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POPULATION AND LIFE HISTORY CHARACTERISTICS OF COEXISTING SMALL MAMMAL SPECIES IN A GRASSLAND HABITAT

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A thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg in fulfilment of the requirements for the degree of Doctor of Philosophy.

Johannesburg, 2009

DECLARATION

I declare that this thesis is my own unaided work. It is being submitted for the degree of Doctor of Philosophy in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.



(signature of candidate)

October 2009

ABSTRACT

Many factors have been proposed to facilitate coexistence between small mammals in arid areas. However, little is known about factors promoting coexistence of small mammals outside arid systems. The Namaqua rock mouse, *Michaelamys namaquensis*, and the Rock sengi, *Elephantulus myurus* frequently occur together on rocky outcrops throughout southern Africa. I investigated whether dietary and/or microhabitat partitioning, differences in habitat use, life history strategies or competitive coexistence or a combination of these factors promoted coexistence of these species on rocky outcrops in the highveld region of South Africa. Monthly trapping on permanent grids was conducted over 2 years. There was a high degree of overlap in diet and microhabitat preferences. Thus, these factors in all probability do not operate alone in facilitating coexistence of the two species. However, there were slight seasonal differences between the species, especially in arthropod consumption. *Michaelamus namaquensis* occurred at higher densities than *E. myurus* and tended to start breeding slightly later. Both species had similar home range sizes and thus there was no indication for macrohabitat separation, but the spatial distribution of individuals indicates that *M. namaquensis* is polygynous whereas *E. myurus* is monogamous. Although life history characteristics are essentially phylogenetically constrained, small seasonal differences in dietary preferences may allow the species to breed slightly asynchronously. *Michaelamys namaquensis* tended to breed later in the season than *E. myurus* which would reduce competition for shared resources. This is reinforced by behavioural studies which indicated that *M. namaquensis* and *E. myurus* actively avoid each other. Neither species appeared to modify their biologies, in terms of home range use and breeding, except *M. namaquensis* females which travelled shorter distances when *E. myurus* was experimentally removed. This may indicate that *M. namaquensis* females have to search less for shared resources, a prediction of specialist-generalist coexistence. Thus, a combination of factors, rather than a single factor acting alone, promote coexistence between *M. namaquensis* and *E. myurus*.

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Chapter 1
Introduction

Motivation for the study

Not much is known about small mammal co-existence outside of desert and arid ecosystems. In these arid systems, various mechanisms, such as differences in diet, time of activity and habitat preferences have been proposed in facilitating co-existence (Brown, 1989b; Perrin & Kotler, 2005). In southern Africa, most studies relating to small mammal co-existence have been done in the semi-arid and arid regions of the karoo (Kerley *et al.*, 1990; Monadjem & Perrin, 2003). These, like most other studies concerning co-existence, have focused on species belonging to at least the same order if not family or genus (Perrin, 1980; Ben-Natan *et al.*, 2004). In southern Africa, two poorly studied species, the Namaqua rock Mouse *Michaelamys namaquensis* (previously *Aethomys namaquensis*; Rodentia: muridae) and the Rock Sengi *Elephantulus myurus* (Macroscelidea: Macraoscelididae; previously the Rock elephant shrew) coexist on rocky outcrops. My study is unique, as although there have been many studies documenting the interactions and coexistence of larger mammal species of different orders (see for example Arsenault, 2007), very few, if any, have looked at the coexistence of representatives of small mammalian orders. Additionally, in the studies on grazing mammals, much emphasis has been placed on food resources and the role of competition and facilitation, both spatial and temporally (Schoener, 1974; Schoener, 1983; Hobbs *et al.*, 1996), while small mammal studies also place emphasis on other factors, such as cover availability (Coppeto *et al.*, 2006; Innes *et al.*, 2007; Manor & Saltz, 2008). The main objective of my study therefore was to study possible mechanisms of coexistence between *M. namaquensis* and *E. myurus* on rocky outcrops in the highveld region of South Africa.

Co-existence

Species co-existence can be facilitated through variability in the environment and the ability of individual species to specialise and exploit this variability (Perrin & Kotler, 2005). Coexistence may also be promoted by mechanisms that reduce interspecific competition (Kinahan & Pillay, 2008) and thus improve overall fitness. In desert ecosystems, these mechanisms include dietary partitioning, habitat and clump size selection and aggressive interference (Brown, 1989b; Kalcounis-Ruppell & Millar, 2002). Differential use of these resources, especially in space and time, may facilitate co-existence

(M'Closkey, 1976; Brown, 1989b; Yunger *et al.*, 2002; Zhang, 2003; Bonesi & Macdonald, 2004; Harris *et al.*, 2006). Spatial differences are based on the macro vs. micro-habitat selection. Thus, factors such as cover availability, differences in microclimate, substrate, predation risk & food availability become important (Chesson, 1986). Temporal differences on the other hand involve variations that act on daily (e.g. resource renewal and availability), lunar (e.g. predation risk) and annual (climate, precipitation) time scales (Chesson, 1986). Thus, for coexistence there needs to be an axis of environmental heterogeneity and a trade-off between interacting species, resulting in each species having a place on that axis where it is the superior competitor (Kotler & Brown, 1988; Brown, 1989b; Abramsky *et al.*, 1990; Perrin & Kotler, 2005). In other words, coexistence needs variability in at least one shared resource that competing species require. The species are able to coexist by using a particular, variable aspect (e.g. low resource abundance) better than competing species. However, other factors may also play a role. Kryštufek *et al.* (2007) suggest that some assemblages may be structured by morphology (e.g. body size) and behaviour (e.g. aggressive interactions), and Brown & Zeng (1989) emphasise the importance of population ecology in promoting coexistence. Perrin & Kotler (2005) proposed that, since there were no differences in resource use and activity in a small mammal community in the Kalahari, differences in reproduction and the seasonal importance of various food resources might promote coexistence. Frequently, mechanisms promoting coexistence do not act independently and several may act simultaneously (Chesson, 1986). Additionally, the same species may employ different mechanisms to coexist in different environments (see for example Merriam's kangaroo rat *Dipodomys merriami*; Kotler & Brown, 1988).

Specialists vs. generalists

Species may be able to coexist as they respond differently to environmental fluctuations (Moro & Morris, 2000; Stilmant *et al.*, 2008). Thus, communities may be composed of species that vary from having very narrow habitat requirements (specialists) to very broad habitat requirements (generalists; Ben-Natan *et al.*, 2004; Manor & Saltz, 2008). Although generalists may have a variety of accessible and profitable options, they often have clear resource preferences and will rank these depending on availability, whereas specialists tend to be more efficient at using specific resources (Stilmant *et al.*, 2008), although this may have costs in terms of habitat, time or energy constraints (Townsend *et al.*, 2000). Where there is overlap, the generalist can exploit resources not

used or underused by the specialist (Morris, 1996; Perrin & Boyer, 2000). Thus, specialists and generalists are able to co-exist with the expectation that specialists should be able to out-compete less well adapted species (Manor & Saltz, 2008). However, most communities are composed of species of varying competitive abilities (Chesson, 1986). An alternative explanation is that factors such as predation and competition (between individuals of both the same and different species) maintain populations below an equilibrium point where generalists would exploit all patches, regardless of the density of the specialist (Morris, 1996). This would also promote co-existence through different resource utilisation and/or activity patterns (Archer, 1970; Kalcounis-Ruppell & Millar, 2002). However, when using generalists and specialists to explain coexistence, the scale of measurement must be considered as there may be a scale where a specialist uses a patch preferentially while generalists show no preference. For example, a dietary specialist may forage in a greater area than a generalist due to availability of resources. Alternatively, a smaller species may utilise a smaller area than a larger species (Makarieva *et al.*, 2005).

Mechanisms of coexistence

Various mechanisms have been proposed to promote coexistence. Those that have received attention in promoting small mammal coexistence include spatial and/or temporal variation in diet and habitat, predator avoidance and time of activity.

Diet

Dietary partitioning relies on differences or modifications of the diet resulting in species utilising different aspects of the food resource (Kinahan & Pillay, 2008). Diet selection depends not only on the variety of resources available (including the energy content, abundance and distribution), but also the species of consumers present, their numbers and morphological and physiological characteristics that may affect their foraging behaviour (Chesson, 1986).

Coexistence through dietary partitioning may thus be promoted by the degree of specialisation – if many specialist species are present, there is a reduction in the amount of dietary overlap, but if methods of resource acquisition are similar, there may be an increase in dietary overlap (Chesson, 1986) which increases competition. However, species do not always consume all available resources, and/or these resources are not necessarily consumed in the proportions in which they are available (Brown & Lieberman, 1973). Consequently, a species may dominate the use of resources due to intrinsic factors such as the size and shape of resources and the species foraging efficiency (Kalcounis-Ruppell &

Millar, 2002) or extrinsic factors depending on spatio-temporal availability of resources (Ben-Natan *et al.*, 2004). These differences may promote co-existence.

Temporal differences in food resource use (e.g. through seasonal rotation – when species use the same resource at different times of the year) may also aid coexistence. Optimal foraging theories predict that each species will have a period when it is the most efficient forager. Thus, due to higher efficiency and lower foraging costs in comparison to other species in the community, the density of efficient foragers is often higher. Thus competitive coexistence may be promoted through asynchronous changes in density (Brown, 1989b; Yunger *et al.*, 2002). For example, potential competitors may vary in their harvesting efficiency depending on resource abundance. This may result in other trade offs, e.g. in the Negev desert, the Greater Egyptian gerbil *Gerbillus pyramidium* monopolises resources when they are abundant while Allenby's Gerbil *Gerbillus andersoni allenbyi* harvests these resources when resource density is low (Ovadia *et al.*, 2005).

Habitat

The concept of habitat selection is controversial due to the differences of scale. This is because habitat preferences may occur at different scales, i.e. what an individual selects within a home range may be very different to what it associates with in a smaller area, e.g. cover availability may be more important on a smaller scale. Jorgensen (2004) attempted to simplify the matter for small mammalogists by defining a microhabitat as those environmental factors affecting individual behaviour while macrohabitat is the spatial area in which individuals perform their biological functions. Thus, in my study, microhabitat selection is concerned with where in the patch an individual was found in terms of vegetation structure and cover availability whereas macrohabitat refers to the home range area of the individual.

Regardless of scale, habitat selection may facilitate species co-existence through various mechanisms (Rosenzweig, 1981). Selection may occur in space (e.g. through distinct microhabitat preferences or distribution of food resources; Kotler & Brown, 1988; Jorgensen, 2004), time (e.g. through tradeoffs or variation in resource availability; M'Closkey, 1976; Brown, 1989a) or through interspecific interactions (e.g. the presence of other consumer species that may change the value of the habitat by making certain resources unavailable; Douglass, 1976; Kerley *et al.*, 1990). Differences in any of these may also be related to physiology and predation risk. For example, in desert systems with granivores, larger species (e.g. Kangaroo rats *Dipodomys*) tend to dominate open areas where there is a greater chance of encountering seeds but also greater predation risk;

Kangaroo rats are bipedal and can run faster whereas smaller quadrapedal species (e.g. Deer mice *Peromyscus*) tend to dominate bush areas. Here, microhabitat selection exists as there is a trade off between foraging efficiency and predation risk (Brown, 1989b).

Predator avoidance and time of activity

If one species is more susceptible to predation (due to size, locomotion, physiological constraints, morphological constraints or lack of crypsis), that species should modify its behaviour to become less conspicuous, such as forage under bushes rather than in the open (Shargal *et al.*, 2000; Cramer & Willig, 2002; Sundell *et al.*, 2008). These changes may then affect microhabitat selection. Temporal influences become important when two ecologically similar species partition time, thereby facilitating coexistence – when two or more species preferentially occur in the same habitat, different activity times may promote their coexistence. If there is no temporal separation, one species may be forced into a suboptimal habitat because of competitive exclusion. In semi-arid Chile, the Degu *Octodon degus* excludes Darwin's leaf-eared mouse *Phylloris darwini* and the Olivaceous field mouse *Akodon olivaceus* from certain areas at specific times (Yunger *et al.*, 2002).

Competitive coexistence

The competition theory assumes that at competitive equilibrium, densities are maintained (Ferreira & Van Aarde, 1999), and may thus act to structure communities (Hughes *et al.*, 1994; Manor & Saltz, 2008). Competitive coexistence may be emphasized when there is spatial or temporal variation in resource abundance or a non-equilibrium between resource and consumer dynamics (Chesson, 1986). Demonstrating that two species use different parts of a resource (e.g. seeds vs. culms of a grass) 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 utilisation may enhance the chances for competition (Conley, 1976). Competitive interactions that promote coexistence may be direct (e.g. fighting) or indirect (e.g. use of a scarce resource so that it is unavailable for other species; Amarasekare, 2002). Both direct and indirect competition can lead to competitive exclusion where one species replaces another or by small behavioural changes of a particular species resulting in a decrease in competition.

The role of behaviour

Behavioural interactions have received little attention in studies of co-existence (Perri & Randall, 1999; Harris *et al.*, 2006), yet some of the most important biotic factors influencing small mammal communities are the interactions both within and between species (Douglass, 1976; Holbrook, 1979; Hughes *et al.*, 1994; Meserve *et al.*, 1996; Ferreira & 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). The interactions may also be asymmetrical due to several reasons, such as the larger species displacing the smaller species (Perri & Randall, 1999; Pinter-Wollman *et al.*, 2006), especially in aggressive encounters (e.g. *O. degus* and *A. olivaceus*; Yunger *et al.*, 2002), prior association (the dear enemy phenomenon; Temeles, 1994), or because some species are more sensitive to the degree of resource overlap (Schoener, 1983), so that the specialist dominates over the generalist. Additionally, these interactions may affect species differently and influence the same species differently in different locations (Meserve *et al.*, 1996; Dammhahn & Kappeler, 2008). Competitive release occurs when in the absence of one species, another species increases its home range, density or range of food eaten (Chesson, 1986).

Although there are some studies on interspecific competition in small mammals, these interactions are poorly understood, as these have been measured differently and at different temporal and spatial scales, making results incomparable (see examples in (Meserve *et al.*, 1996; Abramsky *et al.*, 2001). Results are also often clouded due to the effect of intraspecific competition. Intraspecific competition should occur at a higher density than interspecific competition since resource use is essentially the same within a species (Perri & Randall, 1999; Perrin *et al.*, 2001; Zhang, 2003; Dammhahn & Kappeler, 2008). Thus, as the strength of intraspecific competition increases, individuals are more likely to shift their resource use and potentially come into contact with and compete with another species (Grant, 1972). Thus behaviours that minimise aggression (e.g. avoidance) are also important in structuring small mammal communities. For example, Ord's kangaroo rat *Dipodomys ordii* and *D. merriami* coexist at high densities with large amount of overlap, and coexistence is possible through avoidance rather than aggression (Perri & Randall, 1999).

The influence of space use

Mutually exclusive home ranges provide evidence of avoidance rather than aggression as a behavioural mechanism promoting coexistence. However, the presence of other species is just one factor influencing home range overlap. Other biological factors include population density, sex, age and body size, while ecological factors may include season and food availability and distribution (Burt, 1943; Wolff, 1985; Ostfeld, 1990; Ribble *et al.*, 2002; Priotto *et al.*, 2002; Schradin & Pillay, 2006; Pasch & Koprowski, 2006; Cooper & Randall, 2007). Difference in space use would be expected to promote coexistence since ecologically similar species may occupy adjacent, non-overlapping home ranges (Bleich & Price, 1995; Christopher & Barrett, 2006). However, these home ranges may vary depending on resource availability (Orland & Kelt, 2007). Thus studies of spatial distribution (i.e. dispersion of individuals) may also contribute to understanding patterns of co-existence between ecologically similar species (Ferreira & Van Aarde, 1999; Ribble *et al.*, 2002; Priotto *et al.*, 2002), as it gives an indication of resource partitioning, one of the underlying mechanisms promoting co-existence (Rosenzweig, 1981; Kalcounis-Ruppell & Millar, 2002; Jorgensen, 2004; Bonesi & Macdonald, 2004).

Home ranges also give an indication of the social structure of species (Schradin & Pillay, 2005; Cooper & Randall, 2007). Polygynous species tend to have a high degree of intraspecific overlap, especially between the females and thus also tend to occur in higher densities (Ribble & Stanley, 1998; Priotto *et al.*, 2002). Promiscuous species also tend to have high densities with a high degree of overlap between both sexes, since males are unable to monopolise widespread females (Ostfeld, 1990; Ribble & Stanley, 1998; Jackson, 1999). Monogamous species tend to exclude individuals of the same sex while having a high degree of overlap with one individual of the opposite sex. These species tend to occur at low densities (Gaulin & FitzGerald, 1988). These differences in density and spatial organisation bring about differences in the intensity of resource use and hence may promote coexistence (Perri & Randall, 1999; Yunger *et al.*, 2002; Harris *et al.*, 2006).

Can differences in life histories play a role?

Life history characteristics (such as fecundity and longevity) and population dynamics (including densities and dispersal) that allow species to minimise or avoid competition may promote coexistence (Brown & Zeng, 1989; Dammhahn & Kappeler, 2008) as these traits may be an adaptive response to the environment (Neal, 1986).

Life history theories predict a trade-off between reproductive investment and survivorship (Brown & Zeng, 1989). In unstable or highly variable environments, species may maximise productivity while those species occurring in more stable environments may maximise efficiency (Pianka, 1970; Perrin & Swanepoel, 1987; Willan & Meester, 1989; Mills *et al.*, 1992). This theory assumes variable adult mortality, but if juvenile mortality is variable these stategies are reversed (Neal, 1986), because juvenile survival rates are more influenced by environmental conditions in comparison to adult survival rates (Chesson, 2003). Thus, under strong competition, the dominant species may greatly reduce the density of other species (Chesson, 1986). The subdominant species is able to coexist as long as there are periods of strong recruitment (i.e. successful rearing of offspring when conditions are more favourable). How differing survival rates in unstable environments promote coexistence, especially if there is a limiting resource, is the basis of the lottery model of competition (Chesson, 1986). Essentially, small mammals can be classified into three types according to density responses (and the related reproductive and survival rates) to the environment (French *et al.*, 1975). As such, type I have high reproductive potential and low survival resulting in large density fluctuations, whereas type III have low reproductive rates and high survival with little variation in density, and type II fits inbetween these theoretical classifications (French *et al*., 1975). However, all the above ideas recognise that the organism's interpretation of the environment, rather than environmental stability itself may be important in determining the strategy employed (Neal, 1986).

Although the importance of both abiotic and biotic factors as regulators of small mammal breeding and density fluctuations is acknowledged (Perrin & Boyer, 2000), most work on African small mammals has focused on abiotic factors, such as the timing and quality of rainfall (Perrin & Swanepoel, 1987; Keesing, 1998a) and hence food availability (Perrin & Boyer, 2000). Although it is often difficult to separate out individual factors (Neal, 1986), variables such as photoperiod and temperature may also have an effect (Bronner, 1986; Muteka *et al.*, 2006). Biotic factors (e.g. physiological, morphological and behavioural characteristics) may also influence the breeding season of small mammals, but the relative importance of these factors can have different effects on species living in the same locality (Neal, 1986), and as such, temporal patterns in breeding may be due to inter- and intra-specific interactions (Ims, 1990). If species share the same resource, competition is reduced if the population dynamics of these species is asynchronous (e.g. through temporal differences in breeding season; Chesson, 1986), such as in a small mammal

community in the Kalahari where, at least between Gerbils *Tatera* spp. and the Striped field mouse *Rhabdomys* spp., differences in the breeding strategy and slight seasonal differences in breeding are thought to promote coexistence (Perrin & Kotler, 2005).

The importance of coexistence

Coexistence has both ecological and evolutionary importance but it is hard to bridge the gap between these two time scales. One of the problems associated with determining an ecological or evolutionary effect is that they both often have the same outcome: under both the ghost of competition past theory (Connell, 1980) and the competition exclusion principle, species with the potential to compete should exhibit behavioural, physiological or morphological differences to minimise competition (Townsend *et al.*, 2000). Many authors also question the robustness of coexistence systems both ecologically (Christensen *et al.*, 2002) and evolutionary (Mougi & Nishimura, 2007).

Evolutionary significance

Evolution may drive the niches of competitors apart until they no longer compete or the strength of competition is decreased to such an extent that species can coexist, but this is expressed at the ecological level (Townsend *et al.*, 2000). In order to help understand these systems, questions need to be asked regarding past and present competition and whether this competition is not due to chance or spatial-temporal variations. Additionally, what is the significance of competition as an evolutionary force? Abramsky & Sellah (1982) attempted to answer the latter question looking at Allenby's Gerbil, *Gerbillus allenbyi* and Tristram's Jird *Meriones tristrami* and found that although *M. tristrami* occupies sand dunes where *G. allenbyi* does not occur, when they occur together, it does not use sand dunes, even if *G. allenbyi* is removed. This implies evolutionary effects rather than ecological effects and invokes the idea of phenotypic plasticity, rather than phylogenetic constraints.

Local biodiversity can be affected by phenotypic plasticity (Miner *et al.*, 2005). This plasticity may change the behaviours, life history characteristics and demography of a population over various time scales. The co-evolution of these changes in behaviour, life history and demography due to interactions between coexisting species may influence evolutionary dynamics (Christensen *et al.*, 2002).

Ecological consequences

Coexistence has many important ecological influences, as it may act in the regulation of population density and resource use (Perri & Randall, 1999). For example, population density may be kept low due to competitive interactions which many authors (see Brown (1989b), Morris (1996), Morris *et al.* (2000), Amarasekare (2002), Amarasekare (2003) and Mougi & Nishimura (2007) for examples) view important in the maintenance of coexistence. Understanding species interrelationships and hence coexistence may also help predict the effect of environmental changes. Tilman's Theory of Resource Heterogeneity predicts that at high resource availability, species that are effective at using this resource should be dominant (Townsend *et al.*, 2000), but also that species richness may increase as a result of increased resources. In supplemental feeding experiments in the Sonoran Desert, Orland & Kelt (2007) found that, unlike during ENSO (El Nino Southern Oscillation) events, which increase resource availability, small mammal species richness, especially of rare species decreased as dominant species manipulated the food resource. This has important implications for managing for diversity. Although the biodiversity conservation is mainly concerned with extinctions, animals need to be able to coexist in order to reduce the probability of extinctions occurring (Townsend *et al.*, 2000).

The study animals and site

The Namaqua rock mouse *Michaelamys namaquensis* and the Rock sengi (also known as the Rock elephant shrew) *Elephantulus myurus* co-exist on rocky outcrops throughout southern Africa, but specifically on the highveld grassland region, where they are often the only two small mammal species in the community (*pers. obs.*). However, little is known about their biologies and nothing is known about mechanisms promoting their co-existence.

The Namaqua Rock Mouse Michaelamys namaquensis

Michaelamys namaquensis is a small (~50 g), crepuscular murid rodent that lives in social family groups that often number 10 or more individuals (De Graaff, 1981; Fleming & Nicolson, 2004; Skinner & Chimimba, 2005). It is widespread but prefers rocky areas, as it has physiological (e.g. reduced metabolic rates) and behavioural adaptations (e.g. hides during the heat of the day) for such areas (Fleming & Nicolson (2004) and references therein). *Michaelamys namaquensis* is polygynous (Fleming & Nicolson, 2004) and breeds during the warm, wet months (September to May; Fleming & Nicolson, 2004) with a litter

size of between 1 – 5 (De Graaff, 1981; Skinner & Chimimba, 2005). It may have unstable population cycles associated with high mortality (yet may have a life span of up to two years) and high reproductive potential (Muteka *et al.*, 2006). This high reproductive potential results in densities that vary between 8.1 and 11.8 individuals/ha in the southern Cape (Fleming & Nicolson, 2004) and a nest density 1.5 – 2 nests/ha in thornveld savanna (Meyer & Brandl, 2005). It has been suggested that *M. namaquensis* responds to changes in photoperiod, with males becoming reproductively active sooner than females, but other factors such as rain, temperature and the presence of secondary plant compounds have also been acknowledged as important influences on their reproduction (Muteka *et al.*, 2006). *Michaelamys namaquensis* show no sexual dimorphism (De Graaff, 1981; Rautenbach, 1982; Skinner & Chimimba, 2005), and are reported to be dietary generalists, feeding on stems, seeds and arthropods (De Graaff, 1981; Fleming & Nicolson, 2004; Skinner & Chimimba, 2005). Recent literature has suggested the separation of the *Aethomys* genus into two separate genera, *Aethomys* and *Michaelamys* based on cranial and molecular differences (Chimimba, 2005), with the suggestion that *A. namaquensis* be reclassified as *M. namaquensis*. This study reflects this current thinking.

The Rock Sengi Elephantulus myurus

Elephantulus myurus is a macroscelid, part of the uniquely African mammalian superorder, Afrotheria. Based on molecular data, there appears to be a basal split between Afrotheria and other placental mammals 101 – 108 million years ago (Murphy *et al.* 2001), resulting in the Afrotheria, and especially sengi's and their sister taxa having unique characteristics and behaviours, many of which are more similar to small cursorial herbivores than other small mammals (Ribble & Perrin, 2005). In particular, sengi are apparently monogamous and are thus of interest in terms of the evolution of monogamy as no other mammalian order is totally monogamous (Ribble & Perrin, 2005).

Elephantulus myurus is slightly larger (~60 g) than *M. namaquensis* (Skinner & Chimimba, 2005). It is a monogamous macroscelid (Skinner & Chimimba, 2005) that is thought to be crepuscular (Neal, 1982b). Although there is little information regarding the diet and microhabitat preferences of *E. myurus*, it is considered to be an insectivore and known to occur on rocky outcrops (Neal, 1982b; Skinner & Chimimba, 2005). It occurs in low population densities, and may enter a state of torpor during winter (Mzilikazi & Lovegrove, 2004). There is a paucity of information regarding the life history characteristics of *E. myurus*, but based on some studies of *E. myurus* and other sengi

species, they are thought to be summer breeders (Ribble & Perrin, 2005; Skinner & Chimimba, 2005), although other species (e.g. Rufous sengi *Elephantulus rufescens* and Smith's Rock sengi *Elephantulus rupestris*) are known to breed throughout the year (Neal, 1982b). Sengis have 3 litters/season on average, with 1 – 2 precocial pups/litter (Neal, 1982b, Ribble & Perrin, 2005). The life span of *E. myurus* is 1 – 2years (Neal, 1982b).

The study site

The 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 around 650 mm per year, and average temperatures fluctuate between 12.5 °C in winter to 26 °C in summer. Vegetation on the reserve is varied and comprises of grasslands (dominant species: *Aristida* spp., *Eragrostis* spp. and *Hyparrhenia* spp. with short sparse shrubs), interspersed with rocky outcrops along ridges (dominated by *Burkea africana*, *Ochna pulchra* and *Protea caffra*, larger shrubs and some grasses) and has been described as Bakenveld (Acocks, 1988). There are two perennial rivers on the reserve. The reserve was used for various agricultural purposes 3-8 years before the study commenced in 2002.

Study questions, objectives and aims

This study aimed to examine factors that might promote the co-existence of *M. namaquensis* and *E. myurus*. As mentioned above, although, these two species frequently occur together elsewhere, they are the only two small mammal species occurring on rocky outcrops in the eZemvelo study site. Specifically, my study had 5 aims, as listed below.

1. To determine and compare the patterns of microhabitat use and diet of the two species, using faecal analysis and by relating habitat variables to capture success. Based on the literature available, it was expected that *M. namaquensis* would be a dietary generalist, while *E. myurus* would be a dietary specialist. A large degree of microhabitat overlap was expected as both species are adapted to rocky outcrops (De Graaff, 1981; Fleming & Nicolson, 2004; Skinner & Chimimba, 2005). Macrohabitat choice is often dependant on other factors, such as microhabitat preferences, competition, predation, activity times and foraging efficiency (Rosenzweig, 1981; Abramsky *et al.*, 1990; Abramsky *et al.*, 2001). As both species are are closely associated with rocky outcrops and have similar activity times, macrohabitat was not considered to be a major factor promoting co-existence.

2. To describe and compare the population biology (e.g. in terms of life history characteristics, demography and reproduction) of *M. namaquensis* and *E. myurus* on rocky outcrops in highveld grasslands, using mark-recapture techniques. Although the life history characteristics and population dynamics of *M. namaquensis* have been studied elsewhere (Fleming & Nicolson, 2004), these have not been studied on the highveld region of South Africa. It is, however, expected that they will follow reported trends. Any information regarding the population biology of *E. myurus* will add to the scant data available. These data are used to determine similarities and differences between the two species and whether these similarities and/or differences facilitate co-existence.
3. To determine home range size and use, including intra- and interspecific overlap, of *M. namaquensis* and *E. myurus*. These data can be used to infer how the social and spatial structure of the two species may promote coexistence.
4. To determine how the presence/absence of one species affects the other by conducting removal experiments. An absence or reduction of one species is expected to affect the population dynamics of the remaining species in various ways. Factors such as breeding season are not expected to change due to evolutionary constraints, whereas population characteristics such as density, dispersal and recruitment and home range size are expected to increase or decrease depending on the strength of competition and recruitment levels within the species.
5. To study the behavioural interactions between *M. namaquensis* and *E. myurus* using field based staged dyad encounters. The extent of tolerance and aggression between the two species is expected to reflect the degree of competition between them.

