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Original article

## Effect of high density on the short term *Calomys musculinus* spacing behaviour: A fencing experiment

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## ABSTRACT

We studied the short term spacing behavioural responses of corn mice (*Calomys musculinus*) with regard to population density in four 0.25 ha enclosures (two control and two experimental) in the 2007 breeding season. The goal of this research was to test the hypothesis that spacing behaviour only operates among *C. musculinus* adult females. We estimated 207 home ranges to study: 1) the home range size and the overlap degree of adult males and females in relation to population density; 2) the settlement distances of juveniles to the centre of activity of their mothers and the home range overlap proportion between them and their mothers in relation to population density. We found that home range size and overlap degree in *C. musculinus* adults were determined by sex and density. At high population density males had significant smaller and more exclusive home ranges, and this might reflect induced territoriality derived from social restrictions. Female home range sizes remained similar irrespective of population density, and they kept exclusive home ranges in both control and experimental enclosures. Thus, females maintained their territories independent of the population density values. The settlement distances of juveniles from their mothers and the overlap proportion between them and their mothers were independent of population density. We conclude that spacing behaviour only operates among *C. musculinus* adult females and it could have a role in regulating population abundances limiting the number of females that acquire breeding spaces.

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## 1. Introduction

Social behaviour is an important component of population dynamics because of its potential impacts on variation in birth and death rates and dispersal (Krebs et al., 2007). Although social behaviour encompassing a wide range of behaviours, most of them focus on aggressive interactions between individuals or spacing behaviour (Heske and Bondrup-Nielsen, 1990). Spacing behaviour limits population numbers of several microtine species (Lambin and Krebs, 1991). On the one hand spacing behaviour in spring confines the number of individuals able to reproduce (Taitt and Krebs, 1985) and on the other hand aggressiveness of adults influences juvenile survival and recruitment (Boonstra, 1978). Thus, spacing behaviour has a strong influence on demography of rodent populations. Following Madison (1980) and Bondrup-Nielsen (1985, 1986)

we considered that individuals exhibit spacing behaviour when they maintain their home range size and territoriality independently of population density values. Then when all space is occupied by conspecific these individuals prevent others from settling (Bondrup-Nielsen, 1985). Therefore, spacing behaviour has a stabilizing influence on annual population dynamics by limiting the number of breeding individuals (Tamarin, 1983; Bondrup-Nielsen and Ims, 1986; Heske and Bondrup-Nielsen, 1990).

In voles and mice, home range size has often been considered to decrease when density increases while the amount of overlap among home ranges often increases with density (Bondrup-Nielsen, 1985; Ims, 1987, 1988; Nelson, 1995a,b, 1997; Bond and Wolff, 1999; Ochiai and Susaki, 2002). However, this pattern is not always observed (Bondrup-Nielsen, 1986; Ostfeld, 1990). Responses from home range size and overlap to high population density are variable and flexible and depend to large extent on sex, age and relatedness of individuals (Lambin and Krebs, 1993; Ochiai and Susaki, 2002; Wolff et al., 2002; Wolff, 2003; Moorhouse and MacDonald, 2005). For example, in promiscuous and polygynous voles, male home range size and overlap degree are negatively correlated with high population density (Ostfeld et al., 1985; Ostfeld, 1986; Nelson, 1995a,b, 1997; Bond and Wolff, 1999; Moorhouse and Macdonald, 2008),

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meanwhile females maintain their territories independent of population density (Saitoh, 1981; Ostfeld, 1985; Ostfeld et al., 1985; Heske, 1987; Erlinge et al., 1990).

