Behavioral interactions between a coexisting rodent *Micaelamys namaquensis* and macroscelid *Elephantulus myurus*

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**Abstract** A number of mechanisms are known to influence coexistence in small mammal communities. However, the role of behavioral interactions in promoting species coexistence is under-represented in the literature. We studied the behavioral interactions of two coexisting small mammals, the Namaqua rock mouse *Micaelamys namaquensis* (Rodentia) and the Rock sengi *Elephantulus myurus* (Macroscelidae), which have high dietary and microhabitat overlap. Using wild-caught individuals, intra- and interspecific dyadic encounters were staged in tanks on a neutral rocky outcrop. Interspecific dyads displayed significantly more active avoidance behavior. There was no support for the prediction that the larger, more specialist species, *E. myurus*, is behaviorally dominant over *M. namaquensis*. Intraspecific encounters of *E. myurus* showed significantly more passive avoidance and amicable behavior, whereas the behavior of *M. namaquensis* did not differ between intra- and inter-specific encounters, both of which were characterized by low levels of aggression and amiability. Thus, due to the lack of aggression, direct competition appears weak and instead mutual avoidance may reduce or minimize interspecific interactions, potentially promoting coexistence.

**Key words** Avoidance, Coexistence, *Elephantulus myurus*, Intraspecific behavior, Interspecific behavior, *Micaelamys namaquensis*

Coexistence can occur as a result of spatio-temporal variability in resource abundance, density dependent resource utilization rates, and non-equilibrium between resource and consumer population dynamics (Brown, 1989; Zhang, 2003). Coexistence may also be promoted by mechanisms that reduce interspecific competition (Kinahan and Pillay, 2008) and thus improve overall fitness. These mechanisms include dietary partitioning, habitat and clump size selection, and aggressive interference (Brown, 1989; Kalcounis-Ruppell and Millar, 2002). Frequently, mechanisms promoting coexistence do not act independently and several may act simultaneously (Chesson, 1986). Additionally, the same species may vary the mechanisms used to coexist in different environments (see, for example, Merriam’s kangaroo rat *Dipodomys merriami*; Kotler and Brown, 1988). Behavioral interactions acting as mechanisms that promote coexistence have been extensively studies in many small mammal communities, both within and between species (Douglass, 1976; Holbrook, 1979; Hughes et al., 1994; Meserve et al., 1996; Ferreira and Van Aarde, 1999; Zhang, 2003; Ovadia et al., 2005). These interactions may be exploitative (i.e. by using a resource, individuals deprive others from using it) or due to interference (i.e. individuals are restricted by others from gaining access to a resource (Schoener, 1983), both of which may result in differential use of resources and aggression.

Demonstrating that two species use different parts of a resource does not indicate the absence of competition and thus competitive interactions; similarly, competition cannot be inferred if two species use the same resource (Conley, 1976; Holbrook, 1979; Schoener, 1983). However, increased similarity of resource utilization may enhance the chances for competitive interactions (Conley, 1976). These interactions can influence species coexistence in many ways: the larger species may displace the smaller species, especially in aggressive encounters (Perri and Randall, 1999; Pinter-Wollman et al., 2006). Alternatively, because some species are more sensitive to the degree of resource overlap (Schoener, 1983), the specialist may dominate the generalist. Additionally, due to spatial differences in species composition and interactions, competition may affect species differently and influence the same species differently in different locations. The long term results of these interactions sometimes only become apparent after a lag period (Meserve et al., 1996). Thus, whether or not competitive interactions occur between coexisting spe-
cies can be influenced by several factors, and the outcome is not always predictable.

Interspecific behavioral interactions are normally prominent during the breeding season due to defense of food and nest resources (Garcia and Arroyo, 2002). Such interactions have been previously reported in small mammals (Abramsky et al., 2001) but the findings have been confounded by the use of different measurement protocols and measurements being taken over different temporal and spatial scales (for example, snapshots or over several years), making results incomparable (Meserve et al., 1996). The strength of interspecific competition is often related to intraspecific competition: as the intensity of intraspecific competition increases, individuals are more likely to shift their resource use and thus potentially come into contact with and compete with another species (Grant, 1972). However, the frequency of intraspecific interactions is expected to be higher than interspecific interactions due to high resource overlap.

