



Female Intrasexual Territoriality and its Potential Adaptive Significance: The Pampean Grassland Mouse as an Ecological Model Species

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Abstract

Territorial behaviour in female small mammals has been proposed as a mechanism to defend limited ecological resources or their pups against conspecific infanticidal or predators. Female territorial behaviour very often is associated with reproductive activity due to the fact that frequency and intensity of aggression are exhibited mainly when females are pregnant or lactating. In vole and mice species, female territoriality would be a counterstrategy to prevent the killing of their pups by conspecific breeding females. To study whether female territoriality is a strategy for pups or nest defence against infanticidal breeding females, and whether time invested in nursing young affects aggressive response of mothers, we used the Pampean grassland mouse (*Akodon azarae*) as an ecological model species. We conducted resident–intruder tests between lactating females. Differences in residency time (48 vs. 72 h) of focal females in their home territory were also included in the analysis. In all cases, the pups of both resident and intruder mothers were placed with the nesting material from their reproductive cages. Resident mothers were always more aggressive than intruders and they were even more aggressive when they spent more time nursing their pups. Contrarily, intruder females exhibited the greatest values of submissive behaviours. Our results show that female territoriality of *A. azarae* would represent a strategy to protect pups from potentially infanticidal females. We discuss the extent of female intrasexual territoriality and its potential adaptive significance in relation to strategies which lead to increase their reproductive success.

Introduction

Spacing pattern, behavioural interactions and mating system are some of the main manifestations of the reproductive strategies of individuals within population (Emlen & Oring 1977; Ostfeld 1985, 1986; Wolff 1985; Solomon & Keane 2007). As each sex has different constraints on reproduction, males and females have generally evolved different strategies to maximize reproductive success (Kokko & Jennions 2008; Aloise King 2013). In mammals, because gestation and lactation basically emancipate males from having to provide parental care, males typically compete with

each other for access to receptive females, while females typically compete with each other for food and exclusive space to rear offspring (Clutton-Brock 1989; Frank & Heske 1992; Shier & Randall 2004).

Several studies have focused on aggressiveness and territoriality in relation to mammalian mating systems (Clutton-Brock 1989; Gese 2001; Loughran 2007; Réale et al. 2009; Steinmann et al. 2009; Steinmann & Priotto 2011). In polygynous species, male aggressiveness leads to an increase in reproductive success by defending territories containing breeding females (Clutton-Brock 1989; Shuster & Wade 2003; Waterman 2007); meanwhile, female territorial behaviour

has been proposed as a strategy for defence of food resources (Hrdy 1979; Ims 1987; Ostfeld 1990; Tamarin et al. 1990; Blondel et al. 2009). However, due to the fact that female territoriality typically occurs during the breeding period and then declines in the non-reproductive season, it has been exclusively associated with reproductive activity (Hrdy 1979; Wolff 1993; Ylönen et al. 2004). Several studies have reported that female aggression is triggered by pregnancy and lactation (Mallory & Brooks 1978, 1980; Ayer & Whitsett 1980; Rozenfeld & Denoel 1994). Thus, increased levels of aggression by pregnant or lactating females should increase the chances of keeping intruders away from the nest site (Koskela et al. 1997; Agrell et al. 1998). In vole and mice species, it has been reported that female territoriality would be a strategy to prevent the killing of their pups by conspecific non-siring males (Ylönen et al. 1997; Agrell et al. 1998; Blumstein 2000; Coda et al. 2011; Opperbeck et al. 2012). The potential benefit for males of committing infanticide would be to increase its fitness via nutritional gain, increase the relative proportion of their own genes into the population by reducing the future competition between their own and strange young or gain a quick access to reproductive females (Sherman 1981; Hausfater & Hrdy 1984; Ebensperger 1998; Wolff & Peterson 1998; Ebensperger et al. 2000; Ylönen & Horne 2002; Wolff & Macdonald 2004; Ebensperger & Blumstein 2007). Maternal counterstrategies to male infanticide may include the early termination of pregnancy (Bruce 1959, 1960; Heske 1987), the choice of a dominant male (Horne & Ylönen 1996; Lopuch & Matula 2008), the exclusion of intruder males from their nest sites through aggressive behaviours (Agrell et al. 1998; Wolff & Peterson 1998; Ebensperger & Blumstein 2007) or mating with multiple males to confuse paternity (Cicirello & Wolff 1990; Wolff & Macdonald 2004; Sommaro et al. 2015). However, several authors suggest that female territoriality is mainly directed towards females that attempt to dispossess them from their territories (Sherman 1981; Brooks 1984; Wolff 1993). Infanticide by females has been considered a reproductive strategy that would allow infanticidal females' access to an exclusive rearing area, inherited from the defeated opponent (Sherman 1981; Wolff & Cicirello 1989, 1991; Koskela et al. 1997; Wolff & Peterson 1998). Thus, territorial defence by victim mothers has been proposed as a counterstrategy to prevent infanticide by breeding females (Agrell et al. 1998; Ebensperger 1998; Wolff & Peterson 1998; Ebensperger & Blumstein 2007; Steinmann et al. 2009).