Outline of thesis

Following this introduction, there are five experimental chapters. The experimental chapters have been written as individual papers for submission to various journals. Thus, there is some overlap between the chapters, especially in terms of the present introduction and those of the individual chapters, and in the methods. Similarly, there is overlap between the discussions and conclusions of the individual chapters and the concluding chapter at the end of the thesis. However, as none of the chapters have been published yet, a full reference list is provided at the end of the thesis.

The first experimental chapter (chapter 2: Dietary overlap and microhabitat use in a co-existing rodent and macroscelid in a grassland habitat) corresponds to the first objective mentioned above, the second experimental chapter (chapter 3: A comparison of the life history characteristics and population dynamics between two co-existing small mammals, *Michaelamys namaquensis* and *Elephantulus myurus*) corresponds to the second objective above, the third experimental chapter (chapter 4: Spatial organisation of coexisting *Michaelamys namaquensis* and *Elephantulus myurus*) relates to the third objective above, the fourth experimental chapter (chapter 5: Effects of species removal on the population dynamics and space use of coexisting small mammals) corresponds to the forth objective above and the last experimental chapter (chapter 6: Behavioural interactions between a coexisting rodent and macroscelid) relates to the fifth objective above. The main discussion points and conclusions of the study are discussed in the final chapter (chapter 7).

Chapter 2

Dietary overlap and microhabitat use by a coexisting rodent and macroscelid in a grassland habitat

Abstract

Little is known about factors promoting coexistence of small mammal species in southern Africa. Studies elsewhere report that, among other factors, differences in diet and microhabitat preferences promote coexistence. I investigated the diet and microhabitat use of coexisting *Michaelamys namaquensis* (Rodentia) and *Elephantulus myurus* (Macroscelidea). Faecal analysis confirmed that *M. namaquensis* is a dietary generalist while *E. myurus* is a dietary specialist. The proportion of arthropods in the faeces of *E. myurus* was significantly higher than in the feaces *M. namaquensis* which contained more leaves and seeds. However, *M. namaquensis* faeces contained significantly more arthropods in the rainy season when arthropods decreased in frequency in *E. myurus* faeces. Only arthropods differed in frequency of occurrence between species. In terms of microhabitat selection, *M. namaquensis* was associated with low amounts of dead material and *E. myurus* was associated with shorter grass. However, both species associated with areas of low grass and high rock cover. Despite dietary overlaps and similar microhabitat associations, *M. namaquensis* and *E. myurus* seem to coexist by varying their use of resources seasonally.

Keywords: coexistence; diet; *Elephantulus myurus*; grasslands; *Michaelamys namaquensis*

Introduction

Species coexistence can be facilitated through variability in the environment and the ability of individual species to specialise and exploit this variability (Perrin & Kotler, 2005). Thus mechanisms reducing interspecific competition and improving overall fitness may function to promote coexistence (Kinahan & Pillay, 2008). Specialisation could result in species exploiting a specific part of the environment differently to other coexisting species (Ben-Natan *et al.*, 2004), thereby facilitating the coexistence of generalists and specialists (Manor & Saltz, 2008). Although generalists may have a variety of accessible and profitable options, they often have clear resource preferences and will rank these depending on availability, whereas specialists utilise a few or a narrow range of similar resources (Townsend *et al.*, 2000) and tend to be more efficient at using this resource

(Stilmant *et al.*, 2008). Where there is overlap and the specialist is dominant, the generalist can exploit resources not used or underused by the specialist (Perrin & Boyer, 2000; Morris, 1996). However, specialisation may have costs in terms of habitat, time or energy constraints (Townsend *et al.*, 2000), resulting in a trade-off between tasks (Rosenzweig, 1981), and may ultimately result in niche separation between coexisting species (Townsend *et al.*, 2000).

A number of mechanisms such as dietary, habitat and clump size selection and aggressive interference promote coexistence of rodents in mainly desert ecosystems (Kalcounis-Ruppell & Millar, 2002; Brown, 1989b). Thus differential use of these resources, especially in space and time may facilitate coexistence (Bonesi & Macdonald, 2004; Yunger *et al.*, 2002; M'Closkey, 1976), especially in seasonally-varying environments (Bilenca & Kravetz, 1998).

Dietary partitioning relies on differences or modifications of the diet resulting in species utilising different aspects of the food resource (Kinahan & Pillay, 2008). Diet selection depends not only on the variety of resources available, but also the species of consumers present, their numbers and morphological and physiological characteristics. Species do not always consume all available resources, and/or these resources are not necessarily consumed in the proportions in which they are available (Brown & Lieberman, 1973). Consequently, a species may dominate the use of resources due to intrinsic factors such as the size and shape of resources and the species foraging efficiency (Kalcounis-Ruppell & Millar, 2002) or extrinsic factors depending on spatio-temporal availability (Ben-Natan *et al.*, 2004). These differences may promote coexistence. However, if there is a high amount of overlap, species may differ in other factors, such as choice of microhabitat, to reduce potential contest (Garb *et al.*, 2000).

Habitat selection may facilitate species coexistence (Rosenzweig, 1981) because of (Jorgensen, 2004) food distribution. Additionally, the presence of other consumer species may change the value of the habitat (Kerley *et al.*, 1990) by making certain resources unavailable. These changes may be in space (e.g. through distinct preferences; Kotler & Brown, 1988), time (e.g. through tradeoffs or variation in resource availability; Brown, 1989b; M'Closkey, 1976) or through interspecific interactions (Douglass, 1976).

The Namaqua rock mouse *Michaelamys namaquensis* and the rock elephant sengi *Elephantulus myurus* coexist on rocky outcrops throughout southern Africa, but specifically on the highveld grassland region, where they are often the only two small mammal species in the community (*pers. obs.*). However, nothing is known about

mechanisms promoting their coexistence. *Michaelamys namaquensis* is a small (~50 g), crepuscular murid rodent, and is reported to be a dietary generalist, feeding on stems, seeds and arthropods (Skinner & Chimimba, 2005; Fleming & Nicolson, 2004; De Graaff, 1981). Little detail regarding the diet and microhabitat preferences of *E. myurus* is known, although it is insectivorous and is slightly larger (~60g) than *M. namaquensis* (Skinner & Chimimba, 2005) and also appears to be crepuscular in the study area.

Although there are a few studies on coexistence in southern African small mammals, these have been done mainly on rodent species in arid and semi-arid areas. This study is unique since it examined coexistence between an omnivore and insectivore (representing two different mammalian orders) in a grassland habitat. I aimed to assess whether diet and microhabitat selection may facilitate the coexistence of these species as they are the only two species occurring in rocky outcrops in the study area. Because the concept of habitat selection is controversial due to differences in spatial scale, I adopted the definitions proposed by Jorgensen (2004) in which microhabitat selection is defined as those environmental factors affecting individual behavior; in contrast, macrohabitat selection is the spatial area in which individuals perform their biological functions. In other words, the microhabitat of an organism may be assessed by where the organism is frequently found within the greater area where it lives (macrohabitat which incorporates home ranges). I hypothesised that differences in food resource and microhabitat use would promote coexistence between the two species. I thus predicted that: 1) *Elephantulus myurus* would have more arthropod remains in its faeces compared *M. namaquensis* which would be less selective 2) Although both species were expected to associate with areas of high rock cover, *M. namaquensis* was expected to prefer grassy areas since it is known to eat grass seeds and *E. myurus* is thought to be a habitat specialist.

Methods

Trapping was carried out in a grassland reserve (eZemvelo) near Bronkhorstspruit (25^{o}42’ 26” S 28^{o} 01’ 02” E) in the highveld region of South Africa. The region receives summer rainfall of around 650 mm per year, and daily average temperatures fluctuate between 12.5 ^{o}C in winter to 26 ^{o}C in summer. Vegetation is varied, comprising grasslands (*Aristida* spp., *Eragrostis* spp. and *Hyparrhenia* spp.) on gentle slopes with short, sparse shrubs, and rocky outcrops scattered along ridges with trees (mainly *Burkea africana*, *Ochna pulchra* and *Protea caffra*), larger shrubs and some grasses. The reserve was used for various agricultural purposes 3-8 years before the study commenced.

Eight permanent grids (measuring 70 m x 70 m) at least 200m apart were established in rocky outcrops. PVC live-traps (29 x 6 x 7 cm) were placed 10 m apart with one trap/station (i.e. 49 traps/grid) for 4 consecutive nights approximately every 5 weeks from September 2002 to August 2004, except during February and March 2004 when unseasonable flooding prevented trapping. Seasons were classified according to rainfall: early rain from September to December, late rain from January to April and dry from May to August (Neal, 1991). Traps were covered (to buffer fluctuating environmental temperatures), baited with a mixture of oats, raisins, salt, oil, sunflower seeds and peanut butter and checked every morning and evening and rebaited when necessary.

The following procedures were carried out humanely according to ASM guidelines and approved by the University of Witwatersrand Animal Ethics Committee (clearance no.: AESC 2002/81/3). All trapped individuals were sexed, weighed and their reproductive status noted: males were classed as scrotal (testes descended) or non-scrotal (testes in the abdominal cavity), and females were classed as perforate or non-perforate, depending on whether or not the vagina was open. Reproductive condition was hard to assess in *E. myurus* males as testes are abdominal and thus reproductive condition was only noted where status was easily seen. Thereafter they were permanently marked using toe clipping and released at the point of capture. Additionally, the trap station where the animal was caught was recorded and for the first capture of individuals each session, all faecal material removed from the trap and stored in epindorf tubes for later assessment.

Faecal Contents. - Approximately 1.5 ml of faecal pellets (randomly selected) from each individual from each trapping session were soaked in 70% alcohol for approximately 24 hours at which stage the faeces began to disintegrate. The alcohol mixture was then transferred into small Petri dishes ($\pm$5 cm diameter) and the remaining pellets dissected. After the alcohol had evaporated, the sample was randomly scanned three times under a dissecting microscope (40x magnification; Kerley, 1992; Perrin & Swanepoel, 1987) to determine the relative proportion of stems, leaves, seeds, arthropods (and other faunal parts) and unidentifiable plant and animal remains (Swanepoel, 1980; Drozdz, 1967). The frequency of dietary items (i.e. how often the item occurred) in the faeces was also determined.

The data were arcsine transformed and analyzed using a General Linear Model (GLM) for multiple dependents. Tukey HSD post hoc tests were performed to identify specific differences. Fisher's Exact Test was used to test for differences in frequency of occurrence of food items between species and the sexes within each species. Seasonal

variation in the frequency of occurrence of faecal components was tested using χ^2 tests. Bonferroni sequential adjustments were done for Fisher's Exact and χ^2 tests. There were no significant differences in the unidentifiable remains between the species, nor in their amount or frequency of occurrence and hence this category was not considered further.

Dietary overlap between the species was calculated using the formulae

$$A_{jk} = \frac{\sum_i^n p_{ij}\ p_{ik}}{\sum_i^n p_{ij}^2} \quad \text{and} \quad A_{kj} = \frac{\sum_i^n p_{ij}\ p_{ik}}{\sum_i^n p_{ik}^2}$$

where p_{ij} and p_{ik} are the use of the *i*th resource by species *j* and *k* respectively (Pianka, 1973). A high value indicates a high degree of overlap which would increase the potential for competition.

Microhabitat Selection. - Each station on all grids was sampled seasonally for the proportion of grass material (alive: dead), litter (grass and leaf), rocks, shrubs and bare ground using a $1m^2$ quadrant centered at each trap station (Bilenca & Kravetz, 1998; Gonnet & Ojeda, 1998). The maximum, minimum and two other random measures of grass height were recorded. Vegetation density, plant greenness and the amount of cover (vegetation and rocks) available for small mammal species in each quadrant was categorized according to a scale of 0 to 5, representing 0% and 100% respectively, increasing in increments of 20%. Microhabitat associations for each species were examined by comparing the number of individuals trapped at each station with the above variables. Due to low trapping success, data were pooled across seasons, arcsine transformed and analyzed separately for each species. A General Discriminant Analysis was used to determine whether or not there was any association or relationship between trapping success and microhabitat variables at each station. Although traps were baited and this may have influenced microhabitat selection, this was assumed not to have influenced trap selection as traps were placed in a variety of microhabitats. A Correlation Matrix was used to determine the direction of any associations between trapping success and microhabitat variables.

Results

The faeces of a total of 220 *M. namaquensis* individuals and 53 *E. myurus* individuals were analysed, which apart from one *E. myurus* individual, were all trapped in the morning. Trapping success varied depending on the season and year.

Faecal Contents. - I assumed all faeces collected represented the natural diet of the individual due to the short time spent in traps (<1 h) and gut retention times (Woodall & Currie, 1989). A total of 401 faecal samples were analyzed. GLM results indicated that faecal content was significantly influenced by species ($F_{5, 377}$ =95.0; $p < 0.01$), season ($F_{20, 1251} = 3.6$; $p < 0.01$) and the species x season interaction ($F_{20, 1251} = 3.9$; $p < 0.01$), but there was no difference between the sexes ($F_{5, 377} = 0.6$; $p = 0.69$). *Michaelamys namaquensis* had a higher proportion of vegetative material (stems and leaves) and seeds in the faeces than *E. myurus*, while 60% of the faeces of *E. myurus* consisted of arthropods (Figure 2.1.).

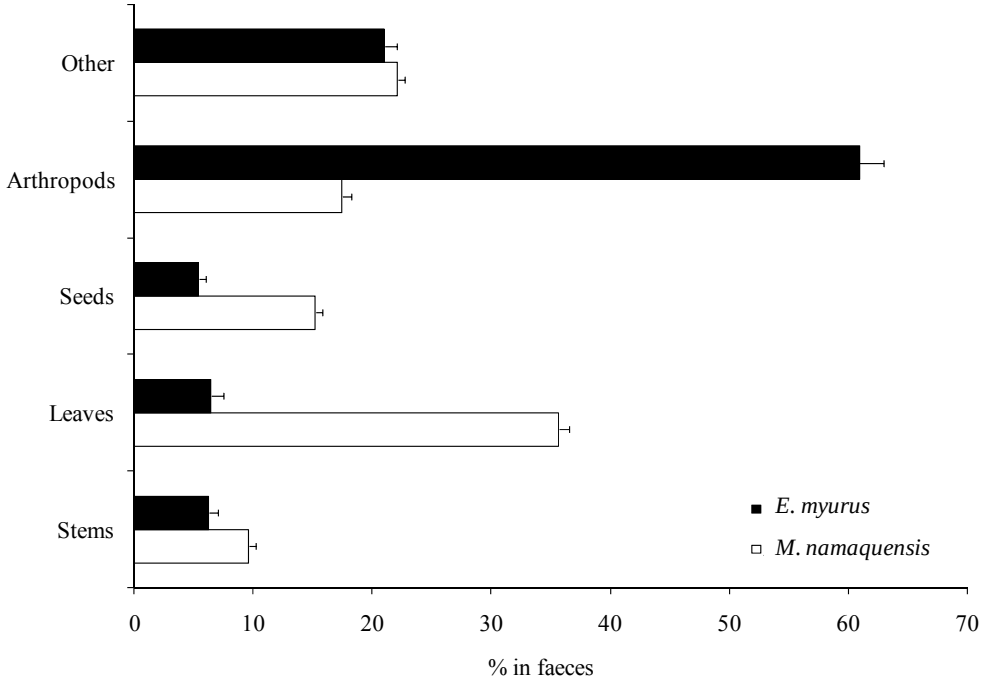


Figure 2.1. Mean (± SE) percentage of components in the faeces of *Michaelamys namaquensis* and *Elephantulus myurus*.

Overall, the faeces of *M. namaquensis* contained less leafy material in the late rain season, while there was no variation in the amount contained in *E. myurus* faeces, perhaps as leafy material, like seeds are only important in the diet of *E. myurus* when the amount of arthropods in the diet decreases (Figure 2.2.). The amount of seeds in the faeces of *M. namaquensis* varied annually, with a peak in the dry season of the second year (2003 – 2004), while the least amount occurred in the dry season of the first year (2002 – 2003).

The fewest arthropod remains in *E. myurus* faeces occurred during the late rain season, with a peak occurring in the dry season, especially in the second year. This contrasts with *M. namaquensis*, which showed a peak in arthropods in the late rain season

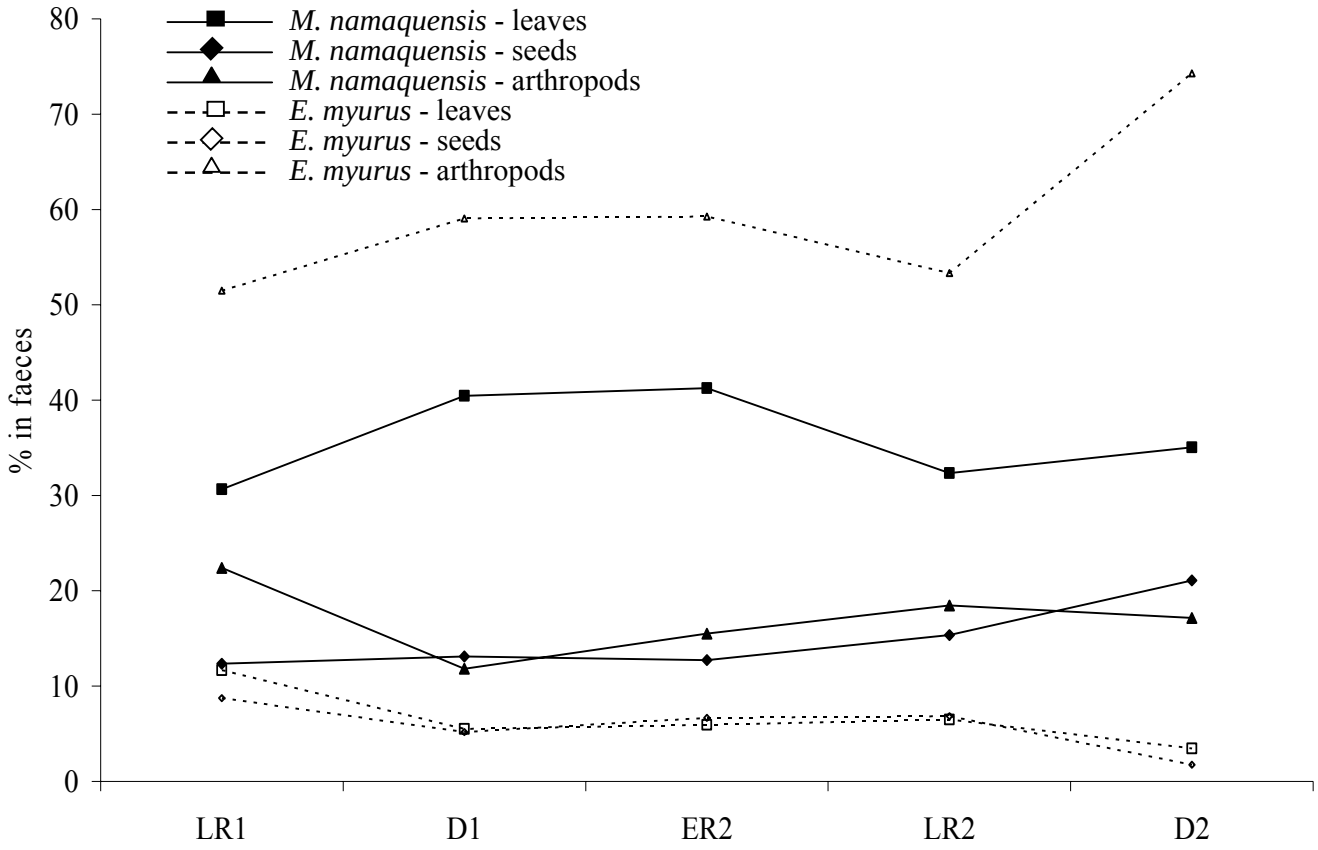


Figure 2.2. Seasonal variation in faecal contents for *Michaelamys namaquensis* and *Elephantulus myurus*. LR = Late Rain, D = Dry, ER = Early Rain, 1 = Year 1 (2002 – 2003), 2 = Year 2 (2003 – 2004).

and a decrease in the dry season. There was a higher frequency of seeds ($p = 0.001$; Fisher's exact test) and leaves ($p = 0.001$) in the faeces of *M. namaquensis* compared to *E. myurus*, but no significant difference in the frequency of arthropods or stems (both $p > 0.05$). There was no significant difference in the frequency of faecal components between the sexes for both species (*M. namaquensis*: stems $p = 0.48$, leaves $p = 0.06$, seeds $p = 0.22$ and arthropods $p = 0.76$; *E. myurus*: stems $p = 0.79$, leaves $p = 0.64$, seeds $p = 0.62$ and arthropods $p = 1.00$). Except for arthropods, the frequency of all other components varied seasonally for *M. namaquensis* (stems: $\chi^2_4 = 12.72$, $p = 0.013$; leaves $\chi^2_4 = 12.04$, $p = 0.017$; seeds $\chi^2_4 = 26.83$, $p < 0.001$; arthropods $\chi^2_4 = 6.75$, $p = 0.15$), but with no clear patterns or trends (e.g. the frequency of stems in the faeces was lowest in the dry season in year 1 and highest in the dry season in year 2). Neither stems nor arthropods varied seasonally for *E. myurus* (stems: $\chi^2_4 = 4.42$, $p = 0.353$; arthropods $\chi^2_4 = 8.41$, $p = 0.078$), but leaves and seeds both varied seasonally with no clear patterns or trends (leaves: $\chi^2_4 = 67.85$, $p < 0.001$; seeds: $\chi^2_4 = 17.49$, $p = 0.001$). Overall, the faecal contents of *E. myurus* overlapped with those of *M. namaquensis* by 44% with the highest degree of overlap in the late rain season (58%) and lowest in dry season (33%). *Michaelamys namaquensis*

overlapped more with *E. myurus* (86%), the highest level occurring in the late rainy season (99%) and the lowest in the dry season (71%).

Microhabitat Selection. - General Discriminant Analysis models and Correlation Matrices revealed that *M. namaquensis* was significantly associated with low proportions of dead grass material, litter and sparse vegetation density (Table 2.1.). In addition, *M. namaquensis* showed a negative correlation with the percentage live grass material and bare ground, and a positive correlation with areas of high rock cover and shrub cover.

Additionally, *M. namaquensis* showed no significant association or correlation with grass height, but did associate with cover, although with no correlation to the amount available. *Elephantulus myurus* significantly associated with sparse vegetation density. It was correlated with low amounts of grass (both alive and dead) and litter and positively correlated with the amount of rock. Its presence was associated with, but not correlated with, vegetation greenness and maximum grass height. Both small mammal species were associated with *Loudetia simplex* and *Enneopogon cenchroides***,** although this may have been because these were also the dominant grass species. Both *M. namaquensis* and *E. myurus* did not associate with *Aristida* spp. and *Pogonarthria squarrosa*.

The microhabitat associations between the species is therefore relatively similar, especially at low capture frequencies (i.e. although the overall effect is not strong (r = 0.35), a low frequency of *M. namaquensis* captures is positively correlated with a low capture frequency of *E. myurus*. For example, both species tended to avoid areas with large amounts of grassy and litter material (Table 2.1.). However, high capture rates of both species are associated with areas with high proportions of rock (Table 2.1.).

Discussion

Faecal Contents. - There are several explanations for seasonal variation in diet and although rain is not directly implicated, due to it's seasonality, rainfall may influence diet composition and quality by altering the abundance of various dietary items (Perrin & Swanepoel, 1987). However, this depends on the geographic region, the small mammal species present, and the seasonal and local availability of food (Rabiu & Rose, 1997). The percentage of stems in the faeces of both species and the percentage of leaves in faeces of *E. myurus* did not vary seasonally, probably as these items did not contribute significantly to the diet (see also Churchfield, 1987; De Graaff, 1981). The seasonal variation of leaves in the faeces of *M. namaquensis* could reflect the availability of fresh material as well as the availability of other dietary items in the environment as the amount of leaves peaked in

Table 2.1. General Discriminate Analysis and Correlation results for microhabitat preferences of *Michaelamys namaquensis* and *Elephantulus myurus*.

* Significant at 0.05.

Habitat variable		Df (effect, error)	*M. namaquensis*				*E. myurus*			
			Mean value at Capture Rate		GDA (F value)	Correlation (*r* value)	Mean value at Capture Rate		GDA (F value)	Correlation (*r* value)
			None	High			None	High		
% cover	Alive	(3, 138)	9.5	4.7	0.99	-0.31*	8.9	8.2	0.98	-0.34*
	Dead	(3, 138)	14.5	7.5	0.95*	-0.41*	13.5	7.4	0.97	-0.43*
	Litter	(3, 138)	13.3	6.9	0.94*	-0.29*	12.4	6.7	0.99	-0.30*
	Shrub	(3, 138)	3.4	0.3	0.97	0.16*	4.0	1.2	0.98	0.12
	Rock	(3, 138)	6.0	37.4	0.97	0.46*	9.7	17.2	0.99	0.43*
	Bare	(3, 138)	11.6	5.0	0.95	-0.22*	9.7	18.6	0.99	-0.05
Vegatation characterstics	Green	(3, 136)	2	2	0.97	-0.10	2	2	0.93*	-0.02
	Density	(3, 136)	3	4	0.86*	-0.29*	3	4	0.87*	-0.33*
	Cover	(3, 136)	2	2	0.91*	0.10	2	1	0.99	-0.16
Grass Height (mm)	Maximum	(3, 141)	690.8	861.3	0.96	0.00	720.1	633.1	0.94*	-0.15
	Minimum	(3, 141)	30.1	31.0	1.00	0.06	30.2	30.3	0.98	0.09
	Average	(3, 141)	100.9	108.4	0.97	0.13	109.7	118.8	0.99	0.01

the faeces collected towards the end of the dry season and beginning of the rain season when leafy material was green, with the least recorded from faeces collected in the late rain season, when leaves are not as nutritious (Owen-Smith, 2002). Arthropods in the faeces of *M. namaquensis* decreased in the dry season in both years which corresponded to an increase in the amount of leaves, and in the second year, the amount of seeds. The proportion of seeds increased in the second year, when there was a decrease in green material, possibly as a result of lower availability due to aseasonally late rains (data collected on reserve). Similarly, in Mozambique, *M. namaquensis* consumed more green plant material in the dry season when no insects were found in its diet (Gliwicz, 1987; Gliwicz, 1985).

Elephantulus myurus consumed mainly arthropods, with seasonal trends of arthropods in the faeces opposite to those of *M. namaquensis*, i.e. the proportion of arthropods in the faeces increased in the dry season and decreased in the late rain season when the proportion of seeds in the faeces increased. These patterns are similar for *E. myurus* in Zimbabwe, where although no seasonal trends were reported, the diet consisted of 70% insects with the remainder made up of plant material and seeds (Churchfield, 1987). Seasonal variation in the diet has also been reported in other African small mammals (Claunitzer *et al.*, 2003).

In terms of diet, coexistence between species is possible if each species prefers a particular food item or a group of food types and has increased foraging efficiency for these items (Garb *et al.*, 2000). This would result in dietary partitioning and/or differences in foraging efficiency, both of which would facilitate coexistence (Brown, 1989b). In the present study, the major component of dietary overlap between the species was arthropods which overlapped in terms of proportion and in frequency of occurrence, potentially increasing competition, especially as *E.myurus* especially is thought to be an ambush hunter. The scope of the present study however does not allow us to evaluate whether or not these small mammals are be consuming the same or different arthropod species. However, the intensity of any competition for arthropods may be seasonal (i.e. in the late rainy season when overlap is the highest) and dependent on the seasonal dietary requirements of *M. namaquensis* and *E. myurus*, as occurs for the omnivorous *R. pumilio* and herbivorous vlei rat *Otomys irroratus* (Curtis & Perrin, 1979) and for *Mastomys* spp. and *Lemniscomys rosalia* (Field, 1975).

Microhabitat Selection. - The presence of both small mammal species was associated with a low proportion of grass cover (alive and dead), plant litter and vegetation

density, and a high proportion of rock cover. Additionally, *M. namaquensis* showed a significant non-association with cover but did associate with a low amount of bare ground and a high proportion of shrubs. *Elephantulus myurus* did not associate with tall grass or vegetation greenness. Thus, although there is a relatively large amount of habitat overlap between the species, there are some differences in microhabitat selection, which might represent the degree of differentiation of the two species, with *M. namaquensis* associated with a wider range of habitat parameters and *E. myurus* having a much narrower range of associations. In the arid Kalahari, *M. namaquensis* prefers areas with cover rather than the edges of vegetation clumps or open areas (Kerley *et al.*, 1990), which might explain its association with a higher proportion of shrubs in the present study, but contrasts with the non-association with cover. This could be related to differences in habitat type since overall cover availability in the arid Kalahari is lower than in the grasslands. Not much literature is available regarding the microhabitat preferences of *E. myurus*. Additionally, the individuals of the different species may perceive the heterogeneity of the patches differently (Cameron & Spencer, 2008).

