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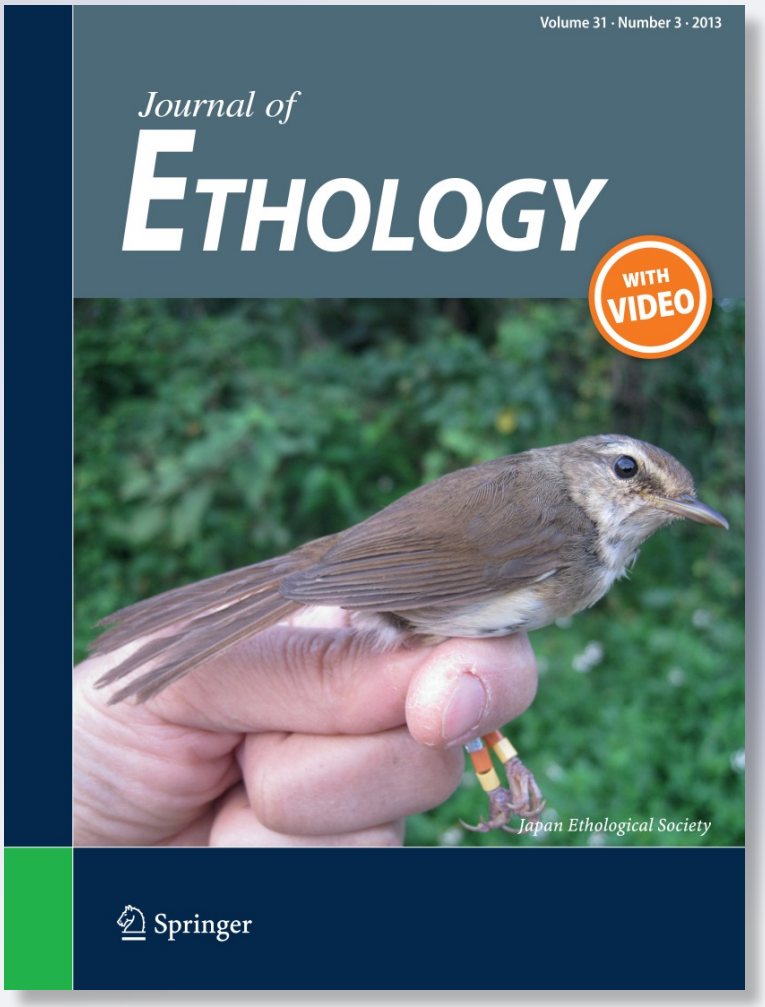

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ARTICLE

Inter-male aggression with regard to polygynous mating system in Pampean grassland mouse, *Akodon azarae* (Cricetidae: Sigmodontinae)

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Abstract Based on the hypothesis that, in *Akodon azarae*, polygyny operates through female defence, we studied inter-male aggression in order to test the following predictions: during the breeding period (1) resident males are more aggressive than intruder males in the presence of females (FP), and (2) aggressive behaviour is independent of male condition (resident or intruder) in the absence of females (FA). To test our predictions, we used the resident male behavioural response towards an intruder male in relation to FP or FA. We conducted 30 encounters in FP and 27 in FA in 0.79-m^2 round enclosures placed in the Espinal Reservation. Our results support the prediction that, in FP, the intensity of aggressive behaviour exhibited by males varied in relation to resident or intruder condition. Resident males showed high levels of aggression towards intruders, and intruders exhibited the greatest values of submissive behaviours with residents. In FA, the intensity of aggressive behaviour did not vary in relation to resident or intruder condition. Both resident and intruder males exhibited low aggressive behaviour and inter-male encounters resulted mainly in non interactive behaviours. Our results support the hypothesis that, in *A. azarae*, the polygynous mating system operates through female defence.

Keywords Aggressive behaviour · Cricetidae · Mating system · Polygyny · Resident motivation · Territoriality

