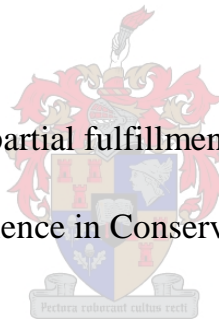# Small Mammal Communities in the Transformed Landscapes of the Western Cape Lowlands and Their Role in Alien Invasion into Fynbos Remnants

by

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at

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Co-supervisor: Dr. Sonja Matthee

Date: December 2008

Declaration

By submitting this thesis electronically, I declare that the entirety of the work contained therein is my own, original work, that I am the owner of the copyright thereof (unless to the extent explicitly otherwise stated) and that I have not previously in its entirety or in part submitted it for obtaining any qualification.

……………………………
Signature

Chapangara James Mugabe
…………………………..
Name in full

26 November 2008
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Date

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First, I would like to thank the Lord, Jesus Christ, for through Him I can do all things. I am greatly indebted to my supervisors, Dr. Cornelia B. Krug and Dr. Sonja Matthee for their support, guidance and advice. I would also like to extend my profound gratitude to the following;

Dedication

This thesis is dedicated to the special people in my life especially my parents,

Mr. & Mrs. K.C. Mugabe and to Mbuya Mai Charisi Tsangamwe with love.

Abstract

The fynbos eco-region in the Western Cape lowlands has been extensively transformed by anthropogenic activities such as agriculture and urban development, as well as invasive alien plants. Elandsberg Private Nature Reserve and Farms lies on Swartland Alluvium Fynbos and has been largely fragmented by agricultural crop production, whilst Riverlands Nature Reserve together with the Pella Research Site, which lie on Atlantis Sand Fynbos, are under severe threat from the invasive woody alien Port Jackson Willow (*Acacia saligna*) which forms dense stands in the lands adjacent the nature reserve. Habitat transformation has resulted in subsequent loss of habitat and a reduction in habitat value for small mammal communities by creating a mosaic of optimal and sub-optimal habitats. The success of *A. saligna* is, in part, attributed to its production of copious amounts of small hard-shelled seeds and well established soil seed banks. In the first part of this study we investigated the effect of habitat transformation on resident small mammal communities by comparing small mammal species richness, diversity and abundance between natural and transformed habitats as well as between the two vegetation types. We also investigated the population demographics of the striped mouse (*Rhabdomys pumilio*) in the different habitats. Our study shows that whilst fragments of natural habitats, especially at Riverlands and Pella, may be playing an important role in harbouring rare and possibly endangered species, transformed habitats are also important as secondary habitats providing both cover as well as seasonal food resources. Reproduction and body condition in *R. pumilio* were dependent on seasonal changes such as availability of water and food resources in the habitats. The second part of this study was carried out to investigate the effect of alien plant invasion on the resident small mammal communities at Riverlands Nature Reserve and to determine the role of small mammals in the removal and predation of *A. saligna* seeds. Rodent species richness, diversity and abundance were very low in the *A. saligna* stands compared to the adjacent fynbos vegetation. The interaction of rodents with seeds (removal or predation) was dependent upon seed size and seed abundance in the habitats. Whilst rodents may play an important role in predator limitation in the acacias, it is also possible that they may be playing a significant role in dispersing the seeds of acacias into the fynbos. More work is required to fully understand the role small mammals play in seed predation, dispersal and limitation in alien invaded fynbos systems.

Opsomming

Die mens se invloed en bedrywighede het die Fynbos van die Weskaap Provinsie se laagliggende areas onomkeerbaar gesteur en verander. Invloede en bedreigings wat uitstaan is landboupraktyke, verstedeliking en uitheemse indringerplante. Elandsberg Privaat Natuurreservaat en Riverlands Natuurreservaat, asook Pella navorsingstasie was die studie area van dié betrokke studie. Elandsberg word gekenmerk aan Alluviale sandfynbos wat grotendeels deur landboubedrywighede, soos byvoorbeeld canola en graag produksie, gefragmenteer is. Riverlands en Pella, beide met 'n natuurlike plante groei bekend as Atlantis sandfynbos word grotendeels deur digte stande van die uitheemse indringer plant, *Acacia saligna* bedreig. Die twee bogenoemde vorme van habitat versteuring het daartoe gely dat habitat kwaliteit van kleinsoogdier spesies nie na wense is nie. *Acacia saligna* se sukses word toegeskryf aan die hoë saadproduksie, wat akkumuleer in gevestigde saadbank en aggressiewe hergroei van dié spesie.

Dié studie fokus eerstens op die implikasies van habitat versteuring op kleinsoogdier gemeenskappe, met spesifieke verwysing na spesiesrykheid, spesiesdiversiteit en hoeveelhede. Populasie demografie die streepmuis (*Rhabdomys pumilio*) in verskillende habitatte is ook gedokumenteer. Resultate toon daarop dat natuurlike habitat wel belangrik is vir sekere skaars spesies, veral in die Pella en Riverlands studie areas. Tog kan sekondêre habitattipes, soos bv. indringer ruigtes wel belangrike bedekking en addisionele voedsel aan spesies bied. Voortplanting en die kondisie van *R. pumilio* was egter meer afhanklik van seisoenale faktore, meer spesifiek water en voedsel bekombaarheid in beide natuurlik en versteurde habitatte.

Die tweede deel van dié studie het die effekte van indringer plantegroei op die kleinsoogdier gemeenskappe bestudeer, asook die rol van kleinsoogdiere op die verspieding en predasie van *A. siligna* sade in Riverlands. Die kleinsoogdier spesiesrykheid, diversiteit en hoeveelhede was beduidend laer in *A siligna* stande relatief tot die aangerensende Atlantis sandfynbos. Verder was die interaksie tussen *A siligna* sade en kleinsoogdiere direk afhanklik van saadgrootte en hoeveelheid. Verder dui resultate daarop dat kleinsoogdierpopulasies wel kontrasteerende rolle kan speel op die saadbanke van *A. siligna*. Predasie op *A. siligna* sade kan 'n betekenisvolle rol speel op beprekte hergroei van dié indringer, maar saadverspreiding mag ook bydra tot die vestiging van jong *A. siligna* spruite in aangrensende fynbos. Daar word egter meer navorsing in die aspekte verlang om breedvoerige bestuursmaatreëls te formuleer.

Thesis structure

Chapter 1 provides a general introduction and background to habitat transformation in the Western Cape lowlands, its effects on small mammals and the role of small mammals in the invasion of the fynbos by *A. saligna*.

Chapter 2 is a review of current literature available on the effect of habitat transformation on small mammal assemblages in different habitats and ecosystems. It also looks at the role of small mammals in seed predation and secondary dispersal in relation to the role they might be playing in the invasion of the fynbos by alien plants such as *A. saligna*.

Chapter 3 investigates the effects of habitat transformation on rodent communities in the Western Cape lowlands, paying particular attention to species diversity, richness and abundances in the transformed and untransformed habitats. It also looks at the demography of the striped mouse *Rhabdomys pumilio* in optimal and sub-optimal habitats.

Chapter 4 investigates the responses of small mammals to alien invasion and the role played by these rodents in seed dispersal and predation in an alien invaded fynbos remnant.

Chapter 5 is a concluding discussion linking the conclusions from chapters 3 and 4 and suggesting management measures for implementation. This chapter discusses recommendations for use of small mammals as environmental indicators and considerations for fragment sizes in new developmental areas. The possible use of small mammal monitoring to inform conservation management decisions on the control of the invasive *A. saligna* is also discussed.

This thesis follows the referencing style of the Journal of Ecology.

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Chapter 1

General Introduction

1.1   Introduction to the Cape Floristic Region and the fynbos biome

The Cape Floristic Region (CFR), comprising an area of 87 892 km^2 at the southwestern tip of Africa (Cowling & Heijnis 2001), is one of the world's most botanically diverse regions. The hallmark feature of the CFR's biodiversity is the exceptionally high diversity and endemism of vascular plants and invertebrates (Cowling *et al.* 2003). The CFR is listed as a Centre of Plant Biodiversity (Davis *et al.* 1994), an Endemic Bird Area (Stattersfield *et al.* 1998) as well as a centre for diversity and endemism for vertebrates such as mammals (Brooks *et al.* 2001), freshwater fish, amphibia and reptiles (Skelton *et al.* 1995; Impson *et al.* 1999; Brooks *et al.* 2001) and many invertebrate species (Picker & Samways 1996). Out of an estimated 9 030 species of vascular plants occurring there almost 70% of them are endemic (Goldblatt & Manning 2000). The CFR is thus home to 44% of the estimated 20 500 species that occur in all of southern Africa (Arnold & de Wet 1993). The most dominant plant families include the Asteraceae, Fabaceae, Iridaceae, Aizoaceae, Ericaceae, Proteaceae and Restionaceae (Goldblatt & Manning 2002). Other peculiarities of the Cape flora include the dominance of fine-leaved sclerophyllous shrubs.

