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The influence of adult female absence on the spacing behaviour of juvenile corn mice, *Calomys musculinus*: a removal experiment

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We tested the hypothesis that the absence of adult females promotes a restriction in spacing behaviour in juvenile male *Calomys musculinus* at the beginning of the breeding period. Our study was carried out in four 0.25 ha enclosures (two control and two experimental enclosures), between December 2004 and February 2005. Mothers were removed from the experimental enclosures. Home range size depended on the sex of juveniles and the treatment. Female home range sizes were always smaller than those of males. Male home ranges were larger in control enclosures than in experimental enclosures. Treatment and overlap type (intra- and inter-sexual) were not independent. The overlap proportions of male home ranges were lower in experimental enclosures than in control enclosures, in both overlap type (male/male, male/female). The intra- and inter-sexual overlap proportions of female home ranges were independent of treatment. The results are discussed in the light of spacing behaviour and competition for resources.

Introduction

Space use can vary within a species due to differences in habitat quality, food quantity and quality, sex, age, population density, familiarity of breeding partners, receptive female abundance and distribution, and absence of conspecific adults (Ostfeld *et al*. 1985, Wolff 1985, Ims 1987, 1988, Ylönen *et al*. 1988, Pusenius & Viitala 1995, Hubbs & Boonstra 1998, Priotto & Steinmann 1999, Priotto *et al*. 2002, Steinmann *et al*. 2005). Many studies have reported that the absence of adults or parents influence differences in the spacing behaviour of juvenile voles within the breeding period (Madison 1980, Rodd & Boonstra 1988, Wolff 1992, Ylönen *et al*. 1995). In some small rodent species the aggressive behaviour of adults toward juveniles depends on which sex is territorial. Thus, spacing behaviour can be influenced by both adult males (Hearley 1967, Flowerdew 1974, Steinmann *et al*. 2005) and adult females (Bondrup-Nielsen 1986). The presence of adult males and the absence of adult females may inhibit both the movement and the sexual activity of juvenile males (Saitoh 1981, 1983, Rodd & Boonstra 1988, Wolff 1999).

Studies carried out by Ylönen and Mappes (1995) and Steinmann *et al.* (2005, 2006) support the hypothesis of the importance of female distribution in determining male space use during the breeding period. Moreover, the reduced overlap of male movements in the breeding season, when females remain in one place, could indicate an increase in competition between males as a mechanism to monopolise an aggregation of receptive females (Ostfeld 1985, Ims 1987).

Calomys musculinus (Muridae, Sigmodontinae) is the dominant rodent species of central and north-western Argentina, and its ecology is mainly studied due to its role as a reservoir of the Junin virus, etiological agent of the Argentine Hemorrahgic Fever (AHF) (Busch *et al.* 1984, Mills & Childs 1998). It inhabits Pampean agrarian ecosystems and is found in a variety of habitats including natural pastures, crop-field edges, cultivated fields undisturbed after harvest, border areas protected by wire enclosures with little agricultural disturbances, roadsides, and railway banks (Polop *et al.* 1985, Busch *et al.* 2000).

The *C. musculinus* breeding period begins in mid-September and finishes at the end of April (de Villafañe 1981), and females and males reach sexual maturation in synchrony (L. Sommaro pers. comm.). In this species, differences in home range size and home range overlap are determined by sex and breeding period (Steinmann *et al.* 2005). Considering the sexual differences in home range sizes, intra- and inter-overlap degree, a lack of paternal care, and that the key resource for reproductive males is receptive females, Steinmann *et al.* (2005) suggest a promiscuous-polygynous mating system for *C. musculinus*. Females keep exclusive home ranges in both breeding and non-breeding periods. Thus, in *C. musculinus*, territoriality is a female characteristic (Steinmann *et al.* 2005).

Research regarding the spacing behaviour of juvenile corn mice, *C. musculinus*, at the beginning of the breeding period and in absence of adult males, was carried out by Steinmann *et al.* (2006). In large outdoor enclosures we conducted an experiment to test the hypothesis that the absence of adult females, at the beginning of the breeding period, decreases the home range size and consequently the degree of intra- and inter-sexual (male/females) home range overlap of juvenile males.

Materials and methods

Our study was carried out in Espinal Reservation of the campus of the National University of Río Cuarto (33°07´S, 64°14´W), between December 2004 and February 2005. Phytogeographically, this region corresponds to “Provincia del Espinal, Distrito del Algarrobo”, which is a low plain (elevation 600–900 m). Our study area was a natural pasture with a high vegetative cover, interspersed with bushy and weedy species, that is very similar to the natural habitats of *C. musculinus*.

