BEHAVIORAL COUNTER-STRATEGIES AGAINST INFANTICIDE IN CORN MOUSE FEMALES, *Calomys musculinus*

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ABSTRACT: Based on the hypothesis that in *C. musculinus* both female territorial behavior and promiscuity are counter-strategies against infanticide by females and males respectively, our objective was to test the following predictions: (1) mother aggression deters infanticide by females; (2) previous matings prevent infanticide by males. We conducted 116 behavioral encounters between mothers and intruders to study the nest related behaviors. Mother-pups units (Mu) were grouped in three treatments in relation to the intruder feature: 55 Mu were placed with siring males, 27 Mu and 34 Mu were housed with non-siring males and reproductively active females, respectively. We also calculated offspring survival rate for each treatment. The nest related behaviors varied among the three groups tested. Mothers showed high rates of aggressive behavior towards females. In presence of siring males mothers remained calm inside the nest. When the intruders were non-siring males mothers exhibited high rates of nest defense behavior. The lowest survival rate was registered in presence of the non-siring males, while the highest rates were registered in presence of females or siring males. The absence of aggressiveness and the high rate of nest defense by mothers against siring and non-siring males respectively, would support that promiscuity acts as a counter-strategy against infanticide by males. Mother aggressive behavior against intruder females would show that female territoriality may be an effective way of pup protection.

RESUMEN: Contraestrategias comportamentales contra el infanticidio en hembras de *C. musculinus*. Bajo la hipótesis de que la territorialidad intra-sexual y el apareamiento múltiple por parte de las hembras de *C. musculinus* actúan como contra-estrategias para evitar el infanticidio cometido por hembras y machos respectivamente, nuestro objetivo fue probar las siguientes predicciones: 1) la agresión de la madre impide el infanticidio por hembras, 2) los apareamientos previos previenen el infanticidio por parte de machos. Estudiamos comportamientos relacionados al nido en 116 unidades madre-cría (Mc) agrupadas en tres tratamientos en relación a las características del intruso: 55 Mc alojadas con los padres de las crías; 27 Mc y 34 Mc alojadas con machos sin experiencia sexual con la madre y con hembras reproductivas, respectivamente. En cada tratamiento se calcularon las tasas de sobrevida Las madres fueron agresivas hacia las hembras. En presencia de los padres las madres permanecieron tranquilas en sus nidos. La menor tasa de sobrevida se registró en presencia del macho no padre; las mayores en presencia del padre y hembras reproductivas. La ausencia de agresividad y las altas tasas de defensa del nido exhibidas por las madres hacia los padres y los machos extraños respectivamente, apoyan la hipótesis que propone la promiscuidad como contraestrategia al infanticidio por machos. La respuesta altamente agresiva de las madres hacia las hembras intrusas sería una estrategia efectiva para la protección de sus crías.

INTRODUCTION

Infanticide is assumed to be an adaptive behavioral strategy in response to intense competition for resources (Hrdy, 1979; Mallory and Brooks, 1980; Wolff and Cicirello, 1989; Wolff, 1993; Agrell et al., 1998; Wolff and Peterson, 1998). Females may commit infanticide mainly as a form to obtain exclusive access to breeding space, and males in order to gain access to reproductive females (Sherman, 1981; Agrell et al., 1998; Wolff and Peterson, 1998; Ylönen and Horne, 2002). In several species of voles, infanticide is common enough to significantly contribute to juvenile mortality and population regulation (Boonstra, 1978; Lidicker, 1979; Caley and Boutin, 1985; Ylönen et al., 1997; Wolff and Peterson, 1998; Ylönen and Horne, 2002; Vihervaara et al., 2010). Thus, infanticide should be a sufficient evolutionary force to cause counter-adaptations against it (Agrell et al., 1998). These counter-strategies include the early termination of pregnancy (Bruce, 1959, 1960), direct aggression by the mother against intruders (Ostermeyer, 1983; Maestripieri, 1992; Parmigiani et al., 1994), female promiscuity (Hrdy, 1974, 1977, 1979), and territoriality (Sherman, 1981; Brooks, 1984; Wolff, 1993). From all these different mechanisms to prevent infanticide, it has been proposed that mothers evolve different counter-strategies to prevent infanticide for both females (Sherman, 1981; Ostermeyer, 1983; Brooks, 1984; Maestripieri, 1992; Wolff, 1993; Parmigiani et al., 1994; Wolff and Macdonald, 2004), and males (Bruce, 1959, 1960; Huck et al., 1982; Ostermeyer, 1983; Elwood, 1985; Elwood and Kennedy, 1990; Maestripieri, 1992; Parmigiani et al., 1994). An effective way for the mother to reduce the risk of infanticide by females is defending the young or the area around the nest (Wolff, 1993; Agrell et al., 1998; Wolff and Peterson, 1998; Rödel et al., 2008). According to Wolff (1985, 1993), Bujalska (1991) and Wolff and Peterson (1998), the ultimate cause of female aggression towards other breeding females is the pup-defense that would lead to territoriality. Thus, female territoriality is

mainly directed towards adult females, and not towards males (Mallory and Brooks, 1980; Wolff and Cicirello, 1989; Wolff, 1993).