A widespread characteristic of territorial behaviour is that residents (territory owners) almost invariably defeat intruders irrespective of their fighting abilities. The value asymmetry hypothesis proposes that residents win as a result of their greater investment and local experience in comparison with the challengers (Maynard Smith & Parker 1976; Maynard Smith 1979; Parker & Rubenstein 1981; Krebs 1982; Stamps 1987; Beletsky & Orians 1989). For example, the previous experience of a breeding female with a familiar area including critical resources to rear offspring would lead to enhance their own fitness through a major motivation to defend this known territory (Ostfeld 1985; Koskela et al. 1997; Steinmann et al. 2009). Thus, the asymmetry in the value of resources would also affect the aggressive behaviour of individuals.

Akodon azarae, commonly known as the Pampean grassland mouse, is the numerically dominant rodent species in the Pampean agrarian ecosystems of central Argentina (Gomez et al. 2015). *Akodon azarae* has a polygynous mating system that operates through female defence, in which a minority of males (40%) monopolize several fertile females leaving other males without access to them (Bonatto et al. 2012, 2013a). In this species, during the breeding period, male home range sizes are always larger than females (240 and 160 m², respectively), show longer movement distances than females (63.5 and 25.6 m, respectively) and female intrasexual overlap percentages are always lower than those of males (7% female/female and 12% male/male) (Priotto & Steinmann 1999; Gomez et al. 2011; Bonatto et al. 2012, 2015; Ávila et al. 2016). According to Batzli & Henttonen (1993), an overlap degree significantly lower than the expected by random placement (minor than 10%) would indicate that individuals are avoiding one another (keeping exclusive or non-overlapping home ranges). Thus, territoriality of breeding females in *A. azarae* initially was assumed based on the little overlapping degree recorded between female home ranges (Priotto & Steinmann 1999; Bonatto et al. 2012). Considering that *A. azarae* females are more sensitive than males to ecological resources (Bonaventura et al. 1992), Bonatto et al. (2013b) carried out an experimental study to test that female territorial behaviour is a strategy to guarantee these resources. Although the results of this study did not support interfemale territoriality as a strategy for defence of food and shelter, it did not provide evidence to reject outright female intrasexual territorial behaviour. Bonatto et al. (2013b) proposed that an alternative explanation to territoriality of *A. azarae* females would be pups or

