emlen and Oring 1977). The greater the degree of imbalance in the OSR, the greater the expected variance in reproductive success among members of the limited sex and the degree of polygyny.

Akodon azarae (Fischer 1829) (Cricetidae: Sigmodontinae) has a polygynous mating system (Suárez 1996, Suárez and Kravetz 1998a, 2001, Bonatto et al. 2012). Bonatto et al. (2012) found sexual differences in body size, with males being larger than females, and proposed that the reproductive success of *A. azarae* males depends on their spatial ability to increase the number of receptive females to ensure optimal mating. During the breeding season in wild populations with a sex ratio close to 2 (male/female), males show longer movement distances than females (45 ± 7 m), whereas in the non-breeding period, movement distances become similar between sexes (Gomez et al. 2011). In enclosed populations with a sex ratio of 1:1, Bonatto et al. (2012) found that at the beginning and middle of the breeding season, the average home range size of reproductive males (RMs) is larger than that of females (240 and 160 m², respectively) and that the intra-sexual overlap percentages are low (12% male/male, 7% female/female). Males do not overlap their home ranges with other males, and this absence of overlapping is maintained both at low and high population density (Bonatto et al. 2012). This spatial avoidance would reflect competition among males for monopolizing the receptive females

(Bonatto et al. 2012). In a more recent study, Bonatto et al. (2013) found that the territorial behavior of *A. azarae* males is strongly related with female defense, and proposed that polygyny operates through female defense. In contrast, females keep exclusive home ranges only at low and moderate densities (Bonatto et al. 2012, Ávila 2013). Bonaventura et al. (1992) suggest that during the breeding season, the territoriality of *A. azarae* females would favor the access to green cover and food, increasing the growth rate and the survival of their offspring.

Considering the background of *Akodon azarae* space use in unbiased sex ratio populations, our objective was to test if the mating tactics of males with a low number of receptive females are determined by the number of receptive females to which they have access or by the number of male competitors with which they interact. To test these hypotheses, and considering that the patterns of space use reflect the mating strategies used by individuals, we measured home range size and overlap degree. In the former hypothesis, we expect that males increase their home range size and intra-sexual overlap degree, whereas in the latter we expect that they decrease both.

Materials and methods

Study species

Akodon azarae (Pampean grassland mouse) together with *Calomys musculus* and *Calomys venustus* (Thomas 1894) are the numerically dominant rodents in agroecosystems of Córdoba province, Argentina (Gomez et al. 2011). This small rodent species (adult average mass, 25 g) is an opportunistic omnivore (Suárez and Bonaventura 2001) and shows continuous activity, being mainly active during daytime and crepuscular hours (Priotto and Polop 1997). This species is found in a great variety of stable habitats with high gramineous cover, including natural pastures, road borders, borders between cultivated fields or pastures, and railway banks (de Villafañe 1981, Bonaventura and Kravetz 1984, Busch et al. 2001). These habitats are characterized by keeping remnant native flora and fauna (Busch et al. 1997, Ellis et al. 1997). *Akodon azarae* is a good indicator of habitat quality owing to its preference for these relatively undisturbed habitats. *Akodon azarae* populations turnover annually, and the individual lifespan is about 12 months (Zuleta et al. 1988, Hodara et al. 2000). The typical population abundance of *A. azarae* at the beginning and the middle of the reproductive period is about 60 individuals/ha (Zuleta et al. 1988, Bonaventura

and Kravetz 1989, Priotto and Polop 1997, Priotto and Steinmann 1999, Gomez et al. 2011), and the sex ratio is typically male biased (male/female=1.83) (Priotto and Steinmann 1999, Bonatto 2013). Breeding occurs mainly in spring and summer (mid-September to mid-March), and there is a marked annual variation in population abundance. Low population numbers occur in spring (September–December), abundance peaks in autumn (May), and decreases dramatically in late winter–early spring (August–September) (Gomez et al. 2011). This species has an average gestation length of 22.7 days and reaches sexual maturity at 60 days (Dalby 1975, de Villafañe 1981). The young are weaned at 14–15 days old and cared for exclusively by females (de Villafañe 1981, Suárez and Kravetz 1998b). *Akodon azarae* has been described as moderately prolific because of the number and size of litters (an average of 3 l of 4.6 pups during a female lifetime), the late sexual maturation, and the low rates of postpartum estrous (de Villafañe 1981).