Variations in levels of population abundance can also affect juvenile dispersal from their natal home range (Andreassen and Ims, 2001). Natal dispersal distance of young males and females is highly variable and dependent partly on the degree of habitat saturation and availability of vacant territories or mating partners (Wolff and Lundy, 1985; Wolff et al., 1988; Lambin et al., 2001; Wolff, 2003). Although the causes of natal dispersal can differ between species, populations and sexes, the ultimate causes of natal dispersal are generally inbreeding avoidance, intra-sexual mate competition and resource competition (Dobson, 1982; Pusey, 1987; Wolff, 1993, 1994; Zedrosser et al., 2007).

*Calomys musculus* (Muridae, Sigmodontinae) is the dominant rodent species of central Argentina, and it is mainly studied due to its role as reservoir of Junin virus, the etiological agent of the Argentine Hemorrhagic Fever (AHF) (de Villafañe and Bonaventura, 1987; Mills and Childs, 1998). *C. musculus* is a short-live grassland mouse and a good settler of disturb habitats (Busch et al., 2000). It inhabits pampean agrarian ecosystems and is found in a variety of habitats including natural pastures, crop-fields, cultivated fields undisturbed after harvest, border areas protected by wire fences with little agricultural disturbance, road borders, borders between cultivated fields or pastures, and railway banks (Busch et al., 2000). *C. musculus* populations in central Argentina region are characterised by seasonal density changes with low density during winter (June–August) and peaks during late summer (February–March) or mid autumn (April–May) (Mills and Childs, 1998). The reproductive period of this species begins in mid-September and finishes at the end of April (Mills and Childs, 1998). Juvenile females of *C. musculus* reach sexual maturity between 32 and 40 days of age and juvenile males between 35 and 39 days of age, with a mean weight close to 16.5 g (de Villafañe, 1981; Sommaro et al., 2009). *C. musculus* has a gestation length of 21 days, and each female can produce many pups in her lifetime (a maximum of 10 litters, with a mean of 6 pups per litter) (Mills et al., 1992). Females show a high frequency of postpartum estrus, which implies that a new pregnancy may overlap with the lactation of the previously produced litter (de Villafañe and Bonaventura, 1987; Busch et al., 2000). *C. musculus* has a promiscuous mating system, and during the breeding period females keep exclusive home ranges and actively defend breeding spaces (territories). Female holders of breeding territories show highly aggressive behaviour towards other females associated with the defence of their reproductive space (Steinmann et al., 2009). Reproductively active females of *C. musculus* would defend an exclusive area to avoid infanticidal females as an adaptation for pup defence. Laconi and Castro-Vázquez (1998) and Laconi et al. (2000) found that lactating *C. musculus* females displayed high levels of aggressive behaviour towards sexually mature females, and that the presence of another female near the nest is deleterious for litter survival. Thus, territoriality in corn mice female would act as a counter-strategy that may have evolved to reduce the risk of losing pups by infanticidal females (Steinmann, 2006). Therefore, young females entering population will be at risk of competition with resident adult females and should disperse. *C. musculus* males have home ranges twice as large as those of females with high intra- and inter-sexual home range overlap, and exhibit high level of intra-sexual tolerant and amicable behaviours (Steinmann et al., 2005, 2009).

Even though we have studied many aspects of space use in *C. musculus*, (Steinmann et al., 2005, 2006a,b, 2009) we never tested the effect of density on its spacing response. Thus, the goal of this research, based on the hypothesis that spacing behaviour only operates among *C. musculus* adult females, was to test the following predictions: (1) home range sizes and overlap degree of

adult female are independent of population density values, (2) home range sizes and intra- and inter-sexual home range overlap degree of adult male decrease in relation to population density increase, (3) at high population density juvenile females settle farther away from their mothers than juvenile males, (4) at high population density overlap proportions between juvenile females and their mothers are lower than overlap proportion between juvenile males and their mothers.

