



Effects of high density on spacing behaviour and reproduction in *Akodon azarae*: A fencing experiment



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ABSTRACT

We studied the short term spacing behavioural responses of Pampean grassland mouse (*Akodon azarae*) with regard to population density in four 0.25 ha enclosures (two control and two experimental) in the 2011 breeding season. Based on the hypothesis that *A. azarae* breeding females exhibit spacing behaviour, and breeding males show a fusion spatial response, we tested the following predictions: (1) home range size and intrasexual overlap degree of females are independent of population density values; (2) at high population density, home range size of males decreases and the intrasexual home range overlap degree increases. To determine if female reproductive success decreases at high population density, we analyzed pregnancy rate, size and weight of litters, and period until fecundation in both low and high enclosure population density. We found that both males and females varied their home range size in relation to population density. Although male home ranges were always bigger than those of females in populations with high density, home range sizes of both sexes decreased. Females kept exclusive home ranges independent of density values meanwhile males decreased home range overlap in high breeding density populations. Although females produced litters of similar size in both treatments, weight of litter, pregnant rate and period until fecundation varied in relation to population density. Our results did not support the hypothesis that at high density females of *A. azarae* exhibit spacing behaviour neither that males exhibit a fusion spatial response.

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1. Introduction

Considering that space use is predicted to reflect a trade off between the costs and benefits of residing in a particular area (Davies and Houston, 1984), space use decisions and the resultant

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spacing patterns exhibited by organisms have profound ecological consequences, affecting individual fitness, population dynamics, and evolution of species (Madison, 1980). A common assumption from the point of view of cost-benefit is that conspecific competitor density increases the settling costs in a specific area, affecting space use of individuals (Moorhouse and Macdonald, 2008; Stradiotto et al., 2009; Sommaro et al., 2010; Eccard et al., 2011). The way individuals use space can affect its survival, growth and reproductive success, and finally impact on the social organization of population (Stamps, 1990; Brant et al., 1998; Stamps and Krishnan, 2001; Aloise King, 2013).

Home range size and overlap degree could vary according to population density, and both depend to a great extent on the sex and reproductive conditions of individuals (Ochiai and Susaki, 2002; Steinmann et al., 2006a,b; Stradiotto et al., 2009; Sommaro et al., 2010). Home range size has often been considered to decrease when density increases while the amount of overlap among home ranges often increases with density (Ochiai and Susaki, 2002). According to Ims et al. (1993) this spacing pattern is known as fusion response. However, this relationship does not always appear to be the case (Bondrup-Nielsen, 1986a,b; Ostfeld, 1990; Ims et al., 1993). Thus, responses of the home range size and overlap to high population density are variable and flexible and depend both on sex and age of individuals as on the degree of habitat saturation and availability of vacant territories (Wolff et al., 1988, 2002; Lambin et al., 2001; Wolff, 2003; Moorhouse and Macdonald, 2005, 2008).

In small mammals, Madison (1980) and Bondrup-Nielsen (1985, 1986a,b) considered that individuals exhibit spacing behaviour when they maintain constant size home ranges and mutually exclusive territories, respect to those of conspecifics of same sex independently of population density values. Then, when all space is occupied by breeding conspecific these individuals may limit the size of the breeding population through spatial exclusion and/or by reproductive suppression of individuals of their same sex (Koskela et al., 1997, 1999; Getz et al., 2003; Wolff, 2007; Moorhouse and Macdonald, 2008; Eccard et al., 2011). In small rodents species, if breeding male or female establish territories, or home ranges with little or none intrasexual overlapping degree, the potential exists for spacing behaviour to limit population density (Bondrup-Nielsen, 1985, 1986a,b; Bätzli and Henttonen, 1993; Wolff, 1993, 2003; Steinmann et al., 2009; Sommaro et al., 2010). According to Patterson (1980), Rodenhouse et al. (1997) and Eccard et al. (2011) this would occur through the suppression or delay of breeding activities of non-territory holders. It has been found that spacing behaviour limits the breeding density and reproductive output in *Microtus townsendii* (Taitt and Krebs, 1981, 1982), *Microtus pineatorum* (Brant et al., 1998), *Myodes glareolus* (Bondrup-Nielsen, 1985; Gipps et al., 1985; Oksanen et al., 2007; Eccard et al., 2011), and *Calomys musculus* (Sommaro et al., 2010). Therefore, spacing behaviour and territoriality can act as a density regulation mechanism (Rodenhouse et al., 1997; Sommaro et al., 2010; Eccard et al., 2011). Territoriality of females may be an adaptation for food resource defense (Ostfeld, 1990; Blondel et al., 2009) or for nest site defense and intrasexual infanticide deterrence (Wolff, 1993; Wolff and Peterson, 1998; Steinmann et al., 2009), while males spatial avoidance would reflect competition among them for monopolizing the receptive females (Clutton-Brock, 1989; Schradin, 2004; Blondel et al., 2009; Bonatto et al., 2012). However, vole and mice vary to a large extent in the degree to which they maintain their territoriality: some species always defend territories, other species do so in high-density populations but not in low-density populations, while others do the opposite (Nelson, 1995a,b; Bond and Wolff, 1999; Steinmann et al., 2006a,b; Loughran, 2007; Sommaro et al., 2010; Bonatto et al., 2015).