nest site defence, rather than food and shelter defence. In small rodent species with altricial young, several authors have supported the hypothesis that territoriality fulfil a function of pups and nest site defence, rather than food defence (Wolff 1993; Agrell et al. 1998; Wolff & Peterson 1998). The assumption that interfemale territoriality acts as a mechanism for defence of pups and nest site has already been tested in *Myodes glareolus* (Bujalska 1991; Koskela et al. 1997; Ylönen et al. 1997; Ylönen & Horne 2002), *Microtus pennsylvanicus* (Madison 1980; Webster et al. 1981), *M. agrestis* (Agrell 1995), *Myodes californicus* (Wolff & Cicirello 1991), *Peromyscus leucopus* and *Peromyscus maniculatus* (Wolff 1985; Cicirello & Wolff 1990), *Calomys musculinus* (Coda et al. 2011), *Cynomys ludovicianus* (Hoogland 1985), *Urocitellus columbianus* (Festa-Bianchet & Boad 1982) and *Urocitellus beldingi* (Sherman 1981). Although there are numerous species in which it has been proven that interfemale territoriality evolved as a counterstrategy to prevent infanticide by females, the great majority of them represent ecological model species of Northern Hemisphere. In Argentina, native small mammals are main herbivores of agroecosystems and play a positive role in agricultural systems (Gomez et al. 2015). Thus, and taking into account that *A. azarae* is a very good indicator of habitat quality owing to its preference for relatively undisturbed habitats (Coda et al. 2015), it is very important to understand spacing and reproductive behaviour of this species.

Based on the hypothesis that (1) *A. azarae* females territoriality is a strategy for pups or nest defence from other potentially infanticidal breeding females, and that (2) residence duration affects aggressive response of female residents towards intruder females, the aim of this study was to test the prediction that (1) in the presence of the nest containing their pups, resident females are more aggressive than intruders and (2) females housed into territories during a longer residence period invest more time in aggressive interactions towards intruders than those housed a shorter residence period.

Methods

The Study Species

Akodon azarae (Cricetidae: Sigmodontinae) is a small (adult average weight 25 g) and opportunistic omnivore rodent (Suárez & Bonaventura 2001). This species shows continuous activity, being mainly active during daytime and crepuscular hours (Priotto & 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). *Akodon azarae* populations turnover annually, and the individual lifespan is about 12 mo (Hodara et al. 2000). Both female and male juveniles of *A. azarae* reach sexual maturity between 52 and 60 d of age, with a mean weight close to 15.5 g in females and 16.5 g in males (Bonatto 2013). The reproductive period of this species begins in spring (mid-September) and finishes in autumn (May). *Akodon azarae* has a gestation length of 23 d, 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 young are vulnerable, cared for exclusively by their mothers and weaned at 14–15 d old (Suárez 1996; Suárez & Kravetz 2001). Females of *A. azarae* generally do not mate post-partum (Bonatto et al. 2012).

Sampling and Housing

Between Sept. 2013 and Oct. 2013, we collected sexually mature *A. azarae* in secondary road borders in an agricultural ecosystem located in Chucul location (64°20'W, 32°21'S), Río Cuarto Department, Córdoba Province, Argentina. Following the guidelines approved by the American Society of Mammalogists (Sikes & Gannon 2011), Sherman-type live traps (23 × 8 × 9.5 cm) were checked twice per day (09:00 and 18:00 h). Animals were weighed and sexed in the field and taken to the GIEPCO laboratory located 30 km away from the capture site. Fifty-two females were mated with 52 males in opaque polycarbonate reproductive cages (29 × 18 × 18 cm) at the laboratory. Opaque cages ensured that the animals were visually isolated from their immediate neighbours. The 52 couples were maintained at 21°C on a 16:8 light/dark photoperiod. Rodent Purina laboratory chow and water were provided *ad libitum*, and sunflower and maize seeds were provided as weekly supplements. Dry wood shavings were provided for bedding. For the purpose of recording the occurrence of pregnancy, females' belly shape was daily checked. Of the 52 mated females, 48 became pregnant and gave birth in the laboratory. As soon as pregnancy was evident, siring males were removed from the reproductive cages and individually housed in other room under the same condition described above. Five days after pups were born in the laboratory, they and their mothers were released into an individual enclosure situated in the Espinal Reservation. Thus, 48

lactating females of *A. azarae* were used in the behavioural trials. *Akodon azarae* males were kept in the laboratory to be used in other study.