Differential habitat selection, both spatially and temporally, may facilitate coexistence (Yunger *et al.*, 2002; Kotler & Brown, 1988) through the different abilities (generalist vs. specialist) and behaviors (opportunist vs. selective) of the species present (Rosenzweig, 1981). In the present study, although no spatial differences in microhabitat selection are apparent, *M. namaquensis* has a wider tolerance range than *E. myurus* and might therefore be considered to be less specialized than *E. myurus*. Temporal separation is also unlikely as both species are active at dawn (*pers. obs.*) and were not seen on the grids at any other time. Continuous observation to test this assumption was not possible as both species are cryptic and vision is limited, even during the day due to the habitat (rocky with shrubs).

Habitat differences are often related to foraging efficiencies (Bonesi & Macdonald, 2004), resulting in the specialist dominating over the generalist. Although *M. namaquensis* is less specialized in terms of diet than *E. myurus*, they occur in higher densities than *E. myurus*, and, at least at the microhabitat level of spatial use, do not seem to be excluded from areas preferred by *E. myurus*. Thus the two species do not seem to use or select microhabitats differently based on their specialist/generalist tendencies.

Most studies on microhabitat use emphasize that several factors might be important for habitat selection (Fuller & Perrin, 2001) as species perceive the environment differently, and this may be one of the reasons why no clear associations were found. Other

factors might be the scale of measurement or the factors measured, although the latter is unlikely as 12 different microhabitat variables were measured, with which small mammals are known to associate. Alternatively, generalists and specialists may be able to coexist through behavioral avoidance under high population densities compared to low densities if the species show high amounts of overlap (Wolff, 1985), where competition for resources may reduce the value of the habitat for the species present (Kerley *et al.*, 1990).

Implications for Coexistence. - Among other factors such as time of activity and behavior, coexistence may be promoted by differences in dietary and microhabitat preferences (Kalcounis-Ruppell & Millar, 2002; Brown, 1989b), and usually involves the interplay between an aspect of environmental heterogeneity (e.g. availability of a resource) and how species utilize (e.g. time of use of resource; Kotler & Brown, 1988) and perceive (Stilmant *et al.*, 2008) that aspect. Despite a high amount of dietary and microhabitat overlap in a Chilean scrub small mammal community, coexistence between the kangaroo rat *Dipodomys agilis* and the cactus mouse *Peromyscus eremius*, and to a lesser extent the California mouse *P. californicus*, is possible through differences in the temporal (both daily and seasonal) use of resources (Meserve, 1981). However, elsewhere *P. californicus* coexists with the brush mouse *P. boylii* because of differences in dietary preferences, resulting in different habitat use (Kalcounis-Ruppell & Millar, 2002). Thus within a community, species may perceive different variables as being important which facilitates coexistence (Yunger *et al.*, 2002; Kotler & Brown, 1988). Additionally, when competition for resources increases, factors such as differences in body size and activity times may aid in facilitating coexistence (Abramsky *et al.*, 2001). In southern Africa, despite a high degree of dietary overlap between five small mammal species in the Kalahari, coexistence was facilitated by microhabitat partitioning between three similar sized species, and by different periods of activity (Kerley *et al.*, 1990), while in the Karoo a combination of differences in body size, activity times and cover preferences facilitated the coexistence of up to six small mammal species (Kerley, 1989).

In the present study, there is a high degree of dietary overlap, especially in the late rain season, when the percentage of arthropods in the faeces of *M. namaquensis* was highest yet it was lowest for *E. myurus*. This is surprising as the availability of arthropods probably peaks during this period. Microhabitat selection patterns are not as clear – although *M. namaquensis* seems to have a wider range of microhabitat preferences compared to *E. myurus*, there is still a high degree of overlap, especially at low capture frequencies, and both species associate with areas of high rock cover and low grass cover.

Factors such as differences in body size and activity time are unlikely to be important due to the similarity of these factors between the two species. Thus, if diet and microhabitat preferences facilitate the coexistence of *M. namaquensis* and *E. myurus*, they are not the only factors; differences in the way that the two species perceive the environment and factors such as behavior and differences in population dynamics may contribute to their coexistence, and require further testing.

Chapter 3

A comparison of life history characteristics and population dynamics between two coexisting small mammals, *Michaelamys namaquensis* and *Elephantulus myurus*

Abstract

Most studies of coexistence focus on spatio-temporal resource partitioning as a factor that reduces competition but few have examined the importance of life history traits. Differences in life histories and population dynamics may allow species to use resources differently spatio-temporally. The life history characteristics and population dynamics of two coexisting small mammals, the Namaqua rock mouse *Michaelamys namaquensis* and Rock sengi *Elephantulus myurus* were examined to determine if they promote coexistence between these two species. The density of *M. namaquensis* was always higher than that of *E. myurus*, but seasonal trends shown by both species were the same. This is surprising as specialist (*E. myurus*) densities are usually higher than those of coexisting generalists (*M. namaquensis*). Both species bred in the warm, wet months. Although both species were reproductively active at the same time, juvenile *E. myurus* appeared in the population before *M. namaquensis* juveniles. This difference may be a result of protein availability for *E. myurus* and photoperiod for *M. namaquensis*. Total recruitment and emigration were positively associated with population density for both species and indicate juveniles entering the population and subadults dispersing. The survival of both species was low and there was no sexual dimorphism. Differences in density and breeding season reduce competition and thus although probably not solely responsible, do promote coexistence.

Keywords: breeding season; competition; density; generalist; specialist; temporal differentiation

Introduction

Life history theories predict a trade-off between reproductive investment and survivorship (Brown & Zeng, 1989). There are several theories regarding life history strategies but few of these have universal applicability (Willan & Meester, 1989). One such theory is the *r*-*K* continuum which proposes habitat stability and variability as the main determinants of breeding strategy (Mills *et al.*, 1992; Perrin & Swanepoel, 1987). According to this theory, species that are *r*-selected tend to occur in unstable or highly

variable environments and thus maximise productivity by reducing body size, longevity and age at first reproduction while increasing litter size and thus fecundity (Willan & Meester, 1989). This contrasts with K-selected species which maximise efficiency of resource use and often competitive ability by increasing body size, longevity and size of young but reduce litter size and delay breeding since they occur in more stable, even if adverse, environments (Pianka, 1970). The bet-hedging theory is similar in that it considers number of offspring, their size and development in relation to the environment, but it also relates habitat stability to mortality. Thus, if adult mortality is variable, the predictions are the same as for the *r*- and *K*-theory. However, if juvenile survival is variable, the predictions are opposite to that of the *r*- and *K*- theory (Neal, 1986). Another theory classifies small mammals into three general types (French *et al.*, 1975): Type 1 have high reproductive rate, low survival and high density tolerance resulting in large density fluctuations, e.g. the Multimammate mouse *Mastomys natalensis* (Amarasekare, 2002). Type 2 have moderate reproductive rates, median survival and are moderately tolerant of density resulting in relatively stable populations that seldom reach high densities e.g. insectivores, such as the Southern short-tailed shrew *Blarina carolinensis* (Whittaker & Feldhamer, 2005) and Type 3 have low reproductive rates but high survival and low density, e.g. the Prairie vole *Microtus ochrogaster* (Ozgul *et al.*, 2004). A common theme in these hypotheses is that the organism's perception of the environment, rather than environmental stability itself may be important in determining the strategy employed (Neal, 1986).

Life history characteristics such as fecundity, longevity and dispersal, that allow species to minimise or avoid competition, promote coexistence (Dammhahn & Kappeler, 2008; Brown & Zeng, 1989), since these traits may be an adaptive response to the environment (Neal, 1986). Thus the question to ask is to what extent are life histories similar due to the environment but different due to interspecific competition and resource allocation?

Both abiotic and biotic factors have been proposed as regulators of breeding and density in small mammal communities (Perrin & Boyer, 2000). Most of the previous studies on African rodents have focussed on abiotic factors that may trigger peaks in small mammal abundance, such as the timing and quantity of rain (Keesing, 1998a; Perrin & Swanepoel, 1987). Thus seasonal reproductive changes are often associated with changes in the diet (Perrin & Boyer, 2000). This results in births often corresponding with favourable environmental conditions to maximise survival (Muteka *et al.*, 2006). However,

rainfall is not the only explanation for seasonality of breeding (Neal, 1981) and other factors, such as photoperiod and temperature may also play a role (Muteka *et al.*, 2006; Bronner, 1986), but it is difficult to separate out the influences of these abiotic factors (Neal, 1986). Differences in habitat could affect the demographic parameters of a species (Schradin & Pillay, 2005; French *et al.*, 1975), for example, homogenous environments are more likely to promote reproductive synchrony (Ims, 1990), which may additionally be affected by social and not solely ecological factors (e.g. seasons; Ims, 1990). Additionally, physiological, morphological and behavioural characteristics are likely to have an effect as different species in the same locality may breeding at different times (Neal, 1986). These temporal patterns may also be due to inter- and intra-specific interactions (Ims, 1990).

Mechanisms that reduce interspecific competition and improve overall fitness promote coexistence (Kinahan & Pillay, 2008). Most studies have focused on the spatio-temporal partitioning of resources (Harris *et al.*, 2006), such as food and patch use and cite the need for an axis of environmental heterogeneity and a trade-off between interacting species, resulting in each species having a place on that axis where it is the superior competitor (Perrin & Kotler, 2005; Abramsky *et al.*, 1990; Brown, 1989a; Kotler & Brown, 1988). However, Kryštufek *et al.* (2007) suggest that some assemblages may be structured by morphology (e.g. size) and behaviour, and Brown & Zeng (1989) emphasise the importance of population ecology in understanding coexistence. Perrin & Kotler (2005) proposed that as there were no differences in resource use and activity, differences in reproduction and the seasonal importance of various food resources may promote coexistence in a small mammal community in the Kalahari.

The competition theory assumes that at competitive equilibrium, densities are maintained (Ferreira & Van Aarde, 1999), and may thus act to structure communities (Manor & Saltz, 2008; Hughes *et al.*, 1994). Species may be able to coexist as they respond differently to environmental fluctuations (Stilmant *et al.*, 2008; Moro & Morris, 2000). Thus, communities may be composed of species that vary from having very narrow habitat requirements (specialists) to very broad habitat requirements (generalists; Manor & Saltz, 2008). Additionally, various factors, such as the presence of both intra-and inter-specific individuals (Manor & Saltz, 2008) may prevent populations from reaching their maximum, resulting in seasonal dynamics (Liu *et al.*, 2007), which may promote coexistence.

The Namaqua rock mouse *Michaelamys namaquensis* and the (eastern) Rock sengi *Elephantulus myurus* frequently coexist with each other on rocky outcrops throughout

southern Africa. *Michaelamys namaquensis* is a medium sized (44.1 - 49.5 g) social murid that lives in family groups of often 10 or more individuals and shows no sexual dimorphism (Skinner & Chimimba, 2005; De Graaff, 1981). It is widespread, but prefers rocky areas as it has physiological and behavioural adaptations suited to such areas (Fleming & Nicolson, 2004). Breeding occurs in the warm, wet months (September to May; Fleming & Nicolson, 2004) and litter size ranges from 1 - 5 (Skinner & Chimimba, 2005; De Graaff, 1981). They may have unstable population cycles associated with high mortality and high reproductive potential (Muteka *et al.*, 2006). The life span of *M. namaquensis* has been recorded at 2 years. *Michaelamys namaquensis* density that varies between 8.1 and 11.8 individuals/ha in the southern Cape (Fleming & Nicolson, 2004) and nest density 1.5 – 2 nests/ha in thornveld savanna (Meyer & Brandl, 2005). It has been suggested that they respond to changes in photoperiod with males becoming reproductively active sooner than females, but other factors such as rain, temperature and the presence of secondary plant compounds have also been acknowledged as important influences on reproduction (Muteka *et al.*, 2006).

Elephantulus myurus is slightly larger (60 g; Skinner & Chimimba, 2005). They are insectivorous and thought to be monogamous (Skinner & Chimimba, 2005; Neal, 1982b) and occur in low population densities, and may enter a state of torpor during winter (Mzilikazi & Lovegrove, 2004). There is a paucity of information regarding the life history characteristics of *E. myurus*, but they are thought to be summer breeders (Skinner & Chimimba, 2005), although other sengi species (e.g. Rufous sengi *Elephantulus rufescens* and Smiths Rock sengi *Elephantulus rupestris*) are known to breed throughout the year (Neal, 1982b). Sengis have 3 litters/ season with 1 – 2 precocial pups/litter (Neal, 1982b). The life span of *E. myurus* is 1 – 2years (Neal, 1982b).

The aim of this study was to describe the life history characteristics and population dynamics of both *M. namaquensis* and *E. myurus*. These results were then compared between the two species to assess whether and how similarities and/or differences aid in their coexistence.

Methods

Studies were conducted on a grassland reserve, eZemvelo Nature Reserve (25^{o} 42’ 26”S 29^{o} 01’ 02” E), in the highveld region of South Africa. The reserve is typified by gentle grassy slopes interspersed with rocky ridges vegetated by mainly *Burkea africana*,

Ochna pulchra and *Protea caffra* and receives around 650 mm of summer rainfall per annum with maximum temperatures varying between 12.5 ^{o}C (winter) to 26 ^{o}C (summer).

Intensive trapping surveys on five permanent grids, measuring 70 m x 70 m in rocky outcrops, were performed using mark-recapture techniques. Traps were placed 10 m apart, with 1 trap/station (i.e. 49 traps/grid). Trapping was conducted for four consecutive nights every month from September 2002 until August 2004. However, due to flooding, it was impossible to trap in February and March 2003. PVC live traps (29 x 6 x 7 cm) were baited with a mixture of oats, raisins, salt, oil, peanut butter and sunflower seeds and covered with vegetation to buffer against environmental extremes. Traps were checked and rebaited daily in the early morning and late evening.

All individuals caught were weighed (to the nearest g), measured (body and tail length to the nearest mm), sexed and the reproductive status noted. Males were classed as scrotal (testes descended) or non-scrotal (testes in abdominal cavity) while females were classed as either perforate, or non-perforate, depending on whether or not the vagina was open. Additionally, any signs of lactation or pregnancy were noted. Reproductive condition was hard to assess in *E. myurus* males as testes are abdominal and thus reproductive condition was only noted where status was easily seen. Individuals were released at the station of capture after being individually marked using toe clipping.

Population size was determined using the Jolly-Seber method (mathematical model; Southwood & Henderson, 2000) and Minimum Number Alive (MNA; direct enumeration also sometimes referred to as Minimum Number Known Alive or MNKA; Krebs, 1966; Wolff, 1985); two models were used as they have different assumptions and advantages under different conditions (reviewed in Sullivan & Sullivan, 2004). Small mammal density on each grid was calculated using the population size for that grid and the effective trapping area (i.e. 490 m^2). Breeding season was determined using the Shannon Diversity index by considering the distribution of different age classes across the season (Brown & Zeng, 1989) and also by using the reproductive and age structure, taking into consideration the time lag between peak breeding season and peak in young animals and the proportion of reproductively active individuals. Sex (M:F) and reproductive (Reproductive : Non reproductive) ratios were obtained from trapping data. As there is no standard method of measuring age class in the field (many studies use tooth structure which is only possible with dead specimens (Bronner, 1986; Delany, 1974) and although mass is not a good indicator of age due to climatic effects and resource availability (Mills *et al.*, 1992), it is convenient and easily measured in the field), the age class structure, in

terms of adults and juveniles was determined from a combination of mass and reproductive condition. The frequency of sexually mature (i.e. perforate or scrotal) and immature individuals was plotted against their mass, and a normal distribution fitted to the graph. Individuals with mass above the point where the normal distributions crossed on the plot was considered to be an adult, while those with mass below this point were considered to be juveniles, unless that individual was visibly reproductive active (Armstrong & Van Hensbergen, 1996; Figure 3.1.). Thus adult *M. namaquensis* weighed 38 g or more while adult *E. myurus* weighed 49 g or more.

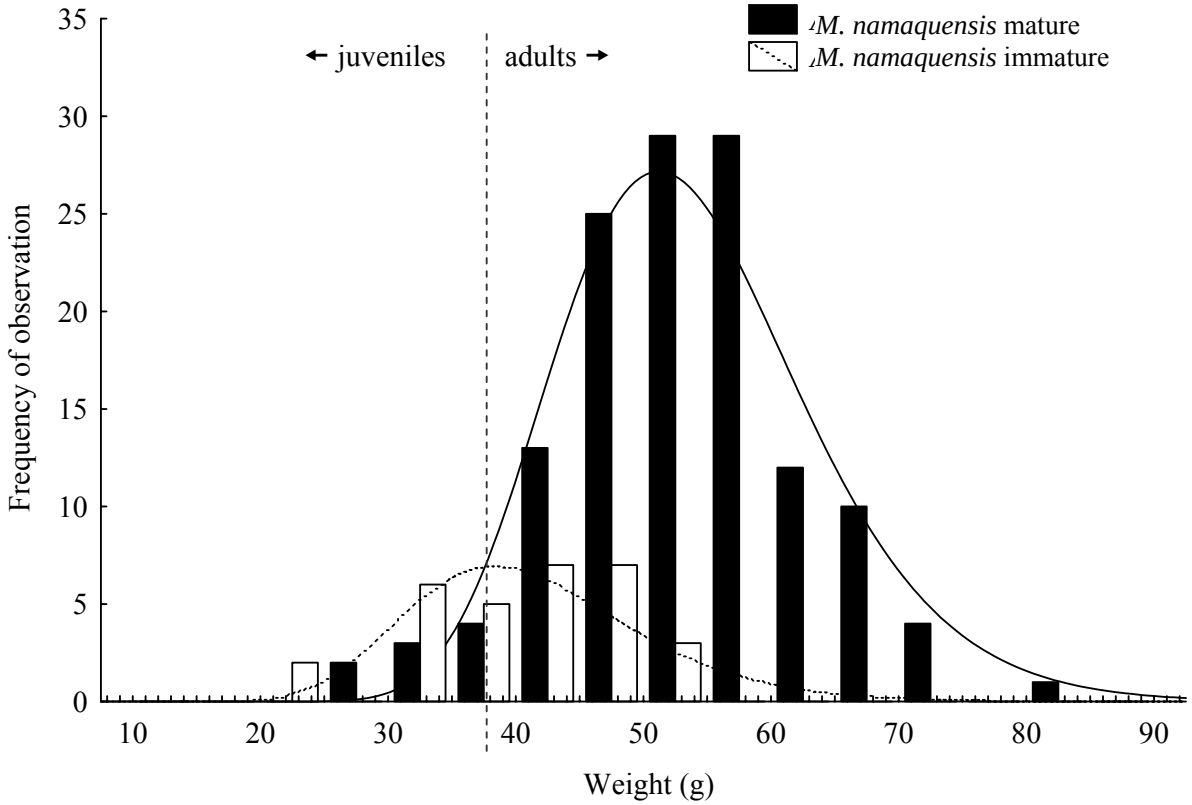


Figure 3.1. The adult-juvenile separation based on mass for *Michaelamys namaquensis*.

Population flux is the result of movements into and out of a population. Both total recruitment (total number of new individuals captured in a grid for each trapping session) and per capita recruitment (proportion of new individuals captured in each trapping session) were determined (Keesing, 1998a). Emigration, or loss from the population, and thus includes mortality and dispersal, was calculated as the proportion of individuals caught in one trapping session and not subsequently caught again. Survival, which is synonymous with persistence for the purposes of this study, was calculated using the first capture and the time taken until the individual was last caught. Sexual dimorphism,

measured as a differences in weight and body size between the sexes, for the species was also determined. All data were catergorised according to three seasons i.e. early rains (September – December), late rains (January – April) and dry season (May – August).

Data were analysed using STATISTICA 6 (Statsoft; www.statsoft.com). All data were tested for normality and the appropriate tests used subsequently. Seasonal differences in trapping success were analysed using an ANOVA. Seasonal variation in density was tested using a 6 x 3 repeated measures MANOVA, with month and season as the independent variables and density as the repeated measures variable. To test for differences in the age distribution, reproductive structure, recruitment and emigration across seasons, data was tested for skewness. Skewness indicates that the data are clustered and thus that the occurrence of these variables (different ages etc.) is not random i.e. occurs in distinct seasons. Differences in the Shannon H values as indicators of seasonal reproduction were tested using a Kruskal-Wallis test. Again, significant differences would indicate that there are distinct reproductive seasons. To test for parity in the sex ratio, χ^2 tests with Bonferonni adjustments for seasons were used. Differences in survival between the species were tested using a Mann Whitney-U test and correlations between season of first capture and survival. Correlations were also used to compare recruitment and emigration values and density. Sexual dimorphism was tested using a General Linear Model (GLM) and Tukey HSD post-hoc tests. All tests used $\alpha = 0.05$.

Results

There was no difference in trapping success across the seasons ($F_{5;\,2.24} = 0.82$, $p = 0.564$; average 5.27% success, range 2.32 – 10.20% success). *Michaelamys namaquensis* (3.46% success, range 2.04 – 4.2% success) was trapped more frequently than *E. myurus* (1.81% success, range 1.3% - 2.03% success).

Wilcoxon matched pairs test revealed that the Jolly-Seber method consistently over-estimated population density in comparison to the MNA method (*M. namaquensis* $T_{37} = 21$, $p = 0.00$; *E. myurus* $T_{37} = 57$, $p = 0.00$; Table 3.1.). There was however a good correlation between the methods (*M. namaquensis*: $r = 0.49$, $p = 0.002$; *E. myurus*: $r = 0.32$, $p = 0.05$). Regardless of method, *M. namaquensis* density was higher than *E. myurus* density (MNA $T_{40} = 23.50$, $p = 0.00$; Jolly-Seber $T_{37} = 63$, $p = 0.00$). However, the trends shown by both species were the same with season having a significant effect on density ($F_{5,\,326} = 9.31$, $p = 0.002$). Additionally, there was a positive correlation between the densities of the species using the MNA method ($r = 0.36$, $p = 0.027$). Density was lowest in

Table 3.1. The densities (mean ± SE) of *M. namaquensis* and *E. myurus* using the Jolly-Seber and MNA methods over the different seasons (ER = early rain, LR = late rain, D = Dry, 1 = Year 1, 2 = Year 2)

	M. namaquensis (individuals/ha)		*E. myurus* (individuals/ha)	
	MNA	Jolly-Seber	MNA	Jolly-Seber
ER1	12.5 ± 0.99	34.2 ± 9.24	8.6 ± 1.12	15.5 ± 3.50
LR1	22.7 ± 1.68	51.5 ± 14.72	9.5 ± 1.18	11.2 ± 0.96
D1	20.2 ± 1.88	31.9 ± 5.68	9.5 ± 0.90	17.7 ± 4.91
ER2	12.2 ± 1.39	14.5 ± 1.61	7.1 ± 0.70	13.4 ± 2.71
LR2	7.1 ± 3.06	12.2 ± 4.08	6.1 ± 0.05	8.7 ± 0.51
D2	11.8 ± 2.18	24.9 ± 4.79	6.1 ± 1.44	12.2 ± 0.05

the late rainy season of the second year but highest in the late rain in the first year of trapping. This inconsistency may be due to the very late rains in the second year, resulting in a decrease of individuals recruited into the population, either through birth or immigration. As a general rule, the population density increased from the beginning of the rainy season, reaching a peak toward the end of the rainy season and having the lowest density in the dry season. When viewed as population growth rates between seasons, although there was only a significant difference using MNA for *M. namaquensis* which had a significantly higher growth rate in the late rain season of the first year in comparison to the rainy seasons of the second year ($F_{16, 13} = 2.32$, $p = 0.067$), all other variables showed a similar trend. Breeding season was established using the reproductive and age structure of the species. Only the distribution of *M. namaquensis* adults was normal (Table 3.2.). Although the data for *E. myurus* adults was not normally distributed, this was not due to skewness. However, the non-normality of the data for *M. namaquensis* and *E. myurus* juveniles was due to a significant left skewed distribution. This left distribution of values was due to *M. namaquensis* juveniles only being present from November to June with a peak in March while E. myurus juveniles were only present from September to February with a peak in November (Figure 3.2.).

Reproductive condition in *E. myurus* was difficult to determine and thus data was only used for individuals who were clearly mature or immature. Reproductive condition was not normally distributed for either species (Table 3.2.) which was not due to a skewed distribution for reproductively active (i.e. scrotal or perforate) individuals. However, for individuals that were not reproductively active, this was due to a skewed distribution

Table 3.2. Results from normality and skewness tests to determine breeding seasonality for *Michaleamys namaquensis* and *Elephantulus myurus*. * indicates significance at α = 0.05

	M. namaquensis		*E. myurus*	
	Normality, W	Skewness (SE)	Normality, W	Skewness (SE)
Adults	0.97	0.29 (0.37)	0.87*	0.33 (0.37)
Juveniles	0.56*	1.85 (0.37)*	0.38*	3.42 (0.37)*
Perforate	0.89*	0.56 (0.37)	0.88*	0.68 (0.37)
Scrotal	0.91*	0.62 (0.37)	0.70*	0.11 (0.37)
Non-perforate	0.84*	0.90 (0.37)*	0.69*	1.46 (0.37)*
Non-scrotal	0.75*	1.79 (0.37)*	0.74*	1.19 (0.37)*

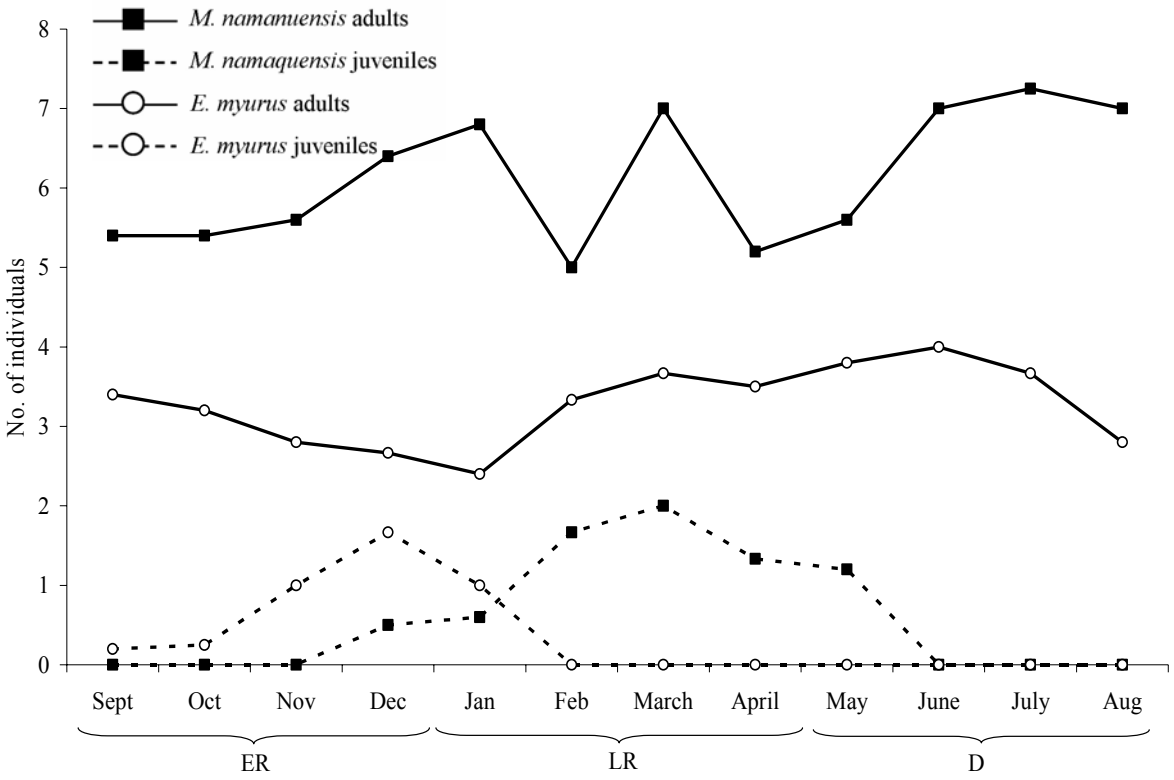


Figure 3.2. The age structure of *Michaelamys namaquensis* (solid square markers) and *Elephantulus myurus* (open circle markers). Adults are indicated by solid lines, juveniles are indicated by dashed lines. ER = early rain, LR = late rain and D = dry.