## 2. Material and methods

This study was carried out on the Espinal Reservation in the National University of Río Cuarto Campus (33° 07' S, 64° 14' W), Argentina, in four 0.25 ha (62.5 m × 40.0 m) field enclosures (control I and II, and experimental I and II) made of galvanized iron sheets extending 0.3 m underground and 0.7 m above ground. A 1 m-wide grass strip was devegetated by herbicide on the inner margin of each enclosure. The enclosures were situated in a stable natural pasture interspersed with woody shrubs and herbaceous weedy species, similar to natural habitats of *C. musculus*. All enclosures had similar vegetation and were considered homogeneous. For a detailed description of the study area and enclosures see Priotto and Polop (2003) and Priotto et al. (2004).

We collected *C. musculus* adults from an area located 30 km away from the study location from September through October 2007, along road borders and borders between cultivated fields and pastures. Sixty-four sexual mature females were mated with 64 sexual mature males in opaque polycarbonate reproductive cages (29 × 18 × 18 cm) at the Ecology Population Researching Laboratory. The 64 couples were maintained at 21 °C on a 14:10 h light: dark cycle (lights on at 06:30 a.m). Rodent Purina laboratory chow and water were available *ad libitum*. Dry wood shaving was provided for bedding.

At the beginning of December 2007, twelve families (each one constituted by the mother, the father and around 6 pups) were placed into each experimental enclosures (mean density 136 mice/enclosure) and 5 families into each control enclosures (mean density 40 mice/enclosure) (Table 1). These average densities in the enclosure populations were comparable with high and low densities for free-ranging *C. musculus* respectively (Mills and Childs, 1998). Before the families were carried to the enclosures their members were sexed, weighed and ear-tagged. Each family was located in the enclosures inside its own reproductive box with wood shaving containing its odour, and 6 h later they were opened allowing the animals to disperse freely into the enclosures. When individuals were released in the enclosures, juveniles were around 30 days of age.

After a settlement period of 5 days, we trapped animals with Sherman live-trap located in a 6 × 10 grid in each enclosure. At each devegetated edge 32 Sherman live traps were placed at 6 m intervals. Animals that were trapped 3 consecutive times in this area were considered dispersers and were removed from the population. Traps were baited with a mixture of peanut butter and cow fat, and placed with an interstation interval of 6 m. Individuals were captured for 10 successive days in December 2007. Given that

**Table 1**

Demographic initial conditions in control and experimental enclosures at Espinal Reservation in the National University of Río Cuarto Campus.

	Low density		High density	
	CE I	CE II	EE I	EC II
Fathers	5	5	12	12
Mothers	5	5	12	12
Pups	27	26	78	77
Offspring sexual rate	1.07	1	1.05	1.05
Population abundance	39 ± 3.078	41 ± 6.568	111 ± 5.535	161 ± 23.400

CE: Control enclosures, EE: Experimental enclosures.

*C. musculus* is mainly nocturnal, traps were set late in the afternoon and checked each morning. Trapped animals were weighed, and sex and reproductive state were recorded. Trap location of each capture was also registered.

To estimate the home-range configuration of each animal, all captures were plotted on graph paper for each trapping session, following the Boundary Strip method (Stickel, 1954). This connected the points halfway between the outermost capture sites and the next closest trap sites by straight lines. This method considers that on average the animal travels halfway to the next trap site during its movement. To estimate home-range size ( $m^2$ ), we selected the minimum convex polygon method (Jenrich and Turner, 1969) for its mathematical simplicity, because it is easy to implement graphically and it is a useful method for comparison with previous studies. The core area was defined as the area of greatest use within the home range. This location may contain a nest, shelter, and food source. In order to identify the core area in each home range we used the Activity Mathematical Centre method (AMC) (Hayne, 1949). However, the true centre of activity of a female is, in fact, where she suckles her offspring rather than the arithmetic mean of her locations of capture in traps (Lambin, 1997). Because of the difficulty of finding the nests of female *C. musculus*, we chose to use the AMC. The AMC is the mathematical centre of the distribution of total captures, taking into account the number of captures at each trap site. The number of captures for each estimated home range varied from 8 to 9 in adults and from 5 to 6 in juveniles. The intra- and inter-sexual home range overlap was estimated for each individual that established home range 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 shared by another animal's home range of the same sex (intra-sexual overlap), or another animal's home range of the opposite sex (inter-sexual overlap), and dividing by the area of the target animal's home range.

