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ORIGINAL ARTICLE

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Territorial defense in a group-living solitary forager: who, where, against whom?

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Abstract Territoriality is of great significance for many species and a characteristic of most group-living animals. Territoriality is thought to lead to increased reproductive success by defending a particular area containing critical resources. I describe several factors that influence territorial aggression in free-ranging striped mice (*Rhabdomys pumilio*), a group-living solitary forager. I induced territorial aggression by attracting mice of different groups using bait either at territory boundaries or in front of nests. Striped mice are territorial and make decisions about whether or not to attack a mouse from another group based upon several factors: (1) the sex of the opponent: males are much more likely to attack strange males than strange females, whereas no sex specific aggression was observed in females; (2) the body size of the opponent: striped mice are much more likely to attack a strange mouse that is lighter than themselves; and (3) the location of encounters: striped mice are much more likely to attack strangers, even those significantly heavier than themselves, in front of the nest than at territory boundaries. These variations in territorial responses between different types of individuals may be due to the different ultimate consequences of territorial aggression for different animals.

Keywords Aggression · *Rhabdomys pumilio* · Striped mouse · Territoriality

Introduction

A territory has traditionally been defined as an area which is defended against conspecifics for an appreciable amount of time (Stamps 1994; Maher and Lott 1995), whereas territoriality is a strategy of an individual to monopolize resources and thereby gain increased fitness (Davies and Houston 1981; Stamps 1994). For example, in some species, such as coyotes (*Canis latrans*), only territorial individuals achieve reproductive success (Gese 2001). The outcome of territorial disputes is expected to be dependent on two factors: (1) the value that the defended resource has for each individual's fitness, and (2) the contestant's fighting ability (resource holding power; Parker 1974; Maynard Smith and Parker 1976). Thus, territorial animals are expected to react in a context-specific manner. This is especially the case if they can reliably assess the value of the resource they fight for and the other contestant's fighting ability (Parker and Rubenstein 1981). For example, male-male contests in bowl and doily spiders (*Frontinella pyramitela*) take longer when the value of the contested female is the same for both males and when both males have the same body size (Austad 1983). In the Anna hummingbird (*Calypte anna*), males are more willing to engage in costly chases instead of cheap displays when the food resource they defend is of higher value (Ewald and Orians 1983). The "dear enemy" phenomenon is another case of context-specific territorial response. Here, territory holders differentiate between familiar neighbors and strangers (Temeles 1994), as reported in the flat lizard (*Platysaurus broadleyi*), where males are less aggressive towards neighbors than against unfamiliar males (Whiting 1999).

Territoriality is also an important phenomenon in group-living animals, including cooperatively breeding species (cichlid *Neolamprologus pulcher,* Taborsky 1984; common marmoset *Callithrix jacchus*, Lazaro-Perea 2001; suricate *Suricata suricatta,* Doolan and MacDonald 1996; European badger *Meles meles*, Kruuk 1978; Damaraland mole-rat *Cryptomys damarensis,* Cooney 2002; house mouse *Mus domesticus,* Gray et al. 2002). To understand group living and cooperative breeding, it is also important to understand group territoriality and its causes and functions. Although we know that territoriality in group-living animals is probably costly (Taborsky

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1984), the mechanisms and potential benefits of participating in territorial defense for different individual group members are still poorly understood (Putland and Goldizen 1998).

Of particular interest is territoriality in group-living solitary foragers, a social system that is more common than previously acknowledged (e.g., Müller and Thalman 2000). Individuals of group-living solitary foragers share one home range and often one sleeping site, but go alone for foraging. Whereas we know that they are often territorial (e.g., Mills 1983; Fietz 2004), the factors influencing their territoriality are poorly understood. In order to understand territorial behavior in a group-living solitary forager, I performed field experiments on the striped mouse (*Rhabdomys pumilio*), which is a medium-sized diurnal muroid rodent (Dewsbury and Dawson 1979). Striped mice live in large groups but forage alone (Schradin and Pillay 2003; Schradin and Pillay 2004). Aggressive encounters between striped mice are often observed in the field and seem to occur along home range boundaries, but it is not known whether these aggressive interactions are between members of different groups (Schradin and Pillay 2004). By inducing encounters between mice of different groups by presenting food at home range boundaries and in front of nests, I studied territorial aggression in striped mice, and predicted the following:

1. If striped mice are territorial, they should show more aggression towards mice from other groups than towards mice from their own group, and they should show more aggression against strangers inside their home range than at home range boundaries (Stamps 1994).
2. For females, the critical resources are food and suitable nest sites to rear offspring (Trivers 1972), resources used by both sexes. Thus, I predicted that females would not show sex-specific territoriality.
3. For males, access to females is another important resource (Trivers 1972), and I expected that males would react less aggressively towards females than towards males.
4. Physical strength in many species is correlated with body weight (e.g., Barlow et al. 1977; Schradin and Anzenberger 2001a). Theory predicts that individuals that are able to assess whether they have a higher fighting ability than their opponents should be more ready to attack, whereas their opponents should withdraw quickly (Parker 1974; Maynard Smith and Parker 1976). Therefore, I predicted that mice are more likely to attack strangers that are lighter than themselves than they are to attack strangers that are heavier than themselves, particularly at territory boundaries, as here both opponents would defend their territory, increasing the symmetry of contest (Maynard Smith and Parker 1976). Note that this is not a prediction about the intensity of aggressive interactions, but of likelihood of attack.
5. Pay-off asymmetry is theoretically expected to affect territorial disputes. This means a weaker individual should be willing to attack a stronger individual if the resource is of higher value for him (Maynard Smith and Parker 1976), as shown previously in black-chinned hummingbirds (*Archilochus alexandri*, Ewald 1985). Thus, I predicted that mice should be more likely to attack larger strangers (with higher fighting ability) in front of their own nest (higher value for residents than strangers, leading to pay-off asymmetry) than at territory boundaries (where no pay-off asymmetry is expected).
6. In the striped mouse, juveniles remain in their natal group after reaching adulthood without breeding (Schradin and Pillay 2004). As they restrain from breeding during this period, I expected them to participate in group territoriality as a possibility to increase their indirect fitness, as such showing helping behavior.

Methods

Study area and period

A field study was performed from September 2001 to January 2002 in Goegap Nature Reserve near Springbok in North-West South Africa (Schradin and Pillay 2003; Schradin and Pillay 2004). The data presented here are from experiments performed about 2 months after the end of the breeding season (unpublished data), from 26 December 2001 until the end of January 2002. Thus, no confounding effects of different hormone levels associated with breeding and estrus were expected.

The habitat at Goegap consists of succulent karoo, with bushes and sandy areas between them. The area is a desert with an annual rainfall of 160 mm that occurs mainly during winter (July to September). The study site consisted of an area of 80×60 m. A map of the study area was drawn, with bushes (n=75) as landmarks drawn into a grid, in which squares represented 2×2 m. Bushes were marked with pieces of plastic for identification.

Study species

The striped mouse is a diurnal muroid rodent (Brooks 1982; Dewsbury and Dawson 1979), with adults of the study population weighing between 40 g and 85 g (both sexes). Studies conducted on striped mice in the grasslands of the eastern parts of southern Africa indicate that striped mice are solitary here (Choate 1972; Perrin 1980; Brooks 1982; Willan 1982). In contrast, direct observations in the succulent karoo revealed that several individuals share one nest and interact amicably with each other in front of nests. Mice share one nest for at least several months, during and after the breeding season. Home ranges of individuals of one nest overlap with each other to a large extent (on average by 91%), but to a much lower extent (13%) with home ranges of mice from other nests (Schradin and Pillay 2004). Thus, I regarded the mice sharing one nest as one group. Each group has a single nest in a dense bush. Groups contain up to 4 breeding females, 1 breeding male, and on average 15 (range: 5–28) non-breeding adult individuals (post-breeding season), which I regarded as adult offspring of the breeding mice (these individuals were observed both as juveniles and as adults at the same nest; Schradin and Pillay 2004). It is not currently known when dispersal occurs, and the only two events of immigration into groups were of two adult males at the start of the breeding season, suggesting that males leave their natal group to immigrate into groups of breeding females (unpublished data). Group members forage alone, but may meet by chance during foraging, sniffing at each other and feeding in close proximity. Size of group home ranges is 1,300 m^2 on average. Therefore, the striped mouse at Goegap is best described as a territorial group-living solitary forager with communal breeding and helpers at the nest (Schradin and Pillay 2004).