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Introduction

In mammals, promiscuity and polygyny have been considered the predominating mating systems (Emlen and Oring 1977; Clutton-Brock 1989; Heske and Ostfeld 1990; Wolff and Macdonald 2004; Waterman 2007). Polygyny is a mating system in which a minority of males control or gain access to multiple females leaving other males without access to them, and females typically mate with only one male (Emlen and Oring 1977; Shuster and Wade 2003; McEachern et al. 2009). Larger male's home ranges that overlap with several females, male territoriality, and sexual dimorphism are considered typical features of voles and mice with a polygynous mating system (Emlen and Oring 1977; Gaulin and FitzGerald 1988; Clutton-Brock 1989; Heske and Ostfeld 1990; Wolff et al. 1994; Waterman 1998, 2007). Polygyny can be classified into defence polygyny (resource defence and female defence polygyny) and male dominance polygyny (lek polygyny and explosive breeding assemblages) (Emlen and Oring 1977; Clutton-Brock 1989). Defense polygyny is the result of an intense reproductive competition between males in order to gain exclusive access to multiple receptive females (Emlen and Oring 1977; Clutton-Brock 1989). According to the strategies that polygynous males use to control receptive

females, Emlen and Oring (1977) proposed a resource defence polygyny and a female defence polygyny. Resource defence polygyny occurs when males gain access to females indirectly by defending essential resources needed by females against conspecific males (Emlen and Oring 1977). In female defence polygyny, males maintain females under their control by aggressive behaviours against rivals, in order to exclude them from the breeding area (Emlen and Oring 1977). Direct aggressive interactions between males are a well-documented mechanism of intra-sexual selection (Darwin 1871; Trivers 1972; Andersson 1994; Cunningham and Birkhead 1998). Several studies have focused on aggressiveness and territoriality in relation to the mating systems of voles and mice (Madison 1980; Ostfeld 1985, 1986, 1990; Nelson 1995a, b; Wolff and Macdonald 2004; Loughran 2007; Réale et al. 2009; Steinmann et al. 2009; Steinmann and Priotto 2011). For males, aggressiveness leads to increase reproductive success by defending territories containing critical resources (Davies and Houston 1981; Wolff 1985; Bondrup-Nielsen 1986; Ostfeld 1986; Stamps 1995; Ylönen et al. 2004). Limiting resources in males are receptive females, whereas for females they are food and space to rear offspring (Ims 1987, 1988; Frank and Heske 1992; Wolff 1993; Shier and Randall 2004; Loughran 2007).

A widespread characteristic of territorial behaviour is that residents, often with less fighting abilities, almost invariably defeat challengers (Beletsky and Orians 1987). 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 and Parker 1976; Davies 1978; Maynard Smith 1979; Parker and Rubenstein 1981; Krebs 1982; Stamps 1987; Beletsky and Orians 1989). Awareness of food resources (Davies 1981) and reproductive investment (Hatchwell and Davies 1992) are further potential factors underlying value asymmetries between residents and intruders (Tobias 1997; Bester-Meredith and Marler 2007). In rodent males, the experience with a familiar area would lead to enhanced owner fitness through a major motivation to defend the territory and acquire mating resources (Ostfeld 1985; Koskela et al. 1997; Johnsson and Forser 2002; Steinmann et al. 2009; Steinmann and Priotto 2011). Thus, the asymmetry in the value of resources would also affect the aggressive behaviour of individuals.

Akodon azarae (Cricetidae: Sigmodontinae) is a small rodent (adult average weight 25 g) commonly known as the Pampean grassland mouse, and is one of the most abundant rodent species in the Pampean agrarian ecosystems of central Argentina (Busch and Kravetz 1992; Gomez et al. 2011). This species is an opportunistic omnivore (Suárez and Bonaventura 2001) and shows continuous activity, being mainly active during daytime and crepuscular hours (Priotto and Polop 1997). *A. azarae* populations turn over annually, and individual lifespan is about 12 months (Zuleta et al. 1988; Hodara et al. 2000). This species has a marked annual variation in population abundance; low population numbers occur in spring (September–December), abundance peaks in autumn (May), and falls dramatically in winter (July–August) (Gomez et al. 2011). The reproductive period of this species begins in spring (mid-September) and finishes in the autumn (May). *A. azarae* has a gestation length of 22.7 days, each female can produce 3 litters in her lifetime (4.6 pups per litter), and they exhibit post-partum oestrous (Dalby 1975; de Villafañe 1981; Suárez and Kravetz 1998, 2001; Bonatto et al. 2012). The young are weaned at 14–15 days old and reach sexual maturity at 60 days with a weight that ranges between 16 and 18 g (Dalby 1975). The presence of males is not important in rearing young (Suárez and Kravetz 1998); the offspring are exclusively cared for by females (de Villafañe 1981). Bonatto et al. (2012) found differences in body size and space use between males and females, with males having larger bodies and home range sizes than females. Even though males always have larger home ranges than females, males that monopolize females have even larger home ranges than those that do not overlap with any female (Bonatto et al. 2012). *A. azarae* males maintain mutually exclusive home ranges, which would reflect competition among males for monopolizing receptive females (Priotto and Steinmann 1999; Bonatto et al. 2012). Based on these backgrounds, and considering the strong female-biased operational sex ratios registered in natural populations of this species, Bonatto et al. (2012) proposed a polygynous mating system in *A. azarae*.