Study site

This study was carried out between November 2010 and January 2011 in the Espinal nature reserve (33°07'S, 64°14'W) in Córdoba province, Argentina. This study period was selected because at the beginning and middle of breeding season, the sex ratio in wild populations of *Akodon azarae* is male biased (Priotto and Steinmann 1999, Gomez et al. 2011). We studied the effect of low female availability on the space use of *A. azarae* males in three 0.25-ha (62.5 m×40.0 m) enclosures. The enclosures were made of galvanized iron sheets extending 0.3 m underground and 0.7 m above ground, and were situated in a natural pasture interspersed with shrubs and herbaceous weedy species. The three enclosures (enclosures I, II, and III) functioned as independent populations. All enclosures had similar vegetation composition, with high percentage of gramineous cover, and were considered homogeneous. A 1-m-wide grass strip was devegetated on the inner margin of each enclosure to establish a matrix.

Study design

In September and October 2010, we collected *Akodon azarae* adults from an area located 30 km away from the study site, along road borders and borders between cultivated fields. In these linear habitats, the wild population abundance of *A. azarae* was 61 individuals/ha, and the sex ratio was male biased (1.71). Adult individuals

were maintained in the laboratory and housed individually in clear polycarbonate cages. All animals were sexed, weighed, and ear-tagged. Mice were maintained on a 16:8 light/dark photoperiod. Rodent chow and water were provided *ad libitum*, and sunflower and maize seeds were provided as weekly supplements. Wood shavings were provided for bedding.

At the beginning of November 2010, 16 adult individuals (12 males and 4 females) were taken to each enclosure. Thus, the population sex ratio (males/females) at the beginning of the study was 3:1. Throughout the study, the sex ratio was maintained by the incorporation of laboratory adult animals. In each enclosure, we set a capture-mark-recapture grid of 6×10 traps with an interstation distance of 6 m. One live trap similar to a Sherman trap was placed at each station and baited with a mixture of peanut butter and cow fat. To identify animals unable to settle down within the enclosures during the study, 32 live traps were placed at 6-m intervals in each devegetated edge (matrix). We assumed that all individuals were able to settle within the enclosures as no animal was trapped in the devegetated edge in each trapping session.

After a settlement period of 25 days, three fortnightly trapping sessions were carried out for six successive nights between December 2010 and January 2011. Traps were checked and closed each morning, and reopened at sunset. Trapped animals were sexed and weighed. Body and tail length were also recorded. The reproductive condition was determined on the basis of external characters (for males, scrotal or abdominal testicles; for females, perforate or imperforate vagina, nipples visible or not, and evidence of pregnancy). We also recorded trap locations. In this study, animals that weighed more and equal to 16 g (females) and 18 g (males) were considered adults (Dalby 1975, de Villafañe 1981).

To estimate the home range configuration of each animal, all captures were plotted on graph paper for each trapping session following the boundary strip methods (Stickel 1954). To estimate the home range size (m²), we used the minimum convex polygon method (Jenrich and Turner 1969) for its mathematical simplicity and convenience for comparison with previous studies. In each trapping session, the intra-sexual home range overlaps were estimated for each individual by the method suggested by Batzli and Henttonen (1993). This method assumes that when the home range overlap is significantly lower (≤10%) than it would be expected by random placement, individuals are avoiding one another, and this is considered as an evidence of territorial behavior (Wolff et al. 1983, Batzli and Henttonen 1993, Wolff 1993, Steinmann et al. 2009). Inter-sexual overlap values (male/female)

were only calculated to identify those males that overlapped their home ranges >10% over female home ranges. We considered as RMs those that overlapped their home ranges >10% with female home ranges in at least two of the three trapping sessions, and as non-reproductive males (NRMs) those that overlapped $\leq 10\%$ and males that established home range without inter-sexual overlap. In this study, there was no overlapping between the NRM and RM home ranges. Assuming that inter-sexual overlap values >10% reflect mating (Clutton-Brock 1989), in this study, the OSR was calculated for each trapping session as $OSR = \text{number of RM} / \text{number of breeding females that established home ranges}$.