We set up four 0.25 ha enclosures (two control and two experimental enclosures) made of galvanized iron sheets extending 0.3 m underground and 0.7 m above ground. For a detailed description of the study area and enclosures *see* Priotto and Polop (2003), and Priotto *et al.* (2004). In each enclosure, six reproductive shelters were enclosed with a concrete circle of 1 m diameter and 0.7 m height and were covered by iron mesh. On the inner margin of each enclosure, a 1-m-wide grass strip was devegetated with herbicide.

Parent *C. musculinus* were from an area located 30 km away from the place of study. Between mid-September and October 2004, parents were mated in the laboratory in 16 individual reproductive boxes. The mice were maintained on a reversed 16:8 light/dark photoperiod and each couple was housed in clear polycarbonate cages. Wood shavings were provided for bedding, and water and Purina laboratory chow were continuously available. After offsprings were weaned in the laboratory, the mothers were removed from those eight boxes that were aleatorily placed into the experimental enclosures (four in each one). In those eight boxes chosen to be placed into the control enclosures, both parents remained with the offspring (eight parents in each one). The offspring and their parents were weighed and ear-tagged for permanent identification. The sex and birth date of all animals were recorded. Thus, during this study, the age of the offspring was known. After this, the animals were taken to the enclosures, and then each family group was located in a reproductive shelter. After three days the reproductive shelters were opened and the animals dispersed into the enclosures. Thus, in the experimental enclosures there were four fewer reproductive females than in the control enclosures.

At the beginning of the study there were 34 males and 36 females of *C. musculinus* in the control enclosures, meanwhile in the experimental enclosures there were 37 males and 24 juvenile females. In each enclosure there was a CMR grid of 6 × 10 traps with an interstation interval of 6 m. One Sherman live trap was placed at each station and baited with a mixture of peanut butter and cow fat. Monthly censuses (trapping sessions) were carried out in each enclosure during eight successive nights. In order to detect those animals that were not able to settle in the habitat area of the plot, in each devegetated edge 28 Sherman live traps were placed at 6 m intervals. Animals that were trapped three consecutive times in devegetated edge areas within each trapping sessions were removed from the population since we assumed that they were not able to settle within the enclosures. The traps were checked each morning during the trapping sessions. Sufficient amount of commercial trout pellets was added weekly to each enclosure. Trapped animals were weighed, and sex and reproductive state were recorded. Reproductive condition was judged on the basis of the following data: position of testicles (scrotal or abdominal) in males; perforate or imperforate vagina, nipples visible or not, and evidence of pregnancy in females. In this study, animals between 25 and 60 days of age were considered juveniles (de Villafañe 1981). Most of the juveniles were reproductively mature after 25 days of age (L. Sommaro pers. comm.).

In December 2004, at the beginning of CMR study, in control enclosures there were 54 juveniles (28 and 26 in each one) and eight adults per enclosure. In experimental enclosures there were 55 juveniles (28 and 27 in each one) and four adult males per enclosure. Therefore, the mean initial population abundance was 70 individuals in control enclosures, and 63 in experimental enclosures.

To study spacing behaviour, home range configuration, size and degree of overlap were considered. To estimate the home range configuration of each animal, all captures were plotted on a graph paper for each trapping session, following the Boundary Strip method (Stickel 1954). To estimate home range size (m^2), we selected the minimum convex polygon method, because of the ease of calculation and its mathematical simplicity. The number of captures for each home-range estimate varied from seven to eight. In each trapping session, the intra- and inter-sexual home range overlap was estimated for each individual reproductively active by the method suggested by Batzli and Henttonen (1993). Thus, we calculated proportional overlap by measuring the area in each home range (the target animal) that was overlapped by another animal's home range of the same sex (intrasexual overlap), or another animal's home range of the opposite sex (inter-sexual overlap), and dividing the result by the area of the target animal's home range. When home range overlap is significantly lower than expected by random placement, it is assumed that individuals are avoiding one another. We consider this as evidence of territorial behaviour (Batzli & Henttonen 1993).

The population size for each sampling was estimated with the minimum number of animals alive (MNA) method, expressed as the number of animals per hectare. MNA was used because it is a reasonable index to estimate population size (Kesner & Linzey 1997), and Slade and Blair (2000) emphasize the importance of using MNA when a single area with a fixed protocol is used. The population density was compared among treatments using repeated-measures ANOVA. Each trapping session was the repeated measures factor (beginning of December, the end of December 2004, January and February 2005).