The climate in the CFR is largely Mediterranean with mainly winter rainfall although the eastern part of the CFR receives substantially more summer rainfall (Goldblatt & Manning 2002). Even though rainfall is limited almost throughout the CFR, vegetation varies conspicuously with soil type and available moisture. For example, forest vegetation is typical of the deeper soils where precipitation is high and evenly spread throughout the year. In lower and more seasonal rainfall and different soil types, forest gives way to shrubby or herbaceous vegetation types. On sandy soils forest gives way to a sclerophyllous vegetation (fynbos) in which species diversity decreases and composition changes until rainfall minimums reach about 300 – 250 mm p.a. when a succulent shrubland becomes dominant (Mucina & Rutherford 2006). On the clay soils forest gives way to fynbos and then to the characteristic renosterveld, a shrubland dominated by shrubby, microphyllous Asteraceae. At precipitation levels below 100 mm p.a., renosterveld is increasingly dominated by succulent perennials (Mucina & Rutherford 2006). The CFR has been identified as a biodiversity hotspot of global significance (Mittermeier *et al.* 1998; Myers *et al.* 2001). Because of its

vulnerability to processes that threaten this unique biodiversity (Rouget *et al.* 2003), it is therefore a global priority for conservation action.

1.2   Habitat transformation and invasive plants in the Fynbos Biome

The fynbos biome, which strictly comprises three different, fragmented vegetation types: fynbos, renosterveld and strandveld, is a fire-prone ecosystem characterized by small leafed, evergreen shrubs and predominantly winter rainfall (Mucina & Rutherford 2006). The fynbos biome takes its name from fynbos – the dominant vegetation in the region. Fynbos vegetation typically occupies sand stone derived soils (Cowling & Holmes 1992), and occupies 67% of the area of the fynbos biome and 56% of the area in the Cape Floristic Region (Rebelo *et al.* 2006).

By the late 1940s, large-scale agricultural transformation of the lowlands within the fynbos biome had taken place and the extent of alien tree and shrub infestation showed a marked increase in the early 1960s (Cowling & Pressey 2003). From the mid 1970s onwards, threats to the CFR's biodiversity began escalating dramatically. By the mid 80s, urbanization, especially in the form of informal settlements, increased massively in the CFR (Cowling & Pressey, 2003). In addition, the political and economic stability of post-apartheid South Africa saw an upsurge in investment in tourism facilities, especially along the coast where many habitats were already extensively transformed by resort development and alien plant infestations. Consequently, even greater pressure was placed upon the biodiversity of lowland areas, which were already most in need of protection.

The lowland fynbos has been extensively transformed by agriculture, urbanization and alien invasions (Richardson *et al.* 1996), resulting in the fragmentation of natural habitat (Rebelo 1992). On the shale derived soils of both the west and south coastal lowlands (Renosterveld and Swartland alluvium fynbos), the natural vegetation has been reduced by agriculture, largely production of cereal and pasture crops, to less than 10% of its original extent (McDowell 1988; Rebelo 1992; Kemper 1997). More recent work has suggested that only about 3% of this vegetation remains as isolated patches or fragments on slopes too steep for cultivation (von Hase *et al.* 2003). Sand fynbos also has a long history of transformation. By the 1980s, agriculture and aforestation accounted for 49% of the transformed area, with alien invasive *Acacia* species accounting for a further 36% (Rebelo *et al.* 2006).

The remaining natural vegetation within the fynbos biome is still under further threats such as ongoing transformation and fragmentation, invasion by alien woody species and overgrazing. Most of the remaining renosterveld fragments are less than one hectare in size (von Hase *et al.* 2003), and are rather isolated from each other. They are, therefore, not likely to provide useful habitats for a wide range of faunal diversity. In addition, habitat transformation creates barriers restricting or preventing the movement of biota (Goldingay & Whelan 1997). Many renosterveld fragments, for example, are isolated from each other on steep slopes and rocky outcrops (van Wyk 1995; von Hase 2003), thus they lack connectivity and might therefore, not serve as refugia for floral and faunal populations in neighbouring fragments. In addition, habitat transformation results in a matrix of natural habitats surrounded by transformed habitats, which are inhospitable to and unsuitable for many indigenous plants, insects, mammals and birds (Fuller & Perrin 2001). This subsequently leads to local extinctions (Frank & Wissel 1998) which are a cause for concern within the fynbos ecoregion given that many plant and animal species are endemics.

Plant invasions pose a serious threat to ecosystems worldwide (Cronk & Fuller 1995). Based on the Red Data plant species, the biggest threat to fynbos ecosystems is by invasive aliens, followed by agriculture and urbanization (Le Maitre *et al.* 1996; Rebelo 2001). Once established in a new environment, most invasive alien plants alter ecosystem processes and reduce local biodiversity (Richardson *et al.* 1992; Maron & Connors 1996; Mack *et al.* 2001). In the coastal lowlands of the Western Cape, *Acacia saligna* (Labill.) Wendl. is one of the most important invasive species (Macdonald & Jarman 1984). Together with *A. cyclops* (A. Cunn.) Ex G. Don., they were introduced to South Africa from the southwestern Australia in the mid-nineteenth century to stabilize shifting sand dunes (Shaughnessy 1980). *Acacia saligna* dominates in sand-plain lowland fynbos vegetation (Moll *et al.* 1984) where dense stands increase fuel loads and therefore fire intensities (van Wilgen & Richardson 1985). They also result in increased litter production, soil nutrient availability and erosion rates thereby significantly compromising the high plant diversity of invaded areas (Holmes & Cowling 1997).

The success of the acacias in the CFR has, in part, been attributed to their production of prolific quantities of long-lived, soil-stored seeds (Holmes 1990a, b). The state-funded Working for Water Programme was launched in 1995 and even though considerable progress in reducing the alien plant problem in some montane water catchments was made (van

Wilgen *et al.* 1996); everywhere else, threats to the biodiversity of the CFR have continued to escalate (Cowling & Pressey 2003). Because of the difficulties faced in implementing chemical and mechanical control, *A. saligna* has been made a target for biological control using the gall-forming fungus, *Uromycladium tepperianum,* and preliminary results have shown a reduction in seed production in *A. saligna* stands (Wood & Morris 2007). Holmes (1990a) had previously hypothesized that, with decreased seed production, rodent seed predation would increase. Since most of the *A. saligna* plants in our study site are infected with the gall-forming fungus, the expected decline in seed production would, therefore, be expected to provide a platform for intense rodent seed predation. Few studies have investigated rodent predation on *A. saligna* seeds in fynbos ecosystems (e.g. Holmes 1990a, b). However, in Australia, the native home of the acacias, rodent predation greatly reduces the seed banks in *Acacia* stands (MacDonald 1984).

1.3 Small mammals

Small mammals are an integral part of all terrestrial ecosystems as predators, consumers, prey, burrowers and seed dispersal agents (Bayne & Hobson 1998; Avenant 2000). This faunal group constitutes the main prey biomass that directly influences abundance and diversity of predator species (Salamolard *et al.* 2000) and contributes largely to the dynamics of the food webs. Small mammals are also important for the dissemination of plant products (Butet *et al.* 2006). In fynbos, small mammals are known as pollinators (Wiens *et al.* 1983) and seed dispersers (Midgley & Anderson 2005). Small mammal species are considered particularly sensitive to habitat changes and their species richness, abundance and diversity has been shown to be strongly correlated with vegetation structure and complexity (Kerley 1992), thus predictable fluctuations in these small mammal attributes occur as vegetation composition and production change with disturbances as well as with seasonal changes in agricultural production systems. Together with habitat transformation, plant invasions are also linked with a reduction in vertebrate diversity (Macdonald & Richardson 1986). Small mammal studies can form a basis for monitoring ecosystem functioning and may facilitate the management of nature reserves and future development of natural areas (Avenant 2000). In southern Africa, extensive research has been done on various aspects pertaining to small mammals. These include studies on the behaviour, biology and distribution of small mammals (e.g. Wirminghaus & Perrin 1993; Els & Kerley 1996; Avenant 2000; Andrews & O'Brien 2000; Eccard *et al.* 2000; Krug 2002; Giere & Zeller 2005). However, to date, very little research has been conducted on the effect of habitat transformation on small mammal

communities in the CFR. In addition, research is needed on the contribution that small mammals can have towards the control and or dispersal of seeds of alien plants. The aim of this thesis is to investigate the effect of habitat transformation on small mammal communities in the Western Cape lowlands and also their role in alien invasion into fynbos remnants.

1.4   Objectives

The objectives of the study were:

- To compare the small mammals species richness, diversity and abundance between transformed and natural habitats.
- To establish the usefulness of transformed areas as habitats for small mammals.
- To record seasonal changes in small mammal species abundances, diversity and richness as well as species specific attributes for the striped mouse (*R. pumilio*).
- To establish the effect of invasive alien *A. saligna* on small mammal communities in an alien invaded fynbos system.
- To determine the role of small mammals in the predation and removal of *A. saligna* seed.