Two similar-sized crepuscular small mammal species, the Namaqua rock mouse *Micaelamys namaquensis* (mean mass 47.5 g; range 33–57.9 g; Skinner and Chimimba, 2005) and the Rock sengi *Elephantulus myurus* (mean mass 60 g; range 48–98 g; Skinner and Chimimba, 2005), coexist on rocky outcrops in southern Africa. They have similar microhabitat and dietary requirements, especially in the late rainy season, when there is potentially a high degree of resource overlap, although *E. myurus* is assumed to be more specialized, both in terms of diet and habitat requirements, than *M. namaquensis* (Lancaster and Pillay, submitted). Because of resource overlap and potential interspecific competition for resources, we asked whether behavioral mechanisms promote coexistence between *E. myurus* and *M. namaquensis*. The aim of our study was to investigate the behavioral interactions of coexisting *M. namaquensis* and *E. myurus* in intra- and interspecific dyadic encounters in neutral arenas. Assuming that behavioral interactions promote coexistence in the two species, we predicted that one species would be dominant over the other species, resulting in higher levels of aggression in interspecific than intraspecific dyads. Specifically, we expected that the larger, more specialized *E. myurus* would be dominant over the smaller, more generalist *M. namaquensis*. Since interactions are influenced by prior association (e.g. “dear enemy” phenomenon; Temeles, 1994), we studied the interactions between intraspecific and interspecific dyads that had made prior contact (i.e. from the same trapping grid) and that had not had the potential to have made prior contact (i.e. originated from different trapping grids). According to the “dear enemy” phenomenon, we predicted that unfamiliar conspecifics would display higher levels of aggression than familiar conspecifics (McGuire and Getz, 1998; Zuri and Rado, 2000), and we questioned whether a similar outcome was likely with different species.

1 Materials and Methods

Our study was conducted at eZemvelo Nature Reserve (25°42’26”S, 29°01’02”E), Gauteng Province, South Africa. The region receives summer rainfall of approximately 650 mm per year with mean daily temperatures ranging from 12.5°C in winter to 26°C in summer. Vegetation on the reserve consists of grasslands, interspersed with rocky outcrops along ridges. Our study was conducted in the late rainy season (December 2005 to February 2006), when dietary and micro-habitat use overlap was expected to be highest (Lancaster and Pillay, submitted).

*Micaelamys namaquensis* and *E. myurus* are the only two small mammal species found on rocky outcrops in our study site. Individual *M. namaquensis* and *E. myurus* were trapped using PVC live-traps (29 × 6 × 7 cm) placed randomly on three different rocky outcrops. Traps were baited (with a mixture of oats, raisins, sunflower seeds, salt, peanut butter and oil), and were covered with vegetation to buffer against temperature extremes. The traps were checked at dawn and dusk. Individuals were weighed and placed in individual holding cages (26 × 20 × 14 cm) overnight before they were used in experiments. During this time, they were provided with water, Epol® mouse pellets and seeds *ad libitum*.

Experiments were conducted on a neutral rocky outcrop. Three types of dyads were established: *M. namaquensis* × *M. namaquensis*, *E. myurus* × *E. myurus* and *M. namaquensis* × *E. myurus*. Only adults were used. For each dyad type, there were 10 same sex replicates. For dyads involving familiar animals (i.e. trapped on the same rocky outcrop), individuals were used twice, once in an intraspecific dyad and once in an interspecific dyad, with a minimum rest period of 3 hours (see Drickamer, 2001). The order in which animals were used (intra- vs interspecific dyads) was randomly determined. The short period between re-use in dyads allowed us to meet the ethical requirements of using as few individuals as possible and keeping them for the shortest period possible in captivity to prevent disruption of their natural activities (e.g. territorial defence). Indi-
v iduals were kept for a maximum of three days. Before their release onto their rocky outcrop, individuals were individually marked using fur-clipping to ensure that they were not re-used in experiments.

Only males were used in dyads with unfamiliar animals (i.e. trapped on different rocky outcrops), as too few females were captured to meet statistical requirements. Individuals were used twice as described above and were marked and released on their rocky outcrop of origin.