Trapping and marking of striped mice

Striped mice were live trapped using metal traps (26×9×9 cm) from 16 to 24 December 2001. Trapping was performed until unmarked individuals were no longer trapped. Traps were placed around bushes in which groups were nesting. Locations of nests were known from previous observations. Traps, baited with a mixture of bran flakes, currants, sea salt and salad oil, were placed in the shade and checked every 15 min. Trapped mice were sexed, weighed and individually marked. A number was written with a fine brush on the side of each animal using the black hair dye Inecto Rapid.

Experimental design

Nests were observed in the early morning and late afternoon with the naked eye and the use of 10×25 binoculars from a distance of 2–6 m. I recorded which individuals were present at each nest, so that group affiliation of individual mice was known. Members of five groups inhabiting the study area and of two additional adjacent groups (which were used to investigate sociality in another study; Schradin and Pillay 2004) were individually known, but several other adjacent groups were also present, whose members were not known.

Experiments were performed during the main activity period of mice, i.e. between 0600 and 0900 hours and between 1600 and 1900 hours. Approximately 30 g of bait (mixture of bran flakes, currants, sea salt and salad oil) were presented in one single pile at home range boundaries of the five groups and in front of three nests (the exact locations of the two other group nests were unknown). I used 30 g of bait since this quantity was sufficient to enable 45 min of observations. Not all the bait was consumed during this period, suggesting that it was a superabundant resource. Home range boundaries were determined before onset of experiments by focal observations of individually marked mice whose home range patterns were recorded onto a map of the study area, using the minimum convex polygon method (Schradin and Pillay 2004). During the entire study, 1,500 g of bait was used. Each location where bait was presented was continuously observed for 45 min, after which another location was chosen for observations. Animals were observed using focal animal sampling of 3 min for each focal individual; 3 min was chosen as this enabled data sampling from several individuals. Observations started when two individuals met for the first time at the bait, with one individual randomly chosen as focal individual. After the first focal individual had been observed for 3 min, another individual was randomly chosen as the focal animal. Whenever possible, the same numbers of females and males was used as focal animals. Each animal was used only once as a focal animal during an observation period at one spot, but could have been the focal animal on the same day at two or more different spots (mean values for each individual were calculated after experiments to avoid pseudo-replication; see below). The following behavioral patterns (see also Perrin et al 2001) were recorded, together with the identity of individuals other than the focal animal: (1) feeding next to another individual without any aggressive interactions; (2) aggression of low intensity (edging out another individual with the body or kicking at another individual with the hind legs); and (3) aggression of high intensity (chasing one individual from the bait or fights, i.e. two mice stand on their hind legs, facing toward each other). Injurious fights were never observed.

Data analyses and sample sizes

Encounters were categorized into three classes based on the behavior shown by the focal mouse: non-aggressive (mice fed next to each other without any aggression shown), low aggressive (the focal mouse showed only low but no high aggression), or high aggressive (the focal mouse showed behavior of high aggression towards the opponent, independent of whether this was preceded by behavior of low aggression). Each focal mouse could meet a specific other mouse several times, i.e. on several days and several locations. For each pair of animals, I calculated the percentage of non-aggressive, low aggressive, and high aggressive encounters over all their encounters (each focal animal with each encountered individual). For each focal animal, I subsequently calculated the percentage of encounters with mice from its own group that were of low or high intensity of aggression, using the previously calculated averages of each dyad. The same calculations were made for encounters with mice from other groups (paired data design) and for all other comparisons (e.g. aggression against same and different sex individuals). In this way I maintained for independence of data and controlled for pseudoreplications.

Altogether, 50 individual males and 51 individual females were observed at least once as focal animals. Data from some mice were excluded from analysis, because their group affiliation was not known (these individuals were probably from groups outside my study area), and some of the remaining individuals were observed only once or a few times, such that insufficient data were collected for statistical analysis. Thus, statistical analysis was based on data from 35 focal males and 33 focal females, in 588 focal observations (277 on focal females and 311 on focal males) and a total of 1,988 encounters (852 with focal females and 1,136 with focal males).