Data analysis

We used the linear mixed model (LMM) to examine the relationships between each response variable (home range size and home range overlap) and predictor variables. We only considered home range size and overlap degree of breeding females and RM. In the analysis of home range size, the predictor variables were sex (fixed factor with two levels) and trapping session (fixed factor with three levels). In the analysis of home range overlap, the predictor variables were overlap type (fixed factor with two levels: male/male, female/female) and trapping session. We used the same statistical methods to compare populations with male-biased sex ratio and populations with a 1:1 sex ratio studied by Bonatto et al. (2012). In the latter, the age of individuals and total densities of *A. azarae* enclosure populations were similar to those registered in our study. Besides, vegetation composition, percentage of plant cover, and weather characteristics (temperature and precipitation) were also similar to those reported in our study. We were able to make this statistical comparison because in both studies, the trapping sessions were conducted at the same date of the year and male reproductive condition was identified in the same way. For these analyses, we added sex ratio (fixed factor with two levels: sex ratio 1:1, sex ratio 3:1) as a predictor variable. In all cases, we included enclosure and individual as random factors, as home range estimations were recorded for each individual in each enclosure in the three trapping sessions. The Akaike information criterion (AIC) was used as a measure of the fit of a model (the smaller the AIC, the better the fit). Model comparison was based on differences in AIC values (ΔAIC); when ΔAIC was greater than two units, the model with the lowest AIC was considered as a better statistical description of the process that generated the data. The best

resulting models were analyzed using analysis of variance (ANOVA). Because equal variance is the most important assumption underlying ANOVA (Crawley 2007), we checked this assumption by using Bartlett's test (Crawley 2007). When this assumption could not be met, the variable was transformed. Statistical analyses were carried out using program R version 2.12.2, NLME library.

Results

From early December 2010 to early January 2011, 51 *Akodon azarae* adults (36 males and 15 females) were captured 828 times in enclosures I, II and III. Densities of *A. azarae* populations were relatively constant during this study: 14 individuals per enclosure (56 ± 1.15 individuals/ha) in early December, 13 (52 ± 1.73 individuals/ha) in late December, and 12 (52 ± 1.53 individuals/ha) in early January. Because the current pregnancy rate is a consequence of previous mating and spacing tactics, we considered the pregnancy rate registered in the trapping session after that spacing data were obtained. Thus, for late December, early January, and late January correspond a pregnancy rate of 41.6%, 75%, and 91.7%, respectively. We were able to calculate the pregnancy rate corresponding to late January because our study was part of a broader one that lasted until late March. In this study, we added only one adult male per enclosure between the trapping sessions of late December and early January. During the study, we captured only two juveniles in enclosure III in early January.

During this study, 87 home ranges of 29 different reproductive adults of *Akodon azarae* (19 males and 10 females) were estimated: 57 RM home ranges and 30 female home ranges. In addition, we estimated 19 home ranges of 13 NRMs. Thus, 40.6% of adult males did not gain access to receptive females. Although during this study, population sex ratios were maintained male biased 3:1, the OSR were 1.58 ± 0.38 , 1.58 ± 0.29 , and 1 ± 0.62 in the three trapping sessions. The average home range sizes were 254.94 ± 106.17 m² for females and 296.93 ± 131.96 m² for RMs (Figure 1). The average home range size of NRM was 196.66 ± 93.63 m². LMM analysis revealed that there were two approximating models with similar support ($\Delta AIC < 2$) for describing home range size. Both models included an interaction effect between sex and trapping session but with different random effect structure (Table 1). To differentiate which random factors are required in the model, we used ANOVA to compare the two models. This analysis revealed that there was no significant effect attributable

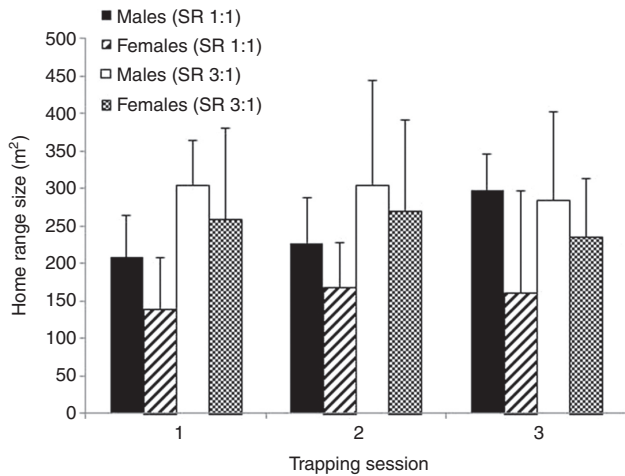


Figure 1 Home range size (mean+SD) in relation to sex and trapping session, in *Akodon azarae* enclosure populations with male/female sex ratios of 3:1 (SR 3:1) and 1:1 (SR 1:1, obtained from Bonatto et al. 2012).

Table 1 Model selection based on AIC comparison of LMM describing home range size and overlap of *Akodon azarae* populations with a sex ratio of 3:1.