(Table 3.2.). Both species had very few, if any, reproductively active individuals during the dry season with most individuals reproductively active in the rainy season (Figure 3.3.). Non-reproductively active individuals showed opposite trends with a peak in the dry season and fewer individuals present in the rainy season (Figure 3.3.). These data are

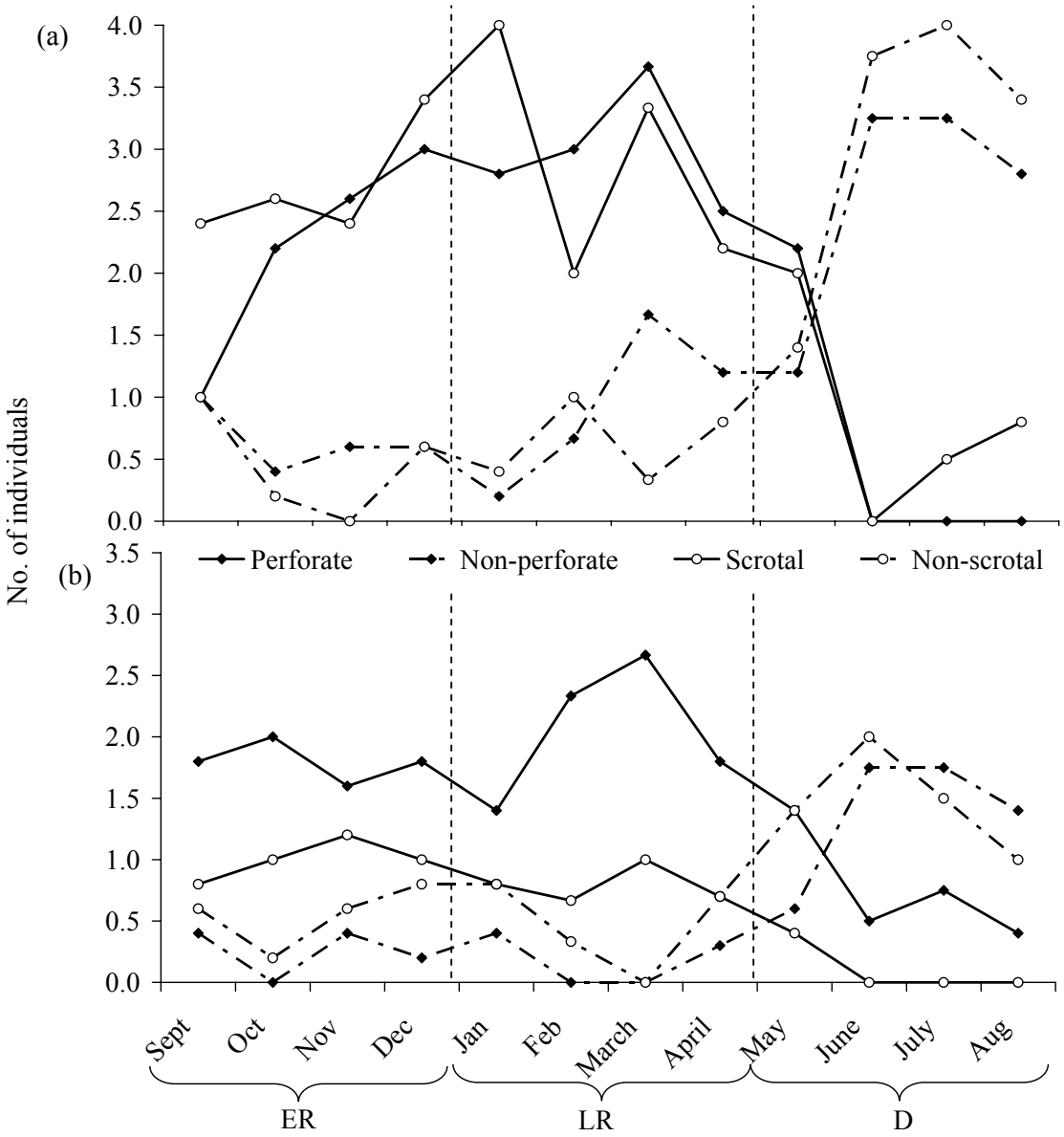


Figure 3.3. The reproductive condition of (a) *Michaelamys namaquensis* and (b) *E. myurus*. Reproductively active individuals are indicated by solid lines, reproductively inactive individuals by dashed lines, females by solid diamond markers and males by open circle markers. ER = Early Rain, LR = Late Rain, D = Dry.

reinforced by the Shannon Diversity data where both species had significantly different H-values for reproductive individuals in the different seasons (*M. namaquensis*: $H_{5,16} = 11.60$, $p = 0.041$; *E. myurus*: $H_{5,16} = 13.31$, $p = 0.021$). Thus it is clear that both species breed in the rainy season and stop breeding in the dry season. *Elephantulus myurus* starts breeding earlier than *M. namaquensis* as their juveniles start appearing in the population sooner than *M. namaquensis* juveniles.

Apart from the per capita recruitment of *M. namaquensis*, all other recruitment and emigration values were significantly not normal. This can be explained by skewed distribution for total recruitment and emigration for both species and per capita recruitment for *E. myurus*, but not for per capita emigration for either species (Table 3.3.). Total recruitment and total emigration were positively correlated with population density for *M. namaquensis* (recruitment: r = 0.54, p = 0.005; emigration: r = 0.33, p = 0.046; Figure 3.4.) but not for *E. myurus* (recruitment: r = 28, p = 0.090; emigration: r = 0.27, p = 0.110 Figure 3.4.).

Table 3.3. Normality and skewness values for recruitment and emigration for *Michaelamys namaquensis* and *Elephantulus myurus*. * indicates significance at $\alpha = 0.05$.

	M. namaquensis		*E. myurus*	
	Normality, W	Skewness (SE)	Normality, W	Skewness (SE)
Recruitment	0.91*	0.75 (0.36)*	0.74*	1.56 (0.36)*
Per capita recruitment	0.95	0.17 (0.36)	0.81*	0.95 (0.36)*
Emigration	0.91*	0.72 (0.36)*	0.80*	0.93 (0.36)*
Per capita emigration	0.94*	0.24 (0.36)	0.85*	0.30 (0.36)

There was no difference in survival between the sexes of each species (*M. namaquensis*: $U_{65, 74} = 2391.5$, p = 0.947; *E. myurus*: $U_{20, 17} = 158.0$, p = 0.674) or between the species ($U_{139, 37} = 2537.5$, p = 0.902). For *M. namaquensis*, the average survival was 2.6 months but the median value was only 1 month, with an interquartile range of 1 – 3 months and range of 1- 22 months. *Elephantulus myurus* showed a similar trend with an average survival of 3.1 months but median survival of 1 month with an interquartile range of 1 – 2 months and a range of 1 – 22 months. There was no correlation between season of first capture and survivoral either (*M. namaquensis*: r = -0.08, p = 343; *E. myurus*: r = -0.17, p = 0.316).

The sex ratio did not differ significantly from parity for either species, regardless of season (Table 3.4.). Additionally, the sexes of both species were of a similar size and mass (*M. namaquensis*: $F_{3, 188} = 0.74$, p = 0.529; *E. myurus*: $F_{3, 57} = 1.36$, p = 0.264) but season greatly influenced the mass of individuals (*M. namaquensis*: $F_{15, 159} = 2.39$, p = 0.002; *E. myurus*: $F_{12, 151} = 2.61$, p = 0.003; Table 3.5.) with *M. namaquensis* individuals significantly lighter in the early rainy season compared to the dry season and *E. myurus*

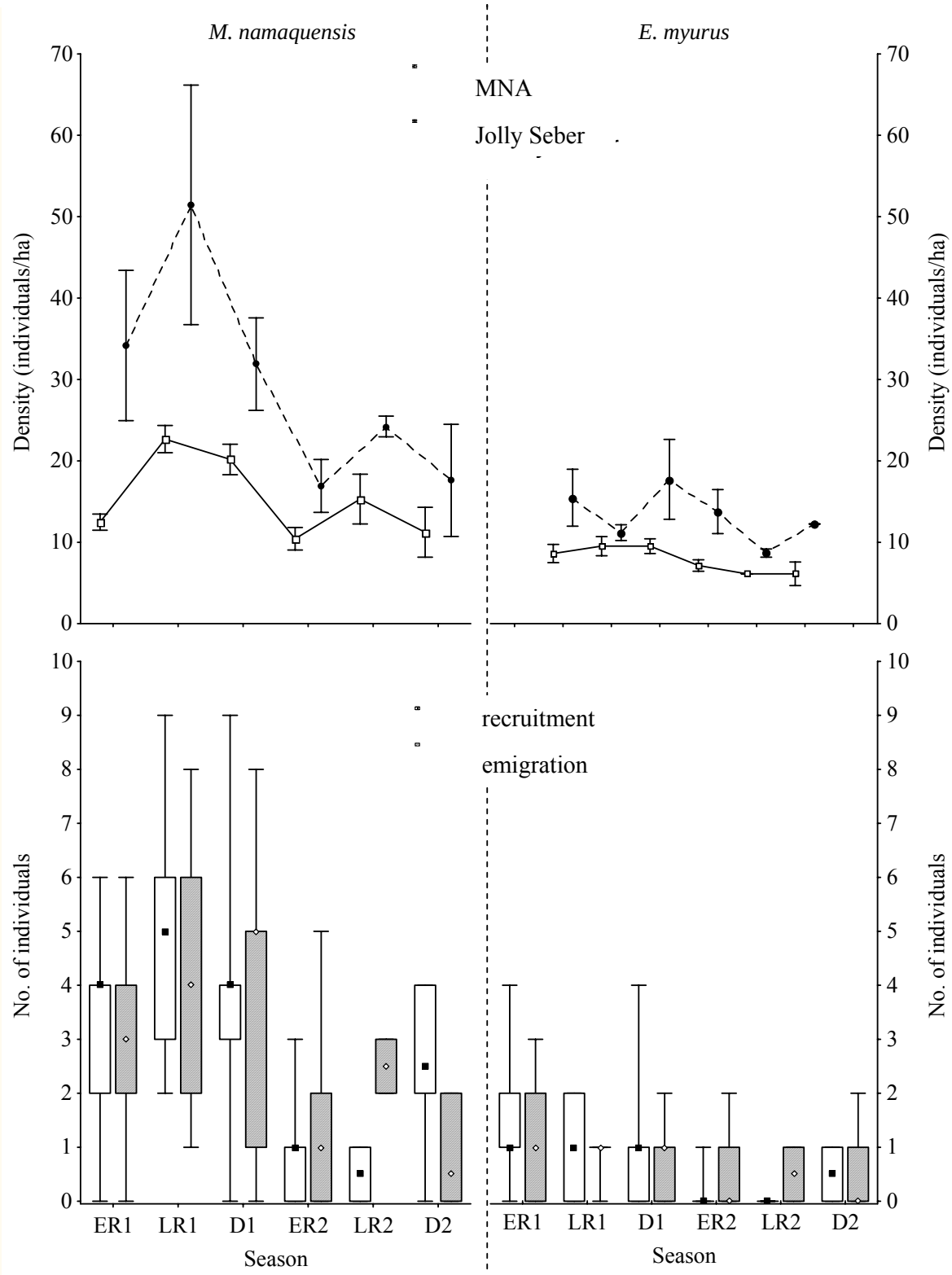


Figure 3.4. Changes in population density, using both Jolly-Seber and MNA methods, in the seasons (top) as compared to recruitment and emigration levels (bottom) for *Michaelamys namaquensis* (left) and *Elephantulus myurus* (right).

Table 3.4. Chi squared results for parity between the sexes between the seasons for *Michaelamys namaquensis* and *Elephantulus myurus*. (ER = early rain, LR = late rain, D = Dry, 1 = Year 1, 2 = Year 2)

	M. namaquensis	E. *myurus*
ER1	$\chi 28 = 3.38$, p = 0.091	$\chi 28 = 14.69$, p = 0.935
LR1	$\chi^2_8 = 7.45$, p = 0.511	$\chi^2_8 = 9.39$, p = 0.689
D1	$\chi^2_8 = 7.08$, p = 0.472	$\chi^2_8 = 9.09$, p = 0.665
ER2	$\chi^2_5 = 2.49$, p = 0.221	$\chi^2_5 = 2.33$, p = 0.199
LR2	$\chi^2_1 = 1.00$, p = 0.683	$\chi^2_1 = 0.33$, p = 0.436
D2	$\chi^2_4 = 0.79$, p = 0.060	$\chi^2_4 = 2.00$, p = 0.264

Table 3.5. Sexual dimorphism in terms of body length, body and tail length and mass for *Michaelamys namaquensis* and *Elephantulus myurus*. Values given as mean (± SE).

	M. namaquensis		*E. myurus*	
	F	M	F	M
Mass (g)	51.6 ± 1.01 (27 – 81)	52.7 ± 0.76 (38 – 73)	63.98 ± 1.41 (50 – 86)	68.0 ± 1.59 (54 – 82)
Body length (mm)	102.1 ± 0.95 (80 – 125)	105.4 ± 0.80 (84 – 126)	121.9 ± 1.31 (96 – 138)	120.1 ± 1.57 (98 – 131)
Body & Tail length (mm)	245.8 ± 2.52 (202 – 290)	243.6 ± 2.27 (192 – 282)	245.8 ± 1.71 (208 – 267)	243.2 ± 2.22 (220 – 262)

individuals significantly heavier in the early rain season in comparison to the late rain and dry seasons.

Discussion

As natural environments are dynamic, the processes promoting similarities and differences in population variables may change in space and time (Chesson, 2003; Brown & Zeng, 1989). This is evident when examining the patterns of density of *M. namaquensis* and *E. myurus*. *Michaelamys namaquensis* density varied between 7.1 and 51.5 individuals/ha, depending on the method used and season. These values are similar to those reported in the literature (5 – 62 individuals/ha; Rickart, 1981). The density of sengis is generally low (Yarnell & Scott, 2006; Stuart *et al.*, 2003), which is supported by the current data for *E. myurus*. The lower densities that were recorded in the second year for both species are probably a result of the late rains reducing the opportunity for breeding. A

similar result was found by Rickart (1981) for a community of small mammals in the Eastern Cape. For both species, the MNA value is a more accurate descriptor of density than the Jolly Seber method due to the assumptions made by the Jolly Seber method (Hammond & Anthony, 2006; Bronner, 1986) and the low sample sizes (Manor & Saltz, 2008) of this study. Surprisingly, regardless of method, the density of the generalist, *M. namaquensis* was always higher than that of the specialist, *E. myurus*. This contrasts with most other studies where the specialist density is usually higher than the generalist (Manor & Saltz, 2008; Kalcounis-Ruppell & Millar, 2002; Shargal *et al.* 2000). Under optimal conditions, specialists tend to outperform generalists but this is reversed when conditions become unpredictable, since the costs of being a generalist are small in comparison to the benefits gained by the plasticity in behavioural and/or physiological mechanisms (Manor & Saltz, 2008). Additionally, densities of insectivores tend to be lower and more stable than those of murids (French *et al.*, 1975), which are frequently reported to have seasonal variances in abundance, reflecting seasonal breeding (Mahlaba & Perrin, 2003; Willan & Meester, 1989; Bronner, 1986; Brooks, 1982; Coetzee, 1975). This can be further explained by energy flow through trophic levels since *M. namaquensis* is a primary consumer while *E. myurus* is a secondary consumer. As less energy is passed on to the second trophic level, a lower density of *E. myurus* may be expected (Townsend *et al.*, 2000).

Three main cues, or a combination thereof, are recognised to influence seasonal reproduction, namely abiotic factors (such as food availability and photoperiod), internal factors (e.g. endogenous rhythms) and social cues between individuals (Ims, 1990; Neal, 1986). Abiotic factors, such as rain are not likely to affect breeding directly as there is usually a lag time of two to three months between rainfall and evidence of breeding (Bronner, 1986), but rather affects breeding indirectly through food availability (Neal, 1982a). Thus, rainfall may still contribute to the timing of the reproductive seasonality and could explain inter-year variation in population numbers and demography (Monadjem & Perrin, 2003; Willan & Meester, 1989). This means that reproduction should be concentrated during times when conditions are favourable (Muteka *et al.*, 2006; Brown & Zeng, 1989). Although both species bred in the wet summer months as predicted by the literature (Muteka *et al.*, 2006; Skinner & Chimimba, 2005; Fleming & Nicolson, 2004), and regardless of gestation period (sengi species are reported to have a gestation of around 61 days (Neal, 1982b), while *Michaelamys* species have a gestation of 29 days; Linzey & Chimimba, 2008), there was temporal separation of breeding: juvenile *E. myurus* started

appearing in the population in September reaching a peak in December with no juveniles found from February onwards while *M. namaquensis* juveniles only started appearing in November with a peak in March. For *E. myurus*, seasonal breeding is most likely due to protein availability as conception would have occurred in the dry season which corresponds with a peak in insect consumption (unpublished data, see Chapter 2). The proteins provided by insects are an important source of dietary protein for small mammals (Ostfeld & Manson, 1996; Field, 1975). This reason is unlikely for *M. namaquensis* as insect consumption in this species peaked in the late rainy season. Additionally, previous studies at eZemvelo have shown that the clear seasonal reproduction shown by *M. namaquensis* is probably regulated by photoperiod, although other factors such as food availability and quality may have an effect (Muteka *et al.*, 2006). The fact that neither species bred during winter is typical of small mammals in seasonal environments as winter places high energetic demands on small mammals (Muteka *et al.*, 2006; Gockel & Ruf, 2001). Males become sexually active earlier in the reproductive season and thus breeding season tends to be determined by females in southern Africa (Perrin & Boyer, 2000; Bronner, 1986). This prediction is true for *M. namaquensis* with no perforate females being recorded in the dry winter season, while scrotal males were trapped every month except for June. *Elephantulus myurus* females appeared to mature earlier than the males, but this may be an artefact of the data as reproductive condition in *E. myurus* is hard to assess.

Population size fluctuations are due to differences in recruitment (movements into the population through birth and immigration) and emigration (movements out of the population through dispersal and death; Bronner, 1986). For both species, total recruitment and emigration had skewed distributions implying that there are seasonal differences in these parameters. As population size is accounted for in per capita recruitment and per capita emigration, differences in these parameters may be masked. The seasonal differences in total recruitment and emigration can be explained by individuals entering into the population through birth at the beginning of the breeding season and leaving the population towards the end of the breeding season either through dispersal or death during winter. Additionally, density and total recruitment and emigration are positively correlated in *M. namaquensis* with a peak in recruitment in late rainy season of the first year and the dry season of the second year. This corresponds with peaks in juvenile appearance, and thus births are likely to be the main contributor to recruitment. Likewise, both Perrin & Swanepoel (1987) and Bronner (1986) related pulses in the recruitment of *M. natalensis* and the Bushveld gerbil, *Tatera leucogaster* respectively to seasonal breeding. A peak in

dispersal was found mainly in the dry season of the first year. This could be due to individuals dispersing from the natal area at maturity or due to low over-winter survival as found by Bronner (1986) for *M. natalensis*. No relationship between density and recruitment or emigration was found for *E. myurus* perhaps due to their low trapability as found by Rickart (1981) for the Cape sengi, *Elephantulus edwardii*. Similarly, patterns of recruitment and reproduction in the Dune hairy-footed gerbil *Gerbillurus paeba* were not associated with any peaks in population density (Perrin & Boyer, 2000).

Life expectancy of murids is generally much lower than that for dietary insectivores (1.8 months vs. 7.4 months; French *et al.*, 1975). In the present study, both species had low survival rates, with that of *E. myurus* only slightly higher than that of *M. namaquensis*. This may be explained by the high number of individuals caught during a single capture session and never again. However, maximum survival was high with both species having individuals that survived for 22 months. Survival may also be influenced by factors that were not directly measured, such as time of birth, mass and population density (Whittaker & Feldhamer, 2005).

Many small mammal species in southern Africa have a sex ratio that approximates 1:1 (see Yarnell & Scott (2006), Monadjem (1999), Ostfeld & Manson (1996), Perrin & Swanepoel (1987) and Bronner (1986) for examples). This was confirmed in the present study. Additionally, previous studies (Fleming & Nicolson, 2004) have reported that *M. namaquensis* does not show any sexual dimorphism in terms of mass or length but, as in this study, mass was lower just prior to the breeding season, possibly due to the thermoregulatory demands of winter (Gockel & Ruf, 2001). Results for sengis are varied, with Stuart *et al.* (2003) reporting sexual dimorphism for *E. edwardii* while Yarnell & Scott (2006) report no sexual dimorphism for the Short snouted sengi *Elephantulus brachyrhynchus*. In order to breed successfully, *E. myurus* may need to increase its mass thereby increasing their body condition, as seen in the early rainy season. Seasonal variations in mass have been found for *M. natalensis* (Bronner, 1986), *T. leucogaster* (Neal, 1991), the Yellow necked mouse *Apodemus flavicollis* and the Bank vole, *Clethrionomys glareolus* (Gockel & Ruf, 2001), with explanations of increasing or decreasing mass due to stress of breeding and the thermoregulatory costs of winter.

The relative importance of demographic parameters depends on the success strategy of the species (French *et al.*, 1975). In terms of life history strategies, *M. namaquensis* tends towards *r*-selection with Type 1-like parameters (see introduction). They tend to have large litters, frequently with large fluctuations in density, recruitment

and emigration, both between years and between seasons (7.1 individuals/ha – 22.7 individuals/ha) with a relatively large over-winter mortality. To compensate for this, females especially appear to sacrifice growth for sexual maturity, breeding in their season of birth, a common trait in murids (French *et al.*, 1975). As in Muteka *et al.* (2006), this is observed as a decrease in the average mass of reproductively active females over the breeding season. Although the reproduction in the present study is apparently concentrated in the late rainy season, *M. namaquensis* appears to have some plasticity in the timing of reproduction as previous studies have recorded juveniles in the population from as early as October (Fleming & Nicolson, 2004) to as late as May (Muteka *et al.*, 2006), which is similar to *T. leucogaster* (Neal, 1991). *Elephantulus myurus* on the other hand tends to be more *K*-selected with characteristics more typical of Type 2 selection than Type 3, probably due to the unpredictability of the environment. *Elephantulus myurus* tends to have relatively stable population densities with little seasonal variation (6.1 individuals/ha – 9.5 individuals/ha). Total recruitment and emigration are significantly skewed and not related to population density but appear to correspond to reproductive season. With little fluctuations in the population density and based on the literature (Yarnell & Scott, 2006; Skinner & Chimimba, 2005; Stuart *et al.*, 2003), it appears that *E. myurus* has a few small litters a year with females emphasising growth to increase over-winter survival to breed in the next season. This is further emphasised by the restricted breeding season reported here in comparison to that reported for *E. myurus* and other sengis elsewhere (Yarnell & Scott, 2006; Skinner & Chimimba, 2005; Stuart *et al.*, 2003).

In the present study, the timing of fluctuations in the densities of the species was similar. Although competitive coexistence may be promoted by species densities changing out of phase (Brown, 1989a), it stands to reason that any changes of the species that reduce spatial or temporal overlap will promote coexistence. Brown & Zeng (1989) propose that similar fluctuations in population characteristics of species using similar resources may be due to convergent similarities rather than phylogeny because, as in the present study, the species differed in their relatedness. Alternatively, species have evolved traits elsewhere but interspecific interactions that allow for differences in factors such as abundance and resource use may promote coexistence (Brown & Zeng, 1989). In this way, subdominant species (normally the generalists) may have higher densities than the dominant species (normally the specialists) if competition is an important regulator of population size (Harris *et al.*, 2006). For this to happen, the relative strength of intra-specific competition must be greater than interspecific competition (Dammhahn & Kappeler, 2008).

The fact that both species have a more restricted breeding season to that reported elsewhere may be an important factor promoting coexistence as it potentially reduces interspecific competition (Kinahan & Pillay, 2008) without negatively impacting on the fitness of either species. Separation in breeding season was found to promote coexistence in the Common spiny mouse *Acomys cahirinus* and the Golden spiny mouse, *Acomys russatus* (Shargal *et al.*, 2000). In this system, although the specialist, *A. russatus* was dominant in terms of numbers, it was more restricted in its breeding season and seems to be displaced more often by the smaller *A. cahirinus* (Shargal *et al.*, 2000). Similarly, *E. myurus*, the larger, more specialised of the two species studied, has a more restricted breeding season than *M. namaquensis*. In the same way, life history trade-offs rather than niche separation are proposed to best explain the pattern of co-occcurence between the Grey mouse lemur *Microcebus murinus* and Madame Berthe's mouse lemur *Microcebus berthae* (Dammhahn & Kappeler, 2008). It is difficult to tell whether the difference in breeding seasonality of *E. myurus* and *M. namaquensis* is due to the way the species experience their environment (Moro & Morris, 2000) or due to competitive interactions over resources necessary for reproduction. However, in combination with other factors, differences in the life history characteristics, such as timing of reproduction and density fluctuations, may reduce overlap and hence competition between *M. namaquensis* and *E. myurus*.

Chapter 4

Spatial organisation of coexisting *Michaelamys namaquensis* and *Elephantulus myurus*

Abstract

The home range characteristics of a species reflect its spatial and social organisation. Using live trapping, we investigated the home range characteristics of two coexisting small mammals, the Namaqua rock mouse *Michaelamys namaquensis* and the Rock sengi *Elephantulus myurus*, to examine the level of intra- and inter-specific home range overlap. There were no differences in the average distance travelled between captures or home range size between species or the sexes (both within and between species). The percentage home range overlap with individuals of the same and different sex did not differ for *A. namaquenis* females. However, the home ranges of *M. namaquensis* males and both sexes if *E. myurus* overlapped significantly more members of the opposite sex (in size and number) than members of the same sex. This confirms that *M. namaquensis* is polygynous while *E. myurus* is monogamous. Interspecific overlap in terms of percentage overlap did not differ for *M. namaquenis* females or either sex of *E. myurus* but *M. namaquensis* males overlapped more with *E. myurus* individuals than other *M. namaquensis* individuals. Neither sex nor species had an effect on the proportion of interspecific individuals overlapped. The home ranges of both species overlapped broadly and hence factors other than spatial organisation are important for their coexistence.

Keywords: coexistence; home range; social system; overlap

Introduction

The spatial organisation of a species varies spatio-temporally, and reflects the social organisation of that species (Cooper & Randall, 2007; Salvioni & Lidicker, 1995). One common determinant of spatial organisation is home range overlap. A high level of home range overlap is indicative of group-living and the converse is true for solitary species (Cooper & Randall, 2007; but see review in Schradin & Pillay, 2005). Home range overlap is influenced by several biological factors, such as population density, sex, age, body size and ecological factors, such as season and food availability and distribution (Cooper & Randall, 2007; Schradin & Pillay, 2006; Ribble *et al.*, 2002; Priotto *et al.*, 2002; Ostfeld, 1990; Wolff, 1985; Burt, 1943). For small mammals, female distribution tends to

be determined by resource abundance, distribution and renewability, factors that are important for reproduction (Ostfeld, 1990). In contrast, male distribution is apparently regulated by female spatial distribution (Ribble & Stanley, 1998; Ostfeld, 1990). Thus, if females have a clumped distribution (i.e. overlapping home ranges), males tend to be territorial in order to monopolise access to females, resulting in a polygynous mating system (Priotto *et al.*, 2002; Ribble & Stanley, 1998). However, if females have non-overlapping, extensive home ranges (i.e. territorial), males are unable to monopolise a group, and instead visit several females, often resulting in scramble competition (Jackson, 1999) and a promiscuous mating system, so that male home ranges are large, overlapping and non-territorial (Ribble & Stanley, 1998; Ostfeld, 1990). For monogamous species, the home ranges of single males and single females will overlap (Gaulin & FitzGerald, 1988).

Studies of spatial organisation may also contribute to understanding patterns of coexistence between ecologically similar species (Priotto *et al.*, 2002; Ribble *et al.*, 2002; Ferreira & Van Aarde, 1999). Since ecological and resource partitioning may be the underlying mechanisms of coexistence (Bonesi & Macdonald, 2004; Jorgensen, 2004; Kalcounis-Ruppell & Millar, 2002; Rosenzweig, 1981), it would be expected that ecologically similar species would occupy adjacent, non-overlapping home ranges (Christopher & Barrett, 2006; Bleich & Price, 1995), but that these may vary depending on resource availability (Orland & Kelt, 2007). Nevertheless, interspecific home range overlap is possible and is underpinned by environmental heterogeneity, which influences spatial or temporal differences in resource availability, predation and climatic factors (Kotler & Brown, 1988). In addition, a portion or the entire home range of one species, often the specialist, may be included in that of another species, normally the generalist (Bleich & Price, 1995).

Space use may also be influenced by variation in food distribution and abundance and the variety of acceptable food resources. Thus in unpredictable environments, or under high population density, home range size may be larger as distances travelled to find resources in order to meet energy requirements increases (Pasch & Koprowski, 2006).