All tests were performed using a two-tailed Wilcoxon matched-pairs sign test (Siegel and Castellan 1988) or a two-tailed Mann-Whitney *U*-Test, and the sequential Bonferroni adjustment was used to correct for multiple comparisons (Rice 1989; Chandler 1995). I give *P*-values of the Wilcoxon-Test and *U*-Test as "*P*", Bonferroni corrected alpha values as "*P*‘". Along with Wilcoxon test (*t*) statistic, I also provide the initial sample size (*n*) as well as the number of zero differences within this sample (*0*) which is crucial for determining the *P*-value using the Wilcoxon test (Siegel and Castellan 1988). All analyses were performed using the software InStat.

To determine whether mice are more likely to attack individuals lighter than themselves, data on body mass from the trapping season at the end of December were used (all mice lose some weight during the dry summer, and weight loss is constant across individuals; unpublished data). Mice that were considered as being lighter/ heavier, must have had weighted at least 1 g less / more than the focal mouse.

To test whether adult offspring staying in their natal group participated in territorial defense, I excluded data for potential breeding adults, i.e., animals weighing over 50 g (indicating that they were born during the previous breeding season; unpublished data), females that had visible teats (indicating that they had lactated), and males that were scrotal.

Results

Territoriality

Mice showed more aggression towards mice from other groups than towards mice from their own group (*t*=106, *n*=68, *0*=14, *P*<0.0001, *P*‘<0.003; Fig. 1). Mice showed low aggression significantly more often against mice of their own group (*t*=55.5, *n*=68, 0=42, *P*=0.0023, *P*‘=0.003; Fig. 1). On average, 5.1% of encounters with group members were classified as low aggression, whereas 1.8% of encounters with strangers were classified

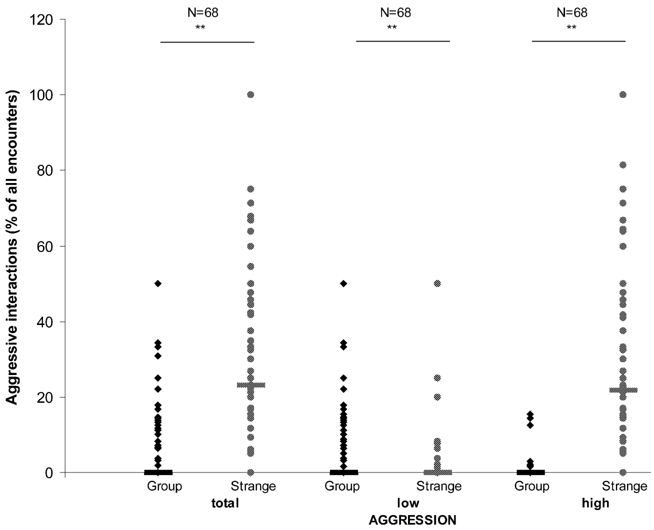

Fig. 1 Aggression of focal striped mice (*Rhabdomys pumilio*) towards mice of their own group (*group*) and towards mice from other groups (*strange*), for all aggressive encounters (*left*: total), encounters with a low level of aggression (*middle*: low; edging and kicking) and a high level of aggression (*right*: high; chasing and fighting). Individual data points, median (*bars*) and sample size are shown. ** *P*<0.01

as low aggression. Mice nearly never showed high aggression towards members of their own group, but significantly more often towards strange mice (*t*=9.5, *n*=68, *0*=16, *P*<0.0001, *P'*<0.003; Fig. 1).

Sex specific aggression

Males did not show higher aggression towards strange males than strange females (*t*=100, *n*=31, *0*=6, *P*=0.093). Some of the males included in this analysis were observed on only a few occasions (i.e. with less than three opponents of either the same or opposite sex or both). When these males were excluded from the analysis (with the remaining males having on average 17.8 encounters with both sexes combined), males were significantly more likely to behave highly aggressively towards strange males than towards strange females (*t*=40.5, *n*=22, *0*=2, *P*=0.0136, *P'*<0.03; Fig. 2). For females, no sex specific aggression was evident, either before (*t*=97, *n*=30, *0*=10, *P*>0.7) or after correction for data with low numbers of opponents (*t*=68, *n*=20, *0*=4, *P*>0.99; Fig. 2). There was no difference between males and females in aggression against females (Mann-Whitney *U*-Test, *U*=235.5, *P*>0.7, *m*=20, *n*=22) or males (Mann-Whitney *U*-Test, *U*=232, *P*>0.7, *m*=20, *n*=22) from other groups.