Taking into account that for most rodents food resources do not determine spacing patterns or mating systems in moderate climate environments (Wolff 2007), and that *A. azarae* is an habitat specialist species that inhabits stable areas with a high gramineous cover and evenly distributed food resources (de Villafañe et al. 1977; Bonaventura and Kravetz 1984; Busch et al. 1984, 2001), we propose that, in *A. azarae*, a polygynous mating system operates through female defence more than through resource defence.

Thus, the aim of this study was to test the prediction that, during the breeding period, resident males in the presence of females are more aggressive than intruder males, but in the absence of females aggressive behaviour is independent of male condition (resident or intruder).

Materials and methods

Sampling and housing

This study was carried out on the Espinal Reservation in the Universidad Nacional de Rio Cuarto Campus (33°07′S,

64°14′W), Argentina. The Espinal Reservation is situated in a natural pasture and comprises herbaceous weedy species interspersed with woody shrubs, and has a high percentage of uniformly distributed gramineous cover. All these characteristics are typical of natural habitats of *A. azarae*. Between December 2010 and February 2011, and between December 2011 and February 2012, we collected *A. azarae* adults from an area located 30 km from the study location, along road borders and borders between cultivated fields and pastures. We considered as adults those animals that weighed more than 16 g (females) and 18 g (males) (Dalby 1975; de Villafañe 1981). Captured animals were weighed, and sex and reproductive state were also recorded. Reproductive condition was judged on the basis of external characters. Females were classified as: non-breeding, if they had an imperforate or perforate vagina but without evidence of pregnancy or suckling; breeding, if they were pregnant (swollen belly) or suckling (visible and well-developed nipples). Males were classified as: non-breeding, if they had abdominal testes; breeding, if they had scrotal testes. Neither non-breeding males and females nor pregnant females were used in this study. Thus, 174 *A. azarae* adults (114 males and 60 females) were used in the behavioural trials. Animals were singly housed in opaque polycarbonate cages (29 × 18 × 18 cm) in the laboratory. Opaque cages ensured that the animals were visually isolated from their immediate neighbours. Individuals were maintained at 21 °C on a 14:10 h light:-dark cycle (lights on at 0630 hours). Rodent laboratory chow and water were available ad libitum, and sunflower and maize seeds were provided. Wood shavings were provided for bedding. No animal remained in the laboratory for more than 4 days until their release into an individual enclosure situated in the Espinal Reservation.

Field procedures

We studied inter-male aggression of *A. azarae* in 0.79-m^2 round individual enclosures placed in the Espinal Reservation. Each enclosure was limited by a concrete circle of 1 m diameter and 0.5 m high. 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 and 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 used the resident male behavioural response towards an intruder male in relation to female presence (FP) or absence (FA). In resident–intruder tests, the intensity of fighting in male rodents is affected by weight, previous experience of animals, physiological characteristics and/or housing conditions (Brain et al. 1980; Parmigiani and Brain 1983; Cairns et al. 1985; Lister and Hilakivi 1988; Hilakivi-Clarke and Lister 1992). Intruders with different housing conditions than residents could increase their likelihood of being defeated by residents (Valzelli 1973; Barnett 1975; Albert et al. 1992; Kaliste-Korhonen and Eskola 2000; Matsumoto et al. 2005; Bartolomucci et al. 2009; Kraak 2012). In order to avoid traits that provide advantages or disadvantages for any opponent, we choose intruders with similar weight, reproductive and physiological conditions (being housed with or without a receptive female) than residents. To comply with the resident–intruder paradigm (Barnett 1975), 48 h prior to the behavioural tests, 54 males were placed individually (FA tests) into the enclosures, and 60 males were housed in pairs with a female (FP tests). One hour before the start of the inter-male behavioural encounters in FP tests, females were removed from the enclosures in order to avoid behavioural interference between male opponents and the female. We assumed that the scent from urine left by a female through her daily activities within the enclosure during the 48 h provided enough evidence of her presence. Female scent marks notice the identity and reproductive condition to potential mates (Thomas and Wolff 2003; Wolff et al. 2002; Wolff 2007). Scent marks allow conspecifics to obtain information about the identity of an individual because the odours remain within the environment after the donor has left a particular area (Brown and Macdonald 1985; Harvey et al. 1989; Ferkin et al. 1997; Steinmann et al. 1997; Rich and Hurst 1999; Thomas 2002; Hurst and Beynon 2004; Hurst 2009). For each inter-male trial, we distinguished two male conditions: territory resident (male housed in the enclosure where the encounter was performed), and territory intruder (intruder in the enclosure in which the encounter was made). Animal condition (resident/intruder) was randomly assigned before each trial.