The tendency of males to kill unrelated offspring to increase their own chance of mating provides a basis for the interrelationship among uncertain paternity, infanticide and promiscuity (Cicirello and Wolff, 1990; Ebensperger, 1998; Wolff and Macdonald, 2004). Promiscuity is relatively common among mammals, and several hypotheses have been proposed for the adaptive significance of multi-male mating by females (Agrell et al., 1998; Wolff and Macdonald, 2004). Due to the fact that males without parental care do not recognize their own offspring (Agrell et al., 1998), it has been suggested that copulation alone is enough to inhibit infanticidal behavior (Elwood, 1977, 1980; vom Saal and Howard, 1982; Brooks and Schwarzkopf, 1983). Thus, in voles and mice where infanticide seems to be common, promiscuity to confuse paternity is the main female strategy to avoid infanticide by males (Cicirello and Wolff, 1990; Wolff, 1997; Agrell et al., 1998; Stockley, 2003; Wolff and Macdonald, 2004). The uncertain paternity hypothesis assumes that copulation inhibits males from killing the future young pups for a period of time long enough for the young to be weaned (Elwood and Ostermeyer, 1984; Cicirello and Wolff, 1990; Wolff and Cicirello, 1991; Agrell et al., 1998; Wolff and Macdonald, 2004).

C. musculinus has a promiscuous mating system (Laconi and Castro-Vazquez, 1998; Steinmann et al., 2009) in which males do not contribute to the construction of the nest, there is no nest co-habitation by a male-female pair, and there is no parental care by males (Cutrera et al., 1988; Yunes et al., 1991). In an outdoor enclosures study, Steinmann et al. (2009) found that *C. musculinus* females keep exclusive home ranges, show strong intra-sexual territorial behavior and highly aggressive behaviors towards other conspecifics females. In that study, where food resource was abundant and homogeneously distributed, and more than 93% of adult females were

simultaneously pregnant and lactating, it was assumed that female territoriality may be an adaptation for pup defense more than an adaptation for food defense. Taking into account that female territorial behavior in voles would have evolved as a mechanism to deter infanticide by females (Wolff, 1985, 1993; Bujalska, 1991; Agrell et al., 1996; Wolff and Peterson, 1998; Wolff and Macdonald, 2004; Loughran, 2007), territoriality in *C. musculinus* females could be associated with the defense of their own reproductive space to avoid infanticidal females (Steinmann et al., 2006a, b, 2009).

Steinmann et al. (2005, 2006a, 2009) found that in enclosure populations females exhibit low levels of aggressiveness towards males, and share largely their home ranges with more than one male. Steinmann et al. (2005, 2006a) found that *C. musculinus* males have large home ranges that overlap with several females and males, while females have smaller home ranges crossed by both transient and resident males but never by breeding females. In these studies, the enclosure size and the length of the study, plus the spacing and mating systems of the species would allow any male to copulate with all females within the population. We may assume that in wild populations of *C. musculinus* females mate with the first male they encounter independently of its condition of neighboring or non-neighboring male. This apparent absence of preference by *C. musculinus* females reflected by their spacing behavior may suggest that females can obtain benefits from multi-male matings that may lead to uncertainty of paternity (Steinmann et al., 2009).

Based on the hypothesis that in *C. musculinus* both female territorial behavior and promiscuity are counter-strategies against infanticide by females and males respectively, our objective was to test the following predictions: (1) mother aggression deters infanticide by females; (2) previous matings prevent infanticide by males.

MATERIALS AND METHODS

The study species, the corn mouse *Calomys musculinus*

The ecology of *C. musculinus* was mainly studied in relation to its role as reservoir of the Junín virus, the etiological agent of the Argentine Hemorrhagic Fever (AHF). *C. musculinus* is a granivorous small mouse that shows a wider habitat and trophic niche than other coexisting rodent species in rural landscape of central and north-western Argentina (Mills et al., 1991; Busch et al., 2000). It inhabits pampean agrarian ecosystems and is found in a variety of habitats including natural pastures, cropfields, 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. musculinus* populations are characterized by seasonal density changes with low density during winter and peaks during late summer or early autumn (Mills et al., 1991, 1992; 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). *C. musculinus* has a gestation period of 20-21 days, and each female can produce many pups in her lifetime (6 pups per litter) (Mills et al., 1992). Juveniles of *C. musculinus* reach sexual maturity at around 35 days of age, with a mean weight close to 16.5 g, and females show a high frequency of postpartum estrus (de Villafañe and Bonaventura, 1987; Sommaro et al., 2009).