The effect of density on the settlement behaviour of juveniles was analysed considering the settlement distance of juveniles with respect to their mother (distance in meters from the AMC of each juvenile to the AMC of its mother) and the home range overlap between the mothers and their offspring (percentage of overlap between mother/daughters and mother/sons).

The population density was estimated using the jackknife estimator in program CAPTURE (White et al., 1982) incorporated as an independent module into program MARK (White and Burnham, 1999). Prior selection of a default closed population estimator is useful when sample sizes are small for model selection in CAPTURE (Boulanger and Krebs, 1994; Pocock et al., 2004).

In our experimental design we used two control and two experimental enclosures as independent observations. To analyse adult home range size, adult intra- and inter-sexual home range overlap (males/males, females/females, males/females), settlement distances of juveniles to their mothers and overlap proportion between juveniles and their mothers in relation to sex (mother/daughter, mother/son) and treatment and their interactions we used two-factor ANOVA tests. When significant differences between levels were observed Tukey post hoc tests were performed. Variance homogeneity assumption was tested by Bartlett's test.

### 3. Results

In control enclosures, 64 of 73 ear-tagged *C. musculus* were captured 254 times and in experimental enclosures 187 of 203 ear-tagged individuals were captured 860 times. During our study, the population densities were  $39 \pm 3.078$  mice in control enclosure I and  $41 \pm 6.568$  mice in control enclosure II. The densities in experimental enclosures I and II were  $111 \pm 5.535$  and  $161 \pm 23.400$  mice respectively. In the study, no animal was trapped 3 consecutive times

in live traps placed in the devegetated edge areas. Thus, we assumed that all animals were able to settle within the enclosures.

Sixty-nine home ranges were estimated in control enclosures (27 and 42 established by adults and juveniles, respectively) and 138 in experimental enclosures (43 and 95 established by adults and juveniles, respectively).

Even though the statistical analysis with two replications could be weak, our result showed a clear pattern. The adult home range size depended on sex and density (interaction:  $F_{1,4} = 250.5$ ,  $p < 0.001$ ). Female home range sizes were similar at high and low density ( $p = 0.755$ ), whereas male home ranges were smaller at high than low densities ( $p < 0.001$ ) (Fig. 1). Adult overlap proportion varied in relation to density and intra- and inter-sexual overlap (interaction:  $F_{2,6} = 43.092$ ,  $p < 0.001$ ). The female intra-sexual overlap proportions were independent of density ( $p = 0.260$ ). The average overlap proportions among female home ranges were always less than 3%. The overlap proportions of male home ranges (males/males and males/females) were lower at high than low densities ( $p$  values  $< 0.001$ ) (Fig. 2). Besides, at low densities males overlapped their home ranges with 4–7 females, while at high densities the inter-sexual overlap occurred only with 1–3 females and did not exceed 13 % of overlapping.

The settlement distance of juveniles to the centre of activity of their mothers was independent of density ( $F_{1,4} = 1.807$ ,  $p = 0.250$ ; low density:  $12.750 \text{ m} \pm 5.454$ , high density:  $17.350 \text{ m} \pm 3.488$ ) and sex ( $F_{1,4} = 0.792$ ,  $p = 0.424$ ; female:  $13.528 \text{ m} \pm 4.067$ , male:  $16.573 \text{ m} \pm 5.772$ ). The interaction was not statistically significant ( $F_{1,4} = 0.580$ ,  $p = 0.489$ ). The overlap proportions between juveniles and their mothers were also independent of density ( $F_{1,4} = 6.352$ ,  $p = 0.0654$ ; low density:  $7.154 \pm 0.970$ , high density:  $5.553 \pm 0.791$ ) and the sex ( $F_{1,4} = 0.213$ ,  $p = 0.669$ ; mother/daughter:  $5.785 \pm 0.392$ , mother/son:  $5.321 \pm 1.228$ ). The interaction was not statistically significant ( $F_{1,4} = 1.684$ ,  $p = 0.264$ ). At low and high densities the average overlap proportions among juveniles and their mothers were always less than 8%.