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Chapter 2: Literature Review

2.1   Effects of habitat transformation and fragmentation on small mammals

Habitat transformation and fragmentation are usually associated with land systems where conservation competes poorly with other forms of land use such as agriculture and urbanization (Kemper *et al.* 1999). Such human induced changes to the landscapes have direct implications for animal populations (Schmidt-Holmes & Drickamer 2001). Small mammals, compared to other wildlife species, are sensitive to habitat alterations (Zou *et al.* 1989), as they have specific requirements for food and cover, and exhibit, to some extent, limited vagility. Because of differences in behaviour, vulnerability to environmental variability and habitat specialization rodent species can show diverse demographic responses to habitat alterations (Ims & Andreassen 1999).

Plant structural heterogeneity resulting from disturbance is attractive to small mammals, as it provides a range of resources in the habitat throughout the year (Fuller & Perrin 2001). Monotypic plant communities, characteristic of most agricultural production systems, usually contribute little towards wildlife habitat value and landscape plant diversity (Olson & Brewer 2003). Small mammal community structure and species richness are related to biotic and abiotic variables such as habitat and vegetation structure, complexity, area, productivity, predation, trampling and grazing, surrounding landscape and the distance between similar habitats and the presence of exotic plant and animal species (Kerley 1992; Els & Kerley 1996; Avenant 2000). Small mammal populations are sensitive to habitat changes (Avenant 1996) and habitat alterations may thus reduce small rodents species richness and diversity through habitat simplification (decreased herbaceous layer, increased bare soil), changes in food availability, or reduced refuges, resulting in areas of lower species diversity, richness or abundance (Keesing 1998; Avenant 2000). However, increased small mammal diversity has been reported in some disturbed habitats. Studies in South America showed that neotropical small mammals often increase in abundance and species richness after disturbances such as fragmentation and logging (e.g. Lambert *et al.* 2003, 2005). The rationalization for this is that successional faunal species often tend to coexist for short periods (Avenant 2000).

Previous studies have shown a connection between the presence or absence of small mammal indicator species and disturbance in natural ecosystems (e.g. Avenant 1996). Habitat

transformation is often related to a decrease in small mammal richness. For the above-mentioned reasons, small mammals are considered as useful indicators of health and function in terrestrial ecosystems (Sullivan *et al.* 2003) and hence research on small mammal communities has increased dramatically in recent years. A number of studies have looked at the effect of habitat fragmentation on small mammal assemblages, and most focused on their systematics and patterns of overall abundance and species richness (e.g. Kerley 1992; Bayne & Hobson 1997; Olson & Brewer 2003). Direct monitoring of small mammals may be a relatively quick and cheap method of indicating healthy/unhealthy ecosystem functioning and may facilitate the management of nature reserves and future development of natural areas (Avenant 2000). Assessments of small mammal populations can thus be used to gauge ecological conditions and wildlife habitat value of transformed habitats including agricultural cropping systems (Olson & Brewer 2003).

2.2   Alien invasive plants in fynbos: the role of small mammals in seed removal

Alien invasive acacias in fynbos

Natural ecosystems worldwide are under siege from a growing number of invasive alien species (Cronk & Fuller, 1995; Richardson & van Wilgen 2004). Besides their effects on agriculture, forestry and human health, biological invasions are also widely recognized as the second largest global threat (after direct habitat destruction) to biodiversity worldwide (Walker & Steffen 1999). South Africa has a long history of problems with invasive alien species (Richardson & van Wilgen 2004) and alien plants are considered one of the major threats to biodiversity within the CFR (Rebelo 1992). Fynbos communities are highly susceptible to invasion and have been invaded mainly by trees and shrubs (Richardson *et al.* 1997). The principal invaders are trees and shrubs in the genera *Acacia, Hakea* and *Pinus* (Higgins *et al.* 1999), and large areas of lowland fynbos are invaded by *A. saligna* and *A. cyclops* (Milton 1980).

Regular fires in fynbos open invasion windows for the alien *Acacia* species, which produce large amounts of seeds and have a relatively short juvenile period of less than five years (Richardson *et al.* 1992; Holmes & Cowling 1997). Once established, these alien acacias alter ecosystem processes and reduce local biodiversity (Richardson *et al.* 1992), thereby eroding the natural capital, compromising ecosystem stability and threatening economic productivity.

The trees form dense stands in the invaded areas, seriously reducing the high indigenous plant biodiversity of invaded areas (Holmes 2002). Other changes to natural processes include increased fuel loads and therefore increased fire intensities, increased littler production, soil nutrient availability and erosion rates as well as reduced diversity of vertebrates (Wood & Morris 2007). Whilst aliens may have the advantage over indigenous plants of having escaped most of their co-evolved natural enemies (Milton 1980), in order for them to successfully invade new habitats, seed dispersal is essential.

Acacia spp. seed production, dispersal and predation

The success of *A. saligna* and *A. cyclops* in South Africa has been attributed in part to their copious production of long-lived, hard-coated seeds which accumulate in large soil-stored seed banks (Henderson 1998) and efficient seed dispersal (Knight 1988). Annual seed production by *A. saligna* and *A. cyclops* is approximately 10 000 and 3 000 seeds per square meter of canopy cover, respectively (Milton & Hall 1981). *Acacia* seeds ripen in early summer and are shed soon after dehiscence in December (Holmes 1990a). Most of the seeds fall directly to the ground (Holmes *et al.* 1987) and a large proportion remain dormant because of a water impermeable testa (van den Berckt 2002), resulting in the accumulation of large seed banks in the soil. Little is known about the long term survival of *A. saligna* seeds (van den Berckt 2002) but about 45% of the annual seed production is normally eliminated during the first year in the absence of predation and another 15% in the second year following seed fall (Holmes 1989). In Australia, ants and birds (O'Dowd & Gill 1986) disperse *Acacia* seeds. In fynbos, efficient dispersal by rodents has been ruled out as there are no seed caching rodent species in the fynbos (Slingsby & Bond 1985). The acacias also appear to be pre-adapted to short-distance dispersal mutualisms with ants (Slingsby & Bond 1983). The significance of these mutualisms is that their seeds can escape rodent predation (Holmes 1990b). Ant species in the fynbos are important in maintaining seed banks of indigenous Proteaceae and in the same manner might play a critical role in the accumulation of alien *Acacia* seed banks (Holmes 1990b).

The gall-forming rust fungus *Uromycladium tepperianum* (Morris 1991) and the seed-feeding beetle *Melanterius compactus* were introduced in 1987 and 2001, respectively, as biological control agents for the woody alien acacias and these measures have contributed to significant reductions in seed production in most *A. saligna* stands (Wood & Morris 2007). With the

reduction in seed production, the proportion of seed eaten by rodents may increase thereby further reducing recruitment into the *Acacia* soil seed bank (Holmes 1990b).

In the *Acacia* invaded fynbos systems, seed removal has also been shown to be related to seed availability. Holmes (1990) showed an inverse relationship between seed availability and seed removal, with more seeds being removed prior to seed fall when seed availability was at its lowest. Holmes also hypothesized that a reduction in the availability of *Acacia* seeds would result in increased proportions of the seeds being predated upon by rodents. In another study on the seed banks of alien acacias in the fynbos, Holmes *et al.* (1987) showed a small annual decrease in *A. saligna* seed banks with felling of standing *Acacia* plants. This decrease may be largely the result of predation (Holmes *et al.* 1987). However, Milton (1980) suggests that rodents take only an estimated 1% of the available seed per year. In fynbos ants also remove seed from the litter layer because they are attracted by the aril of the seed of *A. saligna*. They do not destroy the seed but are responsible for its burial. This behaviour takes the seed out of the predators' reach and is partly responsible for the maintenance of the soil seed bank (Holmes 1990a). Despite this, dispersal by ants is thought to be unimportant (Milton & Hall 1981) as ants only move seeds no further than 3 m (Bond & Slingsby 1983).

Seed traits affecting predation and dispersal

Animal dispersed seeds possess traits that, in addition to affecting germination, growth and development, also influence seed predation, removal and scatter-hoarding by animals (Xiao *et al.* 2006b). Innate seed traits such as size, nutritional quality, and morphological and chemical defenses can influence seed predation, removal and caching by granivorous rodents (Xiao *et al.* 2006a). This in turn affects seed survival and seedling recruitment. Xiao *et al.* (2006b) suggested that these seed traits are primary factors in determining seed preferences by seed eating animals. Seed size, therefore, plays a vital role in plant life history such as seed production, predation, dispersal, germination and early growth of seedlings, and plant communities (Xiao *et al.* 2005). In general, large seeds are expected to have higher seed predation and lower survivorship than small seeds (Moyles *et al.* 2003). This negative relationship between dispersability and seed size holds for many plant species, but seems not to hold for large-seeded plant species primarily dispersed by seed caching rodents (Jansen *et al.* 2004).