Sampling and housing

In September and October 2007 we collected a total of 254 *C. musculinus* individuals (158 females and 96 males) along borders between roads and cultivated fields at Chucul (64° 20' W, 32° 21' S), Río Cuarto department, Córdoba province, Argentina. Trapped animals were taken to the Ecology Population Researching Laboratory of the Río Cuarto University and mated within 24 hours after their capture. Trap locations and mating date were recorded. Sexual maturity was determined based on body mass ($\geq$ 16.5g) (Sommaro et al., 2009), and individuals were mated with partners of similar weight. Due to the fact that the number of males was a limiting factor, at first we only used 96 reproductive pairs. Each couple was housed in an opaque polycarbonate cage (40 x 28 x 18 cm) and 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, and corn and sunflower seeds were provided as weekly supplements. Dry wood shaving was provided for bedding. Cotton and chaff were placed in one corner in order to provide nest material. Couples were checked twice a day in order to register pregnancy evidence and to determine the date of parturition. Siring males were removed from their reproductive cage when pregnancy evidence was registered. These males were mated with the 62 females that still remained unmated. From the 158 matings, 150 were successful: 116 mothers remained with their pups as mother-pups units (Mu), and 34 acted as nest intruders. Litter sizes were registered when new-born pups were discovered.

Mother-intruder behavioral interaction study

In this study we used 116 Mu. Mu were grouped in three treatments in relation to the intruder feature: 55 Mu were grouped with the male who had sired the pups (siring-male) (SM); 27 Mu were housed with a non-siring male (male that never copulated with the mother) (NSM); 34 Mu were grouped with a reproductively active female (F). The number of Mu by treatment depended on the availability of the types of intruders. In each rearing cage containing the Mu, a siring-male, a non-siring male or a female was introduced in the opposite corner where the nest was placed. This was performed two days after parturition to avoid behaviors associated with the postpartum estrous. Adult non-siring males of *C. musculinus* that acted as intruders in our study were trapped in November 2007 in the area where females were captured. Before an intruder was placed into the rearing cage, it was marked on its back with a yellow watercolor marker pen (Origi-nal Hi-Liter, fluorescent yellow, ACMI, Mexico) for visual identification. When the intruders were cornered due to the constant mother's aggression, they were removed in order to avoid serious injuries. Behavioral interactions were registered from the moment the intruder was placed into the rearing cage. According to Wolff and Cicirello (1991) and Steinmann et al. (2009) observations lasted five minutes subdivided into one-minute intervals. The descriptions of nest related behavioral patterns are shown in **Table 1**. We calculated the rate of each behavior for each opponent as: Number of time intervals in which the behavior was observed / total number of time intervals (5), maximum rate value for a given behavior = 1. We expressed the rate of each behavior as percentage.

At the end of the behavioral interaction observations, the intruders that still remained in the rearing cages and the mothers with their pups were daily checked until weaning. The litter size and the presence of injuries in both mother and intruder were recorded. When any individual registered evidence of aggressiveness, it was removed in order to avoid new injuries. To evaluate the effectiveness of the mother behavioral response against the intruder we calculated survival rate for each treatment as: Number of pups at weaning / litter size at the time the intruder was introduced. The research on live animals was performed in a humane manner following Ethic Committee of SAREM (www.sarem.org.ar).

Statistical analyses

Kruskal-Wallis tests were used to analyze the different types of nest related behaviors (**Table 1**) in relation to intruder condition (SM, NSM, F). We conducted Mann-Whitney U-tests as post hoc tests in order to assess which groups differed significantly. Survival rate of pups per treatment was analyzed

Table 1

Nest related behavioral patterns observed in *Calomys musculinus* under laboratory conditions.