### 4. Discussion

Female spacing behaviour is one of most commonly observed pattern in promiscuous rodents (Heske and Bondrup-Nielsen, 1990). Females are presumed to display territorial behaviour directed at protection of nestlings from infanticidal females, whereas spacing of males are based on food availability or abundance of potential female mates (Wolff and Schaubert, 1996; Wolff and Peterson, 1998; Bond and Wolff, 1999; Getz et al., 2005). Therefore, home-ranges size would be expected to differ between sexes and in relation with

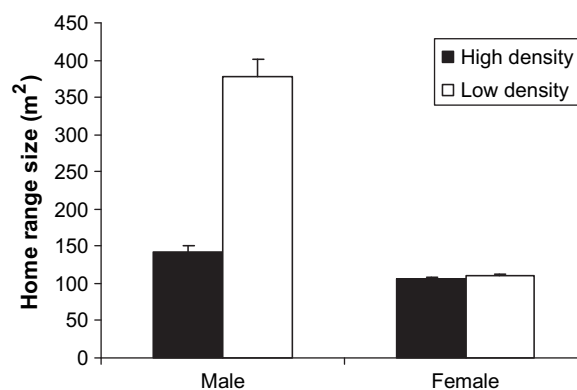


Fig. 1. Adult home range sizes ( $\bar{x} \pm SD$ ) of *Calomys musculus* in relation to treatment and sex.



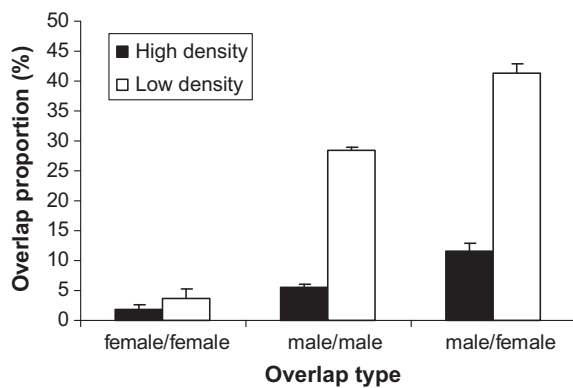


Fig. 2. Percentages of home range overlap ( $\bar{X} \pm SD$ ) of *Calomys musculus* adults, in relation to treatment and overlap type: female/female, male/male and male/female.