Response variable	Fixed effect	Random effect	AIC
Home range size	Sex*trapping session	Individual	1031.64
	Sex*trapping session	Enclosure/ individual	1033.41
Home range overlap	Overlap type*trapping session	Enclosure/ individual	605.64
	Overlap type*trapping session	Individual	606.78

The models include different fixed and random effect structures. Models are ordered by ΔAIC; only models with ΔAIC ≤ 4 are shown.

to differences between enclosures (L. ratio=0.23, p=0.63). Thus, the best model only included an individual random effect. In Table 2, we provide full factor models. Differences between sexes in home range sizes were not significant (Table 2, Figure 1).

The female/female overlap percentages were always <7% (female overlap average values 4.09±2.83%), and the lowest intra-sexual overlap value was observed in the last trapping session (close to 0%). However, RM/RM home range overlap values quadrupled those registered between females (15.82±2.18%). LMM analysis also revealed that there were two approximating models with similar support (ΔAIC<2) for describing overlap values. Both models included an interaction effect between overlap type and trapping session factors with a different random effect structure (Table 1). Similarly to the

Table 2 Effect of sex and trapping session on home range size, and overlap type and trapping session on home range overlap: summaries of two way ANOVAs for home range size and overlap degree of *Akodon azarae* populations with a sex ratio of 3:1.

Response variable	Fixed factors	df	F value	p-Value
Home range size	Sex	1	2.18	0.14
	Trapping session	2	0.34	0.71
	Sex*trapping session	2	0.02	0.98
Home range overlap	Overlap type	1	33.80	1.16e-7 ^a
	Trapping session	2	0.57	0.57
	Overlap*trapping session	2	1.56	0.22

Level of significance: ^ap<0.05.

previous analysis, we used ANOVA to compare these two models. This analysis revealed that there was no significant effect attributable to differences between enclosures (L. ratio=3.14, p=0.07). The best model only included an individual random effect. The overlap average values of female/female were always lower than male/male; however, the greatest differences were observed in the last trapping session, when females slightly shared their home ranges, while males reached the greatest overlapping values (Figure 2). However, there were significant differences only between overlap types (Table 2).

To know if there was a significant change in the home range size and overlap degree between pregnant and non-pregnant females, we used a one-way ANOVA test. This revealed that both home range size (F=0.01, df=1, p=0.94)

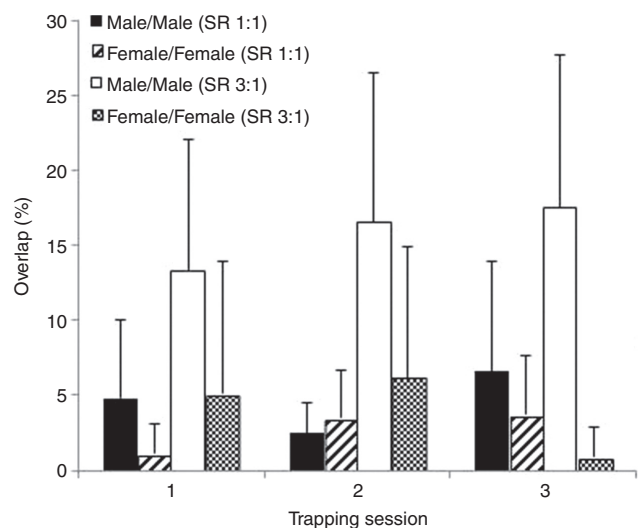


Figure 2 Home range overlap (mean+SD) in relation to overlap type and trapping session, in *Akodon azarae* enclosure populations with male/female sex ratios of 3:1 (SR 3:1) and 1:1 (SR 1:1, obtained from Bonatto et al. 2012).

and overlap degree ($F=3.48$, $df=1$, $p=0.07$) did not vary in relation to pregnancy condition. However, we cannot assure whether this lack of differences in home range size and overlap degree between pregnant and non-pregnant females is caused by the absence of effects of reproductive condition or because of the small sample size. To find differences in these parameters, it would be crucial to increase the sample size from 15 to 20 females, which would increase the statistical power from 60% to 90%. One needs to be cautious about some biologically significant effects that might have been missed because of the small sample sizes (Steidl et al. 1997, Lin et al. 2004).