BEHAVIOR	DESCRIPTION
Nest permanency (NP)	The mother remains inside the nest, nursing or grooming the pups.
Nest defense posture (NDP)	The mother stands on top of the nest containing the pups on four feet and tenses her body towards the intruder, pointing the nose at it. Sometimes this posture ends with a bite attempt.
Aggression (Ag)	The mother leaves the nest rushing and leaping at the intruder with kicks and bites, often combined with pilo-erection. This behaviour is often performed after NEA.
Nest entrance attempts (NEA)	Repetitive and directional movements of the intruder towards the nest attempting to enter the nest with the pups.

by Kruskal-Wallis tests, and we conducted Mann-Whitney *U*-tests as post hoc tests in order to assess which groups differed significantly. To control treatment-wise error rate, we used the Bonferroni correction for multiple tests.
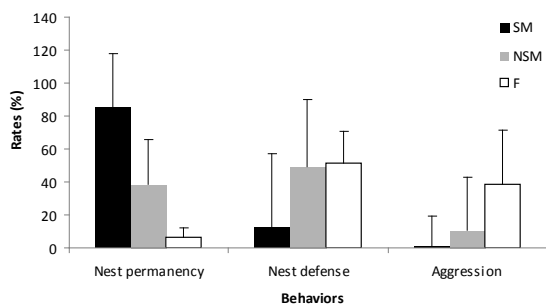
RESULTS

The nest related behaviors varied among the three groups tested (F, NSM, SM): Nest permanency: $H_{2, 116} = 58.0005$, $P < 0.001$; Nest defense posture: $H_{2, 116} = 38.4992$, $P < 0.001$; Aggression: $H_{2, 116} = 48.7898$, $P < 0.001$; Nest entrance attempts: $H_{2, 116} = 43.7811$, $P < 0.001$. Nest permanency of mothers was different among the three groups (P values < 0.0083, after Bonferroni corrections). In presence of siring males, mothers remained calm inside the nest most of the time; if the intruders were non-siring males the time spent inside the nest was two-fold lower. When intruder females were present this behavior reached the lowest value due to the fact that mothers repeatedly left the nests (**Fig. 1**).

Nest defense posture (NDP) varied in relation to intruder type. Mothers exhibited low rates of NDP in presence of fathers and higher rates of this behavior in presence of female and non-siring male intruders (P values < 0.0083, after Bonferroni corrections) (**Fig. 1**). In presence of intruder females the normal pattern of mothers' behavior was to display NDP during the first two minutes of the encounter. Afterwards mothers quickly emerged from the nest and attacked fiercely the intruder females. Thus, although rates of NDP behavior exhibited by mothers were similar with the non-siring males and the intruder females, mothers were much more aggressive towards females than towards males,

independently of their condition (SM or NSM) (**Fig. 1**) (P values < 0.0083, after Bonferroni corrections). The rate of aggressive behavior of mothers against female intruders was threefold greater than against non-siring males (**Fig. 1**). Although no significant difference was found in relation to male condition (P = 0.1641), aggressive behavior between mothers and siring males was rarely observed (**Fig. 1**).

Nest entrance attempts (NEA) were different among the three groups (P values < 0.0083, after Bonferroni corrections). Siring males tried to enter the nest only in few occasions and in these cases mothers' tolerance to fathers was reflected by low rates of aggression. Contrarily, the rates of NEA exhibited by non-siring males were three-fold higher than those registered for siring males (**Fig. 2**). The strength of nest defense behavior exhibited by mothers reflected the attempts of the non-siring males to enter the nest (**Fig. 1**). Intruder females spent most of the time attempting to enter the nest (**Fig. 2**). Despite mother aggressiveness, intruder females displayed repetitive movements approaching to the nest instead of retreating and remaining submissive in order to avoid injuries (**Fig. 2**). These attempts to enter the nest were immediately exhibited by the intruder females when they were placed into the rearing cages. Although intruder females continuously attempted to enter the nest with the pups, they were never able to hurt or kill anyone. Due to the fact that mother aggressiveness towards intruder females increased during the course of the trial, most of the intruder females were removed from the rearing cages before the trial was ended in order to avoid serious injuries. This removal could have affected the real estimation of aggressive behavior rates exhibited by mothers against female intruders. The remainder intruder females were removed from

Fig. 1. Rates of nest permanency, nest defense and aggression behaviors (mean +SD) of the *Calomys musculinus* mothers against siring males (SM), non-siring males (NSM) and females (F).
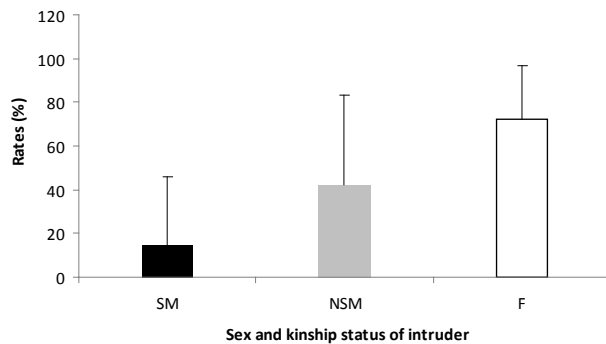
the rearing cages around two days after they were placed with the Mu because they were injured by the mothers.