Akodon azarae (Cricetidae: Sigmodontinae) has a polygynous mating system that operates through female defense (Bonatto et al., 2013), in which a minority of males controls or gains access to multiple females leaving other males without access to them. In semi-natural populations Bonatto et al. (2012) found that only 40% of adult males gained access to receptive females, so the average operational sex ratio of *A. azarae* was 0.59 (± 0.14). During the breeding season males have larger home ranges than females (240 ± 104.2 and 160 ± 89.7 m², respectively) and show longer movement distances (Gomez et al., 2011; Bonatto et al., 2012). In a previous study, Bonatto et al. (2012) found that in enclosure populations with sex ratio unbiased, both breeding females and males of *A. azarae* are territorial. However, at high density of males, male home range size and intrasexual overlap degree increased meanwhile females remains the same (Bonatto et al., 2015). Even though we have studied many aspects of space use in *A. azarae* both in natural and enclosed populations (Priotto and Steinmann, 1999; Bonatto et al., 2012, 2015) we never tested the effect of breeding density on spacing behaviour. Thus, the goal of this research, based on the hypothesis that *A. azarae* females exhibit spacing behaviour and males show a fusion spatial response, is to test the following predictions: (1) home range size and intrasexual overlap degree of females are independent of population density values, (2) at high population density, home range size of males decreases and the intrasexual home range overlap degree increases. In addition, in order to determine if female reproductive success decreases at high population density we analyzed pregnancy rate, size and weight of litters, and period until fecundation in both low and high enclosure population density.

2. Material and methods

2.1. The study species

A. azarae (Pampean grassland mouse) is one of the most abundant rodent species in Pampean agrarian ecosystems of central Argentina (Gomez et al., 2011). This small rodent species (adult average weight 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 (Busch et al., 1997). These habitats are characterized by keeping remnant native flora and fauna (Busch et al., 1997). *A. azarae* is a good indicator of habitat quality owing to its preference for these relatively undisturbed habitats (Martinez et al., 2014; Coda et al., 2015). *A. azarae* populations turn over annually, and individual lifespan is about 12 months (Hodara et al., 2000). Breeding occurs mainly in spring and summer (September to April) with a marked annual variation in population abundance. Low population numbers occur in spring (September–December), at the beginning of breeding period (about 40 individuals/ha), reaching about 100 individuals/ha at the end of this period (March–April) (Priotto and Polop, 1997; Priotto and Steinmann, 1999; Gomez et al., 2011).

Both juveniles female and male of *A. azarae* reach sexual maturity between 52 and 60 days of age, with a mean weight close to 15.5 g in females and 16.5 g in males (Bonatto, 2013). *A. azarae* has a gestation length of 23 days, and each female can produce a maximum of 4 litters, with a mean of 4.6 pups per litter (Bonatto, 2013). In this species the offspring is cared exclusively by females (Suárez and Kravetz, 2001). Females show a high frequency of postpartum estrus (63%), which implies that a new pregnancy may overlap with the lactation of the previously produced litter

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