Influence of body mass on aggression

I examined whether mice showed more highly aggressive behavior towards strange mice that weighted less than themselves compared to strange mice that weighed more.

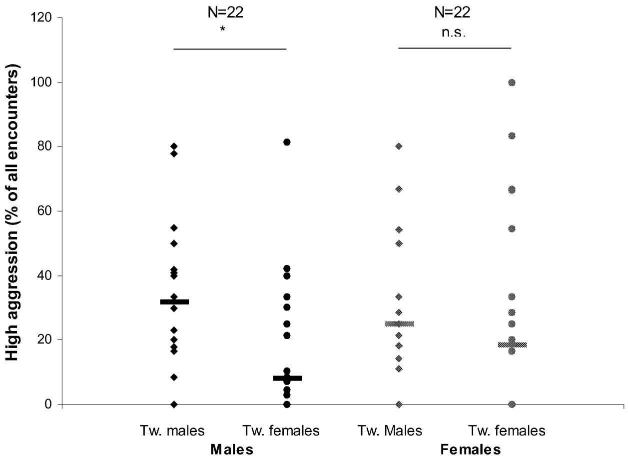

Fig. 2 High aggression of focal males (*left*) and females (*right*) shown towards strange males or females. Individual data points, median (*bars*) and sample size are shown. * *P*<0.05

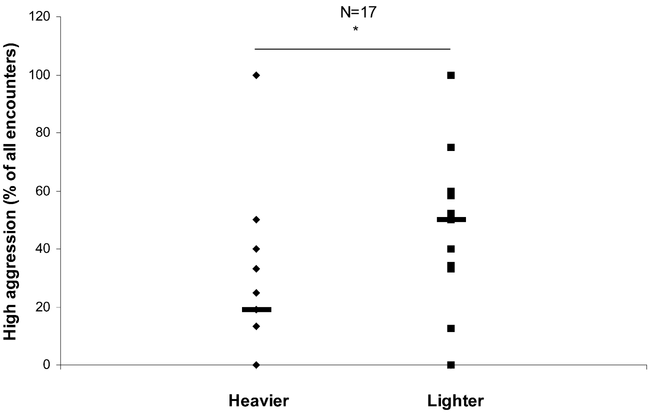

Fig. 3 High aggression of mice towards strangers that were heavier than themselves (*left*) and towards strangers which were lighter than themselves (*right*). Individual data points, median (*bars*) and sample size are shown. * *P*<0.05

To correct for the sex specific aggression by males but not females, I used data only from encounters between focal males and strange males, but included encounters between focal females and both sexes in the analysis. Mice were more aggressive towards mice from other nests that were lighter than themselves compared to strange mice that were heavier (*t*=33, *n*=17, *0*=0, *P*<0.04; Fig. 3).

The influence of location on encounters

I explored whether mice more readily showed high aggression towards strange mice in front of their own nest compared to those encountered at territorial boundaries. Again, because of sex specific aggression by males but not females, I used data only from encounters between focal males and strange males, and between focal females and both sexes in the analysis. Mice attacked strangers about 3 times as often in front of their own nest than at

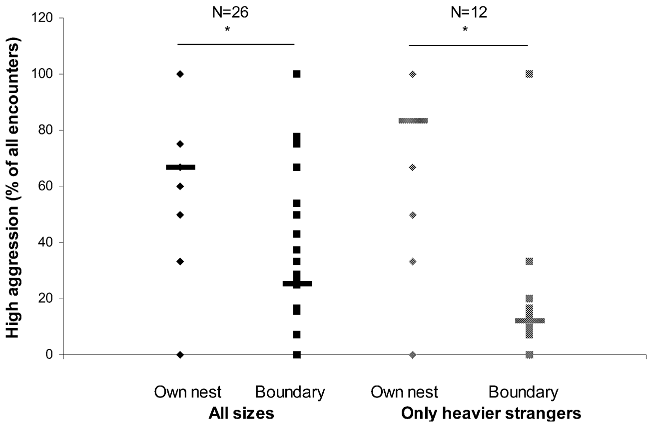

Fig. 4 High aggression of mice towards strangers in front of the nest of their own group (*own nest*) and at the territory boundary (*boundary*). Responses towards all strangers independent of size (*left*) and only against strangers that were heavier than the focal mice themselves (*right*) are shown. Individual data points, median (*bars*) and sample size are shown. * $P<0.05$