Study Design

We studied interfemale territorial behaviour of *A. azarae* in 48 round individual enclosures of 0.79 m² each one, placed in the Espinal Reservation in the National University of Río Cuarto Campus (64°14'W, 33°07'S), in Córdoba province, Argentina.

The individual enclosures are arranged in two parallel and interspersed rows, separated from each other by 4 m, in a fenced area of 500 m². Each enclosure was limited by a concrete circle of 1 m diameter and 0.5 m high, with an open bottom which allows individuals to scent ground odours. Due to the fact that the height of 0.5 m allowed individuals to escape from the enclosure, we covered each of them with an iron mesh. In this study, we considered the enclosures as territories (Wilson 1975; Stamps 1994; Maher & Lott 1995; Wolff 2007). Each enclosure was provided with water, rodent laboratory chow and sunflower and maize seeds *ad libitum*. In addition, to provide refuge, one open and locked trap, similar to a Sherman live trap, was located within each enclosure. To test our predictions, we measured the resident female behavioural response towards an intruder female in relation to residence duration into their respective territories (RD). In resident–intruder tests, the intensity of fighting in female rodents is affected by weight, previous experience of animals, physiological characteristics and/or housing conditions (Cairns et al. 1985; Lister & Hilakivi 1988; Hilakivi-Clarke & Lister 1992). Intruders with different housing conditions than residents could increase their likelihood of being defeated by residents (Matsumoto et al. 2005; Bartolomucci et al. 2009; Kraak 2012). To avoid traits that would bias our results, we choose pairs of resident–intruder females with similar weight (body mass \pm 2 g), and alike litter size and pups age. To comply with the resident–intruder paradigm (Barnett 1975), 48 h prior to the behavioural tests, 24 females with their offspring were placed individually into 24 different enclosures (RD1), and other 24 females with their offspring were housed into 24 different enclosures, 72 h prior to the behavioural tests (RD2). Thus, offspring of RD2 females were one day older than in those of RD1 females. In all cases, the pups of both resident and intruder mothers were placed with the nesting material from their reproductive cages. Half an hour before the start of each interfemale behavioural test, pups were removed from the enclosures to avoid

behavioural interference between female opponents and the pups. Scent marks allow conspecifics to obtain information about the identity of an individual as the odours remain within the environment after the donor has left a particular area (Ferkin et al. 1997; Steinmann et al. 1997; Thomas 2002; Hurst & Beynon 2004; Hurst 2009). Several studies of male dominance (Hurst 1990a; Rozenfeld & Rasmont 1991; Horne & Ylonen 1996; Klemme et al. 2006; Korpela et al. 2011), residence status (Hurst 1986, 1990a,b,c; Rich & Hurst 1998, 1999), recognition of familiar and unfamiliar conspecific (Restrepo et al. 2004; Brennan & Kendrick 2006; Keller et al. 2008; Hurst 2009), intra-sexual detection of female reproductive condition (Hurst 1990c; Heise & Rozenfeld 1999) and mate choice (Ferkin et al. 1997; Johnston et al. 1997a,b; Klemme et al. 2006) have been developed through urine odours exposure in voles and mice. According to these authors, this method based on scent memory has been found to be reliable and has the advantage of avoiding injuries caused along encounters. Thus, we assumed that the scent from urine and faeces left by pups during the residence period provided enough evidence of their presence. During the trials, each litter was kept in opaque polycarbonate cages (29 × 18 × 18 cm) situated outside the territories, with dry wood shavings for bedding and a bundle of strands of cotton as nesting material. For each interfemale trial, we distinguished two female status: territory resident (female housed in the enclosure where the encounter was performed) and territory intruder (intruder in the enclosure in which the encounter was made). Animal status per couple resident–intruder was randomly assigned before each test.