Some studies, however, have shown that large seeds are more likely to be removed and cached rather than eaten in-situ (Vander Wall 1990: Vander Wall *et al.* 2003). In addition, Xiao *et al.* (2005) showed that dispersal by scatter-hoarding rodents clearly increases with both interspecific and intraspecific seed size (Xiao *et al.* 2005). Granivorous rodents thus often prefer to remove and cache larger seeds or seeds with high fat content (Xiao *et al.* 2005). Several hypotheses exist to explain this trend. For example, greater food value makes larger seed size more attractive to seed eaters according to the optimal foraging theory (Stephens & Krebs 1986). In addition, increased handling time can increase the predation risk for granivorous rodents and this means smaller seeds are more likely to be consumed *in situ.* Large seeds and nuts generally have a greater nutritional value for rodents than small ones and may therefore be more attractive for them to cache as food reserves (Jansen & Forget 2001) or eat.

Plants that use their propagules to co-opt animals as dispersal agents must balance the costs of seed predation with the benefits of dispersal (Xiao & Zhang 2006). Successful post dispersal germination is a key measure that reflects these costs and benefits (Price & Jenkins 1986). Whether a given tree species benefits from dispersal by seed caching rodents or other animal seed dispersers depends on; (1) the number of the dispersed seeds from the seed sources e.g. parent plant; (2) the proportion of seeds consumed and cached after dispersal; (3) dispersal patterns (i.e. scattered or clumped); (4) post dispersal seed shadows (i.e. spatial patterns of the dispersed seeds); (5) seed deposition patterns (e.g. substrates and micro sites). Although it is not understood how plants evolved to balance seed predation and seed dispersal via scatter-hoarding animals, the short distance mutualism between acacias and ants in the fynbos might be a significant adaptation aiding them to escape rodent predation (Holmes 1990b).

Secondary dispersal of seeds by food caching animals is not well documented in Australia and Africa (Vander Wall *et al.* 2005) and few, if any, studies have evaluated the role of animals in the ecology of invasive plant species in the fynbos, particularly the woody *Acacia* species. Animal seed dispersal is a dominant mechanism of dispersal in many temperate and tropical forests and has the potential to accelerate forest regeneration and restoration (Wunderle 1997). Many of the plants that are dispersed by ground foraging animals drop seeds or nuts at maturity to facilitate seed harvest by these ground foraging animals (Vander Wall 2001). After they are shed from the parent tree, and depending on size and other seed

traits, seeds are often removed and consumed or scatter-hoarded by seed eating rodents (Price & Jenkins 1986). Although many of these seeds and nuts are consumed, some of the seeds are scatter-hoarded (Vander Wall *et al.* 2003) and some of these seeds survive to establish seedlings (e.g. Zhang & Wang 2001; Li & Zhang 2003; Xiao *et al.* 2004a).

Rodent seed predation and dispersal

In many ecosystems, granivorous rodents are mainly seed predators rather than seed dispersers (Hulme & Benkman 2002). There have been conflicting reports about the role of rodents in seed dispersal in fynbos ecosystems. Slingsby & Bond (1985) ruled out the possibility of rodent seed dispersal in fynbos because of the absence of seed caching rodent species. However, Knight (1988) suggested that generalist avian and rodent frugivores might be responsible for the spread of seed of *Acacia* species into un-infested habitats. More recently, evidence has emerged of rodents playing important roles as seed predators (Holmes 1990a, b) and scatter-hoarders (Midgley & Anderson 2005) in fynbos systems.

A number of variables, including seed density, distance from parent tree, microhabitat, macrohabitat (forest vs. field or tree fall gap), seed species, season of dispersal and site specific interactions among predators (Meiners & LoGiudice 2003) can affect the behaviour of seed predators. Small mammals have been shown to play important roles in forest ecology, acting as seed predators and dispersers in French-Guiana (Forget 1991) and China (Zhang & Wang 2001). Increases in their abundances have been shown to negatively affect forest regeneration and succession (Terborgh *et al.* 2001). It is possible that seed caching rodents (and other seed dispersing animals as well) can help restore tree diversity in fragmented forests and therefore there is need to evaluate the potential contributions of these animals to forest restoration (Xiao *et al.* 2004). These potential contributions are of considerable interest given the increasing rate of anthropogenic disturbances and invasions in the ecoregion.

2.3   Predictions and hypotheses

Based on the reviewed literature the following predictions and hypotheses can be made;

i.   Habitat transformation is expected to negatively affect small mammal communities. Species richness, diversity and abundance are expected to be lower in transformed habitats than in natural habitats.

ii.   Habitats transformed by invasive alien *A. saligna* will harbor fewer rodent species and lower abundances.

iii. Rodent will contribute to the dispersal of alien seeds. Seed availability and size are expected to be important factors on whether seeds are removed or eaten *in situ*.

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Chapter 3

Small mammal communities in transformed landscapes with particular focus on the demographics of *Rhabdomys pumulio*

Abstract

The fynbos eco-region of the Western Cape lowlands has been extensively transformed by anthropogenic activities such as agriculture and urban development, as well as invasion by alien plants. These transformations have resulted in subsequent loss of habitat and a reduction in habitat value for small mammal communities by creating natural (optimal) and transformed (sub-optimal) habitats. In this study, we investigated the effect of habitat transformation on small mammal communities by comparing small mammal species richness, diversity and abundance between natural and transformed habitats as well as between two vegetation types (sand fynbos and alluvium fynbos). We also investigated seasonal dynamics in species-specific attributes such as body mass, body condition index, and reproduction of the striped mouse (*Rhabdomys pumilio*) in the different habitats. A total of 308 individuals representing seven different species were captured in both the natural and transformed habitats. Transformed habitats in general, had lower species richness, abundance and diversity compared to the adjacent natural habitats. Reproduction and body condition in *R. pumilio* were dependent upon seasonal changes such as availability of water and food resources in the habitats, while reproductive activity of rodents captured in the transformed habitats was related to percentage vegetation cover and to average plant height. Our study shows that whilst fragments of natural habitats may play an important role in harboring rare and possibly endangered species, transformed habitats are also important as secondary habitats providing both cover as well as seasonal food resources for rodents.

3.1   Introduction

Human induced changes of landscapes have direct implications for resident animal populations (Schmidt-Holmes & Drickamer 2001). In the Western Cape, the natural vegetation of the lowlands has been replaced by urban developments, farmland and invasive alien plant species. At the first of our study sites, Elandsberg Private Nature Reserve and Farms (hereinafter referred to as Elandsberg), agricultural crop production has led to a high degree of transformation of the natural vegetation. Although the reserve protects the largest remaining tract of Swartland Alluvium Fynbos (Midoko-Iponga 2004; Mucina & Rutherford 2006), most of the surrounding natural vegetation remnants are rather small and isolated. Riverlands Provincial Nature Reserve and the Pella Research Site which comprise the second site (hereinafter referred to as Riverlands and Pella), are part of the Atlantis Sand Fynbos (Mucina & Rutherford 2006), and are under intense pressure from invasive woody alien plants on the surrounding lands as well as small holder farming development. Such transformation in the Western Cape lowlands has led to the destruction of natural habitats. The fragmentation of natural vegetation can affect resident small mammal communities in a number of ways. For example, crop monocultures, which are typical of most agricultural production systems, usually contribute very little towards wildlife habitat value and landscape plant diversity (Olson & Brewer 2003). Whilst cropping seasons may be able to provide food and cover for some rodent species, fallow seasons usually contribute very little habitat value to small mammals (van Wyk 1995), whose dependence on food resources and cover from predation is very high.

Small mammals are considered as agricultural pests causing damage to agricultural products (Butet *et al.* 2006). However, they form an important part of all terrestrial ecosystems (Kerley 1992; Bayne & Hobson 1998; Avenant 2000). Most small mammal species are sensitive to habitat changes (Saetnan & Skarpe 2006), as they have low vagility and require relatively high densities to maintain viable populations (Silva & Downing 1994). In addition, based on species-specific behaviour, vulnerability to environmental variability and habitat specialization (Ims & Andreassen 1999), different species can show diverse demographic responses to habitat alterations. For most animal groups, species diversity and richness not only declines in the event of an ecological disturbance within a habitat (Hoffmann & Zeller 2005), but also with decreasing size and increasing isolation of habitat fragments (Silva

2001). Relatively undisturbed habitat remnants support species rich small mammal communities and may thus serve as important refugia (Ellis *et al.* 1997). Assessments of small mammal populations can be useful in gauging ecological condition and wildlife habitat value of new agricultural cropping systems (Olson & Brewer 2003) and transformed habitats (Hoffmann & Zeller 2005).

Research on small mammals conducted in southern Africa (e.g. Wirminghaus & Perrin 1993; Els & Kerley 1996; Avenant 2000; Andrews & O'Brien 2000; Eccard *et al.* 2000; Krug 2003) helps generate descriptive data that are essential for understanding interactions between the organism and its environment and to assess the effects of man-made changes to the environment (Giere & Zeller 2005). Generalist rodent species such as the striped mouse (*Rhabdomys pumilio*), which has been described as a broad-niche species occupying a wide variety of habitats (De Graaff 1981), provide an ideal opportunity for studying an organism's ability to endure particular habitat disturbances and the influence of different habitats on its population demography (Schradin & Pillay 2005). When a species occurs in different habitats, it is possible to observe differences in its population demography, and reproductive behaviour resulting from the differences in the habitats (Lott 1991).