The Namaqua rock mouse *Michaelamys namaquensis* and the Rock sengi *Elephantulus myurus* coexist on rocky outcrops throughout southern Africa but specifically on the highveld grassland region, where they are often the only two small mammal species in the community (*pers. obs.*). Although they are of a similar size (*M. namaquensis* 47.5g, range 33g – 57.9g; *E. myurus* 60g, range 48g – 98g; Skinner & Chimimba, 2005) and have similar microhabitat and dietary requirements (Chapter 2), they appear to avoid contact

with each other in staged behavioural interactions (see Chapter 6). Little is known about the spatial organisation of both species and how this may influence their coexistence. The aim of this study was to determine the home range size of *M. namaquensis* and *E. myurus*, and the degree of intra-and inter-specific overlap. We predicted that 1. As *M. namaquensis* is polygynous (Fleming & Nicolson, 2004), there would be a large amount of female-female overlap and little male-male overlap but a high degree of male-female overlap. 2. Since *E. myurus* occurs as monogamous pairs (Skinner & Chimimba, 2005), it was expected that the home range of one male would overlap that of only one female; similarly, the home range of one female is expected to overlap with one male. 3. Since individuals of the two species actively avoid one another in behavioural encounters, we predicted that the degree of interspecific home range overlap would be lower than intraspecific home range for *M. namaquensis*. Alternatively as specialists usually have a larger home range area in comparison to generalists, the generalist *M. namaquensis* is expected to have a smaller home range size compared to the specialist *E. myurus*. This would result in a high degree of interspecific overlap for both species.

Methods

This study was conducted in a grassland reserve (eZemvelo Nature Reserve; 25^{o} 48' S 28^{o} 40' E) in the highveld region of South Africa. eZemvelo comprises mainly grasslands interspersed with wooded, rocky ridges. It receives summer rainfall ($\pm$650 mm per annum) with average temperatures fluctuating between 12.5 ^{o}C in winter to 26 ^{o}C in summer.

Intensive trapping surveys on five permanent grids, measuring 70 m x 70 m in rocky outcrops, were performed using mark-recapture techniques. Traps were placed 10m apart, with 1 trap/station (i.e. 49 traps/grid). Trapping was conducted for five consecutive nights every month from September 2004 until April 2005, coinciding with the breeding season of both *M. namaquensis* and *E. myurus*. PVC live traps (29 x 6 x 7 cm) were baited with a mixture of oats, raisins, salt, oil, peanut butter and sunflower seeds and covered with vegetation to buffer against environmental extremes. Traps were checked and rebaited daily in the early morning and late evening.

Each individual caught was weighed, sexed and its reproductive status noted. Males were classed as scrotal (testes descended) or non-scrotal (testes in abdominal cavity) while females were classed as either perforate, or non-perforate, depending on whether or not the vagina was perforated. Additionally, any signs of lactation or pregnancy were

noted. Reproductive condition was difficult to assess in *E. myurus* males, since testes are abdominal and thus reproductive condition was only noted where testes was easily seen. Individuals were released at the station of capture after being individually marked. Because of financial constraints, live-trapping instead of radiotelemetry was used to assess space use. However, many studies have shown a close correlation between the two methods with live trapping consistently under-estimating home range size (Smith, 2007; Ribble *et al.*, 2002; Ribble & Stanley, 1998).

The software programme, Ranges6, was used to establish the average distance travelled between captures, home range size, and overlap of individuals that were caught at least four times at different trap stations (Priotto *et al.*, 2002; Batzli & Henttonen, 1993), using the Minimum Convex Polygon method with 100% cores; this is a well established method used for small mammals (Schradin & Pillay, 2005; Priotto *et al.*, 2002; Batzli & Henttonen, 1993) but see the discussion in Nilsen *et al.* (2008). Statistical comparisons for home range size and distance travelled between species and sexes were made with a General Linear Model (GLM) with Tukey post-hoc tests. Wilcoxon matched pairs tests were used to assess home range overlap and proportion of overlapping individuals. Proportion, rather than real number was used to compensate for the varying trapping success of *M. namaquensis* and *E. myurus*. For these tests, we compared the data for individuals intraspecifically (e.g. home range overlap between same and different sex individuals), and between species (e.g. home range overlap between individuals of same and different species). All statistical tests were two-tailed and $\alpha = 0.05$.

Results

A total of 180 adult *M. namaquensis* (93 females and 87 males) and 67 *E. myurus* (32 females and 35 males) were captured during the study. Of these, 55 *M. namaquensis* females and 43 *M. namaquensis* males were captured at four or more different stations and could be used for the home range size and overlap analysis, and the data from an additional 20 females and 10 males were available for determining the average distance travelled between captures. The trapping success for *E. myurus* was much lower with only 21 and 18 females and males respectively meeting the requirements of four or more captures at different stations for the analysis of home range size and overlap. However, a total of 27 females and 22 males were used to determine average distance travelled.

For *M. namaquensis*, there was no significant difference in home range overlap between females and conspecific females and males (T_{55}=920.5; p=0.209), but the home

ranges of males overlapped significantly more with females than other males (T_{43}=103; p=<0.001; Figure 4.1.). For *E. myurus*, the home ranges of both sexes overlapped significantly more with that of the opposite sex than the same sex (Figure 4.1.): females – T_{21}=14.0; p<0.001; males T_{15}=5.0; p<0.001. Between species comparisons indicated no differences between same species and different species (*M. namaquensis* females: T_{55}=763.0; p=0.957; *E. myurus* females: T_{21}=71.0; p=0.126; *E. myurus*: T_{15}=27.0; p=0.064), except for *M. namaquensis* males which overlapped more with *E. myurus* individuals than with conspecifics (T_{43}=200.0; p=0.001; Figure 4.1.).

The results of the proportion of individuals with overlapping home ranges mirrored those of the home range overlap (Figure 4.2.). The home ranges of female *M. namaquensis* overlapped with a similar proportion of conspecific females and males (T_{55}=741.5; p=0.815). In contrast, the home ranges of male *M. namaquensis* (T_{43}=105.5; p=<0.001) and both sexes of *E. myurus* (females – T_{21}=43.0; p=0.012; males T_{15}=6.0; p<0.001) overlapped with a greater proportion of different sex than same sex individuals. Interspecifically, the home ranges of both sexes of both species overlapped with a similar proportion of conspecifics and heterospecifics: *M. namaquensis*: female - T_{55}=927.0; p=0.190; male T_{43}=612.0; p=0.061; *E. myurus*: female - T_{21}=89.0; p=0.366; male - T_{15}=80.0; p=0.277).

The distance travelled between captures ($F_{1,167}$=2.37; p=0.126) and home range size ($F_{1,130}$=0.52; p=0.471) was not influenced by species identity. In addition, sex (distance travelled: $F_{1,167}$=0.06; p=0.804; home range size: $F_{1,130}$=0.50; p=0.479) and species x sex (distance travelled: $F_{1,167}$=2.61; p=0.108; home range size: $F_{1,130}$=1.45; p=0.230) were not good predictors of these parameters (Table 4.1).

Discussion

Intraspecific home range overlap - Michaelamys namaquensis is polygynous (Skinner & Chimimba, 2005; Fleming & Nicolson, 2004) and thus males are expected to be territorial with large, exclusive home ranges overlapping those of many females who have smaller, intrasexually overlapping home ranges (Reynolds, 1996). Our data support these predictions with *M. namaquensis* males overlapping more with conspecific females than other males while females did not differ in their overlap of males and females. Additionally, both sexes had similar home range sizes. A high level of female overlap by males despite similar home range sizes was also found for wild polygynous

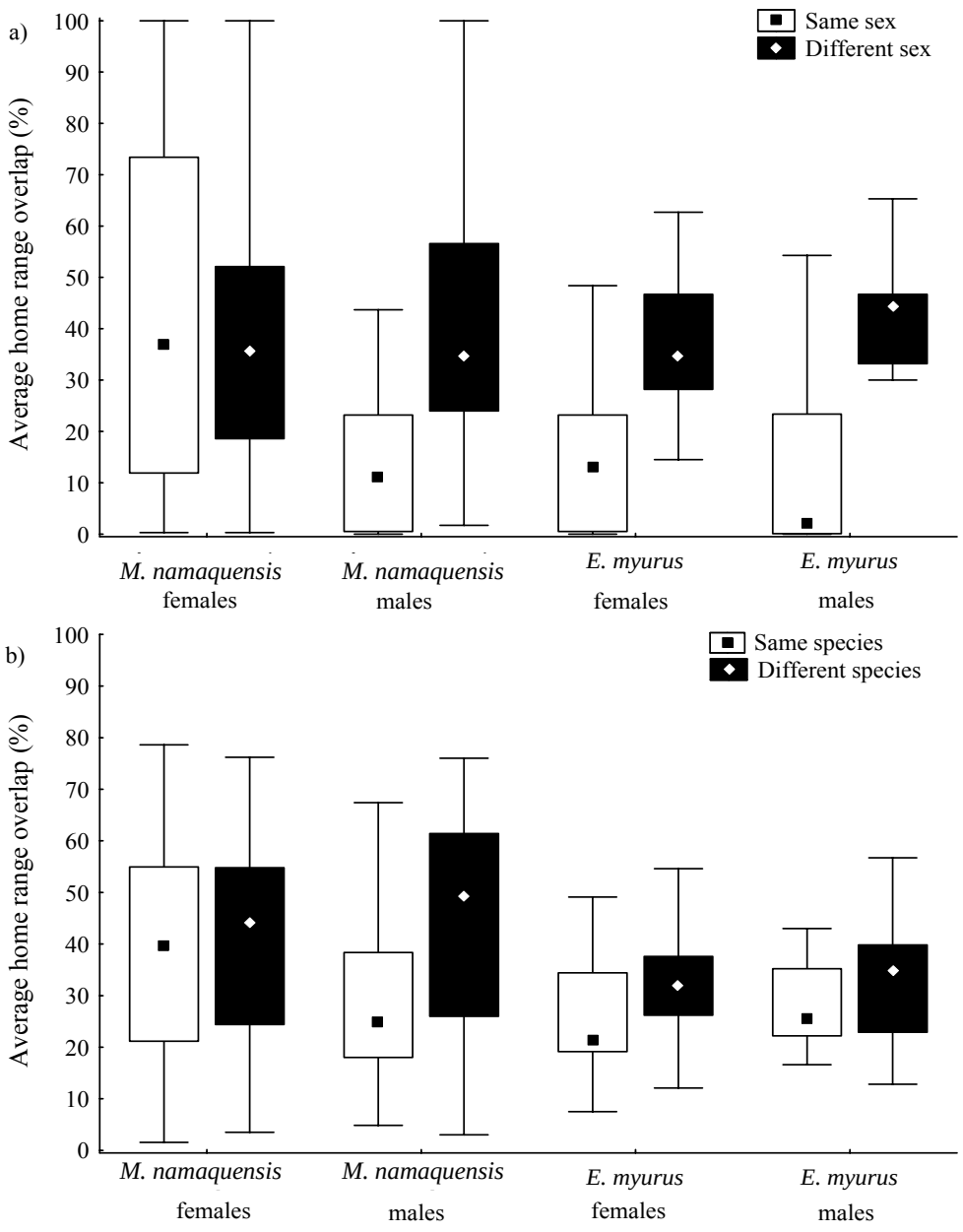


Figure 4.1. Average home range size overlap (%) for a) intraspecific and b) interspecific overlap. Markers indicate the mean, boxes the quartiles and whiskers the ranges.

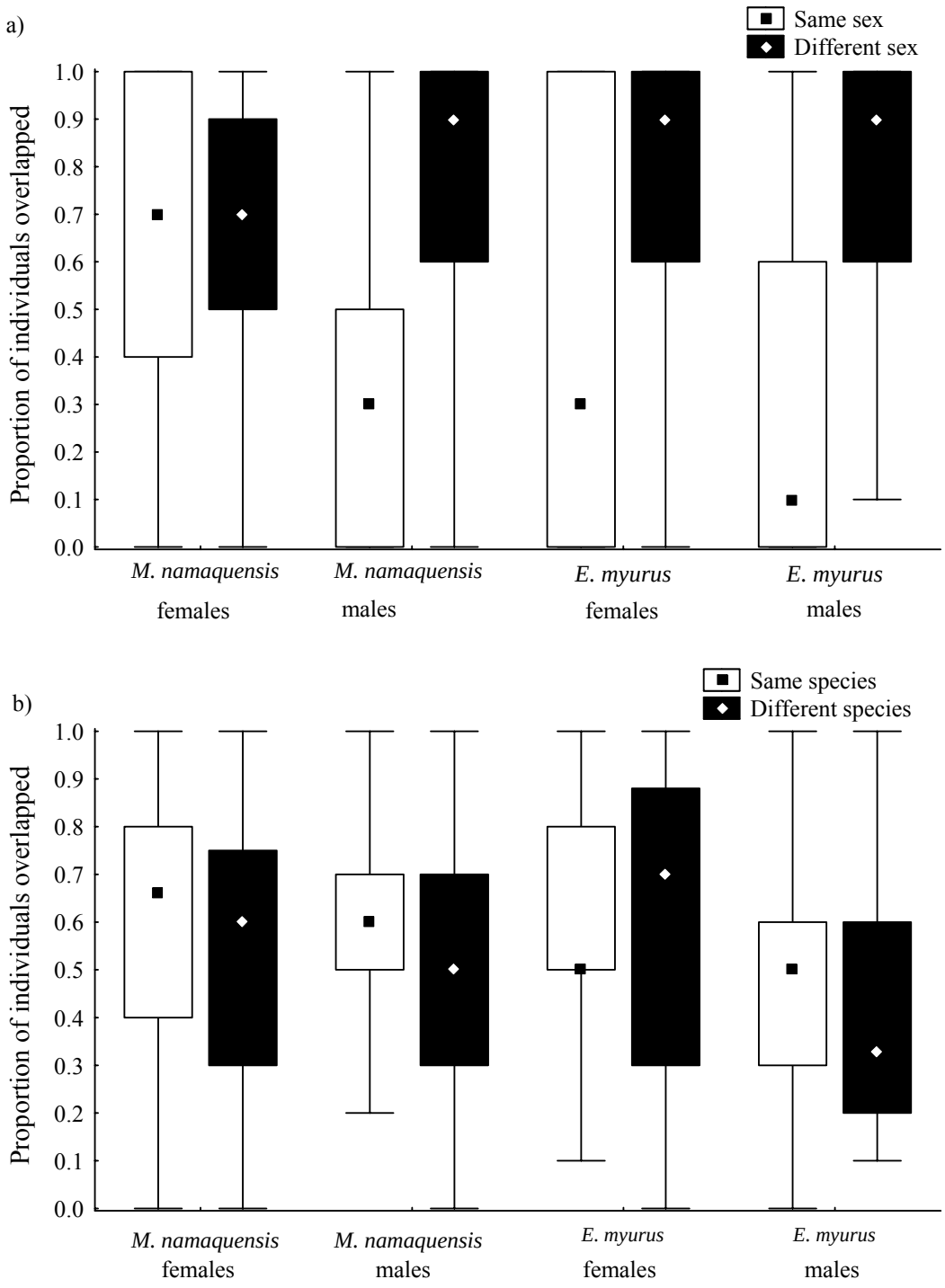


Figure 4.2. Proportion of home ranges overlapping for a) intraspecific and b) interspecific overlap. Markers indicate the median, boxes the quartiles and whiskers the ranges.

Table 4.1. Mean (+ SE) measurements of space use in coexisting *Michalemays namaquensis* and *Elephantulus myurus* females and males.

Species/sex	Distance travelled (m)	Home range size (ha)
M. namaquensis females	41.65 (2.18)	0.11 (0.01)
M. namaquensis males	37.66 (2.03)	0.13 (0.01)
E. myurus females	32.44 (2.57)	0.11 (0.01)
E. myurus males	37.88 (3.21)	0.10 (0.02)

House mice *Mus domesticus* in wheat fields in Australia (Chambers *et al.*, 2000). Like the Northern flying squirrel, *Glaucomys sabrinus* (Smith, 2007), males and females also travelled similar distances between captures.

Most Macroscelidae are monogamous (Skinner & Chimimba, 2005) and thus males and females tend to have similar sized, intrasexually exclusive home ranges (Gaulin & FitzGerald, 1988). Although overlap was relatively low, there was a large amount of variability: both sexes seem to maintain sexually exclusive home ranges that overlapped more with members of the opposite sex than the same sex. Like *M. namaquensis*, both sexes had similar home range size and travelled the approximately the same distance between captures. Thus *E. myurus* is certainly monogamous, although whether this monogamy is facultative or obligative is not yet understood (Ribble & Perrin, 2005). This is reinforced by a low population density on the grids and is similar to the Rufous sengi *Elephantulus rufescens* which was found to occur in pairs with family groups occurring adjacent to each other (Neal, 1982b).

Interspecific home range overlap and home range size - Contrary to the prediction of behavioural avoidance, the results indicate that apart from *M. namaquensis* males which overlapped more with heterospecifics than conspecifics, the percentage of overlap did not differ interspecifically. Additionally, there was no difference in the proportion of individuals of the same and different species which overlapped nor differences in home range size. The non-exclusivity of home ranges implies that *M. namaquensis* and *E. myurus* do not exclude each other spatially. Subdominant species are expected to have larger home ranges to minimise contact with the dominant species (Douglass, 1976) but based on home ranges, neither species is spatially dominant over the other.

One reason for the high level of overlap could be that the overlap occurs temporally and not spatially as assumed here from the trapping data. Temporal separation occurred in the coexistence of the Rice rat *Nesoryzomys swarthi* and Black rat *Rattus rattus* on the

Galapagos Islands, possibly due to interference competition by *R. rattus* (Harris *et al.*, 2006). However, the two species are active at the same time (*pers. obs.*), so that the home range overlap measured here reflects both a spatial and temporal pattern. Additionally, as in a study on the Grey mouse lemur (*Microcebus murinus*) and Madame Berthe's mouse lemur (*Microcebus berthae*), high amounts of home range overlap may be due to high resource overlap, especially in terms of food resources (Dammhahn & Kappeler, 2008). Another reason for the high degree of overlap could be differential use of a core area (Harris *et al.*, 2006). Core areas are usually exclusively maintained (Harris *et al*., 2006) but due to the lack of sensitivity of data, could not be measured in the present study. In a study on native Galápagos rice rats *Nesoryzomys swarthi* and the black rat *Rattus rattus*, it was found that differential core area usage due to slight difference in dietary preferences probably promoted coexistence despite a high amount of spatial and temporal overlap (Harris *et al.*, 2006).

Home range size and overlap are variable (Batzli & Henttonen, 1993) and may be associated with many factors such as behaviour, microhabitat differences and macrohabitat requirements and use. Analysis of intraspecific characteristics revealed that *M. namaquensis* and *E. myurus* have different social organisations, which may also influence space use and hence coexistence (Gaulin & FitzGerald, 1988). The difference in social structure has been used to explain the coexistence of the monogamous Prairie vole *Microtus ochrogaster* and the promiscuous Meadow vole *M. pennsylvannicus* which had a larger home range size, mainly as a result of the large home ranges of scrotal *M. pennsylvannicus* males which travelled large distances in search of receptive females (Gaulin & FitzGerald, 1988). They suggest that in promiscuous mating systems, males increase their home range size during the breeding season to increase their access to females, but decrease it in the non-breeding season to approximately the same size as females. The population density of coexisting species may also influence home range size and overlap (Priotto *et al.*, 2002) or perception of patch quality (Manor & Saltz, 2008) which in turn would affect home range size. For example, the home range of the Brush mouse *Peromyscus boylii* was positively related to the abundance of Pinyon mouse *Peromyscus truei* (Ribble & Stanley, 1998). Similarly, the coexisting, ecologically similar Deer mouse *Peromyscus maniculatus* and White-footed mouse *Peromyscus leucopus* had high levels of home range lap at low population densities, but at high densities, mutual avoidance resulted in territoriality and non-overlapping home ranges (Wolff, 1985).

Several mechanisms are known to operate simultaneously to promote coexistence in rodents (Kotler & Brown, 1988). Our study shows that home range size and overlap do not seem to directly promote coexistence in *M. namaquensis* and *E. myurus*, since both species had similar home range size and extensive home range overlap. However, differences in home range use, microhabitat preferences, behaviour, social organisation and population characteristics (e.g. density) may operate in combination with spatial organisation to promote coexistence between *M. namaquensis* and *E. myurus.* Apart from using more sensitive techniques (e.g. radio-telemetry to assess overlap of core areas of the home range), future studies should consider seasonal variation in home range size and overlap which are known to affect other small mammals in southern Africa e.g. Striped mice *Rhabdomys pumilio* (Schradin & Pillay, 2006).

Chapter 5

Effects of species removal on the population dynamics and space use of coexisting small mammals

Abstract

Although competition and space use are normally invoked as factors promoting coexistence and structuring of communities, recently, differences in life history traits and behaviour have gained attention as possible explanatory factors. The Namaqua rock mouse *Michaelamys namaquensis* and the Rock sengi *Elephantulus myurus* coexist on rocky outcrops in the highveld region of South Africa. This study aimed to establish the effect of removal of either *M. namaquensis* or *E. myurus* on ecology of the remaining species. Seven permanent grids were trapped, of which two grids each were for *M. namaquensis* or *E. myurus* removal and three served as control grids. The density of *E. myurus* was higher on control and *M. namaquensis* removal grids than on *E. myurus* removal grids. There were distinct breeding seasons, with more reproductively active *M. namaquensis* individuals present on removal grids during the early rainy season compared to control grids. Both species had greater juvenile recruitment on removal grids and per capita recruitment of *M. namaquensis* was high on grids from where it was removed. There were no home range or range span differences between grid types but these parameters were significantly greater for *E. myurus* than *M. namaquensis* on *E. myurus* removal grids. Female *M. namaquensis* did not travel as far on *E. myurus* removal grids as they did on control grids. Hence, *E. myurus* is probably restricted in terms of space use by *M. namaquensis* but *E. myurus* may restrict resource acquisition by *M. namaquensis*. These species do compete, most likely for resources such as space and food, which in turn affects various population characteristics.

Keywords: breeding season; density; *Elephantulus myurus*; home range; *Michaelamys namaquensis*; recruitment; removal

Introduction

Many mechanisms that reduce interspecific competition and improve overall fitness have been proposed to promote species coexistence (Kinahan & Pillay, 2008; Harris *et al.*, 2006). It has been suggested that in species assemblages, there is an axis of environmental heterogeneity and trade-offs between interacting species, resulting in each species having a

place on that axis where it is the superior competitor (Perrin & Kotler, 2005). Although there are five main mechanisms that promote coexistence (variation in macrohabitat and microhabitat requirements, spatial and temporal variation in resource use, and dietary partitioning; Kotler & Brown, 1988; Brown, 1989a; Abramsky *et al.*, 1990), recently factors such as interspecific behavioural differences and differences in life history strategies have gained prominence (Dammhahn & Kappeler, 2008; Liu *et al.*, 2007; Christopher & Barrett, 2006; Pinter-Wollman *et al.*, 2006; Perri & Randall, 1999; Brown & Zeng, 1989). Thus, studying population dynamics and their fluctuations may be as important in understanding coexistence as patterns of resource use (Brown & Zeng, 1989).

A dynamic reproductive strategy will enable a individual to vary its life history strategy depending on environmental variability (Willan & Meester, 1989; Perrin & Swanepoel, 1987), and also to minimise or avoid competition by varying particular characteristics, thus promoting coexistence (Dammhahn & Kappeler, 2008). As such, reproductive and life history traits may represent an adaptive response to both biotic and abiotic factors affecting the population and may be an indication of how the organism perceives, and responds to, the environment (Neal, 1986). Brown & Zeng (1989) found that there are processes promoting similarities and differences in life history strategies but that these processes are unpredictable between different populations of the same species and between species. For example, the differences and/or similarities may be due to co-evolution to reduce overlap, interactive sorting or ecological fitting and independent assembly of species. Additionally, attributes such as body size (Perri & Randall, 1999) and relative abundance may reflect non-random differences that may promote coexistence through decreasing competition intensity (Kryštufek *et al.*, 2007).

The importance of competition in structuring a community is well documented (Manor & Saltz, 2008). When resources overlap competition is inevitable (Zhang, 2003), but the intensity of such competition may be altered by the density of the species concerned and the presence of generalists and specialists as they respond to different cues in the environment (Stilmant *et al.*, 2008), varying from very narrow requirements (specialists) to broad requirements (generalists; Manor & Saltz, 2008). However, the relative importance of competition on coexistence is not always apparent. One hypothesis suggests that competition is rare and therefore displacement is not expected (Perrin, 1980), and thus present interactions may be a result of past relationships. Another hypothesis is that superior competitors out-compete other species (Perrin, 1980). From this it follows that if the density of a dominant competitor is decreased, or the species is absent, the

diversity and/or abundance of the remaining community may increase due to higher colonisation and lower extinction rates (Keesing, 1998b) or competitive release (Harris *et al.*, 2006). This means that at a competitive equilibrium, the densities of coexisting species are maintained while those of competing species may have a negative relationship (Ferreira & Van Aarde, 1999). If these relationships are non-linear, it reflects a system where competitive interactions allow a numerical advantage of one species to negatively affect the other species. This is especially evident when there is no realised niche differentiation (Ferreira & Van Aarde, 1999). However, in optimal environments, density can be high without competition having a negative influence on the species concerned (Manor & Saltz, 2008), as competition need not be interference competition to shape community structure. Additionally, competition for resources often results in habitat shifts while a change in density usually reflects the strength of competition (Hughes *et al.*, 1994).

Spatial organisation is another important factor shaping communities (Ribble *et al.*, 2002). Home range size is known to be affected by a number of factors, such as habitat structure, resource availability (Ribble & Stanley, 1998), population density and interference from other species (Wolff, 1985). Although most studies have focused on intraspecific overlap as an indicator of social organisation and mating systems, spatial and social organisation may also be a function of density, not only of conspecifics but also heterospecifics (Ribble *et al.*, 2002). As a result, there may be a minimum threshold density at which individuals become aggressive and defend and maintain territories, below which territories are maintained through mutual avoidance (Wolff, 1985). This minimum threshold density may affect survival and reproductive success (Wolff, 1985).

Michaelamys namaquensis is a medium sized (44.1 - 49.5g), omnivorous murid that lives in family groups (Skinner & Chimimba, 2005; Speakman *et al.*, 1992; Rautenbach, 1982; De Graaff, 1981). It is widespread, but prefers rocky areas as it has physiological and behavioural adaptations suited to such areas (Fleming & Nicolson, 2004). Breeding occurs in the warm, wet months (September to May; Fleming & Nicolson, 2004) and litter size ranges between 1 - 5 (Skinner & Chimimba, 2005; De Graaff, 1981). It may have unstable population cycles associated with high mortality but has a high reproductive potential (Muteka *et al.*, 2006), with densities that vary between 8.1 and 11.8 individuals/ha in the southern Cape (Fleming & Nicolson, 2004) and 1.5 – 2 nests/ha in thornveld savanna (Meyer & Brandl, 2005).

Elephantulus myurus is slightly larger (60g; Skinner & Chimimba, 2005). They are insectivorous and thought to be monogamous (Skinner & Chimimba, 2005; Neal, 1982b)

and occur in low population densities, and may enter torpor during winter (Mzilikazi & Lovegrove, 2004). *Elephantulus myurus* appears to be a summer breeder (Skinner & Chimimba, 2005). Sengis have 3 litters/ season with 1 – 2 precocial pups/litter (Neal, 1982b).

Michaelamys namaquensis and *E. myurus* coexist on rocky outcrops throughout southern Africa, there is a high degree of overlap between the two species in terms of diet and microhabitat use (see chapter 2). There is also a slight temporal differentiation in the breeding season of *M. namaquensis* and *E. myurus* (see chapter 3) and their home ranges overlap (see chapter 4) but they appear to actively avoid each other (see chapter 6).

The aim of this study was to assess whether either *M. namaquensis* or *E. myurus* alter their population dynamics and space use when the density of the other species is reduced by removal trapping. Thus, I made several predictions: 1) Based on their social structure and spatial organisation, it was expected that *M. namaquensis* would increase in density regardless of which species was removed as they live in groups with a high level of home range overlap and have a high reproductive rate. Behavioural studies (see Chapter 6), they are tolerant of other individuals of the same species and thus have high levels of recruitment, thereby increasing the local density. 2) Due to competitive release when *E. myurus* was removed, it was also expected that *M. namaquensis* would have increased reproductive output, further increasing their density. 3) It was expected that *E. myurus* would increase its home range size as they are solitary and appear to have more exclusive home ranges (see Chapter 4) when either species is removed. Additionally, they are slower breeders and occur in much lower densities compared to *M. namaquensis* and thus increasing density, if it occurred, would happen over a much longer time period.

Methods

Field studies were conducted at eZemvelo Nature Reserve (25^{o} 42’ 26” S 29^{o} 01’ 02” E), in the highveld region of South Africa. The reserve is typified by gentle grassy slopes interspersed with rocky ridges that are sparsely populated by mainly *Burkea africana*, *Ochna pulchra* and *Protea caffra*. The reserve receives approximately 650 mm of summer rainfall per annum with maximum temperatures varying between 12.5 ^{o}C in winter and 26 ^{o}C in summer.