To analyse home range size in relation to sex and treatment, and home range overlap percentage in relation to treatment and overlap type (males/males, females/females, males/females and females/males), repeated-measures ANOVA was also used. The repeated measures factor was the trap session. The *F*-statistics for within-subject factors (and their interactions) are inflated in repeated-measures ANOVA when the sphericity assumption is not met (Von Ende 2001), thus the Greenhouse-Geisser corrected probability was used when interactions were statistically significant. In all cases, normality assumption was tested with the Kolmogorov-Smirnov test, and variance homogeneity was tested with Bartlett's test (Sokal & Rohlf 1979).

Results

From the beginning of December 2004 to February 2005 a total of 1335 captures were recorded during 3072 trap nights: 206 and 216 *C. musculinus* individuals were obtained in control and experimental enclosures, respectively. A total of 422 individuals (232 males and 190 females) were ear-tagged. The sex ratio (male/female) mean values ranged from 0.94 to 1.2 in the control and from 1.6 to 1.9 in the experimental enclosures. During the study, the population density did not vary between the control and experimental enclosures ($F_{1,2} = 13.410$, $p = 0.615$), nor in relation to the trapping session either ($F_{1,2} = 14.231$, $p = 0.620$). At the beginning of December, the mean population densities were 22 voles per ha in the control enclosures and 23 in the experimental enclosures: they increased towards February to 28 and 29 in the control and experimental enclosures, respectively.

During this study, ten animals were removed from the enclosure populations because they were trapped 3 consecutive times in live traps placed in the devegetated edge areas. We assumed that the rest of the animals were able to settle within the enclosures. Only reproductively mature animals established home ranges in both control and experimental enclosures.

The home range size was calculated for each trapping session. During the study, 146 home ranges of reproductive individuals of *C. musculinus* were estimated. In the control enclosures 77 home ranges were estimated (40 and 37 male and female home ranges, respectively), and in the experimental enclosures 69 (48 and 21 male and female home ranges, respectively). Thus, the number of male and female home ranges in the control enclosures was similar, whereas in experimental enclosures female home ranges represented only 30% of all home ranges.

When home range size was analysed, the interaction between sex of juveniles and treatment (mother removal), was observed ($F_{1,4} = 148.47$, $p = 0.0002$). In both control and experimental enclosures the female home ranges were similar (Tukey for equal *N*: $p = 0.9999$) and smaller than male home ranges in control ($p = 0.0002$) and experimental ($p = 0.0030$) enclosures. Otherwise, male home ranges were always fewer in the experimental enclosures than in the control enclosures (Tukey for equal *N*: $p = 0.0031$) (Fig. 1). The first-order interaction (treatment × time and sex × time), and second-order interaction (treatment × time × sex) were not statistically significant ($p > 0.05$).

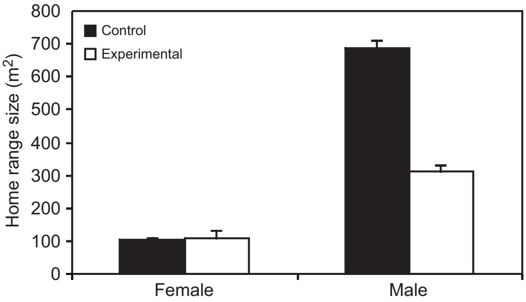

Fig. 1. Home range size (mean + SD) of *Calomys musculinus* juveniles, in relation to treatment and sex.

Treatment and overlap type (intra- and intersexual) were not independent when the overlap proportion was analysed ($F_{3,8} = 32.388$, $p = 0.0002$). The overlap proportions of male home ranges were lower in experimental enclosures than in control enclosures, in both overlap types (intra- (m/m) and inter-sexual (m/f)) (Tukey for equal *N*: $p = 0.0021$ and $p = 0.0004$, respectively). The intra- (f/f) and inter-sexual (f/m) overlap proportions of female home ranges were independent of treatment (Tukey for equal *N*: $p = 0.9999$ and $p = 0.9899$, respectively) (Fig. 2). The interaction between treatment and time was not statistically significant ($p = 0.0592$) when Greenhouse-Geisser corrected probability was applied. The overlap type × time and treatment-overlap type × time interactions were not statistically significant ($p > 0.05$).

Discussion

We found that the home range size and overlap degree in *C. musculinus* were determined by sex and treatment. Even though the home range size and intra- and inter sexual-overlap of males

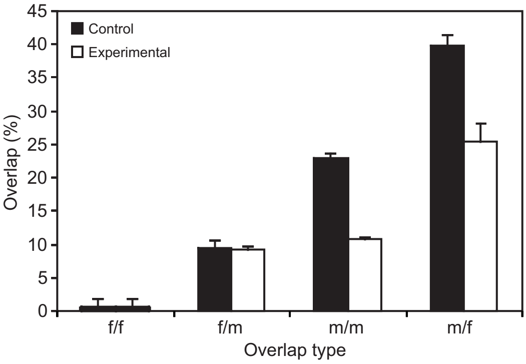

Fig. 2. Percentage of home range overlap (mean + SD) of *Calomys musculinus* juveniles, in relation to treatment and overlap type: female/female (f/f), female/male (f/m), male/male (m/m), and male/female (m/f).