In relation to the statistical comparison between populations with sex ratios 1:1 and 3:1, we found two approximating models with similar support ($\Delta AIC < 2$) for describing home range size and overlap values. In both analyses, the best models included the same fixed factor but with different random effect structure (Table 3). The ANOVA analysis revealed that there were no significant effects attributable to differences between enclosures either in home range size (L. ratio=0.66, $p=0.42$) or overlap (L. ratio=3.69, $p=0.06$). Thus, in both analyses, the best models included only an individual random effect. For home range size, the best model included interaction effects among sex, trapping session, and sex ratio (Table 3). In populations with a sex ratio of 3:1, the male home range sizes increased 18% with respect to those measured in populations with a sex ratio of 1:1 (Figure 1). For overlap values, the best model included an interaction effect among overlap type, trapping session, and sex ratio (Table 3). In populations with a sex ratio of 3:1, the intramale home range overlap increased 50% with respect to that observed in populations with a sex ratio of 1:1 (Figure 2). In both cases, because assumption of homogeneity of residual variances could not be obtained, even when the data were transformed, ANOVA tests were not performed.

Table 3 Model selection based on AIC comparison of LMM describing home range size and overlap of *Akodon azarae* populations with sex ratios of 1:1 and 3:1.

Response variable	Fixed effect	Random effect	AIC
Home range size	Sex*trapping session*sex ratio	Individual	1714.52
	Sex*trapping session*sex ratio	Enclosure/ individual	1715.87
Home range overlap	Overlap type*trapping session*sex ratio	Enclosure/ individual	984.77
	Overlap type*trapping session*sex ratio	Individual	986.46

The models include different fixed and random effect structure. Models are ordered by ΔAIC ; only models with $\Delta AIC \leq 4$ are shown.

Discussion

The home ranges of males were bigger in populations with a male-biased sex ratio than in unbiased populations. The differences in home range sizes between sexes were smaller at low availability of females. The slight differences between male and female home range sizes observed in populations with a sex ratio of 3:1 are because females increased their home range sizes about 69% with respect to the mean size values obtained by Bonatto et al. (2012) in unbiased populations. Considering that food resources and plant cover were abundant and evenly distributed in the enclosures of both studies, an increase in female home range size may be a response to fewer competing females. Besides, it is still economical to maintain larger and exclusive home range at low abundance of competitors, as keeping exclusive home ranges is an adaptation for defense of food and plant cover resource in *Akodon azarae* females (Bonaventura et al. 1992, Bonatto et al. 2012). In the last trapping session, when the majority of females were pregnant, female aggression toward males would also contribute to home range exclusiveness. According to Suárez and Kravetz (2001), pregnant females of this species exhibit high levels of aggressiveness against males to prevent disturbances to the nest.

In this study, the degree of male-male overlap was greater than the overlapping values obtained by Bonatto et al. (2012). In rodents, during the breeding season, space use of males is strongly affected by the search of mate (Dobson 1982, Ostfeld et al. 1985, Ostfeld 1986, Ostfeld and Heske 1993), and female availability is a key resource in determining home range size and degree of intra-sexual overlap (Ylönen and Viitala 1985, Ostfeld and Canham 1995, Ylönen and Mappes 1995, Bond and Wolff 1999, Steinmann et al. 2005, 2006b). Several studies have shown that the space use of voles and mice is influenced by the presence or absence of other individuals and the distribution of resources that may limit fitness (Pusenius and Viitala 1993b, Wolff et al. 1994, Wolff and Schaubert 1996, Fortier and Tamarin 1998, Bond and Wolff 1999, Steinmann et al. 2006b, Steinmann and Priotto 2011). Ostfeld (1990) and Agrell et al. (1996) proposed that changes in space use of males could be predicted by the sex ratio. In the promiscuous species *Calomys musculinus*, males strongly decrease their home range sizes and intra-sexual overlap degrees at low female availability as a consequence of an increase of competition between them for receptive females (Steinmann et al. 2006b, Steinmann and Priotto 2011). Contrarily, in the promiscuous rodent *Microtus canicaudus* (Bond and Wolff 1999) and in the polygynous species *Microtus californicus* (Peale 1848) (Ostfeld et al. 1985, Ostfeld 1986) and *Clethrionomys rufocanus*