Dyadic encounters were staged in neutral arenas (tanks measuring 45 × 30 × 30 cm³), with 3 metal sides, painted a neutral color, and one side of clear PVC to facilitate observations. The floors of the tanks were covered with approximately 2 cm of wood shavings and straw. After every encounter, the tanks were washed with water and alcohol to remove the odours of previous occupants. Dyads were performed early morning, during the peak activity times of both species (pers obs). To identify subjects in same species dyads, individuals were marked dorsally with water-based, non-toxic paint. Individuals in interspecific species interactions were marked in a similar way to reduce experimental bias.

Individuals were randomly placed on either side of an opaque barrier which divided the tank into two. The barrier was lifted after an acclimatization period of 5 minutes, and encounters were videotaped for 10 minutes (Silva de Freitas et al., 2009). Using continuous recording (Martin and Bateson, 1993), the frequency of five behaviors were scored for each dyad member. The behaviours scored were: aggressive (e.g. chasing, attacking, biting), amicable (e.g. allogrooming, naso-nasal sniffing), active avoidance (e.g. moving away from the other individual when it approached), ignore or passive avoidance (e.g. watching the other member) and explore behavior (Fig. 1). Changes in behavior were scored if the behavior was performed for more than 2 seconds. An individual was classified as dominant if, in comparison to its opponent, it exhibited more exploratory and aggressive behavior (see Cranford and Derting, 1983, Pillay, 2000).

Data were analyzed using STATISTICA 6 (StatSoft, USA). Non-normal data were square root transformed to meet the assumptions of normality. A general linear model (GLM) with a multivariate design was used to compare the five behaviors (dependent factors) with dyad type and sex (independent factors). The difference in body mass between dyad members was included as a co-variate in the model. In a second analysis, the behaviors of dyads comprising familiar partners with those that were unfamiliar (i.e. from different grids) was compared using a GLM. Paired t-tests were used to compare the body mass of dyad partners, and \( \chi^2 \) analyses were used to compare the frequency of aggression and explore behaviors of dyad partners in interspecific dyads. All tests were two-tailed and \( \alpha \) was set at 0.05.

2 Results

No dyads engaged in damaging fights. The body mass of individuals did not differ significantly for intraspecific dyads involving familiar partners, for M. namaquensis (male: mean±SE: 49.3±1.87, \( t_\nu=1.48, P=0.173 \); female: 38.8±1.33, \( t_\nu=0.84, P=0.422 \)) and E. myurus (male: 62.3±1.62, \( t_\nu=1.26, P=0.238 \); female: 59.9 ± 1.20, \( t_\nu=1.21, P=0.256 \)) dyads. However, in interspecific dyads, E. myurus was significantly heavier than M. namaquensis (male: 65.7±1.04 vs 54.2±0.49, \( t_\nu=8.95, P<0.001 \); female: 56.4±1.28 vs 45.9±1.84, \( t_\nu=7.50, P<0.001 \). The same pattern was observed in dyads involving unfamiliar partners, as follows: M. namaquensis (51.9 ± 1.07, \( t_\nu=0.97, P=0.356 \)), E. myurus (61.5 ± 1.26, \( t_\nu=0.17, P=0.897 \)) and M. namaquensis x E. myurus (61.0 ± 1.65 vs 54.1 ± 1.53, \( t_\nu=4.25, P=0.002 \).

2.1 Dyads involving familiar individuals

Dyad type was a significant predictor of behavior (\( F_{10,98}=37.23, P<0.001 \)). There was no significant effect of sex (\( F_{3,49}=1.19, P=0.326 \)) and dyad type × sex (\( F_{10,98}=0.75, P=0.136 \)). Interestingly, the difference in body mass between dyad partners (co-variate) was also not significant (\( F_{3,49}=0.99, P=0.434 \)). Tukey post-hoc tests revealed that the intraspecific E. myurus dyads were most aggressive, whereas the intraspecific M. namaquensis dyads were the most amicable (Fig. 1). Interspecific dyads displayed the highest levels of avoidance and ignore behaviors and the lowest levels of explore behavior (Fig. 1).

A high frequency of aggressive and explore behaviors can be used as a dominance measure. We compared the overall frequency of these behaviors in partners of interspecific dyads and found no significant differences (\( P=0.05 ; \chi^2 \) analyses) for either behavior, so we were not able to determine if one species was dominant over the other.