The survival rates of the pups at weaning varied among groups (F, NSM, SM) ($H_{2, 116} = 55.3074$, $P < 0.001$). The highest loss of pups was observed in the NSM group, where the survival rate of the pups was 0.61 (P values < 0.0083, after Bonferroni corrections). Besides, on eight occasions we directly observed non-siring males committing infanticide. In all these cases we immediately removed the non-siring male from the rearing cage. When the mother and her pups were accompanied by the siring male the litter survival rate was 0.94. The maximum survival rates of pups were registered when the mother and her pups were in presence of a female (survival rate = 1).

DISCUSSION

We found that lactating females displayed much more aggression towards females than towards siring or non-siring males. *C. musculinus* females may benefit from killing the offspring of conspecifics to acquire nest sites to raise their own pups (Steinmann et al., 2009). Aggression of mothers against intruder females indicates that the presence of the latter near the nest site becomes a threat to pups (Ylönen and Horne, 2002). Thus, and taking into account that in enclosure populations during the breeding season, corn mouse females are strictly territorial towards other females, and when the latter trespass the mother territory edge, mothers exhibit aggressive behaviors (Steinmann et al., 2009), we can assume that intra-sexual territoriality of *C. musculinus* females evolved as a counter-strategy to infanticide by females. Therefore, high levels

of intra-sexual aggression by lactating corn mouse females may be the primary defensive mechanism for keeping away potential infanticidal females from the nest site. The absence of infanticide by intruder females and the lack of injuries in the offspring found in this study, even though mothers and intruder females clashed in a fierce fight, support the assumption that territoriality increases mother fitness. Territoriality among females has also been proposed as a counter-strategy to infanticide by conspecifics females in many species of small rodents (Madison, 1980; Sherman, 1981; Wolff, 1985, 1993; Koskela et al., 1997; Agrell et al., 1998; Wolff and Peterson, 1998; Ylönen and Horne, 2002).

The use of space by males of *C. musculinus* is strongly related to the search of mate. Males maximize their fitness by moving extensively among multiple estrous female home ranges, whereas females remain philopatric in their own territories (Steinmann et al., 2006a, b, 2009). Therefore, we can assume that in wild populations, associations between *C. musculinus* females and males would be ephemeral. This mating behavior of *C. musculinus* females would support the confusing paternity strategy. In our study *C. musculinus* mothers tolerated the presence of the fathers except when they quickly approached close to the nest. Contrarily, we observed high rates of nest defense when mothers with their pups were in the presence of males that never copulated with them. In promiscuous vole species copulation inhibits males from

killing pups for the time period in which the young would be vulnerable to infanticide (vom Saal and Howard, 1982; Soroker and Terkel, 1988; Cicirello and Wolff, 1990; Agrell et al., 1998; Wolff and Macdonald, 2004). Besides, multi-male mating as a mechanism to create uncertainty of paternity to deter infanticide is expected most frequently in species such as voles and mice in which male turnover rate and encounters with strange males are high (Madison, 1980; Wolff, 1985; Agrell et al., 1996). In *C. musculinus* the high turnover rate and the high probability of encounters between different partners (Steinmann, 2006; Steinmann et al., 2009), would support the confusing paternity strategy. Besides, our results allow us to support the confusing paternity counter-strategy hypothesis in *C. musculinus* females. This based on: *i*) the absence of aggressiveness exhibited by the mothers against the siring males; *ii*) the absence of infanticide by siring males; *iii*) the high rates of nest defense of mothers against non-siring males; and *iv*) the low value of offspring survival rate in presence of non-siring males.

In order to elucidate the mating system of *C. musculinus*, Laconi et al. (2000) compared the influence of different social partners on pup survival. Contrarily to our findings, those authors found that the presence of any partner (siring male, strange male or adult virgin female) placed near a nest occupied by a mother with her litter was detrimental for pups. However, even though the authors found a high percentage of litter loss, they were unable to distinguish if the losses were due to infanticide by males or females or as a consequence of the lack of maternal heat during combat between mother and opponent. The high aggression exhibited by mothers against adult females registered by Laconi et al. (2000), accords with our results.

To conclude, the high offspring survival rates observed in presence of siring males contrary to the low values registered in presence of non-siring males found in our study would support multi-male mating as a counter-strategy to infanticide against males. Besides, the aggressive behavior of mothers against intruder females demonstrates to be an effective way of pup protection and would support that female intra-sexual territoriality acts as a counter-strategy against females in *C. musculinus*.

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