(Sundevall 1846) (Ims 1987, 1988), an increase in the degree of intra-sexual overlap of RMs was reported in populations with low female and high male densities. Additionally, in a study with density manipulation in the polygynous *Microtus agrestis*, Nelson (1995a) found that males increased their home range sizes and intra-sexual overlaps at low density of females to compensate for the few mating opportunities. Similarly, our results suggest that *Akodon azarae* males may adjust their space use to increase their mating opportunities at low density of females. As the increase of overlap degree of *A. azarae* males is a consequence of the enlargement of home range size (Bonatto 2013), the higher intra-sexual overlap would indicate a larger movement rate of males in populations with low female availability. Thus, the larger inter-male overlap observed in this study might reflect a search of additional females as a strategy of compensation for the few mating opportunities. In the mating effort strategy, reproduction should be greater in males that use the most rewarding tactic (Yoccoz et al. 2002, Mysterud et al. 2004, 2005). The most logical benefit to males is the chance of siring multiple litters. Thus, at low availability of females, different males could maximize their fitness by overlapping their home ranges over the ranges of the same females. According to Madison (1980), the overlap between neighboring polygynous males with the home ranges of receptive females supports the notion that overlapping with another breeding male only pays when the chance of increased reproductive success is clear. Thus, at low availability of females, those *A. azarae* males that shared females would obtain more matings than those that did not.

An increase of assistance in rearing offspring and guarding mated females is a behavioral tactic to increase male reproductive success when females are scattered or scarce (Grafen and Ridley 1983, Gruder-Adams and Getz 1985, Clutton-Brock 1989, Storey et al. 1995, Waterman 2007). In the first place, *Akodon azarae* typically does not have nest cohabitation by a male-female pair; males do not contribute to the construction of the nest; and the parental care is carried out exclusively by females, independently of female density (Bonaventura et al. 1992, Suárez and Kravetz 2001, Suárez et al. 2004). Thus, in this species, males are not expected to participate in offspring care. Finally, mate guarding is another beneficial mating tactic by which dominant males increase their reproductive success by investing more on keeping and defending females than the subordinate males (Horne and Ylönen 1996, Waterman 2007). In rodent species, mate guarding is associated with high densities of competing males, dispersing females, and females in post-partum estrus, rather than with a low density of females (Webster and Brooks 1981, Sherman 1989, Waterman 1998, 2007). Mate guarding

is mainly registered in species in which mating is confined to a very short period of the female reproductive cycle (Parker 1974, Webster and Brooks 1981, Grafen and Ridley 1983). Besides, mate guarding is a widespread strategy in species with pronounced sexual dimorphism and intra-sexual differences in body size of males (Le Boeuf 1974, Clutton-Brock et al. 1977, 1982, Davies and Halliday 1979, Poole 1989). We are not able to propose this strategy for *A. azarae* males as reproductive activity extends throughout their life cycles (de Villafañe 1981, Bonatto et al. 2012), and they do not have either pronounced sexual dimorphism or remarkable differences in body size (Bonatto et al. 2012).

As regards female competitive searching tactic, some authors propose that the ability to find receptive females is more important to male reproductive success than overt conflict (Gaulin and FitzGerald 1986, Dewsbury 1988, Ims 1988, Waterman 2007). The sexual selection theory predicts that when one sex is limited in availability (usually females), the other sex competes for access to members of the underrepresented sex (Trivers 1972). It has been proposed that in the breeding period, males compete for acquisition of as many mating partners as possible and that at low densities of females, males are more likely to be aggressive (Krebs et al. 1969, Flowerdew 1974, Krebs 1978, Perrin 1981, Boonstra and Hogg 1988, Boonstra et al. 1993, Nevo 2007, Moorhouse and Macdonald 2008). In this study, even though the initial population sex ratio was strongly male biased, and we strived to maintain a sex ratio of 3:1 during the study, the average OSR (1.39) indicated that almost half of the males were not able to gain access to receptive females. Taking into account that OSR values reflect mating competition (Clutton-Brock and Parker 1992, Kvarnemo and Ahnesjö 1996, Mitani et al. 1996), the OSR observed in this study would suggest inter-male competition. However, we did not observe external signs of fights among males. It is possible that the greatest intra-sexual overlap degree between males increases familiarity, reducing intra-sexual aggressive tendencies as several authors suggest for other vole species (Dewsbury 1988, Ferkin 1988, Ylönen et al. 1990, Pusenius and Viitala 1993a,b, DeVries et al. 1997, Ricankova et al. 2007). Thus, the greatest spatial association between *Akodon azarae* RMs registered in this study would explain the absence of external signs of fights.

In conclusion, we found that under male-biased populations, the increase in home range sizes and intra-sexual overlap degree of *Akodon azarae* males would reflect a transient spatial tolerance tactic to increase their mating opportunities. Our results suggest that at low breeding female availability, the mating tactics of males are determined by the number of receptive females to which they have access.

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