population densities. In this experimental study we found that home range size and overlap degree in adult *C. musculus* were determined by sex and density. Similar results were found in experimental studies of promiscuous rodents in which population density was manipulated. Male home range sizes and overlap degree of *Microtus agrestis*, *Microtus canicaudus* (Nelson, 1995a,b, 1997; Bond and Wolff, 1999) and *Arvicola terrestris* (Moorhouse and Macdonald, 2008) were negatively correlated with population density. According to our results, at low densities *C. musculus* males would increase their home range size to incorporate more female home ranges at low cost with respect to intra-sexual competitive interactions. Even though home range size and intra-sexual overlap of males were always larger than those of females, this was much less evident in experimental enclosures. At high population density males had smaller and more exclusive home ranges, decreasing the space shared among them. Steinmann et al. (2005) documented that the degree of home range overlap of *C. musculus* males is a consequence of their home range size. Thus, the home range size of males in experimental enclosures (38% lower than in control enclosures), and consequently their lower overlap degree, would indicate a minimum movement rate of adult males in these populations. Thus, home ranges of *C. musculus* males responded as an elastic disc (Wilson, 1975) decreasing their size and overlap degree as density increases. So, in the populations the upper limit in the number of breeding males may be reached gradually. In a study carried out in a corn-field during 1993, Steinmann and Priotto (unpublished results) found that at the end of the breeding period with a density of 393 mice/ha and high quantity and quality of forage, *C. musculus* males reduced their home range size close to the range of the trap (100 m<sup>2</sup>), and their inter-male overlap close to 0%. Thus, at high density the smallest and non-overlapping male ranges may reflect induced territoriality derived from social restrictions. According to Bond and Wolff (1999) and Ishibashi and Saitoh (2008), the two main factors that should limit reproductive success of male rodents are the number of females to which it has access and the number of male competitors with which it interacts. Nelson (1995a,b) and Bond and Wolff (1999) also reported that home range sizes of male rodents become smaller in response to density increase of either sex, and that intra-sexual competition appears to set upper limits to male home range size and overlap. The smaller home range size and intra-sexual overlap of *C. musculus* males may be a consequence of inter-male territorial aggression and might allow encounter rates among males reduction. Thus, *C. musculus* male home range sizes may have been restricted by the number of ranges of other individuals with which they overlapped; this implies a social limit on home range size. Nevertheless, population density values higher than those manipulated in this study might induce

a breakdown of male territoriality as observed in some rodent species (Kokko and Rankin, 2006; Loughran, 2007).

*C. musculus* female home range sizes remained similar irrespective of population density. With respect to inter-female overlap, females kept exclusive home ranges in both control and experimental enclosures. Thus, females maintained their territories independent of the population density values. Then, *C. musculus* territorial females may limit the size of the breeding population by constraining other females from settling. However, the strength of spacing exclusion among females would depend on reproductive status, age and relatedness among them (Boonstra, 1984; Heske and Bondrup-Nielsen, 1990; Lambin and Krebs, 1993). *C. musculus* breeding females are more intolerant among them than with juvenile females (Sommaro et al. unpublished results).

According to Bondrup-Nielsen (1985) and Heske and Bondrup-Nielsen (1990) when individuals have mutually exclusive home ranges of constant size the number of home ranges within any patch plot will be equal to patch size divided by the average range size. Thus, when the patch becomes filled with territorial female home ranges, young females attempting to acquire breeding home ranges might disperse in search of available space elsewhere (Bujalska, 1973; Saitoh, 1981), or postpone their maturation avoiding competition with breeding females as it was observed in species of microtines (Anderson, 1980, 1989). The latter would not occur in *C. musculus* since the sexual maturation of juvenile females is independent of adult presence (Sommaro et al., 2009). Although we expected *C. musculus* juvenile females to settle farther away from their mothers at high density due to maternal aggression, our results did not support this prediction. However the low overlap proportion between juveniles and their mothers independently of population density would reflect an active exclusion of the young individuals, near sexual maturity, by their mothers outside the natal site. This exclusion of the offspring by their mothers may be in response to an increment in competition for breeding space between daughters and mothers (competition for resources) and mate avoidance between sons and mothers (inbreeding avoidance). Similar results were observed by Lambin (1994) in *Microtus townsendii*.

In summary, male home ranges were smaller and more exclusive at high densities. Female range sizes remained constant at different population densities and females kept breeding territories irrespective of population abundance. Our results support the hypothesis that spacing behaviour only operates among *C. musculus* adult females. In this species, as it was proposed to *M. townsendii* and *Microtus pennsylvanicus* for Gipps et al. (1981) and Rodd and Boonstra (1988) respectively, male spacing appears to have few influences on population dynamic. On the other hand, spacing behavioural strategy of *C. musculus* females could have a role in regulating population abundances limiting the number of females that acquire breeding spaces. In order to assess the effect of female spacing behaviour on population dynamic it would be important to conduct a long term study of *C. musculus* natural populations.

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