Behavioural Testing

Between Nov. and Dec. 2013, we performed 24 intra-sexual encounters between females: 12 RD1 encounters and 12 RD2. To perform behavioural encounters, we placed into the territories a movable polycarbonate circular opaque arena (COA), 70 cm high (20 cm higher than the enclosure border), 219.8 cm perimeter and 70 cm diameter, with an open ground area (Steinmann 2006; Steinmann et al. 2009; Bonatto et al. 2013a). This open area allowed females to scent pups odours. A removable opaque partition was placed across the centre of the COA at the beginning of each trial, and females (resident and intruder) were placed simultaneously on either side of the partition for a 1-min acclimatization period. After this period, the separator was carefully removed so that interactions between contestants could occur, and then the

resident–intruder test started. The observer was not blind in relation to the opponent's status; before the encounter, to identify the opponents, one of them was marked on its forehead with an odourless yellow water colour highlighter. This kind of marker does not affect individual behaviour in small rodent species (Steinmann et al. 2009; Korpela et al. 2011; Steinmann & Priotto 2011; Bonatto et al. 2013a,b). Trials were performed during one of the activity peak of the Pampean grassland mouse, between 09:00 and 11:00 h (Priotto & Polop 1997). Observations lasted 5 min and were recorded using a full high-definition (1080i) video camera. A tripod to stabilize the video camera to prevent blurred images was added. We measured each behaviour per encounter and for each opponent as duration (in seconds) of a determined behaviour along the 5 min (maximum duration value for a given behaviour 300 s). Behaviours observed during encounters were described according to criteria proposed by Bonatto et al. (2013a,b), and grouped in four behavioural categories: (1) Aggressive (AA, AP, P, F), (2) Submissive (Sb, Es), (3) Cautious (A) and (4) Non-Interactive (Ex, G) (Table 1).

Focal animal sampling (Altmann 1974) was used to record the behaviours. Females and their pups were used only once. While the manipulation of the video camera, tripod and COA were conducted by two persons, the duration of the different behaviours was carried out by a single observer. At the end of this study, mothers with their offspring were kept in the laboratory to be used in other study.

Our research protocol was approved by the Ethics Committee of Animal Research of the National University of Río Cuarto, Argentina (dossier N° 126/16). During the study, animals were treated in humane manner according to current Argentinean Laws (National Law 14346).

Statistical Analyses

We used a generalized linear model (GLM) approach to examine the effects of female status (fixed factor with two levels: resident or intruder) and residence duration (fixed factor with two levels: RD1 or RD2) on time invested in aggressive interactions by the females (response variable). During this procedure, we fit time invested by females in aggressive interactions to a negative binomial distribution (with variance greater than the mean). Statistical analyses were carried out using the R software, version 3.2.2, library MASS (R Development Core Team 2015, www.r-project.org).

Results

Because we never interrupted interfemales' encounters before the time limit, we analysed 240 min of filming of behaviours exhibited by resident and intruder females. This is because neither fights nor pursuits ended in injuries. On average, resident females exhibited aggressive behaviour during the third part of each test (108.67 ± 30.25 s). Contrarily, this behaviour was the least observed among intruders during

Table 1: Behaviours observed in *Akodon azarae* during interfemale paired encounters

Behavioural category	Description of behaviour
Aggressive	<i>Aggressive Approach (AA)</i> : Directional and fast locomotion towards the opponent, often combined with pilo-erection. This behaviour may end in fight. <i>Aggressive Posture (AP)</i> : The animal stands on four feet and tenses its body towards the opponent, pointing the nose at it. Generally, this posture ends in attack. <i>Pursuit (P)</i> : Running after the opponent attempting to bite and chase it. <i>Fight (F)</i> : Both opponents stay supported on their hind legs face-to-face, pushing the opponent with his forelegs, frequently with their mouth open
Submissive	<i>Submissive posture (Sb)</i> : The animal bends its neck laterally, offering the concave side to the opponent, generally with flexion of the contralateral forelimbs, ears down, eyes closed or nearly closed. This behaviour is assumed in response to an aggressive approach or an aggressive posture of the opponent. <i>Escape (Es)</i> : Rapid locomotion directed away from the opponent, generally accompanied by squeaks. This behaviour is exhibited in response to a pursuit. Also, it is how an opponent abandons the fight
Cautious	<i>Alert (A)</i> : Individual remains quiet in one place in attitude of alertness, ears down, maintaining permanent visual contact with its opponent. Generally accompanied by body shakings and sniffing
Non-interactive	<i>Exploratory behaviour (Ex)</i> : Vertical and horizontal environment exploration, individual exploratory movements in all directions along the ground or climbing the lateral fence of the COA. This includes any behaviour in which the animal explores anything of the environment ignoring the other animal. <i>Self-Grooming (G)</i> : Grooming or manipulation of any part of the own body with mouth or forelimbs