Few if any studies have compared small mammal assemblages in the natural and transformed habitats in the Western Cape lowlands. The primary aim of this study was to determine the effect of habitat transformation in the Western Cape lowlands on small mammal assemblages by comparing species richness, diversity and abundance between the natural vegetation remnants and the adjacent transformed habitats. The study also sought to investigate dynamics in species-specific attributes such as body mass, body condition and reproduction in the striped mouse (*R. pumilio*) within the different habitats over the different seasons. The study sought to address the following questions:

1. Do natural habitats have higher small mammal species richness, diversity and abundance than the surrounding transformed habitats?
2. Are there seasonal changes in vegetation structure in the habitats and how do these affect the composition of small mammal communities?
3. Do transformed habitats serve as primary or secondary habitats for small mammals?
4. What differences exist and what changes occur in species specific attributes (e.g. body mass, body condition, reproduction etc.) of *R. pumilio* between sexes, seasons and habitats?

**3.2	Methods**

The study was carried out at Elandsberg Farms and Private Nature Reserve (Elandsberg), and at Riverlands Provincial Nature Reserve and the Pella Research Site (Riverlands and Pella) in the Western Cape Province of South Africa. The trapping of small mammals in the Western Cape lowlands was permitted by Cape Nature (Permit/License No. AAA004-00022-0035) and the study was approved by the Stellenbosch University Subcommittee B Ethics Committee (Ref: 2006B01005).

**3.2.1	Study sites**

Elandsberg

Elandsberg is located in the Tulbagh District of the Western Cape, approximately 25 km north of Wellington between 33°24'S and 33°30'S, and 19°01'E and 19°05'E (Baard, 1990) and covers approximately 4000 hectares of Hawequas sandstone fynbos, Swartland alluvium fynbos, Swartland shale renosterveld and old lands. The lowland portion includes one of the largest remaining patches of Swartland alluvium fynbos in the Cape Floristic Region (Mucina & Rutherford 2006). The Elandskloof Mountains form the eastern boundary of the reserve whilst the southern section is bordered by Krantzkop Ammunition Factory (Department of Defence) and the northern section by the Voelvlei dam (Department of Water Affairs). The western section borders the commercial wheat lands of Elandsberg farms. These lands, consisting of 2600 ha of farmland, maintain merino sheep and cattle, wheat, canola, oats, barley, clover and other crops (Midoko-Iponga 2004).

Elandsberg falls within the Mediterranean climate zone of the south-western part of the Southern African sub-continent. The weather is influenced by the South Atlantic anticyclonic system with dry and hot summers from December to February, and cold and wet winters from June to August (Engelbrecht 1995). The south Western Cape region receives most of its rain in autumn, winter and early spring, usually from May to September (500 mm pa.). At Elandsberg, the average annual rainfall is 687 mm, with 77% of this falling between April and September (Midoko-Iponga *et al.* 2005). Rainfall peaks in June with an average of 114 mm, whereas the average monthly minimum precipitation (10 mm) is observed in December. The mean annual temperature is 17.4 °C, with a winter mean of 12.2 °C and a summer mean of 23.8 °C (Baard 1990). The coldest month in winter, July has an average

temperature of 6 °C whereas the hottest month in summer (February) has an average of 31.3 °C (Baard 1990). Swartland alluvium fynbos is the wettest and hottest alluvium fynbos type and wind predominantly blows from the south for most of the year and becomes northerly in the winter (Mucina & Rutherford 2006). At Elandsberg, small mammal trapping was carried out at four paired study sites covering the transformed and natural areas (Fig 3.1 and Table 3.1).
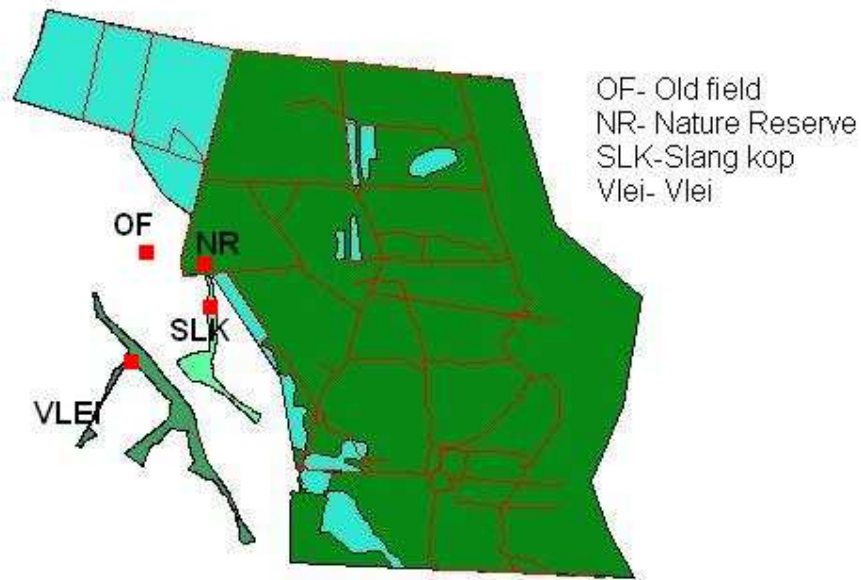
Fig 3. 1 Map of Elandsberg Private Nature Reserve and Farms showing study fragments. Green represents natural vegetation whilst the blue represents abandoned old fields. Red dots indicate the location of the study plots. Map courtesy of B. Wooding, Elandsberg Farms.

Riverlands and Pella

Riverlands and Pella are located 63 km north of Cape Town, off the N7 highway, at approximately 18°37′E and 33°29′S at an altitude of 190 m in the Malmesbury Magisterial district of the Western Cape Province. The native vegetation is classified as Atlantis sand fynbos (Mucina & Rutherford 2006), some of which is located on seasonal wetlands. The climate is Mediterranean, with hot dry summers and cool wet winters (Yelenic *et al.* 2004). Riverlands covers an area of about 1300 ha. Soils of Riverlands and Pella consist of well-drained aeolian acidic sands approximately 1-2 m deep of the Constantia and Clovelly forms (Lambrechts & Fry 1988), according to the South African Binomial classification (MacVicar *et al.* 1997). Pella lies on quaternary sand and receives an average annual rainfall of 400 mm. Vegetation at both sites is sand plain proteoid fynbos and the dominant fynbos species are *Protea scolymocephala, Elegia filacea, Ischyrolepis monanthos, Phylica cephalantha,*

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Leucadendron corymbosum and *Ischyrolepis paludosa, Thamnochortus punctatus, Erica plumosa, Phylica cephalantha, Serruria fasciflora, Leucospermum parile, Metalasia capitata* (Kongor, pers. comm.). Both nature reserves were set aside for the conservation of locally endemic and endangered fynbos species. The conservation status of the Atlantis sand fynbos has been recognized as vulnerable, as some 40% has been transformed and inherent threats include cultivation (agricultural small holdings and pastures), urban development as well as gum and pine plantations. Woody invasive aliens in and around the reserve include *Acacia saligna, A. cyclops* and various species of *Eucalyptus* and *Pinus*.

About 400 indigenous plant species occur at Riverlands Nature Reserve, 41 of which are critically rare or endangered (Killian 1995). Riverlands, a farm that was purchased from Transnet (formerly South African Railways) in 1985 by Cape Nature Conservation because of its high concentration of rare plants (Yellenik *et al.* 2004), consists of a habitat mosaic including uninvaded native fynbos communities, fallow fields and invasive alien vegetation. Through the Working for Water programme, a significant amount of these aliens has been cleared, although dense alien stands on the neighbouring lands still pose problems of potential invasions of the reserve. Riverlands and Pella are both flanked by stands of invasive alien acacias, which are encroaching into the reserves. Invasion by alien acacias results in significant alterations to fire regimes (van Wilgen *et al.* 1998) and subsequent vegetation structure. At this site, two paired plots, one each at Riverlands and Pella, were set up in the natural and transformed areas (Fig 3.2 and Table 3.1).

Table 3. 1 Short description of the study sites chosen at EPNR, Pella Research Site and Riverlands Nature Reserve. A and B denote natural and transformed habitats respectively.

Natural Habitat	Transformed habitat

Swartland Alluvium Fynbos

Vlei A
Fragment dominated by *Elytropappus rhinocerotis*. Bordered on one side by a vlei flooded in winter, on the other sides by wheat fields.

Vlei B
Wheat field with a winter wheat crop. Fallow the rest of the year.

Nature Reserve A
A plot 300m from the edge of the reserve. The dominant shrubs included *E. rhinocerotis*, *Helichrysum* spp, *Hermannia* spp. and *Thesium* spp. as well as an indigenous perennial forb, *Leysera gnaphalodes*.