2.2. Dyads involving unfamiliar individuals

A comparison of dyads involving familiar (same rocky outcrop) and unfamiliar (different rocky outcrop) partners, revealed that dyad type significantly influenced behaviors (\( F_{10,98}=20.07, P<0.001 \)). In addition,
the familiarity of the dyad partners ($F_{5,49}=13.25$, $P<0.001$) and the interaction between dyad type and the familiarity of partners ($F_{10,98}=5.38$, $P<0.001$) were also significant predictors of behavior. There was no significant influence of the difference in body mass of dyad partners ($F_{5,49}=0.13$, $P=0.984$). Tukey post-hoc tests revealed that interspecific dyad types, regardless of familiarity, displayed the lowest aggression, amicability and explore behaviors, and the highest avoidance and ignore behaviors. Differences in familiarity influenced the behavior of intraspecific dyads, which displayed more aggression and avoidance, and less amicable and exploratory behavior in encounters between unfamiliar compared with familiar dyads (Fig. 1).

As in the dyads with familiar partners, there was no significant differences in the frequency of aggressive and explore behaviors ($P>0.05$; $\chi^2$ analyses) between unfamiliar partners in interspecific dyads.

3 Discussion

We conducted intraspecific and interspecific dyadic encounters to assess whether behavioral interactions influence coexistence in M. namaquensis and E. myurus. Agonistic behavior among conspecifics is common, since they have similar resource requirements, such as access to nesting sites, food and mates (Perrin et al., 2001). Thus, for the specialist E. myurus, resource overlap between individuals is probably greater and thus levels of intraspecific aggression should have been predictably higher than in the more generalist M. namaquensis. Additionally, E. myurus forms monogamous pairs whereas M. namaquensis lives in small groups (Skinner and Chimimba, 2005), so that more tolerance would be expected between conspecific M. namaquensis.

In support of our prediction, in intraspecific dyads, M. namaquensis showed greater levels of amicability and lower levels of aggression towards familiar conspecifics. However, E. myurus were also amicable in intraspecific encounters. This may be because of the low population density of E. myurus occurred at low densities on the study site, possibly too low for intraspecific competition to be an important consideration, but it could also be the result of prior familiarity between dyad partners. In fact, despite experiments being conducted in a neutral tank on a neutral rocky outcrop, intraspecific dyads of both species displayed less aggression and more avoidance when dyad partners were familiar rather than unfamiliar. This concurs with the “dear enemy” phenomenon (Temeles, 1994). Nonetheless, familiarity of dyad members did not influence the behavior of interspecific dyads.

Contrary to our expectations of greater aggression in interspecific encounters, no dyad type showed a higher frequency of aggression than any other dyad type, and neither species showed differences in aggression in intra- and interspecific dyadic encounters. One reason for the low levels of aggression in interspecific encounters may be due to both species, but especially E. myurus, showing low levels of exploratory behavior in all encounters, which was not the case when these individuals were housed alone (pers. obs.). Thus, aggression may be avoided, and passive avoidance may be important in conflict resolution behaviors in interspecific encounters (Cheney and Seyfarth, 1982; Kapusta et al., 2007). Consequently, instead of displaying overt aggression, these two species tended to minimize contact with each other. Another possible reason for the low levels of aggression is that competition is likely to occur over some
resource (which was not provided in the neutral arena,) that is important to both species especially if there is a minimum threshold density of either the resource or the individuals at which animals become aggressive (Wolff, 1985).

In behavioral studies of two vole species in captivity, the meadow vole Microtus pennsylvanicus was dominant over the montane vole Microtus montanus, yet they were often caught in adjacent traps in the field. This suggests that interspecific interactions may not be the only factor promoting their coexistence, but may become more important when resource utilization overlaps, resulting in the exclusion of the subordinate species (Douglass, 1976). Similarly, the intensity of interspecific interaction varies seasonally depending on the availability of space (Conley, 1976). These examples support our idea that although active avoidance may minimize interspecific contact, factors other than behavior may be promoting the coexistence of M. nanaquensis and E. myurus, as occurs in coexisting Rice rat Oryzomys longicaudus, Olive grass mouse Akodon olivaceus and Long-haired grass mouse Akodon longipilis (Murua et al., 1987).

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References


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