behavioural trials (12.33 ± 11.28 s). The result of GLM for aggressive behaviour showed that the interaction between female status and previous permanence period into a territory was statistically significant. Even though resident females were always more aggressive than intruders, they were even more aggressive in RD2 (β (SE) = 1.1270 (0.5114); $z = 2.2040$; $p = 0.0275$) (Fig. 1). In contrast, time spent by intruders in aggressive behaviours decreased in RD2 (Fig. 1). Aggressive approach and aggressive posture were the most common behaviours exhibited by resident females in RD1 and RD2. These behaviours were observed in 100% and 95.83% of behavioural trials, respectively. Conversely, fighting was the behaviour less frequent in encounters (33.33%).

Submissive behaviour was practically not exhibited by resident females in intrasexual encounters (Fig. 1). On the other hand, the intruders were always more submissive than female residents, and this was more evident in DR2 (Fig. 1). During the encounters, submissive posture was the most common behaviour exhibited by intruders. In general, intruders displayed submissive behaviour for more than half the duration of each test (166.92 ± 60.18 s) (Fig. 1).

In relation to alert behaviour, resident females exhibited this behaviour more frequently than intruders (78.33 ± 8.75 and 33.79 ± 4.93 s, respectively). This behaviour was less observed in DR2 in both resident and intruder females (Fig. 1). Even though both resident and intruder females exhibited non-interactive behaviours almost during a third of each trial, residents exhibited exploratory and self-grooming behaviour more frequently than intruders (109.93 ± 0.38 and 86.96 ± 0.13 s, respectively) (Fig. 1).

Discussion

In small rodents, interfemale territoriality has been initially proposed as a strategy for food resource defence (Ostfeld 1985, 1990; Ims 1987; Tamarin et al. 1990). Nevertheless, due to the fact that females are mainly territorial during the breeding period (time of greatest food abundance), several authors have proposed that the ultimate function of intrasexual female aggression that may lead to territoriality is pup or nest site defence and that defence of food resource may play a secondary function (Wolff 1993; Agrell et al. 1998; Wolff & Peterson 1998; Steinmann et al. 2009). Considering that infanticide is costly to the victim mother, natural selection should favour maternal counterstrategies to protect their pups. These counterstrategies may include nest protection against predators by staying in the nest or increasing levels of vigilance (Lima et al. 1985; Getz et al. 1992; Brown et al. 2001; Liesenjohann et al. 2011), or against conspecifics males by increasing their levels of aggressiveness or by mating with multiple males (Agrell et al. 1998; Wolff & Peterson 1998; Wolff & Macdonald 2004; Klemme & Ylönen 2010; Sommaro et al. 2015). On the other hand, an effective way for mothers to reduce the risk of infanticide by females is defending the young or the area around the nest (Wolff 1993; Agrell et al. 1998; Ylönen & Horne 2002; Steinmann et al. 2009). Sherman (1981) and Wolff (1993) proposed that territoriality among female mammals functioned as a counterstrategy to infanticide by conspecific females. Although this hypothesis has been discussed extensively, it can be summarized briefly with the following arguments: female territoriality is common in species in which females are