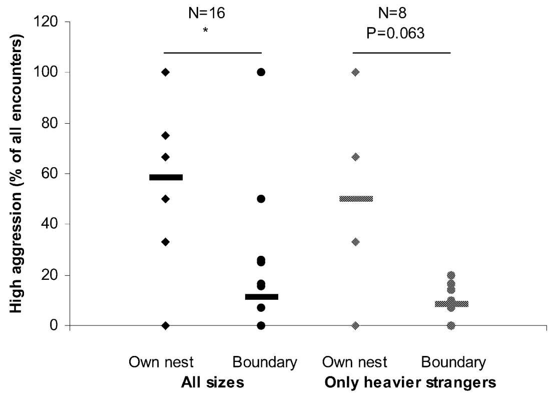

Fig. 5 Aggression of adult offspring staying in their natal group towards strangers in front of the nest of their own group (*own nest*) and at territory boundary (*boundary*). Responses towards all strangers independent of size (*left*) and only against strangers that were heavier than the focal mice themselves (*right*) are shown. Individual data points, median (*bars*) and sample size are shown. * $P<0.05$

territory boundaries (t=45, n=26, 0=4, P=0.008, P'<0.03; Fig. 4). They were also about 5 times more likely to attack strangers that were heavier than themselves in front of their nest than at territory boundaries (t=1.5, n=12, 0=4, P=0.021, P'<0.03; Fig. 4).

Participation of adult offspring in territorial defense

Adult offspring showed more highly aggressive behavior towards strangers in front of the nest of their group than at territory boundaries (t=7, n=16, 0=4, P=0.012, P'<0.05; Fig. 5); the response by adult offspring was not sex-specific (males: t=0, n=8, 0=4, P=0.125; females: t=6, n=8, 0=0, P=0.093). Adult offspring showed on average more aggression towards heavier (10% on average) strangers encountered in front of the nest of their group than when these strangers were encountered at territory boundaries (Fig. 5), but this difference was not significant (t=1, n=8, 0=2, P=0.06). There were insufficient data to test for sex-specific responses.

Discussion

Striped mice are territorial, reacting with a high level of aggression towards mice from other groups (see also Perrin et al. 2001). However, aggression was absent from many encounters with strangers, which was probably due to two factors: (1) food was abundant and mice could feed next to each other for some time, and (2) mice often left the place of food when a new mouse from another group arrived, by this avoiding aggression. In contrast to interactions between mice from different groups, competition between members of the same group over food resulted in only low levels of aggression. This indicates that the conflict between mice from different groups is much higher than between mice from the same group. The reason for this is unknown, but possibly cooperatively breeding females are close kin, as is the case in house mice (*Mus domesticus*, Wilkinson and Baker 1988; Hurst and Barnard 1995). Another explanation would be reciprocal tolerance as a special case of reciprocal altruism (Trivers 1971), in which case mice of one group are only able to nest together because they do not react aggressively against familiar mice independent of genetic kinship.

Male striped mice displayed sex-specific aggression. Males were more aggressive towards males from other groups, which are likely to be reproductive competitors, than towards strange females which are possible future mates (Trivers 1972; Ostfeld 1985). This pattern has wide occurrence in vertebrates, such as cichlids (Schradin and Lamprecht 2000), the Tasmanian native hen (*Gallinula mortierii*, Putland and Goldizen 1998), spotted hyenas (*Crocuta crocuta*, Boyston et al. 2001), callitrichid primates (Anzenberger 1985; Lazaro-Perea 2001), tree shrews (*Tupaia glis*, Kawamichi and Kawamichi 1979), and house mice (Palanza et al. 1996; Gray et al. 2002). I found this effect even after the breeding season had terminated, thus one might question why males should treat females different from males during this period. There is evidence that males are the dispersing sex, leaving their natal group before the next breeding season and immigrating into a neighboring group of cooperatively breeding females (Schradin and Pillay 2003). If this is the case, even the breeding males of the last breading season would have to immigrate into another group the next year, to avoid inbreeding with their daughters staying at home. To facilitate immigration into another group, a male should not attack females, as they otherwise are likely to reject him as breeding male (Parker et al. 2001; Randall et al. 2002).