Behavioural testing

Between December 2010 and February 2011, and between December 2011 and February 2012, we performed 57 encounters between breeding males of similar weight (29 ± 2 g). We conducted 30 encounters in FP and 27 in FA. To perform encounters, we placed into the enclosures a movable polycarbonate circular opaque arena (COA), of 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). This open area allowed males to scent female odours. A removable opaque partition was placed across the centre of the COA at the

beginning of each trial, and males (resident and intruder) were placed simultaneously on either side of the partition for a 1-min acclimation period. After this period, the separator was carefully removed so that interactions between contestants could occur, and then the resident–intruder test started. Before the encounter, to identify the opponents, one of them was marked on its forehead with an odourless yellow watercolour highlighter. This kind of marker does not affect individual behaviour in small rodent species (Bester-Meredith and Marler 2007; Steinmann et al. 2009; Korpela et al. 2011; Steinmann and Priotto 2011). Trials were performed during one of the activity pick of the Pampean grassland mouse, between 0900 and 1100 hours (Priotto and Polop 1997). Animals were used only once in this study. After each behavioural test ended, animals used in the dyadic encounter were released into their natural habitat.

Observations lasted 5 min and were recorded using a video camera. 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). Following Petersen and Helland (1978) and Steinmann et al. (2009), the different types of behaviours were classified as interactive (those behaviours performed with, from or towards the partner) and non-interactive (those behaviours performed individually, not being directed to the opponent). Behaviours observed during encounters were described according to preliminary observations in *A. azarae* and are shown in Table 1.

In order to assess the value of females (receptivity), females removed from enclosures were taken to the laboratory to record mating occurrence. In order to determine mating occurrence and assign male paternity, females were checked twice a day to register the date of parturition.

Data analysis

For statistical analyses, we grouped the different behaviour types in four categories: (1) aggressive behaviour (AA, At, AP, P), (2) submissive behaviour (Sb, A, Es), (3) amicable behaviour (Sp, Ss) and (4) non-interactive behaviour (Ex, Q, G). We had originally planned to use a MANOVA to test these four dependent variables together, since we expected different behaviours in the same animal to be correlated. However, Wilk's λ for each of the independent effects and interaction was not significant ($P > 0.05$), implying a lack of correlation between each variable response. Therefore, it was more appropriate to analyse each behavioural category separately. Thus, two-way ANOVAs were used to test whether condition of individual (resident or intruder) and housing condition (female presence or female absence) affects the duration of each behavioural category in inter-male encounters. Due to the

Table 1 Behaviours observed in *Akodon azarae* during inter-male paired encounters

Behaviour	Description
Interactive behaviours	Aggressive approach (AA): directional and fast locomotion towards the opponent, often combined with pilo-erection. This behaviour may end with intentional movements of boxing and biting
	Attack (At): rushing and leaping at the opponent with kicks and bites
	Aggressive posture (AP): the animal stands on four feet and tenses its body towards the opponent, pointing the nose at it. Generally this posture ends in attack
	Pursuit (P): running after the opponent attempting to bite and chase it
	Submissive posture (Sb): this behaviour is assumed in response to an attack or an aggressive posture of the opponent. 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
	Alert (A): 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
	Escape (Es): this behaviour is exhibited in response to a pursuit. Rapid locomotion directed away from the opponent, generally accompanied by squeaks
	Sniffing partner (Sp): individual either stands close to or follows the partner, while sniffing the oral or genital region of the opponent
	Sharing space (Ss): opponents stay close by and share a common space within the COA. This behaviour may include grooming of the opponent
Non-interactive behaviours	Exploratory behaviour (Ex): 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
	Quiet (Q): the animal lies down or stands motionless except for occasional chewing movements, ignoring the other animal
	Self-grooming (G): grooming or manipulation of any part of the own body with mouth or forelimbs

fact that equal variance is the most important assumption underlying analysis of variance, we checked this assumption using Bartlett's test (Crawlay 2007). When this assumption could not be obtained, the response variable was transformed with natural logarithm. Tukey's Honest Significant Difference multiple comparisons test was used to assess between which levels of each predictor variable the significant differences occurred. Statistical analyses were carried out using R v.2.12.2 (R Development Core Team 2011, http://www.r-project.org).