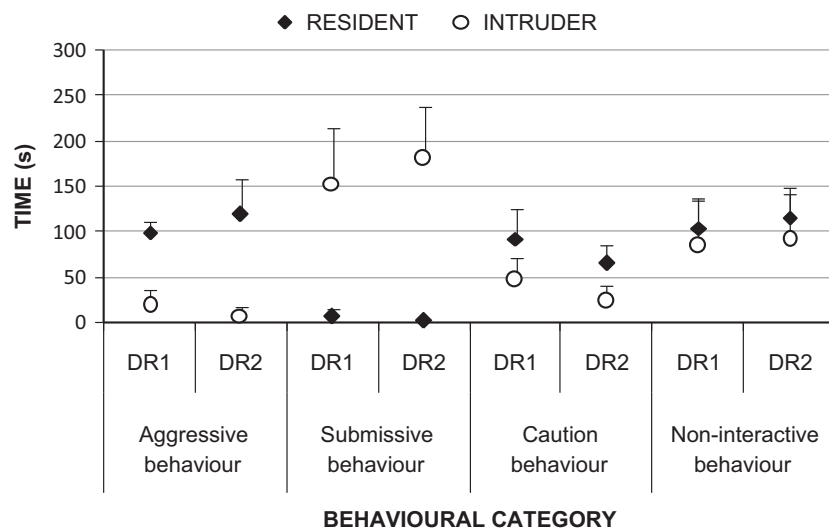


Fig. 1: Mean (+SE) duration (in seconds) of behavioural response per female status (resident or intruder) and residence duration (RD1: 48 h; RD2: 72 h) in interfemale encounters of *Akodon azarae*.

infanticidal, such as carnivores, rabbits and most rodents; females are territorial if their young are altricial, or are housed in protected sites (Ostfeld 1985, 1990; Wolff 1993). Taken together, these data suggest that the occurrence of female infanticide has a large influence on female intrasexual aggression and territoriality (Agrell et al. 1998).

In this experimental study, we tested whether *A. azarae* females perform aggressive behaviours associated with pup or nest site defence. Our results suggested that in pups' presence, resident females were much more aggressive than intruders and that intensity of aggressive behaviour increases with increasing residence duration within their territories. This behavioural dominance was supported by greater values of submissive behaviour exhibited by female intruders. Due to our experimental design lacked a treatment with females without pups (control), we cannot ensure that our results effectively support our hypothesis. However, based on Bonaventura et al. (1992) who proposed that the reproductive success of *A. azarae* females would be determined by its ability to attain green cover and food, Bonatto et al. (2013b) predicted that resident females would perform aggressively towards intruder females linked to food and refuge defence. Nevertheless, these authors found that during behavioural trials, both resident and intruder females spent most of the time exploring the environment, suggesting tolerant coexistence. Taken together, current evidence is more consistent with the hypothesis that *A. azarae* breeding females are aggressive against intruder females as a strategy to protect their offspring, a possibility that could explain interfemale spatial avoidance recorded both in wild and in enclosed populations of this species (Priotto & Steinmann 1999; Bonatto et al. 2012, 2015; Ávila et al. 2016).

Although resident females of *A. azarae* were always much more aggressive than intruders, the rates of aggressive behaviour exhibited by them never reached the highest values registered in females of *Calomys musculinus* (Steinmann et al. 2009). *Calomys musculinus*, a promiscuous cricetid rodent commonly known as corn mice, is numerically dominant in the Pampean agrarian ecosystems of central Argentina, together with *A. azarae* (Steinmann et al. 2009; Gomez et al. 2015). Meanwhile in our study, *A. azarae* resident females spent 30% of the total time of each trial in aggressive displays and *C. musculinus* resident females spent more than 80% exhibiting aggressive behaviours against intruder females (Steinmann 2006; Steinmann et al. 2009). The differences in the degree of aggressiveness exhibited by resident