Three permanent control grids, measuring 70 m x 70 m were established in September 2002. Grids were a minimum of 2 km and a maximum of 4 km apart. PVC live traps (29 x 6 x 7 cm) in a 7 x 7 arrangement with 10 m between traps were used, and baited

with a mixture of oats, raisins, salt, oil, peanut butter and sunflower seeds; traps were covered with vegetation to buffer against temperature extremes. Trapping was conducted for four consecutive nights every month for 2 years except for February and March 2003 when flooding made access to sites impossible. Traps were checked and rebaited daily in the early morning and late evening. In September 2003, an additional 4 grids were established at least 200 m away from the control grids. These grids were used for either *M. namaquensis* removal (2 grids) or *E. myurus* removal (2 grids), with the original grids acting as controls. All removed animals were placed on a grid approximately 1km away from the next closest grid and monitored for signs of re-establishment.

All individuals caught were weighed, measured (body and tail length), sexed and reproductive status and point of capture noted before being individually marked using toe clipping. Males were classed as scrotal (testes descended) or non-scrotal (testes in abdominal cavity), and females were classed as either perforate, or non-perforate, depending on whether or not the vagina was open. Additionally, any signs of lactation (prominent nipples) or pregnancy (distended abdomen) were noted. Reproductive condition was difficult to assess in *E. myurus* males as testes are abdominal and thus reproductive condition was only noted where testes was easily seen. On control grids, individuals were released at the point of capture. On *M. namaquensis* removal grids, *E. myurus* were released at point of capture while *M. namaquensis* were retained and *vice versa* on *E. myurus* removal grids. All retained individuals were kept in holding cages; released on a separate site about 200 m from any other grid a maximum of three hours later and monitored for re-establishment (not reported on here).

For each type of grid, various population characteristics of the two small mammal species were measured and compared to data obtained from control grids. Recaptures in different sessions were treated as separate observations so that home ranges could be calculated. Population size was determined using mathematical models (Jolly-Seber method; Southwood & Henderson, 2000) and direct enumeration (Minimum Number Alive (MNA); Wolff, 1985; Krebs, 1966). Small mammal density was calculated using the effective trapping area (i.e. 490 m^2) of the grid. Breeding season was determined using the reproductive data and age structure, taking into account the time lag between peak breeding season and peak in the numbers of young animals, and the proportion of reproductively active individuals. Based on previous data (see chapter 3), age classes were determined using a combination of weight and reproductive condition (Delany, 1974) with adult *M. namaquensis* weighing 38 g or more and adult *E. myurus* weighing 49 g or more.

Total recruitment (total number of new individuals captured in a grid for each trapping session) and per capita recruitment (proportion of new individuals captured in each trapping session) were determined (Keesing, 1998a). Emigration (i.e. mortality and dispersal) was calculated as the proportion of individuals caught in one trapping session and not subsequently caught. Survival (or persistence) was calculated using the first capture and the time until the individual was last caught (Keesing, 1998a). All data were categorised according to the rainy season i.e. early rains (September – December), late rains (January – April) and dry season (May – August). Additionally, average distance travelled between captures, home range size and overlap was calculated using Ranges6 for individuals on the *M. namaquensis* removal and *E. myurus* removal grids. These parameters were compared with individuals on control grids.

Data were analysed using STATISTICA 6 (Statsoft; www.statsoft.com). For the distribution of age and reproductively active individuals, data sets were arcsine transformed to approximate normality and a General Linear Model (GLM) used to test for experimental and seasonal effects with grid type and season as independent factors and age and number of reproductive individuals set as dependent variables. Kruskal-Wallis ANOVAs were used to compare recruitment and emigration (dependent factors) between the different grids (independent factors; Pyke & Thompson, 1986). To test for differences in survival, a Mann-Whitney U test was used. Differences in weight between individuals (dependent variable) on the different grids (independent variable) were analysed using a GLM. A GLM was also used to test for differences in average distance travelled, home range size and range span (dependent variables) between removal and control grids (independent variables). All statistical tests were two tailed with $\alpha = 0.05$.

Results

A total of 21 *M. namaquensis* females and 28 *M. namaquensis* males were caught on *M. namaquensis* removal grids, and 14 females and 10 males were caught on *E. myurus* removal grids. The numbers for *E. myurus* were much lower with only 4 females and 5 males caught on *E. myurus* removal grids and 5 females and 4 males caught on *M. namaquensis* removal grids. On control grids, 28 *M. namaquensis* females, 33 *M. namaquensis* males, 10 *E. myurus* females and 8 *E. myurus* males were caught.

Although the methods (Jolly-Seber and MNA) used to determine density were significantly correlated (*M. namaquensis*: $R_{21} = 0.57$, $p = 0.008$; *E. myurus*: $R_{21} = 0.51$, $p = 0.02$), they gave significantly different results (*M. namaquensis*: $Z_{22} = 3.74$, $p < 0.001$; *E.*

myurus: $Z_{22} = 3.18$, $p = 0.001$) with the Jolly Seber method consistently overestimating population size in comparison to MNA. Thus, as some of the assumptions made for the Jolly-Seber method were not met (Hammond & Anthony, 2006; Bronner, 1986), and due to the small sample size (Manor & Saltz, 2008), all further analyses are based on the MNA method. For *M. namaquensis*, the type of grid did not affect the density ($H_{2,37} = 2.79$, $p = 0.248$) but grid type did affect the density of *E. myurus* ($H_{2,38} = 21.48$, $p < 0.001$) with multiple comparisons revealing that *E. myurus* densities were higher on control and *M. namaquensis* removal grids than *E. myurus* removal grids (Figure 5.1.).

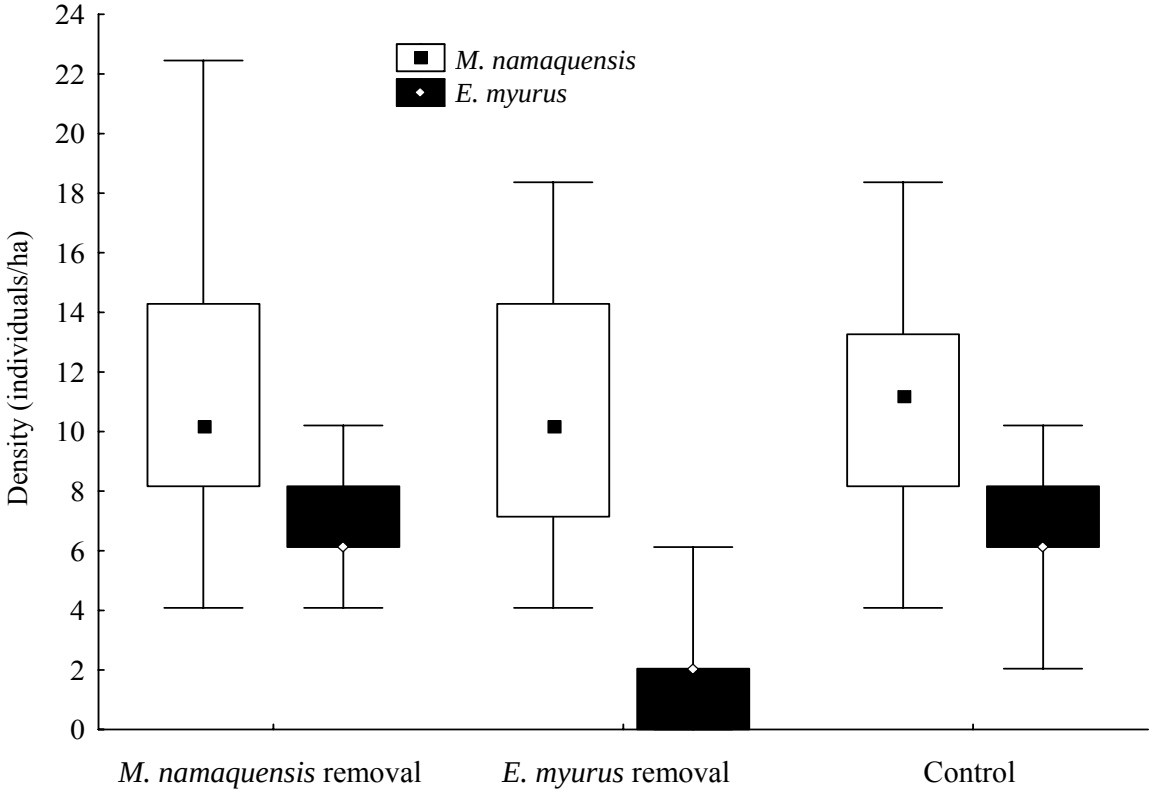


Figure 5.1. Comparison of density obtained from the different grid types. Markers indicate the median, boxes the interquartiles and whiskers the minimum and maximum**.**

Breeding season was determined using the age and reproductive structure of the populations. Both grid type ($F_{8,44} = 4.23$, $p < 0.001$) and season ($F_{8,44} = 4.14$, $p < 0.001$) and their interaction ($F_{16, 68} = 3.14$, $p < 0.001$) had significant effects on the number of adults and juveniles. Tukey HSD post-hoc tests revealed that there were more juveniles than adults of both species on their respective removal grids i.e. more *M. namaquensis* juveniles on the *M. namaquensis* removal grids and more *E. myurus* juveniles on the *E. myurus* removal grids. In terms of season, more juveniles of both species were present in

the early rainy and late rainy seasons compared to the dry season. Additionally, there were more *E. myurus* juveniles on grids in the dry and early rain season (Figure 5.2.).

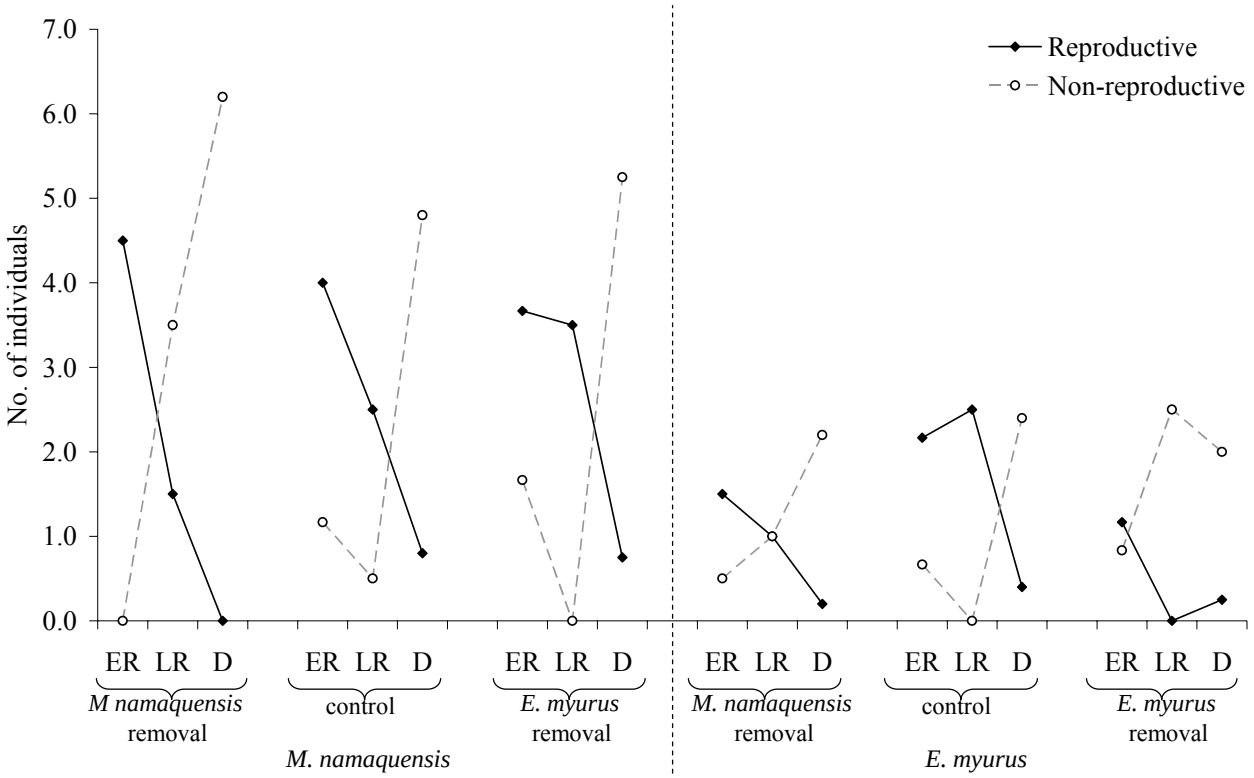


Figure 5.2. The frequency of reproductive (perforate and scrotal) and non-reproductive *Michaelamys namaquensis* and *Elephantulus myurus* in three trapping grid types in the early rain (ER), late rain (LR) and dry (D) seasons.

The occurrence of seasonal breeding was supported by examining the distribution of reproductively active individuals seasonally, which indicated no influence due to type of grid ($F_{8,44} = 0.65$, $p = 0.253$) but a definite seasonal influence ($F_{8,44} = 0.16$, $p < 0.001$); grid type*season was not a significant predictor of reproductive activity($F_{6, 68} = 0.48$, $p = 0.337$). For *M. namaquensis*, more reproductively active individuals were present in the early and late rainy season (Figure 5.2.). There were more reproductively active *E. myurus* in the early rainy season compared to the dry season with non-reproductively active individuals showing the opposite trend (Figure 5.2.).

Due to the small sample sizes reported above, and as no seasonal differences were found in recruitment and emigration in a previous study (see chapter 3), the effects of season were not considered for recruitment and emigration data. For recruitment, Kruskal Wallis tests revealed that only *M. namaquensis* per capita recruitment differed significantly between grid types (*M. namaquensis*: recruitment $H_{2,72} = 4.68$, $p = 0.097$; per capita

recruitment $H_{2,72} = 12.09$, $p = 0.002$; *E. myurus*: recruitment $H_{2,72} = 1.17$, $p = 0.557$; per capita recruitment $H_{2,72} = 1.49$, $p = 0.474$), and multiple comparisons showed a trend for more recruitment on *M. namaquensis* removal grids (Figure 5.3.). There were no significant differences in either emigration or per capita emigration for either species among the grid types (*M. namaquensis*: emigration $H_{2,72} = 4.68$, $p = 0.097$; per capita emigration $H_{2,72} = 12.09$, $p = 0.002$; *E. myurus*: emigration $H_{2,72} = 1.17$, $p = 0.557$; per capita emigration $H_{2,72} = 1.49$, $p = 0.474$; Figure 5.3.). Mann-Whitney U tests showed that grid type had no effect on survival for the year of trapping (*M. namaquensis*: $Z_{24,38} = 0.41$, $p = 0.685$; *E. myurus*: $Z_{4,5} = -1.02$, $p = 0.306$) with *M. namaquensis* having a median survival of 1 month on both the control (range: 1 – 5 months) and *E. myurus* removal (range: 1 – 4 months) grids. Survival was slightly longer for *E. myurus* with a median of 2 months (range: 1 – 5 months) on *M. namaquensis* removal grids and 6 months (range: 1 – 12 months) on control grids.

The absence of a coexisting species did not influence the body condition in terms of mass of either species (*M. namaquensis*: $F_{1, 124} = 2.54$, $p = 0.114$; *E. myurus*: $F_{1, 3} = 0.04$, $p = 0.85$) with mean ($\pm$ SE) *M. namaquensis* mass of 53.1g ($\pm$ 1g) on control grids and 50.6g ($\pm$ 1g) on *E. myurus* removal grids. For *E. myurus*, the mean mass ($\pm$ SE) was 68.7g ($\pm$ 2g) on control grids and 66.5g ($\pm$ 2.3g) on *M. namaquensis* removal grids.

Neither grid type nor sex had significant effects on the distance travelled for *M. namaquensis* (grid type: $F_{1, 383} = 2.34$, $p = 0.130$; sex: $F_{1,162} = 0.99$, $p = 0.322$). However, there was a significant grid type*sex effect ($F_{1, 676} = 4.13$, $p = 0.046$) with females on control grids travelling further than females on removal grids (Figure 5.4.). There were no significant interactions for distance travelled between successive captures for *E. myurus* (grid type: $F_{1, 12} = 0.07$, $p = 0.794$; sex: $F_{1, 170} = 1.00$, $p = 0.330$; grid type*sex: $F_{1, 2} = 0.02$, $p = 0.987$). Likewise, grid type had no influence on either home range size (*M. namaquensis*: $F_{1, 0.42} = 2.77$, $p = 0.106$; *E. myurus*: $F_{1, 0.28} = 2.10$ $p = 0.182$) or range span (*M. namaquensis*: $F_{1, 726} = 3.19$, $p = 0.084$; *E. myurus*: $F_{1, 909} = 2.69$, $p = 0.135$) for either species. However, when comparing home range and range span (the maximum diameter of a home range) of *M. namaquensis* and *E. myurus* on the same grid type, there were differences (Home range: $F_{1, 0.63} = 4.24$, $p = 0.046$; Range span $F_{1, 1581} = 6.27$, $p = 0.016$; Figure 5.5.). Tukey HSD posthoc test revealed that the home range of *E. myurus* on *M. namaquensis* removal grids was significantly greater than on *M. namaquensis* on *E. myurus* removal grids while the span of *M. namaquensis* on *E. myurus* removal grids was significantly less than *E. myurus* on *M. namaquensis* grids.

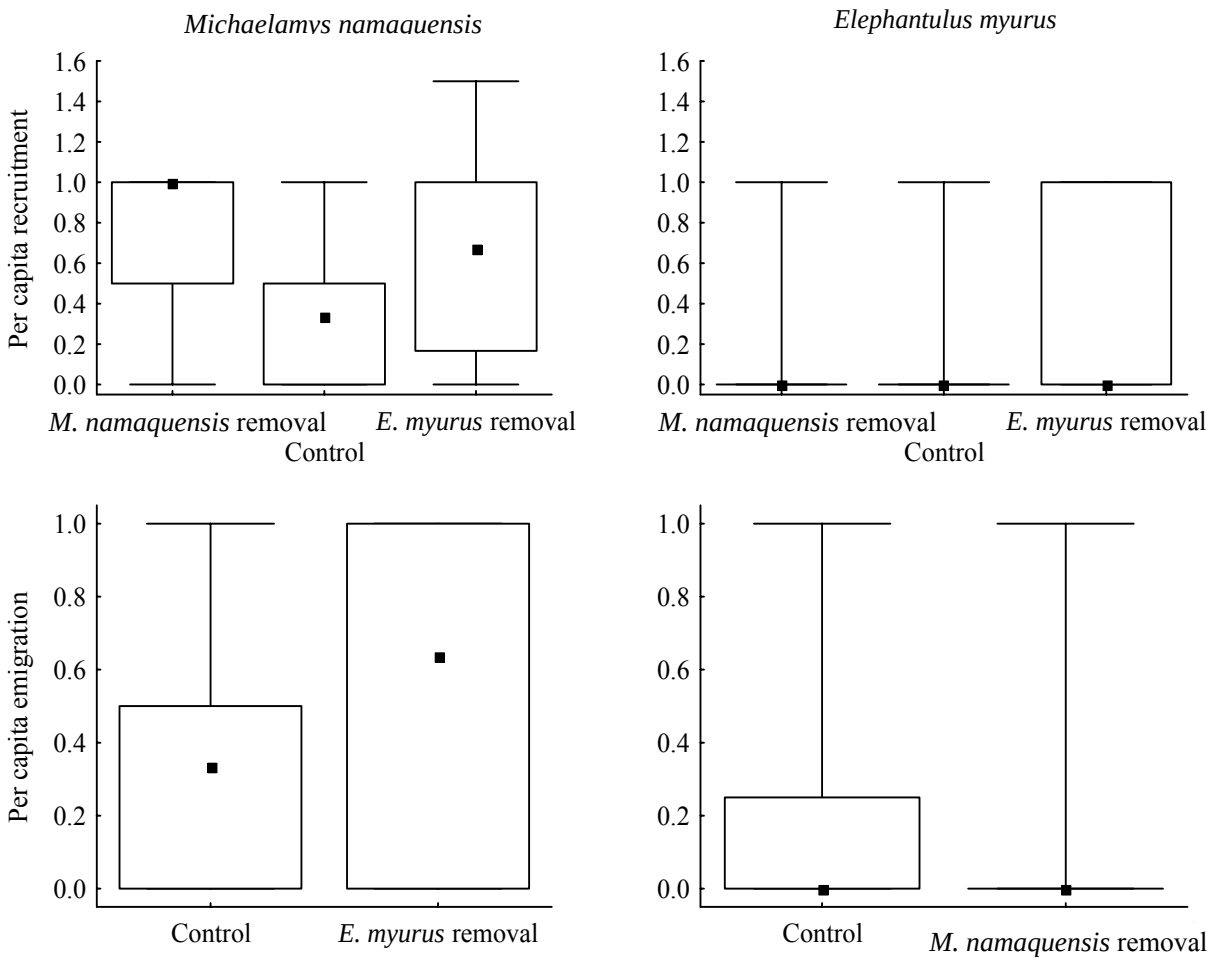


Figure 5.3. Per capita recruitment and emigration of *Michaelamys namaquensis* and *Elephantulus myurus* during removal experiments. Markers indicate the mean, boxes the inter-quartiles and whiskers the range.

Discussion

Many factors, including life history characteristics, competition and environmental factors are said to influence spatio-temporal organisation (Cooper & Randall, 2007; Douglass, 1976) and community structure (Hughes *et al.*, 1994) of different species. I expected that regardless of which species was removed, the density of *M. namaquensis* would increase as it is social and a generalist. Thus, when *M. namaquensis* was removed, I expected that new individuals would enter the population to replace those individuals removed, while when *E. myurus* was removed, the density of *M. namaquensis* would increase due to increased resource availability. The latter would also apply if interspecific competition was an important regulator of population density, as the density of

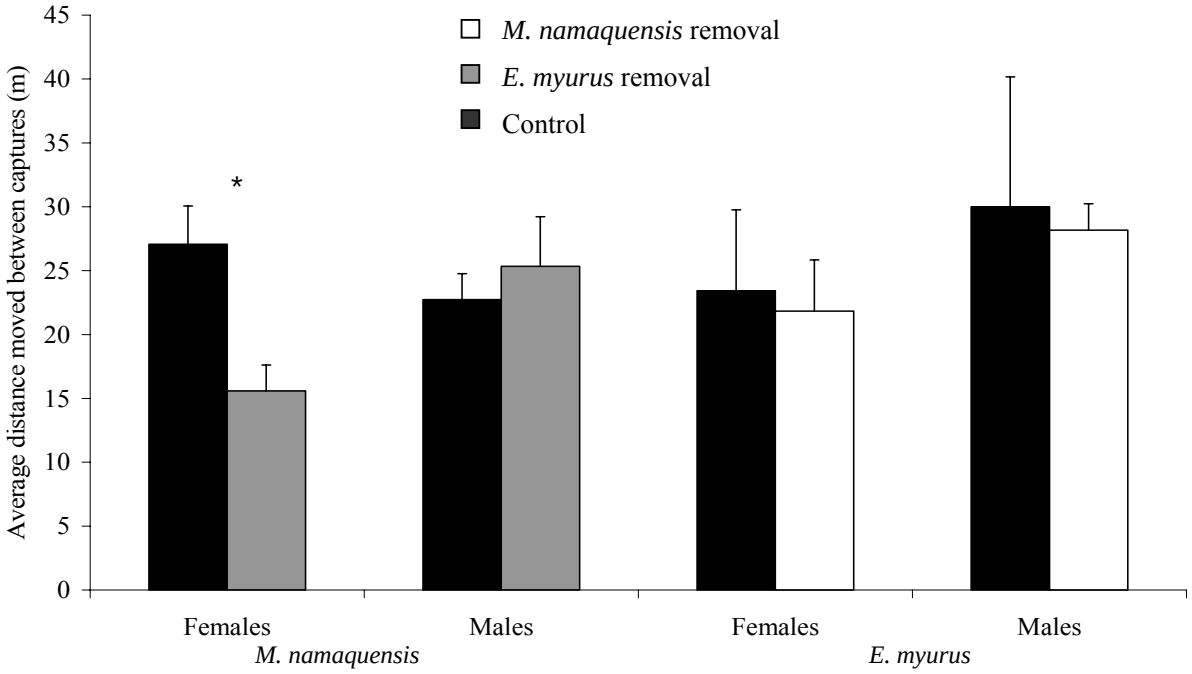


Figure 5.4. Mean (+ SE) distance moved between captures for *Michaelamys namaquensis* and *Elephantulus myurus* when individuals of coexisting species are removed. * indicate differences at $\alpha = 0.05$.

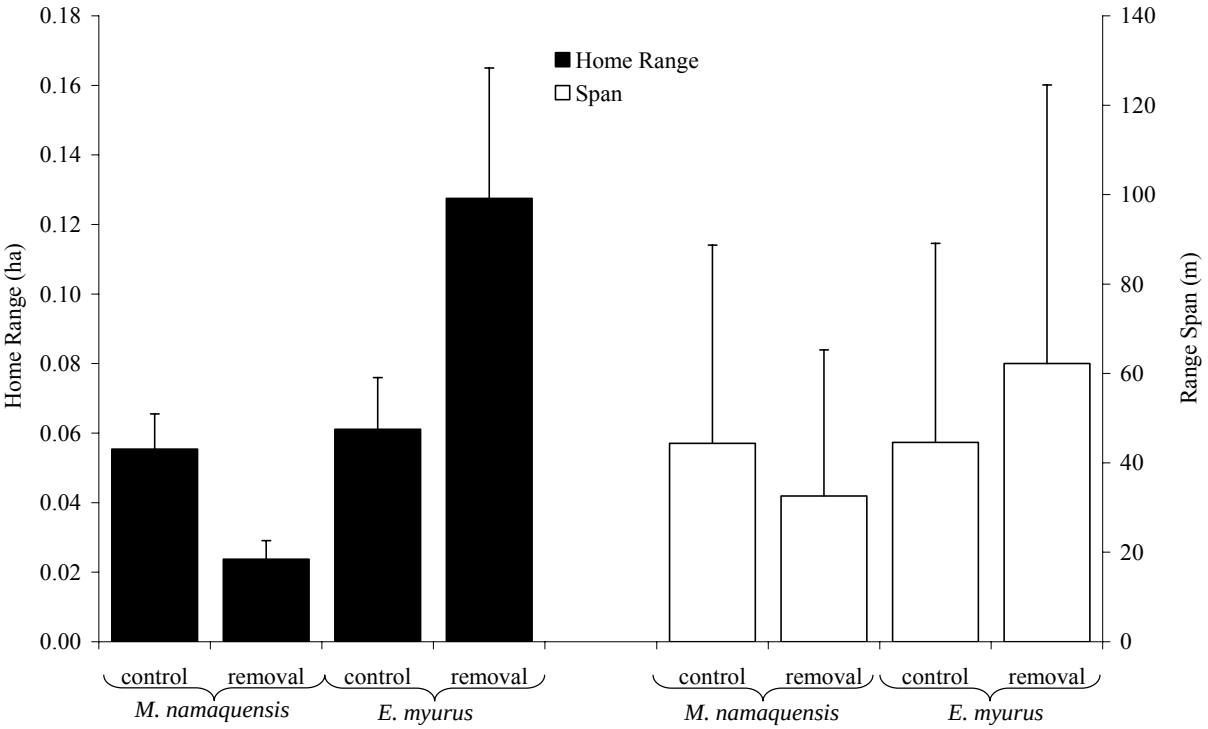


Figure 5.5. Differences in mean home range size and range span for *Michaelamys namaquensis* and *Elephantulus myurus* in the presence and absence of coexisting species. Error bars indicate SE, letters indicate significant differences at $\alpha = 0.05$

subdominant competitor (usually the generalist) should increase when the density of the superior competitor (normally the specialist) is reduced (Harris *et al.*, 2006). However, in the present study, there was no difference in density of *M. namaquensis* between the removal and control grids, indicating that removal of either species did not stimulate increased recruitment by *M. namaquensis*. There was a trend for the *M. namaquensis* removal grids to have a higher density of juveniles, especially in the late rain and early dry season. This could be as a result of seasonal breeding and/or due to increased recruitment as the per capita recruitment by *M. namaquensis* was higher on *M. namaquensis* removal grids than on control and *E. myurus* removal grids.

For *E. myurus*, a larger home range was expected when either *M. namaquensis* or *E. myurus* were removed, as *E. myurus* is a specialist and is solitary-living or forms monogamous pairs (Skinner and Chimimba, 2005; Lumpkin & Koontz, 1986). The lower density on *E. myurus* removal grids is almost certainly as a result of their removal with little recruitment. This also explains why the density of *E. myurus* on the control grid was not different to that of the *M. namaquensis* removal grids, but was higher than on the *E. myurus* removal grids. Low recruitment by *E. myurus* may be a result of aggressive (Ostfeld & Manson, 1996) or avoidance (see chapter 6) behaviour associated with territoriality within this species.