Results

The result of ANOVA for aggressive behaviour showed that the interaction between the condition of an individual and housing condition was statistically significant (Table 2). The response variable was transformed with natural logarithm to obtain equal variances. Although resident males were more aggressive than intruders in both FP and FA, the differences were statistically significant only in FP (Tukey post hoc test: $P < 0.05$). In FP resident males tripled the time invested in aggressive exhibitions in relation to FA tests (Fig. 1).

For submissive behaviour, the result of ANOVA showed that the interaction between the male condition and housing condition was statistically significant (Table 2). The assumption of equal variances was met for this behaviour. Although intruder males were always more submissive than resident males, the difference was statistically significant only in FP encounters (Tukey post hoc test: $P < 0.05$; Fig. 1). Escape was the most common behaviour exhibited by intruders towards residents in FP encounters. This behaviour was observed in 67 % of behavioural trials. On the other hand, in FA encounters submissive postures and attitude of alertness were the submissive behaviours most commonly exhibited by both opponents. They were observed in more than 65 % of the behavioural trials.

In both amicable and non-interactive behavioural categories, equal variances were not obtained, and therefore ANOVAs were not performed. Amicable behaviour was much less observed in inter-male encounters in comparison to other behavioural categories. During the encounters, both resident and intruder males were more amicable in FA tests than in FP tests (Fig. 1). The non-interactive category was the most common behaviour observed in inter-male encounters. Both resident and intruder males exhibited this behaviour in FA for longer than in FP (Fig. 1).

All females housed in the enclosures gave birth in the laboratory after they were removed. This confirms that all matings were successful.

Discussion

In this study, we assumed that males performed behaviours associated with female defence. Our results support the prediction that, in FP, the intensity of aggressive behaviour exhibited by males varies in relation to resident or intruder condition. In the presence of females, *A. azarae* resident males showed high levels of aggression towards intruders, and this behavioural dominance was supported by the greatest values of submissive behaviour exhibited by the intruders. In space use studies, Priotto and Steinmann (1999) and Bonatto et al. (2012) showed that *A. azarae* males have large home ranges that overlap with several females, but do not overlap with other breeding males. This spatial avoidance would reflect competition among males for monopolising the receptive females (Bonatto et al. 2012). Our experimental study shows that *A. azarae* males defend females more than resources. Although in this study we did not score male and female mating during the 48-h cohabitation period, the fact that all females became pregnant and gave birth between 22 and 23 days after they were removed from enclosures allows us to assess female receptivity. This allowed us to assume that the aggressive behaviour of males

Table 2 Effect of animal condition (resident or intruder) and housing condition (female presence or female absence) on duration of aggressive and submissive behavioural categories

Response variable	Fixed factors	*df*	*F* value	*P*
Aggressive behaviour	Animal condition	1	31.903	1.285e−7*
	Housing condition	1	18.710	3.362e−5*
	Animal condition × housing condition	1	8.794	0.004*
Submissive behaviour	Animal condition	1	25.342	1.89e−6*
	Housing condition	1	0.798	0.374
	Animal condition × housing condition	1	9.776	0.002*

Summary of two way ANOVAs for aggressive and submissive behavioural categories in inter-male encounters of *Akodon azarae*