Another reason for territoriality in males is to defend food resources. In the semi-arid succulent karoo, food is a critical resource, and mice lose more than 12% body weight from early summer with a high food abundance to the end of summer, when food is scarce (unpublished data). Thus, defense of a food containing territory is an adaptive strategy. Another critical resource for striped mice is nest sites. Most nests are found in bushes of the species *Zygophyllum retrofractum*, which have hard and spiny branches, providing protection against predators. These bushes are often already occupied by bush karoo rats (*Otomys unisulcatus*), another diurnal rodent. Bush karoo rats and striped mice compete with each other for these bushes as nesting sites, as indicated by the frequent aggressive encounters between these species. As bush karoo rats weigh 3 times as much as striped mice, they win most encounters (unpublished data). Thus, whereas striped mice cannot defend bushes as nesting sites against bush karoo rats, they probably use territoriality to defend good nesting sites against other groups of their own species. Defending the nest site would also include defending pups against infanticide by strangers (Palanza et al. 1996), which occurs in both males and females of the study population (Schradin and Pillay 2003). As my experiment was performed outside the breeding season, defense of pups in the nest against infanticide may be ruled out as an explanation for my results. As was the case for males, food and nest sites are resources important for female reproductive success (Trivers 1972; Ostfeld 1985). Accordingly, females were highly aggressive towards strangers of both sexes (for other taxa see Putland and Goldizen 1998; Schradin and Lamprecht 2000; Lazaro-Perea 2001), as both sexes use these resources.

Differences in body mass are correlated with dominance rank (Barlow et al. 1977; Schradin and Lamprecht 2002), fighting ability and, thus, resource holding power. When two contestants are of different body mass, there is an asymmetry in contest (Parker 1974; Maynard Smith and Parker 1976). Accordingly, I found that striped mice were more than twice as ready to attack strangers that were lighter than themselves than those that were heavier. However, striped mice make their decision whether or not to attack not only on the basis of the weight difference, but also alter their territorial behavior depending on the pay-off asymmetry (Maynard Smith and Parker 1976). The classical experiments of Tinbergen (1972) revealed that male sticklebacks (*Gasterosteus aculeatus*) attack their neighbors more intensely inside their own territory than inside the neighbor's territory (see also Bolyard and Rowland 2000). To my knowledge, this phenomenon has only rarely been demonstrated in other species, despite its general acceptance (Maher and Lott 1995). Striped mice chased heavier strangers away inside their own territory, particularly in front of their own nest, but not at territory boundaries. This indicates that striped mice regard their nesting site as a valuable resource worthy of defense (for house mice see Gray et al. 2002).

Adult offspring staying in their natal group (Schradin and Pillay 2004) participated in defense of the group territory and nest, a behavior pattern that has been acknowledged as an important aspect of helping behavior (Taborsky 1994; Doolan and MacDonald 1996; Lazaro-Perea 2001). Territorial defense by adult offspring could be interpreted as helping behavior in the striped mouse if it leads to fitness benefits of the breeders, and these individuals also help in nest construction and probably infant rearing (Schradin and Pillay 2003; Schradin and Pillay 2004).

There was large variance in the aggressive reaction of mice towards other mice (see Figs. 1, 2, 3, 4, 5). This might be due to individual differences (both motivationally and physically), which is why it is so important that the comparisons were made using a paired data design. For example, as body mass differences influenced aggression, light individuals might represent data points of low aggression, and heavy individuals data points of high aggression. Furthermore, I had the impression that some individuals were generally more aggressive, without being clearly associated to a particular groups (such as breeders or non-breeders, heavier or lighter individuals). A study to test for individual consistency in aggressive behavior (see, e.g., Francis 1990; Schradin and Anzenberger 2001b) would be of great interest.

It is a challenge to understand behavioral rules followed by cooperatively breeding species, particularly the roles and characteristics of individual group members (Emlen 1982; Dunbar 1995; Clutton-Brock et al. 2000). For example, female lions have different roles in territorial defense, and their willingness to participate in territorial defense depends on the situation at a particular time, with some females readily participating in defense while others doing the opposite (Heinsohn and Packer 1995). The factors leading to these individual differences are not understood (Heinsohn and Packer 1995). In the striped mouse, individuals make their decision about whether or not to attack a strange mouse based on where they meet this individual, the sex of this individual, and whether it is heavier or not.

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