Nature Reserve B
Open grassy patch in the nature reserve bordered by a Canola field on one end and an old field on another. The dominant grasses are *Cynodon dactylon* and introduced European grasses of the genus *Briza.*

Old field B
A grassy old field dominated by *C. dactylon* in summer and introduced European grasses (*Briza spp., Lolium* spp., *Poa annua, and Vulpia myuros*) after winter rainfall.

Old field A
A very heterogeneous fragment composed of a mixture of grass and shrub cover. The dominant grass species is *C. dactylon* whilst *E. rhinocerotis* is the dominant shrub.

Slang kop B
Two fields on either side of slang kop. The eastern field was positioned between slang kop and the Nature reserve. The other field was bordered by more fields on the western side. A canola crop provided dense vegetative cover during the winter season. The field was fallow all the other seasons.

Slang kop A
A hilly fragmented measuring 33ha flanked on either side by cereal fields. The vegetation is a heterogeneous mixture of shrubs, grasses and geophytes.

Atlantis Sand Fynbos

Riverlands B
Dense stand of *Acacia saligna* (Port Jackson willow) with a dense litter layer.

Riverlands A
Dense fynbos vegetation at the edge of the Nature reserve bordered by a stand of alien *Acacia saligna*. The dominant plant species include *Protea scolymocephala, Elegia filacea, Ischyrolepis monanthos, Phylica cephalantha, Leucadendron corymbosum* and *Ischyrolepis paludosa.*

Pella B
A stand of alien *Eucalyptus* spp (blue gum) and *A. saligna*. This habitat is part of the nature reserve and alien species are currently being removed.

Pella A
Dense fynbos vegetation at the edge of the Nature reserve bordered by a stand of alien *Eucalyptus* spp (blue gum) and *A. saligna*. The dominant plant species include *Thamnochortus punctatus, Erica plumosa, Phylica cephalantha, Serruria fasciflora, Leucospermum parile, Metalasia capitata.*
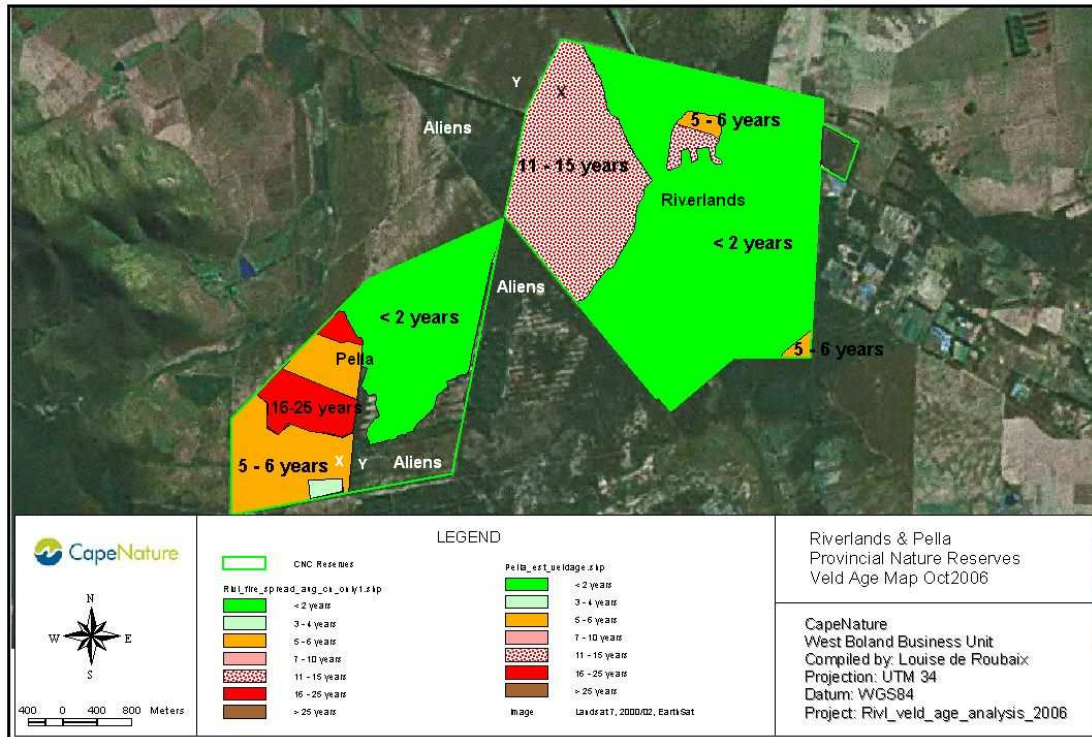
Fig 3. 2 Map of Riverlands Nature Reserve and the Pella study site showing natural Atlantis sand fynbos vegetation of different ages (after fire) and the surrounding stands of *Acacia saligna* in the private land surrounding the reserve. Study plots in fynbos are indicated by an X and plots in aliens are indicated by Y. (Map courtesy of Cape Nature)

3.2.2   Vegetation surveys

Vegetation surveys were carried out on each plot during each trapping session. Line transects were set up along each trap line to determine plant life form, dominant species and percentage canopy cover. Plants were classified into the following life form types: shrubs, grasses, herbs and geophytes. At each sampling point along the line transect, the life forms on either side of each trap station were identified and its height recorded. Points where dead or no plant material was encountered were classified as bare ground. Percentage vegetation cover for each of the transects was then calculated by taking the number of points on the transect where a plant, regardless of life form or height was found and dividing this by the total number of transect points. Percentage vegetation cover for each plot was determined by averaging the percentage vegetation cover for all transects in a plot. Average percentage vegetation cover was calculated for both natural and transformed habitats at Elandsberg and Riverlands and Pella. Average plant height was determined and the dominant plant species were identified for each plot. Factorial ANOVA was used to test for the combined effect of

vegetation type, habitat type and season on percentage vegetation cover and average plant height. Differences in average vegetation cover between seasons and between habitats were investigated using one way ANOVAs and significant differences were determined using Post Hoc Bonferroni comparisons. Statistical analyses were carried out using Statistica for Windows 7® (Statsoft Inc. 2007).

3.2.3 Small mammal surveys

Species richness and abundance of small mammal populations were evaluated using mark-recapture trapping techniques. In order to capture and mark as many rodents as possible, live trapping of small mammal was conducted over five trap nights per session per site, for a total of 900 trap nights. To investigate seasonal changes in small mammal community structure and composition, trapping was carried out quarterly from April 2006 – April 2007, covering the following seasons:

- autumn (February – April);
- winter (May – July);
- spring (August – October) and;
- summer (November – January).

Locally made Sherman-like traps (Super Kill Mouse and Rat Traps®) were used in the study. This type of trap has been used in small mammal studies in fynbos and renosterveld vegetation (e.g. Krug, unpublished), and in the succulent Karoo (e.g. Haveron 2008). Ninety traps were placed 15 m apart in line transects in a 9×10 trapping grid. Trapping grids are more effective in assessing population densities than trap-lines (Gurnell & Flowerdew, 1990) and have been used in previous studies (e.g. Krug 2004, 2007; Hoffmann & Zeller 2005; BIOTA transect analysis). Trap size is one of the factors affecting the effectiveness of trapping effort (Hayes *et al.* 1996) and therefore in this study two trap sizes, small ($150\times50\times50$ mm) and large ($250\times80\times80$ mm), were used alternating in the rows and columns of each grid. For ease of access to the small mammals, the traps were laid out on flat ground with the entrance of the trap flush with the ground. Where possible the traps were placed close to shrubs as some rodents are known to prefer covered areas (Gurnell & Flowerdew 1990), as these present areas of probable high food density and low predation risk (Kotler 1984). At each paired plot, one trapping grid was placed in the fragment of natural vegetation and another in the adjacent transformed land. Mixtures of peanut butter and rolled oats mixed

with various other ingredients have been used effectively in previous small mammals studies (Krug 2002). In this study, the traps were baited with a peanut butter, oats and marmite mix. Dry straw was placed in the traps for bedding to prevent small mammals deaths from cold exposure or overheating. Traps were checked twice daily, in the morning and afternoon, and straw and bait were replaced in traps when necessary. Captured small mammals were removed from the trap using the 'polythene bag technique' (Gurnell & Flowerdew 1990) and identified to species. Each individual was first checked for any previous marking and unmarked individuals were then marked by ear notching (Fig 3.3) to facilitate individual recognition. Marked individuals were recorded as recaptures and the captured small mammals were released near the trap at which they were caught. The traps were re-baited and the straw was replaced where necessary. The following measurements were taken from each captured individual;

(i)   Body mass (to the nearest gram using either a 100 g or 50 g Pescola spring balance).

(ii) Body length – a straight line measurement from nose to anus (to the nearest millimeter using veneer calipers).

(iii) Tail length – a straight line measurement from anus to the tip of the tail (to the nearest millimeter using veneer calipers).

(iv) Ear length (to the nearest millimeter using veneer calipers).