In contrast to my findings, most studies of population densities of coexisting species have found that the dominant, specialist or larger species tends to have a greater density (see for example Caro, 2001) and that when this density is reduced, the density of the subdominant, generalist or smaller species increases (see Christopher & Barrett (2006) and Ferreira & Van Aarde (1999) for examples). However, a reduction in the density of generalists or smaller species does not normally affect the density of the dominant, specialist or larger species (Kalcounis-Ruppell & Millar, 2002). This is typical of situations where interspecific competition drives community structure. However, no differences in density in response to the removal of a species does not necessarily indicate no interspecific competition (e.g. the densities of the dominant Black rat *Rattus rattus* and the Rice rat *Nesoryzomys swarthi*; Harris *et al.*, 2006) and other factors may better indicate the competition between species. Differences in ecological attributes such as density may reflect differences in resource use and may promote coexistence by reducing competition (Kryštufek *et al.*, 2007), especially if similar species respond differently to environmental fluctuations (Moro & Morris, 2000). For coexistence to occur, this interspecific

competition must be weaker than intraspecific competition (Dammhahn & Kappeler, 2008; Zhang, 2003).

The importance of interspecific competition may be reflected by the population dynamics of coexisting species (Brown & Zeng, 1989). The breeding and hence population dynamics of small mammals may be regulated by several factors (Muteka *et al.*, 2006; Lima *et al.*, 2003; Perrin & Boyer, 2000), including the presence of other species in the community (Smith, 2007; Keesing, 1998b; Ims, 1990). However, the relative importance of these factors depends on the life history strategies of the species (French *et al.*, 1975). Both *M. namaquensis* and *E. myurus* had distinct breeding seasons with *E. myurus* breeding restricted to the early rainy season and *M. namaquensis* starting breeding towards the end of the early rainy season and continuing into the late rainy season. This confirms the results of previous studies on these species (see chapter 3). Shargal *et al.* (2000) found that although *Acomys russatus* is dominant in terms of the number of individuals, it is more restricted in its breeding compared to *Acomys cahirinus*, suggesting an overlap in breeding resource requirements. This is similar to the present study in which *M. namaquensis* breeds during the latter part of the breeding season compared to elsewhere in its range (Skinner & Chimimba, 2005; De Graaff, 1981).

In both species of concern, more juveniles in comparison to adults were found on the removal grids. This indicates juvenile recruitment into the population, but is contrary to expectations, since I expected that juvenile recruitment would occur in *M. namaquensis* but not for *E. myurus*, since they have a low reproductive turnover. Only per capita recruitment of *M. namaquensis* on *M. namaquensis* removal grids increased. This possibly represents individuals entering the population to replace those removed during trapping.

In removal experiments, there are two major questions that can be asked about survival (after Pyke & Thompson, 1986) – does a higher proportion of individuals reach a particular age in the removal population than the control and/or is the life span of the individuals greater in the removal or control population? There was no difference in persistence or emigration (a surrogate measure of death rate as this cannot be accurately determined in trapping studies) among removal grid types. This could be an artefact of the trapping and time span of the removal experiments, since in previous studies both species had a maximum persistence of 22 months (see Chapter 3), significantly longer than in the present study which only lasted 12 months. However, no differences in survival were expected because factors that may affect persistence (e.g. predators; Rogovin *et al.*, 2004) were not changed or could not be controlled for (e.g. phylogenetically constraints or

environmental conditions; Reed *et al.*, 2007; Reed & Slade, 2006). Likewise, no differences in emigration were expected.

Habitat quality (including the presence of individuals of the same and different species that may change the quality due to competition for shared resources), population density of both coexisting species, sex, reproductive condition and behavioural responses may interact in a complex way to affect home range size (Getz *et al.*, 2005). Wolff (1985) found that removal of a coexisting species had no effect on the home range size of the White footed mouse *Peromyscus leucopus* and the Deer mouse *Peromyscus maniculatus*, indicating that interspecific interactions had little effect on space use. Similarly, there was no grid type effect on home range size or range span for either species. However, the increase of *E. myurus* home range and range span on *M. namaquensis* removal grids in comparison to *M. namaquensis* on *E. myurus* removal grids in the present study suggests that a high *M. namaquensis* density (as seen on control grids) restricts the space use of *E. myurus*. Likewise, the smaller home range and range span of *M. namaquensis* on *E. myurus* removal grids may be due to increased recruitment even though this recruitment was not significantly greater than on control grids. An unexpected result was that the average distance female *M. namaquensis* travelled on *E. myurus* removal grids was significantly less than on control grids. This possibly indicates that they were travelling shorter distances to access resources, which were previously being utilised by *E. myurus* individuals. As *E. myurus* is primarily an insectivore and insects are an important source of dietary protein in small mammals (Field, 1975), insects might represent a resource that would become available when the density of the specialist, *E. myurus*, is reduced. Under optimal conditions, specialists tend to out perform generalists. However, when conditions become unpredictable, the cost of being a generalist is outweighed by their plasticity of responses, both behavioural and physiological, to unpredictability, and generalists outcompete specialists (Manor & Saltz, 2008).

The role of competition in coexistence of species with similar life histories and behaviour has recently gained much attention in the literature with many studies considering the effects of removal of a competitor on small mammal community structure (Christopher & Barrett, 2006). The expected competition may be inferred in many ways but generally changes in density relate to the strength of competition while changes in habitat use relate to competition for resources (Hughes *et al.*, 1994). In my study, only the density of *E. myurus* changed, with lower densities recorded on *E. myurus* removal grids than control and *M. namaquensis* removal grids. However, in terms of habitat use, female

M. namaquensis travelled significantly shorter distances when *E. myurus* was removed than on control grids or those where *M. namaquensis* had been removed, thus suggesting that *M. namaquensis* and *E. myurus* potentially compete for resources, as suggested by Hughes *et al.* (1994). Nevertheless, changes in both density and habitat use may have direct influences on the life histories of the coexisting species. For example, the dominant and slightly larger Grey mouse lemur *Microcebus murinus* has a clumped distribution resulting in patches of high density while the coexisting Madame Berthe's mouse lemur *Microcebus berthae* has a more random distribution (Dammhahn & Kappeler, 2008). This has direct influences not only on their social structure but also their life history strategies, and Dammhahn & Kappeler (2008) propose that life history trade-offs rather than niche separation best explain the pattern of coexistence. In contrast, there are no clear indications of coexisting Olive grass mice *Akodon olivaceus* or Rice rats *Oryzomys longicaudus* limiting each other in terms of their densities or demographic characteristics (Murua *et al.*, 1987).

In my study, the density of *E. myurus* remained low in areas from which they were removed but there was a high juvenile recruitment. Their densities tend to be stable but relatively low and thus *E. myurus* is more *K*-selected and typifies Type II animals (French *et al.*, 1975; Pianka, 1970).As the specialist in the system, and assuming that specialists are usually dominant, there is probably little competition for resources despite their density being lower than that of *M. namaquensis*. Rather, their home range size may be limited as they had comparatively larger home ranges on *M. namaquensis* removal grids compared to *M. namaquensis* on *E. myurus* removal grids. On the other hand, although *M. namaquensis* also has high recruitment of juveniles on removal grids, their densities tend to be less stable. They thus are a more *r*-selected or Type I species (French *et al.*, 1975; Pianka, 1970). This is supported by the lack of differences in *M. namaquensis* density between the grid types. Even though life history strategies are phylogenetically constrained, there is a trend for *M. namaquensis* breeding to start earlier in the season when *E. myurus* is removed from the system, indicating that *E. myurus* may influence the breeding season of *M. namaquensis*. Additionally, although changes in habitat use were not directly measured, *M. namaquensis* females tended to travel shorter distances on removal grids. These results imply that there was a change in patch use and thus competition for resources (Hughes *et al.*, 1994), especially for those resources which have high overlap e.g. food and microhabitat (see Chapter 2).

Chapter 6
Behavioural interactions between a coexisting rodent and macroscelid

Abstract

A number of mechanisms are known to influence coexistence in small mammal communities. However, studies of the role of behavioural interactions (within and between species) in promoting species coexistence are under represented in the literature. I studied the behavioural interactions of two coexisting small mammals, the Namaqua rock mouse *Michaelamys 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 in the field. Interspecific dyads displayed significantly more active avoidance behaviour, and there was no support for the prediction that the larger, more specialist species, *E. myurus,* is behaviourally dominant over *M. namaquensis*. Intraspecific encounters of *E. myurus* showed significantly more passive avoidance and amicable behaviour, whereas the behaviour of *M. namaquensis* did not differ between intra- and inter-specific encounters, both of which were characterised by low levels of aggression and amicability. Thus, due to the lack of aggression, direct competition appears weak and instead mutual avoidance may reduce or minimise interspecific interactions, potentially promoting coexistence.

Keywords: avoidance; coexistence; *Elephantulus myurus*; intraspecific behaviour; interspecific behaviour; *Michaelamys namaquensis*

Introduction

Coexistence may occur as a result of spatio-temporal variability in resource abundance, density dependant resource utilisation rates and non-equilibrium between resource and consumer population dynamics (Zhang, 2003; Brown, 1989a). As a result, specialists and generalists are able to coexist, since generalists exploit habitats unused or underused by the specialists (Manor & Saltz, 2008). Alternately, factors such as predation and competition (between individuals of both the same and different species) maintain populations below an equilibrium point were generalists would exploit all patches regardless of the density of the specialist (Morris, 1996). This would also promote

coexistence through different resource utilisation and/or activity patterns (Kalcounis-Ruppell & Millar, 2002; Archer, 1970). Many of these interactions may however not be immediately apparent due to a combination of factors, such as metapopulation dynamics and habitat characteristics and preferences (Ferreira & Van Aarde, 1999).

Behavioural interactions have received little attention in studies of coexistence (Harris *et al.*, 2006; Perri & Randall, 1999), yet some of the most important biotic factors influencing small mammal communities are the interactions both within and between species (Ovadia *et al.*, 2005; Zhang, 2003; Ferreira & Van Aarde, 1999; Meserve *et al.*, 1996; Hughes *et al.*, 1994; Holbrook, 1979; Douglass, 1976). 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).

There are many possible outcomes of these interactions that may influence species coexistence. The interactions may be asymmetrical for various reasons such as the larger species displacing the smaller species, especially in aggressive encounters (Pinter-Wollman *et al.*, 2006; Perri & Randall, 1999) or because some species are more sensitive to the degree of resource overlap (Schoener, 1983), so that the specialist dominates over the generalist. Additionally, competitive interactions affect species differently and influence the same species differently in different locations, because of spatial differences in species composition and interactions (Dammhahn & Kappeler, 2008), the long term results of which may only become apparent after a lag period (Meserve *et al.*, 1996). Also, 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 (Schoener, 1983; Holbrook, 1979; Conley, 1976). However, increased similarity of resource utilisation may enhance the chances for competition (Conley, 1976).

Interspecific competition has been found previously in small mammals (Abramsky *et al.*, 2001) but is poorly understood because it has been measured differently and at different temporal and spatial scales (for example, snapshots or over several years), making results incomparable (Meserve *et al.*, 1996). Additionally, 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 among conspecifics (Zhang, 2003; Perrin *et al.*, 2001; Perri & Randall, 1999). Additionally, according to the classical niche theory, coexistence is only possible if the strength of intraspecific competition is greater than that of interspecific competition (Dammhahn & Kappeler, 2008).

Two crepuscular small mammal species, the Namaqua rock mouse *Michaelamys namaquensis* (47.5g; range 33g – 57.9g; Skinner & Chimimba, 2005) and the Rock sengi *Elephantulus myurus* (60g; range 48g – 98g; Skinner & Chimimba, 2005), coexist on rocky outcrops in southern Africa. Previous studies (Chapter 2) have shown that they have similar microhabitat and dietary requirements especially in the late rainy season, when there is potentially a high degree of overlap in resource use, although *E. myurus* is assumed to be more specialised, both in terms of diet and habitat requirements, than *M. namaquensis*.

The aim of this study was to establish intra- and interspecific dyadic encounters in neutral arenas to investigate the behavioural interactions of coexisting *M. namaquensis* and *E. myurus*. Assuming that behavioural interactions promote coexistence in the two species, I predicted that one species would be dominant over the other species, resulting in higher levels of aggression in interspecific than intraspecific dyads. Specifically I expected that the larger, more specialised *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), the interactions between intraspecific and interspecific dyads that had not made prior contact (i.e. originated from different grids) were also studied. According to the dear enemy phenomenon, it was predicted that unfamiliar conspecifics would display higher levels of aggression than familiar conspecifics (Zuri & Rado, 2000; McGuire & Getz, 1998), and I questioned whether a similar outcome was likely with different species.

Methods

This study was conducted at eZemvelo Nature Reserve (25^{o} 42’ 26” S 29^{o} 01’ 02”E), Gauteng Province, South Africa. The region receives summer rainfall of around 650 mm per year, and average temperatures fluctuate between 12.5 ^{o}C in winter to 26 ^{o}C in summer. Vegetation on the reserve comprises grasslands, interspersed with rocky outcrops along ridges.

Michaelamys namaquensis and *E. myurus* are the only two small mammal species occurring on rocky outcrops in the study site. This 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 (Chapter 2). Individual *M. namaquensis* and *E. myurus* were trapped using PVC live-traps (29 x 6 x 7 cm) scattered randomly in three different rocky outcrops. Traps were baited (mixture of oats, raisins, sunflower seeds, salt, peanut butter and oil), covered with vegetation to buffer against fluctuating temperatures, and checked at dawn and dusk. Individuals were weighed and placed individually in holding cages (26 x 20 x 14 cm) overnight, and were provided with water, Epol ® mouse pellets and seeds *ad lib*.

Experiments were conducted on a neutral rocky outcrop (approximately 20m where animals were kept) to decrease the effect of the dear-enemy phenomen. Three types of dyads were established: *M. namaquensis* x *M. namaquensis*, *E. myurus* x *E. myurus* and *M. namaquensis* x *E. myurus*. Dyads were all same sex adults and comprised 10 replicates each. For dyads involving familiar animals (i.e. trapped on the same rocky outcrop), individuals were used twice, once in an intraspecific dyad and again in an interspecific dyad, following a rest period of >3 hours. The order in which animals were used (intra- vs. interspecific dyads) was randomly determined. The short period between re-use in dyads met 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 activities (e.g. territorial defence) in nature. Before their release onto their rocky outcrop, individuals were individually marked (fur-clipped) 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. Again, individuals were used twice (one intra- and one interspecific dyad). After experiments, they were marked as described above and released on their rocky outcrop of origin.

Dyadic encounters were staged in neutral arenas (i.e. tanks measuring 45 x 30 x 30 cm), with 3 metal sides (painted a neutral colour) and one side of clear PVC to facilitate observations. The floors of the tanks were covered with approximately 2 cm of woodshavings and straw. After every encounter, the tanks were washed with water and alcohol to remove odours of previous occupants. Dyads were performed during peak activity times of both species (i.e. early morning). To identify subjects in same species dyads, individuals were marked dorsally with water-based, non-toxic paint. Individuals in different 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 parts. The barrier was lifted after an acclimatisation period of 5 minutes and encounters were videotaped for 10 minutes. Using continuous recording (Martin &

Bateson, 1993), the frequency of five behaviours were scored for each dyad member. The behaviours scored were aggressive (e.g. chasing, attacking, biting), amicable (e.g. allogrooming, naso-naso 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 (walking around the arena). Changes in behaviour were scored if the behaviour was performed for more than 2 seconds.

Data was analysed using STATISTICA 6 (Statsoft; www.statsoft.com). The dyad values for familiar dyad partners (i.e. those from the same grid) were summed. The data set was then square root transformed to meet the assumptions of normality. A General linear model (GLM) with a multivariate design was used to compare the five behaviours (dependent factors) for the dyad types and sex of dyad members (independent factors); the difference in body mass between dyad members was included as a co-variate in the model. In a second analysis, using a similar GLM, the behaviour of dyads comprising familiar partners with those that were unfamiliar (i.e. from different grids) was compared. Paired-t tests were used to compare the body mass of dyad partners, and χ^2 analyses were used to compare the frequency of aggression and explore behaviours of dyad partners in interspecific dyads. All tests were two-tailed and α was set at 0.05.

Results

No dyads engaged in damaging fights. The body mass of individuals did not differ significantly in intraspecific dyads involving familiar partners, for *M. namaquensis* (male: mean $\pm$ SE: 49.3$\pm$1.87, t_9=1.48, p=0.173; female: 38.8$\pm$1.33, t_9=0.84, p=0.422) and *E. myurus* (male: 62.3$\pm$1.62, t_9=1.26, p=0.238; female: 59.9$\pm$1.20, t_9=1.21, p=0.256) dyads. Although *E. myurus* is usually not significantly heavier than *M. namaquensis*, in interspecific dyads, *E. myurus* was significantly heavier than *M. namaquensis* (male: 65.7$\pm$1.04 vs. 54.2$\pm$0.49, t_9=8.95, p<0.001; female: 56.4$\pm$1.28 vs. 45.9$\pm$1.84, t_9=7.50, p<0.001). The same pattern was observed in dyads involving unfamiliar partners, as follows: *M. namaquensis* (51.9$\pm$1.07, t_9=0.97, p=0.356), *E. myurus* (61.5$\pm$1.26, t_9=0.17, p=0.897), and *M. namaquensis* x *E. myurus* (61.0$\pm$1.65 vs. 51.4$\pm$1.53, t_9=4.25, p=0.002). This is a random effect, but may be due to the requirement of not re-using individuals.

Dyads involving familiar individuals - Dyad type was a significant predictor of behaviour in the present study ($F_{10, 98}$=37.23, p<0.001). There was no significant effect of sex ($F_{5, 49}$=1.19, p=0.326) and dyad type x sex ($F_{10, 98}$=0.75, p=0.136). Interestingly, the difference in body mass between dyad partners (co-variate) was also not significant

($F_{5,49}$=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 (Figure 6.1.). The interspecific dyads displayed the highest levels of avoidance and ignore behaviours and the lowest levels of explore behaviour (Figure 6.1.).

A high frequency of aggressive and explore behaviours by individuals in dyads can be used as a dominance measure (see Cranford and Derting, 1983). I compared the overall frequency of these behaviours in partners of interspecific dyads and found no significant differences ($p>0.05$; χ^2 analyses) for either behaviour, so I were not able to determine if one species was dominant over the other.

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 behaviours ($F_{10,98}$=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 behaviour. Again, there was no significant influence of the difference of 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 behaviours, and the highest avoidance and ignore behaviours. Differences in familiarity influenced the behaviour of intraspecific dyads, which showed more aggression and avoidance, and less amicable and explore behaviour in encounters between unfamiliar than familiar dyads.

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

Discussion

The aim of the study was to assess whether behavioural interactions would influence coexistence in *M. namaquensis* and *E. myurus* by assessing the similarities and differences in behaviour of the species in intra- and inter-specific encounters. The factors influencing coexistence between species include the numbers and types of coexisting species present and their patterns of resource utilisation, the environment in which they occur, and spatio-temporal variations in activity (Dammhahn & Kappeler, 2008; Connell, 1983). Specifically, the specialist is expected to be dominant over the generalist (Kalcounis-Ruppell & Millar, 2002; Morris, 1996). The larger species is also expected to

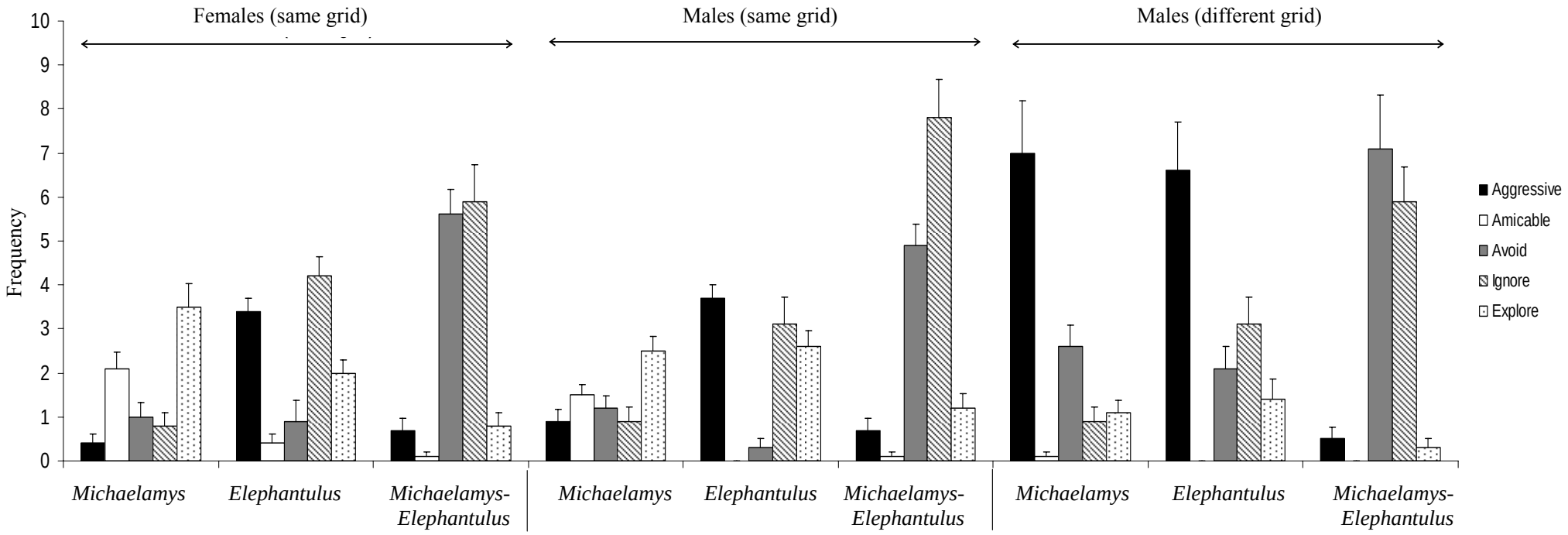


Figure 6.1. Behavioural frequencies (mean ± SE) from three same sex dyad types, two intraspecific (*Michaelamys*; *Elephantulus*) and one interspecific (*Michaelamys-Elephantulus*).

be dominant and more aggressive than the smaller species (Perri & Randall, 1999). In both of the above cases, the more specialised and/or larger species would thus restrict the access of the generalist and/or smaller species to shared resources thus promoting coexistence. Thus, *E. myurus* was expected to be dominant over, and hence display more aggressive behaviour than *M. namaquensis*, which was expected to show more avoidance behaviour in interspecific dyads. However, 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 encounters.

One possible reason for the low levels of aggression is that competition is likely to occur over some resource that is important to both species that was not provided in the neutral arena, especially if there is a minimum threshold density of either the resource or the individuals at which animals become aggressive (Wolff, 1985). Another reason is that both species, but especially *E. myurus*, showed low levels of exploratory behaviour in all encounters, but not when housed alone (*pers. obs*.). Thus, aggression may be avoided, as individuals tended to ignore each other. Passive avoidance may thus be an important conflict avoidance behaviour for *E. myurus*. Therefore, instead of displaying overt aggression, these two species tended to minimise contact with each other. Similarly, when the Rufous sengi *Elephantulus rufescens* and a spiny mouse species *Acomys* spp. co-occur, *E. rufescens* seems to avoid the *Acomys* spp. (Neal, 1982b).

The relative strengths of intra- and interspecific interactions are an important consideration for coexistence (Cranford & Derting, 1983), since if Species A is a superior competitor to Species B, the density of Species B is likely to decrease but if intraspecific competition is stronger than interspecific competition in Species A, the population density of Species A may be self-regulated below the interspecific competition threshold (Connell, 1983). Agonistic behaviour among conspecifics is common, as 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 higher and thus levels of intraspecific aggression should be predictably higher than in the more generalist *M. namaquensis*. Additionally, *E. myurus* forms monogamous pairs whereas *M. namaquensis* lives in small groups (Skinner & Chimimba, 2005), so that some level of tolerance would be expected between conspecific *M. namaquensis*.

Indeed, *M. namaquensis* showed a greater levels of amicability and lower levels of aggression towards conspecifics in dyads with familiar partners. Interestingly, there was no difference in the frequency of behaviours displayed by *M. namaquensis* in intra- and

interspecific interactions. Contrary to expectations, however, more amicable behaviour was shown by *E. myurus* individuals in intraspecific encounters than interspecific encounters. One reason may be that *E. myurus* occurred at low densities on the study site, possibly too low for intraspecific competition to be an important consideration, but this could be the result of prior familiarity between dyad partners.

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, which concurs with the "dear enemy" phenomenon (Temeles, 1994). Nonetheless, familiarity of dyad members did not influence the behaviour of interspecific dyads.

In a study of the behavioural interactions of two vole species in captivity, (Douglass, 1976) showed that the Meadow vole *Microtus pennsylvanicus* was dominant over the Montane vole *Microtus montanus*, yet they are often caught in adjacent traps in the field, suggesting that interspecific interactions may not be the only factor promoting their coexistence, but may become more important when resource utilisation overlaps, resulting in the exclusion of the subdominant species. In support, the intensity of interspecific interactions between Long-tailed voles *Microtus longicaudus* and Mexican voles *Microtus mexicanus* varied seasonally depending on the availability of space (Conley, 1976). Likewise, the Broad-toothed mouse *Apodemus mystacinus* was dominant over the Common spiny mouse *Acomys cahirinus* in Mediterranean afforested landscapes, but this was especially evident when resources where less abundant (Manor & Saltz, 2008). This lends support to a theory that although *M. namaquensis* and *E. myurus* are not aggressive in a neutral arena, despite their similarity in resource use, other factors may be promoting their coexistence. Additionally, competitive interactions did not affect the coexistence of the Rice rat *Oryzomys longicaudus*, Olive grass mouse *Akodon olivaceus* and Long-haired grass mouse *Akodon longipilis* (Murua *et al.*, 1987).

Contrary to expectations, interspecific dyads were characterised by higher levels of avoidance behaviour than aggression. Additionally, *M. namaquensis* and *E. myurus* both responded differently in interactions with intra- and interspecific individuals: *E. myurus* displayed avoidance rather than aggression and *M. namaquensis* behaved similarly in intra- and inter-specific interactions with low levels of aggression and amicability. Thus, although the behavioural mechanism of coexistence between the species is probably different, active avoidance may prevent interactions, or at least minimise interspecific contact between the species. In another study, I showed that high levels of home range

overlap between the species (from 22% in *M. namaquensis* males to 34.3% in *E. myurus* females; unpublished data). Therefore, rather than overt aggression, it is possible that other factors, in addition to active avoidance promote coexistence between *M. namaquensis* and *E. myurus*.

Chapter 7
Discussion

The main objective of this research was to study mechanisms of coexistence between *M. namaquensis* and *E. myurus* on rocky outcrops in the highveld of South Africa. Specifically, dietary overlap and micro- and macro-habitat use (in terms of home range) were compared to assess the similarity of resource use between these species. Population characteristics, such as density, were examined as these may assist in revealing differences in the use of resources. Additionally, species differences in resource and habitat use may be due to behavioural mechanisms, and thus the behavioural interactions of these species were studied. Lastly, to see if competition had an effect, the response of both *M. namaquensis* and *E. myurus*, in terms of population characteristics and home range use, was assessed during removal experiments. The above mentioned characteristics were selected as previous studies have shown their importance in promoting coexistence, especially as they respond to changes and variability in the environment (Brown, 1989b; Perri & Randall, 1999; Perrin & Kotler, 2005). Environmental variability promotes coexistence (Perrin & Kotler, 2005) through specialisation or through spatial and temporal differences in resource use (M'Closkey, 1976; Kotler & Brown, 1988; Brown, 1989b; Mitchell *et al.*, 1990; Yunger *et al.*, 2002; Zhang, 2003; Bonesi & Macdonald, 2004; Ben-Natan *et al.*, 2004; Harris *et al.*, 2006).

Differences in resource use may act to reduce interspecific competition (Kinahan & Pillay, 2008). In desert ecosystems, small mammal coexistence has been shown to be promoted through spatial and temporal differences in diet and habitat selection, which may be mediated by aggressive interference (Brown, 1989b; Kalcounis-Ruppell & Millar, 2002), but little is known about the co-existence of small mammals outside of desert systems. Recently, factors such as morphology, behaviour (Brown & Zeng, 1989) and reproductive characteristics (Perrin & Kotler, 2005) have also gained attention as possible factors promoting coexistence. Seldom do any of these factors act in isolation (Chesson, 1986).

Outcomes from the present study

Time of activity

Temporal partitioning promotes coexistence because if there is a high amount of overlap, one or more species may be forced to be active at different times rather than

occupying suboptimal habitats (Yunger *et al.*, 2002). Additionally, time of activity may also influence susceptibility to predation. Predator susceptibility influences coexistence as species may modify their behaviours to become less conspicuous if they are subject to higher predation risks than other species in the community (Meserve *et al.*, 1996).

Both *M. namaquensis* and *E. myurus* are of a similar size, have similar locomotion patterns and based on trapping data, occur in the same area and are active at the same time. Thus, there is no broad temporal separation and both species would be subject to similar levels of predation. As such, neither predator avoidance nor differences in time of activity are likely to promote coexistence.