Level of significance: * $P < 0.05$

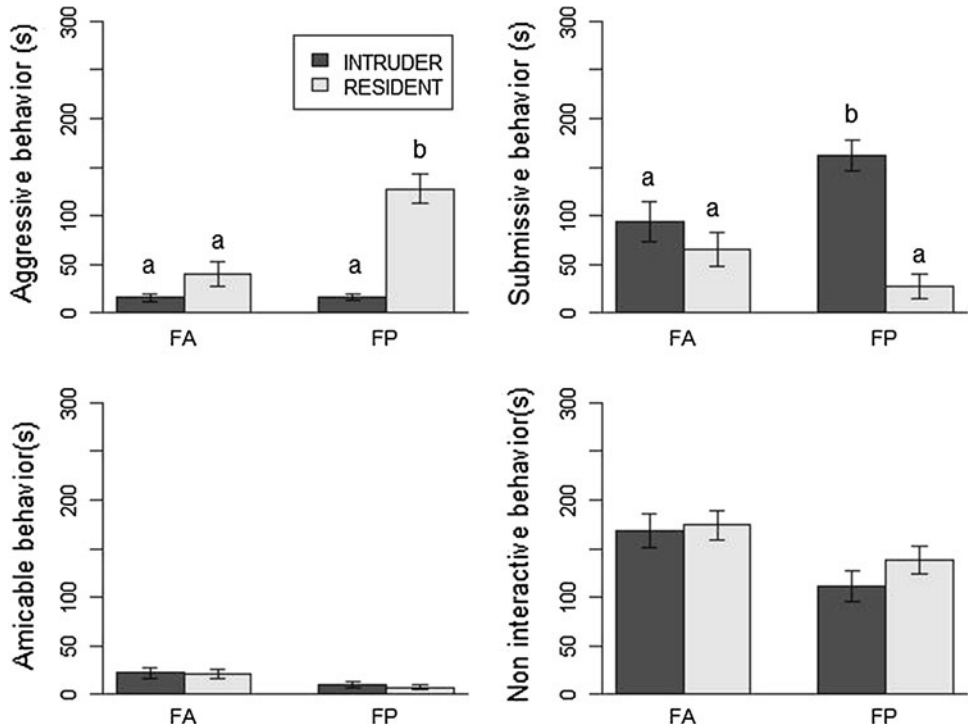

Fig. 1 Mean (±SE) duration (in seconds) of each behavioural category per condition of individual (resident or intruder) and housing condition (*FP* female presence, *FA* female absence) in inter-male encounters of *Akodon azarae*. *Different letters* denote significant differences ($P < 0.05$)

in FP tests is associated with the defence of receptive females. In addition, the fact that this habitat specialist species inhabits stable areas, with a high gramineous cover and evenly distributed food resources (de Villafañe et al. 1977; Bonaventura and Kravetz 1984; Busch et al. 1984, 2001), would be additional evidence to support a female defence polygyny more than a resource defence polygyny. Resource defence polygyny is more common in habitats with uneven resource distribution, while female defence polygyny is predominant in habitats with high plant cover and uniformly distributed food resources (Verner and Willson 1966; Jarman 1974; Emlen and Oring 1977; Ford and Pitelka 1984; Ostfeld 1985, 1987). Grass, herbaceous food, widely scattered seeds and any food resource regularly replenished and widely distributed are probably not defensible for small cryptic rodents (Wolff and Peterson 1998). Female defence strategy in *A. azarae* would be supported by the fact that breeding males of this species typically monopolise clumped receptive females in habitats that guarantee refuge and food resources (Bonaventura et al. 1992; Bilenca et al. 1992; Bilenca and Kravetz 1998; Bonatto et al. 2012). Furthermore, in rodents, it has been difficult to demonstrate experimentally that food resource shortage is a sufficient factor in limiting reproduction (Wolff 1993, 2007; Wolff and Schauber 1996; Wolff and Sherman 2007). Species that seem to be able to defend food resources are those that hoard food, such as red squirrels (*Tamiasciurus hudsonicus*) and kangaroo rats (*Dipodomys* spp.) (Wolff and Peterson 1998; Wolff 2007).

In natural conditions, the aggressiveness of a territory owner can lead to the exclusion of potential rivals. If mate acquisition is directly related to residence duration (Bradbury and Vehrencamp 1998; Johnsson and Forser 2002), the permanence of a male in its territory longer than the 48-h period used in this study would increase its perception of territory value. Therefore, in wild populations, the increased residence time of *A. azarae* males in their territories would lead to stronger aggressive responses against other males that attempt to trespass their breeding territory boundaries. Our experimental design might have caused some obscure side effects and thus reduced the compatibility of the results in relation to a completely natural situation. Nevertheless, due to the specific nature of the question asked in this study, the requirement of similar conditions of both contestants was given priority.

Our findings also support the prediction that, in the absence of females, the intensity of aggressive behaviour in *A. azarae* males does not vary significantly in relation to resident or intruder condition. In FA, both resident and intruder males exhibited low aggressive behaviour, and inter-male encounters resulted mainly in non interactive behaviours. In FA, both resident and intruder males spent most of the time exploring the environment, suggesting tolerant coexistence.

Although the results of the present study support the hypothesis that, in *A. azarae*, a polygynous mating system would operate through female defence, future studies where males have equal access to females but with

resource distribution manipulation within their territories should be developed to better support our hypothesis.

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