females of both species could be related to their mating systems. In promiscuous species, female voles typically mate shortly after delivery with multiple males, both familiar and unfamiliar, while the pups are left in the nest (Ylönen et al. 2004; Coda et al. 2011). Consequently, the females' time available for mate choice should be highly constrained by the trade-off between the time and energy spent on finding a new mate, nursing and protecting their offspring against potential infanticidal females (Wolff & Macdonald 2004; Klemme et al. 2006). In the promiscuous species *C. musculinus*, females show a high frequency of post-partum oestrus which implies that a new pregnancy would overlap with lactation of the previously produced litter (Steinmann et al. 2009). In this species, territory owner females show high levels of aggressive behaviours against female intruders, and never exhibit tolerant or non-interactive behaviours towards them (Steinmann 2006; Steinmann et al. 2009). These authors found that intrasexual aggressions between *C. musculinus* females very often involve direct physical contact that sometimes cause serious injuries and proposed that females' aggression is directly associated with the defence of their own reproductive space. In a later study, Coda et al. (2011) found that intrasexual territoriality in *C. musculinus* females would evolve as a counterstrategy to infanticide by conspecific females. In the promiscuous species *Peromyscus leucopus*, *P. maniculatus* and *Myodes glareolus*, female territory holders also act very aggressively towards females near the nest (Wolff 1985, 1993; Ylönen & Horne 2002). Contrarily, in the polygynous species *A. azarae*, females that maintained exclusive home ranges respect to other females both in wild and enclosed populations did not show any injury evidences even when population densities reached the highest values (Priotto & Steinmann 1999; Bonatto et al. 2012; Ávila et al. 2016). In this study, we found that *A. azarae* female intrasexual aggressions practically did not involve direct physical contact between opponents and that territory owner females exhibited non-interactive behaviours during trials. In a study carried out in natural conditions, Zuleta (1989) found low rates of direct aggression in *A. azarae* resident females during the breeding period, suggesting that intrasexual social intolerance in this season is mediated by chemical signals. In other polygynous species, such as microtine and cricetids rodents with female defence mating systems, females are generally tolerant among them, but exhibit aggressive behaviour towards other females only when they try to cross the boundaries of their territory (Ostfeld 1986; Lambin & Krebs 1991). *Akodon*

azarae mothers also would mainly perform aggressive behaviour as a mechanism to avoid female intrusions into their territory.

Our findings also support the prediction that the intensity of aggressive behaviour in *A. azarae* females varies significantly in relation to residence duration within territories. According to Bradbury & Vehrencamp (1998) and Johnsson & Forser (2002), residence duration of an individual in its territory affects its perception of territory value. This because territory owners, knowing the location of food, hiding places, nesting site, escape routes, among other issues, will be more willing to defend this area (Maynard Smith & Parker 1976; Bester-Meredith & Marler 2007). Thus, the increased previous permanence period into a territory could lead to increasing aggressive response against other individuals that attempt to trespass their territory boundaries. In this study, we registered that although residents were always more aggressive than intruders, the intensity of aggressive behaviour exhibited by *A. azarae* females increases with increasing previous permanence period within the territory. Resident individuals housed into territories during a longer permanence period invested more time in aggressive interactions than those housed during a shorter permanence period. In RD2 treatment, mothers remain with their pups one day more than those under the RD1 treatment. Thus, and according with Trivers (1972), the greater time invested in young nursing would explain the different levels of aggression of *A. azarae* resident mothers better than the different assessment of territories. If the intensity of the defence of the pups is directly related to residence duration (Bester-Meredith & Marler 2007), the permanence of *A. azarae* mothers in their territory longer than 72-h period would increase their aggressive response even more.

In summary, our results suggest that female territoriality of *A. azarae* would represent a strategy to protect pups from potentially infanticidal females and that residence duration of females within their territory affects their aggressive response towards intruder females. Because behavioural reproductive strategies have implications on demography and the social organization of small rodent species, future studies should examine the behavioural response of *A. azarae* mothers towards other types of individuals, including male intruders.

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