Diet

Diet selection depends on numerous variables, including the type, number and seasonal variations of food resources available (Brown & Lieberman, 1973; Perrin & Swanepoel, 1987; Rabiu & Rose, 1997), presence of competing species (Kalcounis-Ruppell & Millar, 2002) and adaptations of the consumer (Kerley, 1989; Abt & Bock, 1998). Coexisting species may be able to modify their dietary requirements, by utilising different parts of the resource or using the resource at different times, which can reduce competition (Kinahan & Pillay, 2008). Thus, especially if there are specialists present, dietary overlap can be reduced but if there are many generalists present, or species with similar dietary requirements, overlap and hence competition is increased, reducing the chances of coexistence (Chesson, 1986).

Although this study confirmed that that *E. myurus* is a specialist, feeding on predominantly insects (Churchfield, 1987; Skinner & Chimimba, 2005), and *M. namaquensis* is omnivorous (De Graaff, 1981; Skinner & Chimimba, 2005), faecal analysis showed that dietary differences alone are unlikely to promote coexistence between *M. namaquensis* and *E. myurus* due to the high level of overlap, especially of seasonally variable and limiting resources. Some components did not vary seasonally (e.g. stems for both species and leaves for *E. myurus*), possibly due to the low significance of these items. However, there was seasonal variation in other components, especially seeds and arthropods. This variation could represent seasonal availability of resources (Claunitzer *et al.*, 2003; e.g. the remains of leaves in the faeces of *M. namaquensis* peaked towards the end of the dry season/beginning of the early rainy season when plant material was green and decreased towards the end of the late rain season when leaves were probably not as nutritious; Owen-Smith, 2002). It may also represent the availability of other resources

(e.g. for *M. namaquensis*, the percentage of seeds increased when the percentage of arthropods decreased in the dry season). Another potential reason with important implications for coexistence is that access to resources may be limited due to other species monopolising access. In this study, there seems to be high overlap in the percentage and the frequency of arthropods in the faeces, especially in the late rain season, indicating possible competition for resources. Although only broad comparisons were made (i.e. not to species/specific part of the food consumed) between *M. namaquensis* and *E. myurus*, the potential for competition is still high, especially when this resource is seasonally limiting. However, the two species may differ in their seasonal dietary requirements, as was found for the omnivorous Striped mouse *Rhabdomys* spp. and herbivorous Vlei rat *Otomys irroratus* (Curtis & Perrin, 1979) and for the Multimammate mouse *Mastomys* spp. and the Single striped mouse *Lemniscomys rosalia* (Field, 1975). Differences in dietary preferences do however promote coexistence in the California mouse *Peromyscus californicus* and the Brush mouse *P. boylii*. These differences result in differences in habitat use (Kalcounis-Ruppell & Millar, 2002), which may also influence microhabitat selection, which also promotes coexistence, as was found by Kerley *et al.* (1990) in a small mammal community in the Kalahari.

Habitat

Within a community, species may interpret and rank different variables as being important which facilitates coexistence (Kotler & Brown, 1988; Yunger *et al.*, 2002). Differences in habitat selection in space (Kotler & Brown, 1988; Jorgensen, 2004) or time (M'Closkey, 1976; Brown, 1989a), due to interspecific interactions (Douglass, 1976; Kerley *et al.*, 1990), individual adaptations or perceived threats (Brown, 1989b) may facilitate species co-existence through various mechanisms (Rosenzweig, 1981).

There is much debate regarding the issue of scale in habitat selection (see Noss (1990) and Kotliar & Wiens (1990), and I used the definitions proposed by Jorgensen (2004), who refers to a microhabitat as those characteristics of a patch where an individual is found in terms of vegetation structure and cover, whereas macrohabitat refers to the habitat/s contained within the home range of an individual.

While microhabitat (i.e. the areas where individuals were most frequently trapped) selection patterns were not clear in my study, the preferences of *M. namaquensis* and *E. myurus* did not differ significantly and there is a high level of overlap in their association with many of the variables measured. This was expected as both species are known to

associate with a high degree of rock cover and thus both species were also associated with a low level of vegetation cover, although the presence *M. namaquensis* was sometimes associated with shrub availability, possibly for protection against predation. Thus, microhabitat selection on its own does not seem to be an important factor promoting coexistence between *M. namaquensis* and *E. myurus*. However, frequently microhabitat differences alone do not promote coexistence. For example, in the Karoo, microhabitat differences act together with differences in body size and activity times to facilitate co-existence of up to six small mammal species (Kerley, 1989).

However, individuals may perceive the heterogeneity of patches differently (Fuller & Perrin, 2001; Cameron & Spencer, 2008), which may be indicated by macrohabitat use. If species with similar requirements occupy adjacent, non-overlapping home ranges, these home range differences may promote coexistence (Bleich & Price, 1995; Ferreira & Van Aarde, 1999; Christopher & Barrett, 2006), especially if home ranges provide a reliable indicator of resource partitioning (Rosenzweig, 1981; Kalcounis-Ruppell & Millar, 2002; Jorgensen, 2004; Bonesi & Macdonald, 2004). Many factors may influence home range distributions (Burt, 1943; Wolff, 1985; Ostfeld, 1990; Ribble *et al.*, 2002; Priotto *et al.*, 2002; Schradin & Pillay, 2006; Pasch & Koprowski, 2006; Orland & Kelt, 2007; Cooper & Randall, 2007), including the perception of patch quality (Priotto *et al.*, 2002), which may be influenced by the density of co-existing species (Manor & Saltz (2008), but see Ribble & Stanley (1998) and Wolff (1985) for examples of other factors such as population density, sex, age, body size and food availability).

Results from interspecific home range overlap indicate that the percentage of overlap did not differ between *M. namaquensis* and *E. myurus*, except for *M. namaquensis* males which overlapped more with *E. myurus* individuals than *M. namaquensis* individuals. This may be due to the high degree of resource overlap between the species, as was found for the Grey mouse lemur *Microcebus murinus* and Madame Berthe's mouse lemur *Microcebus berthae*, where coexistence was facilitated by differential use of a core area (Dammhahn & Kappeler, 2008). While there is a high level of home range overlap between the species, this only indicates spatial overlap and not temporal overlap. Although unlikely to promote coexistence between the two species, temporal overlap does facilitate coexistence between the Rice rat *Nesoryzomys swarthi* and Black rat *Rattus rattus* possibly due to interference competition by *R. rattus* (Harris *et al.*, 2006).

The non-exclusivity of home ranges, together with no differences in home range size between the species, implies that neither *M. namaquensis* nor *E. myurus* is dominant.

It has been hypothesised that subdominant species would have larger home ranges to minimise contact with the dominant species (Douglass, 1976). It is also possible that the subdominant species needs larger areas to search for resources. Thus, when a species is released from this competitive effect, a subdominant species would be expected to decrease its home range size and range span.

Removal experiments reinforced the idea that neither species is completely dominant since there was no difference in home range size or range span for either species when the other species was removed. Similarly, Wolff (1985) found that removal of a coexisting species had no effect on the home range size of the White footed mouse *Peromyscus leucopus* and the Deer mouse *Peromyscus maniculatus*. A strong piece of evidence supporting the hypothesis of co-dominance is that *M. namaquensis* females decreased the distance they travelled between successive captures when *E. myurus* was removed. This implies that *E. myurus* may restrict access to shared resources, either behaviourally or by utilising them first (Hughes *et al.*, 1994), as predicted by the specialist-generalist hypothesis of coexistence (Manor & Saltz, 2008).

Home range size and overlap also give an indication of social organisation (Schradin & Pillay, 2005; Cooper & Randall, 2007). The present study confirmed that *M. namaquensis* is polygynous while *E. myurus* is probably monogamous. Additionally, *E. myurus* occurred at low densities in comparison to *M. namaquensis*. These differences in spatial and social organisation may promote co-existence through differences in the intensity of resource use (Gaulin & FitzGerald, 1988) and have been shown to facilitate coexistence in the Prairie vole *Microtus ochrogaster* and the Meadow vole *M. pennsylvannicus* (Gaulin & FitzGerald, 1988). However, density may not only be a function of home range distribution (e.g. clumped vs. random), but also be a function of life history characteristics (Dammhahn & Kappeler, 2008).

Life history and population dynamics

Life history characteristics that result in species to minimising or avoiding competition may promote coexistence (Brown & Zeng, 1989; Dammhahn & Kappeler, 2008) because these traits may be an adaptive response to a particular set of environment conditions (Neal, 1986). This is because life history characteristics are generally accepted to be the result of a trade-off between reproductive investment and survival (Perrin, 1989) and are generally related to various environmental variables (Pianka, 1970; French *et al.*, 1975; Neal, 1986; Chesson, 1986; Perrin & Swanepoel, 1987; Willan & Meester, 1989;

Mills *et al.*, 1992; Chesson, 2003; Muteka *et al.*, 2006). Both biotic (e.g. physiological and behavioural characteristics; Neal (1986) and abiotic (e.g. rainfall; Perrin & Swanepoel, 1987; Keesing, 1998a) and food availability (Perrin & Boyer, 2000)) factors are known to be regulators of small mammal breeding. However, the presence of other species (Chesson, 1986; Ims, 1990; Keesing, 1998b; Smith, 2007) and hence the importance of competition in coexistence of species with similar life histories and behaviour has recently gained much attention in attempting to explain variation in life history strategies and population dynamics (Christopher & Barrett, 2006). Generally, interspecific competition results in changes in density (related to the strength of competition) or changes in habitat use (competition for resources; Hughes *et al.*, 1994).

Michaelamys namaquensis has large population fluctuations, which typifies *r*-selected or Type I species while *E. myurus* tends towards *K*-selection/Type II species with comparatively lower and more stable densities (Pianka, 1970; French *et al.*, 1975). Apart from lower *E. myurus* densities on *E. myurus* removal grids, density did not vary with removal treatments. Although there was high recruitment of *E. myurus* juveniles on *E. myurus* removal grids, no differences in density may be the result of aggression and territoriality within the species (Ostfeld & Manson, 1996). Recruitment may also be a function of *E. myurus* breeding strategy and low replacement rates, which is supported by no differences in per capita recruitment or emigration on different grid types. *Michaelamys namaquensis* recruitment was not stimulated by the removal of either species, although there was a trend for increased juvenile density on *M. namaquensis* removal grids, which may be due to increased per capita recruitment. It was expected that more *M. namaquensis* juveniles would occur on *M. namaquensis* removal grids due to immigration, but due to low reproductive turnover, this was not expected for *E. myurus*. However, no changes in density were found for either species. Likewise, coexisting Olive grass mice *Akodon olivaceus* or Rice rats *Oryzomys longicaudus* do not limit each other in terms of their densities (Murua *et al.*, 1987). This contrasts with most other studies which tend to find that the subdominant, generalist or smaller species have a lower density than coexisting dominant, specialist or larger species (Ferreira & Van Aarde, 1999; Caro, 2001; Christopher & Barrett, 2006): with the removal of the subdominant, generalist or smaller species not affecting the density of the dominant, specialist or larger species but a reduction in the density of these species usually results in an increase of the former type of species (Kalcounis-Ruppell & Millar, 2002). Although changes in density are typical of competition-driven communities, no change in density does not necessarily indicate a lack

of interspecific competition, as was shown by Harris *et al.* (2006) in *R. rattus* and *N. swarthi*. Despite no changes in density between the two species, differences in density may still promote coexistence through different intensities of resource use, thus reducing competition (Kryštufek *et al.*, 2007) especially if the species react differently to environmental variations (Moro & Morris, 2000; Harris *et al.*, 2006).

Both *M. namaquensis* and *E. myurus* had distinct breeding seasons, confirming results of previous studies (De Graaff, 1981; Skinner & Chimimba, 2005) with *E. myurus* breeding restricted to the early rainy season and *M. namaquensis* starting breeding towards the end of the early rainy season and continuing into the late rainy season. Timing of breeding is often constrained, not only by the environment but also phylogenetically in terms of age of reproduction. *Michaelamys namaquensis* tended to start breeding earlier in the season when *E. myurus* was removed which may indicate that *E. myurus* restricts access to particular resources that are necessary for breeding, although elsewhere in its range, breeding starts earlier (De Graaff, 1981; Skinner & Chimimba, 2005; Muteka *et al.*, 2006). Similarly, although the Golden spiny mouse *Acomys russatus* is dominant in terms of the number of individuals, it is more restricted in its breeding compared to the Common spiny mouse *Acomys cahirinus*, suggesting an overlap in breeding resource requirements (Shargal *et al.*, 2000). Chesson (1986) suggest that slight seasonal differences in breeding strategy which results in asynchronous breeding and hence densities peaking at slightly different times may promote coexistence through reduced competition for shared resources as was found by Perrin & Kotler (2005) in a community of Gerbils *Tatera* spp. and the Striped field mouse *Rhabdomys* spp. in the Kalahari.

Under the lottery model of competition, although the dominant species is expected to have a higher density, subdominant species are able to coexist as long as there are periods of strong recruitment (Chesson, 1986). From breeding and removal studies, it appears that although *E. myurus* (dominant) does not reduce the density of *M. namaquensis* (subdominant), it does restrict the timing of breeding of *M. namaquensis*. Due to differences in resource use, there appears to be some degree of temporal separation in breeding, which would promote coexistence in these two species.

Behavioural interactions and competition

Although behavioural interactions have received little attention in studies of coexistence studies (Perri & Randall, 1999; Harris *et al.*, 2006), these interactions, both within and between species, may influence small mammal community structure (Douglass, 1976; Holbrook, 1979; Hughes *et al.*, 1994; Meserve *et al.*, 1996; Ferreira & Van Aarde,

1999; Zhang, 2003; Ovadia *et al.*, 2005). Although intraspecific competition should always be higher than interspecific due to the similarity of resource use (Connell, 1983; Perri & Randall, 1999; Perrin *et al.*, 2001; Zhang, 2003; Dammhahn & Kappeler, 2008), competitive coexistence may be more pronounced if there is temporal or spatial variation in resource abundance (Chesson, 1986). Small behavioural changes may reduce competition between species, thereby promoting coexistence. Competitive interactions may be direct or due to interference (e.g. fighting or restricting other individuals from gaining access to a resource) or indirect or exploitative (e.g. use of a (scarce) resource so that it becomes unavailable for other individuals; Schoener, 1983). However, competition cannot be inferred if species use the same resource; equally, if species use different parts of a resource it does not indicate the absence of competition (Conley, 1976; Holbrook, 1979; Schoener, 1983).

Although it was expected that *E. myurus* would be dominant and hence display more aggressive behaviour, behavioural studies showed that no dyad type (inter- or intraspecific) showed a higher frequency of aggression. Additionally, neither *M. namaquensis* nor *E. myurus* showed differences in aggression in inter- and intraspecific encounters. This is unusual since normally the specialist and/or larger species is expected to be dominant (although not necessarily through aggression) over the generalist/smaller species (Morris, 1996; Perri & Randall, 1999; Kalcounis-Ruppell & Millar, 2002), thus restricting access to shared resources. A possible explanation is that the shared resource that the species may compete for was not provided in the neutral arena in my study or that there is a minimum threshold density of either the resource or the number of individuals at which animals become aggressive (Wolff, 1985). However, when insects and seeds were provided in a neutral arena, *E. myurus* dominated the food resource (Pillay, *pers. comm.*). Additionally in both Pillay's (*pers. comm.*) study and my study, there were high levels of avoidance in both species suggesting that rather than overt aggression, *M. namaquensis* and *E. myurus* tend to actively avoid each other. Similarly, when the Rufous sengi *Elephantulus rufescens* and a spiny mouse species *Acomys* spp. co-occur, *E. rufescens* seems to avoid the *Acomys* spp. (Neal, 1982b). Perri & Randall (1999) also found that although Ord's kangaroo rat *Dipodomys ordii* and *D. merriami* coexist at high densities with large amount of overlap, coexistence was promoted through avoidance rather than aggression. In the present study, it was also found that at low capture (and by inference, density), *M. namaquensis* and *E. myurus* were likely to be trapped together, but as capture

rates of either species increased, the likelihood of both species being trapped decreased. This implies that they may actively avoid each other at high densities in the field.

Social structure may also be an important factor promoting coexistence. Since *E. myurus* is specialist and possibly monogamous (Skinner & Chimimba, 2005), resource overlap is higher and intraspecific aggression levels should thus be higher than in *M. namaquensis* which is more generalist and group-living and would be expected to be intraspecifically tolerant, especially in individuals occurring in close contact. Although there was no difference in the frequency of behaviours displayed by *M. namaquensis* in intra- and interspecific encounters, they showed greater levels of amicability and lower levels of aggression towards conspecifics, especially if those dyads were with familiar individuals. *Elephantulus myurus* also showed more amicable behaviours in intraspecific vs. interspecific encounters, possibly as their density was too low for intraspecific competition to play an important role.

These results suggest that interspecific interactions may not be the only factor promoting coexistence. Similarly, coexistence in the Rice rat *Oryzomys longicaudus*, Olive grass mouse *Akodon olivaceus* and Long-haired grass mouse *Akodon longipilis* was not facilitated by competitive interactions (Murua *et al.*, 1987). However, behavioural interactions may become important when resource utilisation overlaps significantly, resulting in avoidance behaviours between the two species. Conley (1976) found that the intensity of interspecific interactions between Long-tailed voles *Microtus longicaudus* and Mexican voles *Microtus mexicanus* varied seasonally, while Manor & Saltz (2008) found similar resource-dependent interactions between the Broad-toothed mouse *Apodemus mystacinus* and the Common spiny mouse *Acomys cahirinus*. Another consideration is the density of the coexisting species as as intraspecific competition increases due to increasing density, individuals are more likely to shift their resource use and thus potentially come into contact with and compete with another species (Grant, 1972).

Implications for coexistence

Although there is a high level of dietary overlap between *M. namaquensis* and *E. myurus*, in periods when shared resources are limiting, *E. myurus*, the specialist, does not appear to dominate, either behaviourally or in terms of numbers, over *M. namaquensis* as predicted by the literature. However, *E. myurus* does appear to restrict the movement of *M. namaquensis* females, which travelled less far when *E. myurus* was removed, suggesting that *E. myurus* controls a resource necessary for reproduction. Additionally, *M.*

namaquensis starts breeding slightly earlier in the absence of *E. myurus* which provides support for the idea that *E. myurus* restricts access to a shared resource. Active avoidance also seems to play a role in promoting the coexistence of the two species.

Alternatively, *E. myurus* may not be able to dominate or restrict *M. namaquensis* to the point of competitive exclusion due to the relative densities of the two species – despite occupying home ranges of a similar size, and with equivalent amounts of high overlap between the species, *M. namaquensis* is group-living and thus occurs at higher densities than the pair-living *E. myurus*. Additionally, being a specialist, *E. myurus* in all probability requires a particular set of specific resources in its home range and thus may be restricted in the densities, whereas *M. namaquensis* is more of a generalist and can thus survive in marginal areas if required to do so.

Temporal differences in food resource use (e.g. through differences in seasonal preferences) may also aid coexistence. Optimal foraging theories predict that each species will have a period when it is the most efficient forager, which often corresponds to an increase in density as the most efficient forager has lower foraging costs while its competitor's density is usually lower. Thus competitive coexistence may be promoted through asynchronous fluctuations in the densities of coexisting species (Brown, 1989b; Yunger *et al.*, 2002), which in turn is often related to breeding season. This may result in other trade offs (e.g. in the Negev desert, the Greater Egyptian gerbil *Gerbillus pyramidium* monopolises resources when they are abundant while Allenby's Gerbil *Gerbillus andersoni allenbyi* harvests when there is a low resource density; Ovadia *et al.*, 2005).

Home ranges may also provide evidence for competitive coexistence as mutually exclusive home ranges may imply active defense of an area through aggression. Alternatively, or in addition, home range exclusivity may indicate avoidance rather than aggression as a behavioural mechanism promoting coexistence. If home ranges are overlapping, as in the present study, avoidance probably aids coexistence. This is reinforced as behaviour data revealed little aggression between the species but high levels of avoidance.

There may also be a trade-off between ecological and evolutionary pressures. Ecological factors would promote or exclude species from a community, whereas evolutionary processes would result in selective pressures that shape the traits shown by the species (Chesson, 1986). If these processes work at the same scale, the result would be disruptive selection with each species having a suite of traits that maximise their fitness in

that community, thereby promoting coexistence and limiting the entrance of other species into that community. However, ecological processes are probably operating at a shorter time scale and although species may coexist at a smaller scale, their traits doubtless evolved over a larger time scale (Chesson, 1986).

Evolutionary implications

Evolutionary ecology explains limits by studying key environmental factors, organismal traits and evolution of these traits, with most work focusing on adaptive traits as a mechanism governing community patterns (Sih & Gleeson, 1995). Removal experiments may help in answering whether competition is current or a ghost of competition past (Connell, 1980). If competition is current, then interspecific competition is important but even if current competition is not widespread, past competition may have played a role in present community structure (Townsend *et al.*, 2000). These may however be phylogenetically constrained resulting in a trade off between life history characteristics and competitive ability (Mougi & Nishimura, 2007) and may also depend on the strength and direction of selection pressures (Mougi & Nishimura, 2007). It is thus often difficult to invoke ecological and evolutionary events.

In the present study, although some characteristics (e.g. number of offspring reproduced and interlitter interval) are phylogenetically constrained and thus affect ecological correlates such as density, there is still evidence of competition. However, it is hard to definitively invoke evolutionary or ecological causes of this competition as only a restricted number of variables (such as space use and density) were compared and factors such as changes, if any, in dietary and microhabitat preferences were not assessed.

Ecological implications

The effect of density in the present study may have important implications as when *E. myurus* density was experimentally reduced, *M. namaquensis* individuals started breeding earlier in the season. Additionally, there was high juvenile recruitment. Whether these trends in population dynamics would continue or not is debatable but may lead to outbreaks. It is also important to consider the robustness of systems and it was interesting to note, that even when a species was removed, new individuals appeared to re-colonise the area relatively rapidly.

Future studies

Through the course of this study, many questions have arisen that could not be amswered with the data collected. It would be interesting to investigate dietary preferences in more detail, specifically temporal differences and differences in what species are being consumed by *M. namaquensis* and *E. myurus*. I propose that there is high overlap, particularly in arthropods which may restrict the breeding season of *M. namaquensis*. However, if *M. namaquensis* and *E. myurus* are eating different parts of the food resources, or even different species or orders, this overlap may not be as great as it appears. Additionally, with the advent of satellite imagery that is fine-scaled with more detail and more easily accessible and user-friendly, analysing home range use with environmental correlates may produce interesting results with regards to specific habitat requirements of the species. This would answer the questions of what environmental variables are in the home ranges of *M. namaquensis* and *E. myurus*. Is there a difference between the species in this regard, i.e. can *M. namaquensis* survive with less rocky cover *E. myurus* uses the rocks for hunting? More intensive sampling, perhaps using spooling or radiotracking techniques may also give indications of core areas, where they are and how much they overlap, not only within a species but also between species. Additionally, the strength of competition, and indeed whether the competition is current or coexistence is due to the ghost of competition past (Connell, 1980), may be revealed through addition experiments rather than removal experiments.

Studies comparing these results with other communities that are composed of a couple of species might give more insight as to how these systems work. Additionally, studies of *M. namaquensis* and *E. myurus* in other communities where there are also other species may give a clearer understanding of competitive mechanisms between the species and why *M. namaquensis* and *E. myurus* so frequently occur together, excluding other species.

Conclusion

This study aimed to examine factors that might promote the co-existence of *M. namaquensis* and *E. myurus*, members of different orders of mammals. In this way, my study is unique because although studies investigating coexistence between representatives of larger mammalian orders are common place (Gordon, 1988; du Toit & Owen-Smith, 1989; Dublin *et al.*, 1990; Arsenault & Owen-Smith, 2002), little has been done on coexistence between orders of small mammals. Additionally, most work on small mammal

coexistence has been done in arid areas. My study not only expands the knowledge we have on the biologies of *M. namaquensis* and *E. myurus*, but also provides important information on the coexistence of small mammals from different orders in the grassland ecoregion of South Africa. This ecoregion is highly threatened due to development, agriculture and mining activities (Bredenkamp, 2002). Additionally, understanding coexistence will aid in understanding factors governing biodiversity issues.

Dietary analysis confirmed that *E. myurus* consumes predominantly insects while *M. namaquensis* is less specialised consuming a wide variety of food types. However, there is still a large amount of overlap especially in the late rain and dry season when some resources decrease in availability. Surprisingly, arthropods decrease in the diet of *E. myurus* during the early rainy season when this resource should be most abundant, while *M. namaquensis* increases its diet of arthropods during this season. There was also a high degree of microhabitat overlap, since both species were associated with areas of high rock cover and low proportion of grass cover. There was no difference in home range size when both species were present. Neither did the species vary home range size when the other species was removed. Additionally, overlap between the two species showed no spatial separation. Both species have summer breeding, with *E. myurus* juveniles present in the community before *M. namaquensis* juveniles, implying a slightly earlier breeding season but *M. namaquensis* start breeding earlier when *E. myurus* is removed. Thus, even though the density of *E. myurus* was lower than that of *M. namaquensis*, *E. myurus* may restrict the breeding of *M. namaquensis*, probably through restricting access to resources necessary for breeding, as female *M. namaquensis* travelled less far when *E. myurus* was removed. This restriction results in slightly asynchronous breeding and resource use, which is reinforced by active avoidance between the two species. Thus, as in previous studies examining coexistence in small mammals, coexistence between *M. namaquensis* and *E. myurus* is promoted by a combination of factors rather than one mechanism alone (Figure 7.1.). In other words, the system is elastic and as one variable increases (e.g. overlap in food resources), there is compensation by another variable (e.g. increased avoidance). Maximum competition or overlap would then occur when all factors overlap i.e. in the central circle in Figure 7.1. However, the relative importance of all these factors varies depending on how the species concerned perceives the environment.

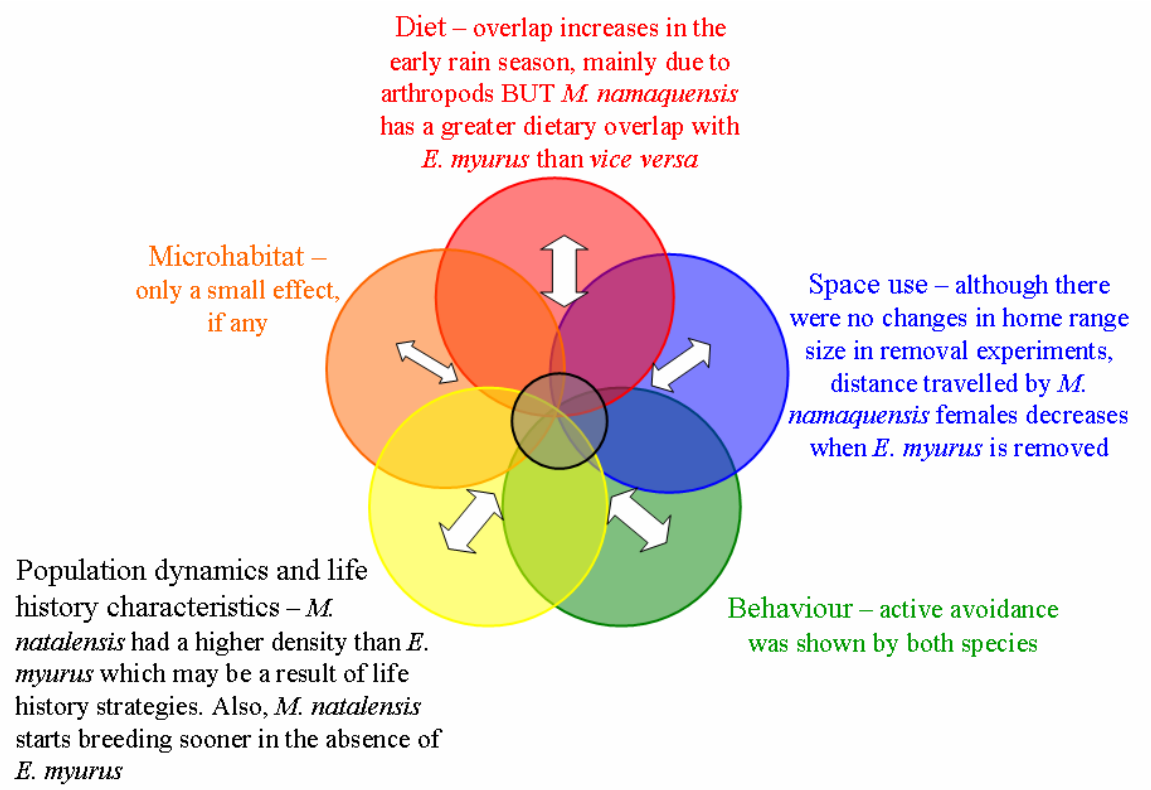


Figure 7.1. Diagrammatic representation of the main mechanisms promoting coexistence in *Michaelamys namaquensis* and *Elephantulus myurus* illustrating the dynamic relationships of these characteristics. Arrows indicate the size and direction of the relationship.

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