(male/male, male/female) were always larger than those of females (female/female, female/male), this was much less evident in the experimental enclosures. Saitoh (1983), Rodd and Boonstra (1988) and Wolff 1999 also found that the presence of adult males and the absence of adult females may inhibit the movements of juvenile males. Steinmann *et al.* (2005) recorded that the degree of *C. musculinus* home range overlap of males is a consequence of their home range size. Thus, the home range size of males in the experimental enclosures (45.2% lower than in control enclosures) and consequently their lower overlap degree would indicate a minor movement rate of juvenile males in experimental populations. Since juvenile *C. musculinus* males — in the absence of adult females — do not disperse more than in their presence (J. Priotto pers. comm.), we do not expect juvenile males to move a greater distance in the experimental enclosures. With respect to intra-sexual overlap, females kept exclusive home ranges in both control and experimental enclosures. Thus, females maintained their territoriality during this study. Similar results were found by Steinmann *et al.* (2006).

In this study, we manipulated populations in order to ensure that the control and experimental populations comprised individuals with known relatedness. In addition, our approach allowed us to control the age distribution of the population and standardize the post-weaning social environment. This was accomplished by controlling the initial spatial distribution and food abundance in the control and experimental enclosures. These manipulations may have caused some obscure side effects and thus reduced the compatibility of the result with respect to the natural situation. Nevertheless, due to the specific nature of the question asked in this study, the requirement of strict control was given priority.

The spacing behaviour of females is determined by the need to defend the nest site and to prevent infanticide (Wolff 1989, 1993), and by food distribution and abundance (Ostfeld 1985, 1990). According to Bujalska (1991) and Wolff (1993), access to food resources may be secondary to identifying space sufficient to prevent infanticide. Male spacing behaviour is strongly influenced by mate searching behaviour (Dobson 1982, Ostfeld *et al.* 1985, Ostfeld 1986, Ostfeld & Heske 1993), and female distribution is a key resource in determining male space use during the breeding season (Ylönen & Mappes 1995, Steinmann *et al.* 2005, 2006). It has been suggested that, during the breeding period, females compete for space while males compete for access to as many mating partners as possible (Boonstra & Hogg 1988, Perrin 1981, Boonstra *et al.* 1993). Because male *C. musculinus* do not provide paternal care, the limiting factor of male reproductive success is access to receptive females (Laconi & Castro-Vásquez 1998, Steinmann *et al.* 2005). Thus, reproductively active females must ensure an exclusive area to avoid infanticide and to supply adequate food for themselves and their offspring (Bondrup-Nielsen 1986, Bujalska 1991, Wolff 1993, Buzzio & Castro-Vazquez 2002).

During the breeding period, adult females are usually gestating or lactating. Postpartum estrus is characteristic of *C. musculinus*, hence males may maximize their fitness by moving within their home ranges in search of postpartum females (Buzzio & Castro-Vazquez 2002). In our study, the removal of adult reproductive females at the beginning of the breeding period could alter spacing behaviour of juvenile males because of a different availability of resources. In experimental enclosures, there were fewer breeding female home ranges relative to control enclosures. Thus, in the absence of adult females, competition between males for receptive females could increase because females are a scarcer resource. This could be expected on the basis of previous empirical studies which showed that in the absence of adult females, males became much more aggressive towards other males (A. Steinmann unpubl. data). Indeed, Bond and Wolff (1999) found that the two main factors that limit male reproductive success are the number of females to which it has access and the number of male competitors with which it interacts. These authors also reported that male home ranges were significantly smaller in populations with high male density and low female density, and that intrasexual competition seems to set upper limits for male home range size and overlap. This, according to our results, may explain the smaller home range size and degree of home range overlap in juvenile males when in the absence of reproductively mature females and in the presence of reproductively experienced males. Alternatively, the removal of adult males leads to higher size and intra- and inter-sexual overlap of juvenile male home ranges, allowing them to access more reproductive females (Steinmann *et al*. 2006). This is consistent with a promiscuous/polygynous mating system, and with the observation that *C. musculinus* females do not show kin discrimination, as one would expect in a non-monogamous species (Laconi & Castro-Vásquez 1998, Steinmann *et al*. 2005).

Our experiment supports the hypothesis that juvenile males — at the beginning of the breeding period and in absence of *C. musculinus* adult females — decrease their home range size and the degree of inter- and intra-sexual home range overlap. This result is likely due to an increase in competition between males for receptive females.

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