(v)   Hind foot length – including claw (to the nearest millimeter using veneer calipers).
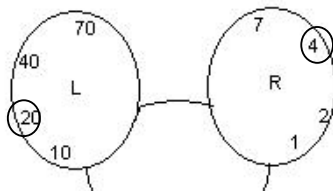
Fig 3. 3 Ear notching used for marking small mammals. The figure represents a small mammal marked number 24 (Adapted from C.B. Krug, unpublished data sheet).

These measurements provided an indication of physiological condition. In addition, mass and pelage characteristics were used to estimate age of the small mammals. The external genitalia were examined to provide information on reproductive activity (Brooks 1974; Gurnell & Flowerdew 1990). In the male, the testes were noted as either withdrawn into the abdominal cavity (abdominal) or descended into the scrotal sacs (scrotal). When the testes appeared to be abdominal but could be stroked down into the scrotal sacs, they were termed to be

'moving' and such adults were classified as reproductively active. In the females, the vaginal orifice was recorded as either perforate (open) or imperforate (sealed). Pregnancy or lactation was also determined for perforate females by gently feeling the abdomen for fetuses or checking for the presence of nipples respectively.

Small mammal communities were described as follows; species richness (S) was the total number of species recorded in each given habitat. Abundance for each small mammal species and total abundance for all species combined were the total number of unique individuals captured excluding recaptures, as trapping effort was strictly the same on each site (Butet *et al.* 2006). For comparisons between habitats at Elandsberg and Riverlands and Pella, we calculated the relative abundances as the total number of captures divided by the total number of trap nights for each habitat type. Species diversity is sensitive to rare species abundance (Engen 1979) and thus accounts simultaneously for species richness as well as the relative contributions of each species (Kelt 2000). The Brillouin index, which is a more accurate measure of diversity in cases when the randomness of sampling cannot be guaranteed (as in small mammal trapping: Haveron 2008), was also calculated and correlated with the Shannon diversity index using regression analysis to check for sampling bias.

Shannon Diversity was calculated as;

$$H = -\sum_{i}^{s} p_i \ln p_{ip};$$

-where p_i is the abundance of a particular species in a sample.

The Brillouin index (HB) was calculated as;

$$HB = \ln N! - \sum \ln n_i! \, / \, N;$$

-where N is the total number of individuals, n_i is the number of individuals in each species (Magurran, 1988).

Abundance, diversity and evenness indices were calculated for natural and transformed habitats at both Elandsberg and Riverlands and Pella. We analyzed the relationship between vegetation attributes (plant form richness - represented by the total number of plant forms in each study plot - and percentage vegetation cover) and small mammal species diversity, richness and abundance (calculated as abundance per trap night) for natural and transformed habitats at Elandsberg and Riverlands and Pella sites using regression correlation analysis. Vegetation data was arc sin transformed before analysis. Small mammal species richness and abundances were compared between natural and transformed habitats within and across the

study sites. Seasonal changes in small mammal abundances were also compared between the habitats and study sites.

3.2.4 *Rhabdomys pumilio* population demographics

Analyses of species-specific data were only performed for *R. pumilio*, as it was the only species with a large enough sample size. Captured individuals were treated as described above. Although striped mice can start breeding with a body weight of around 30 g in grasslands (David & Jarvis 1985), Krug (2002) classified as adults all individuals weighing more than 36 g and as juveniles all individuals weighing less than 35 g. In our study, all breeding adults weighed at least 40 g, which is comparable to Schradin & Pillay (2005), and individuals weighing below 40 g did not show indications of reproductive activity. Therefore we regarded *R. pumulio* individuals as adults when they weighed at least 40 g. Those that weighed between 35-39 g were regarded as sub-adults and those weighing less than 35 g were regarded as juveniles. Body mass was compared in different seasons. To determine sexual dimorphism we compared the body mass of male and female striped mice using female individuals that were neither pregnant nor lactating using a Mann-Whitney U test (Statistica for Windows 7®; Statsoft Inc. 2007). As there was no significant difference between male and female body mass (see below), we used combined data of males and females to investigate the temporal and spatial dynamics in small mammal body mass. We, however, controlled for the influence of pregnancy by excluding all pregnant and lactating females. We also controlled for the influence of growth in young rodents by using only adult and sub-adult rodents (>35 g). The proportions of reproductive rodents as a percentage of total number of adults were calculated for each sex. One way ANOVA was used to test for differences in reproductive activity between sexes, seasons and between habitats. We also used regression correlation to test for relationships between reproductive activity and vegetation cover.

3.2.5 Index of body condition in *R. pumilio*

Body condition refers to the size of energy stored in the body in relation to the structural components of the body (Green 2001). It is an important determinant of an individual animal's fitness, fecundity and survival, and its implications are of great interest to ecologists. Measuring body condition in live animals is a difficult task and numerous non-destructive

methods that are based on relating body mass to linear measures of body size have been developed and used (reviewed by Brown 1996). In this study, body condition was determined for the small mammals using the ordinary least squares (OLS) linear regression of body mass against length of the body size indicator (BSI) as described below. It has been argued that this method provides the cleanest way to separate the effects of condition from the effects of body size (Krebs & Singleton 1993; Jakob *et al.* 1996). To control for the influence of pregnancy, pregnant and lactating females were excluded from the analysis. As no sexual dimorphism was observed, data for males and females were combined in the analysis. A regression analysis was carried out on the relationship between body mass and body length of all *R. pumilio* individuals from both the Elandsberg and Riverlands and Pella study sites. The resultant linear regression model was then used to predict the expected body mass from the observed body length (Krebs & Singleton 1993). The estimation of body condition involved three steps: (1) estimating the regression between body length (X) and body mass (Y) for the population; (2) using this regression to predict body mass from observed skeletal size for each individual; and (3) estimating the condition of each individual from the ratio of observed mass to predicted body mass. The index of condition was calculated as follows:

Index of condition =observed mass/predicted mass

Ideally, the first step of estimating a regression for the population under study should be done on a large data set. In this study, a sample size of n = 241, which included rodents captured from both Elandsberg and Riverlands sites, was used in the analysis. Indices of condition were then compared between males and females, between seasons and between individuals from Riverlands and Pella and Elandsberg. We determined if the observed body masses differed significantly with expected body masses using the χ^2 test. For this analysis, we first combined all the individuals and then treated the sexes separately. Factorial ANOVA was carried out to determine the relative importance of season, site and sex on body condition for *R. pumilio* in both the natural and transformed habitats. Due to the small number of small mammals captured in some transformed habitats, there was not enough data to statistically compare indices of condition between individuals captured in these habitats and those from the natural habitats.

Shannon diversity and evenness indices were calculated in Canoco for Windows (ter Braak & Šmilauer 2002.) and all statistical analyses were carried out in Statistica for Windows 7® (Statsoft Inc. 2007) and Microsoft Excel 2007 (Microsoft Inc. 2006).

3.3   Results

3.3.1   Temporal variation in vegetation and small mammal responses

The vegetation composition was distinct between the different habitats. Shrubs were the most dominant growth form in all natural habitats (Fig 3.4a, c), whilst grasses (mostly alien) and alien trees dominated the transformed habitats at Elandsberg and at Riverlands and Pella respectively (Fig 3.4b, d). There was very little seasonal variation in vegetation cover in the natural habitats ($F = 0.654$, $df = 9$, $p = 0.749$) over the entire sampling period. Notable changes in vegetation cover only occurred during the winter season in the agricultural fields at Slang kop and Vlei fragment, both at Elandsberg, where winter crops, canola and wheat, were grown (Fig 3.4b). The fields were left fallow during the other seasons. At Slang kop, the canola height averaged 65 cm and the percentage vegetation cover in the canola field was more than 70%. In the Vlei fragment sampling for the winter season was carried out in the wheat field when the wheat averaged 80 cm in height. In the transformed habitats at Riverlands and Pella (Fig 3.4d), annual grasses were observed in winter and spring. Annual plants (herbs and seasonal geophytes) were recorded in the natural habitats and in the Elandsberg transformed habitat. As only the tallest plant was sampled at each sampling point, most of the annual plants did not contribute to an overall change in the average plant height. Vegetation cover was significantly lower in transformed habitats than in natural habitats ($F = 29.454$, $df = 44$, $p = 0.000$).

Small mammal diversity and abundance was positively correlated with vegetation cover in the natural and transformed habitats at Elandsberg (Table 3.2). However, it was only in the transformed habitats that the positive correlation between percentage vegetation cover and small mammal diversity was significant ($R^2 = 0.999$, $p = 0.000$). No correlation between small mammal diversity and abundance and vegetation cover was observed in the habitats at Riverlands and Pella (Table 3.2).
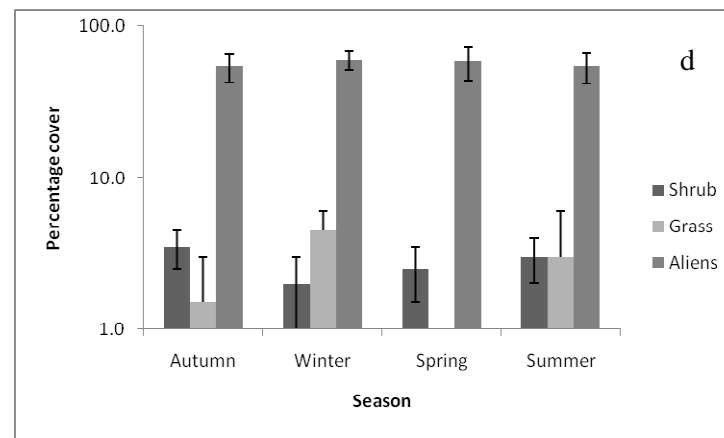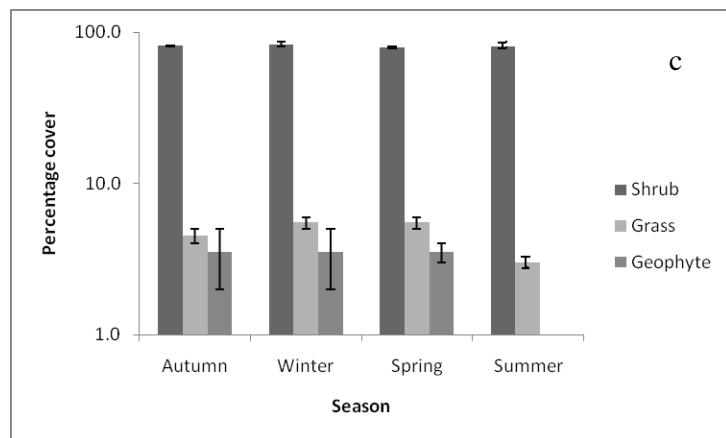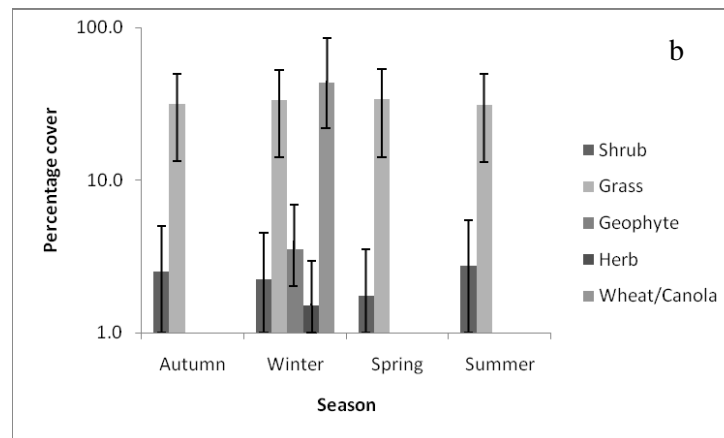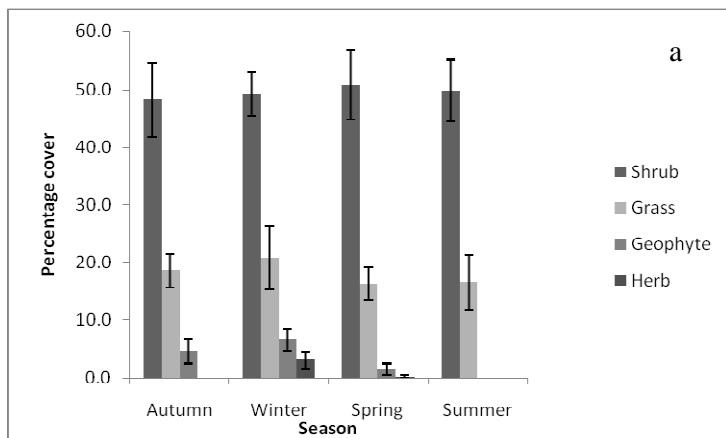
Fig 3. 4 Seasonal changes in percentage vegetation cover ± S.E. of each life form in the habitats. a- Natural habitats at Elandsberg, b-Transformed habitats at Elandsberg, c- Natural habitats at Riverlands and Pella, d-Transformed habitats at Riverlands and Pella.

Table 3. 2 Results of regression correlation analysis between percentage vegetation cover and small mammal species diversity and abundance in natural and transformed habitats at Elandsberg, and Riverlands and Pella. *denotes significance at $\alpha = 0.05$.

Site	Effect	R^2	p	F	df
Elandsberg natural	small mammal diversity	0.901	0.051	18.270	2
	abundance per trap night	0.578	0.240	2.735	2
Elandsberg transformed	small mammal diversity	0.999	0.000*	2097.6	2
	abundance per trap night	0.744	0.138	5.803	2
Riverlands and Pella natural	small mammal diversity	0.000	0.982	0.00063	2
	abundance per trap night	0.040	0.801	0.0825	2
Riverlands and Pella transformed	small mammal diversity	0.101	0.682	0.225	2
	abundance per trap night	0.012	0.891	0.024	2

3.3.2   Small mammals in transformed versus natural habitats

A total of 308 individuals from seven small mammal species were captured over four trapping seasons. *Rhabdomys pumulio* was the dominant species in all the seasons, constituting 81.49% of all the captures and was captured at 10 of the 12 sampled sites (Table 3.3). The other species captured were *Mus minutoides* (pygmy mouse), *Steatomys krebsii* (Krebs's fat mouse), *Mysorex varius* (forest shrew) and *Tatera afra* (Cape gerbil), *Otomys irroratus* (vlei rat), and *Myomyscus verreauxii* (Verreaux's mouse). The rate of recapture was very low (Table 3.3) and since trapping effort was strictly the same for all the sites, the total captures were used for the analysis below.

Even though species richness and diversity were low within most of the individual habitats, natural habitats generally had a higher small mammal species richness and abundance (Table 3.4). At Elandsberg, 199 individuals representing four species were captured in the natural habitats compared to 21 individuals from three species captured in the transformed habitats (Fig 3.5a). *Rhabdomys pumilio*, *S. krebsii* and *M. minutoides* were captured in both transformed and natural habits whilst *M. varius* occurred in the natural habitats only. Similarly, natural habitats at Riverlands and Pella had higher species richness and abundance than the transformed habitats. A total of six species represented by 78 individuals captured in the natural habitats, but only ten individuals from two species (*R. pumilio* and *M. minutoides*) were captured in the transformed habitats (Fig 3.5b). Rodents captured in the natural habitats

at Riverlands and Pella included one *O. irroratus* individual and two *M. verreauxii* individuals.

All transformed habitats combined accounted for 10% of all the captured small mammals. Even though they had lower small mammal species richness and abundances, transformed habitats had higher Shannon evenness than natural habitats at both Elandsberg, and Riverlands and Pella (Table 3.4). At Elandsberg, the Shannon diversity index (H) of 0.836 in the transformed habitats was higher than in the natural habitats (H = 0.232). On the other hand natural habitats at Riverlands and Pella had more diverse small mammal assemblages (H = 1.246) than the transformed habitats (H = 0.693).

3.3.3   Seasonal changes in small mammal species abundance and richness

The small mammal abundance in autumn was the highest, with a total of 161 rodents captured, representing 52% of total captures, while only 39 individuals (13% captures) were captured in spring. The highest species richness (*n* = 7) was recorded in autumn (Table 3.3). In all seasons, natural habitats had higher rodent abundances than their adjacent transformed habitats. Autumn had the highest rodent abundances in all habitats except for Elandsberg transformed, where highest abundances were recorded in winter (Fig 3.6). In natural habitats, the highest abundance of rodents was observed in autumn and this declined from winter through to summer. In spring and summer, small mammal numbers were low in both transformed and natural habitats. When excluding *R. pumilio*, small mammal abundances in the natural habitats at both Elandsberg and Riverlands declined from autumn to summer. In the transformed habitats, however, the highest abundance was observed in winter (Fig 3.6). The total abundance of *R. pumilio* in the natural habitats declined by more than 75% from autumn to winter, and then stabilized at about 40 individuals in the other seasons (Fig 3.7). In the transformed habitats, *R. pumilio* abundance decreased from autumn to summer with no captures in the latter season.

Table 3. 3 Small mammal capture statistics from 12 sampling plots in the study sites at Elandsberg, Riverlands and Pella during the sampling period 2006-2007. Figures show the numbers of unique individuals captured, recaptures are shown in brackets.

Species	No. of captures										% of captures	No. of patches occurred
	Autumn		Winter		Spring		Summer		Total			
Rhabdomys pumulio	134	(27)	43	(17)	34	(8)	40	(8)	251	(60)	81.49	10
Mus minutoides	6	(0)	12	(0)	1	(0)	-		19	(0)	6.17	6
Otomys irroratus	1	(0)	-		-		-		1	(0)	0.32	1
Steatomys krebsii	12	(1)	12	(4)	2	(1)	-		26	(6)	8.44	4
Myomyscus verreauxii	1	(0)	-		1	(0)	-		2	(0)	0.65	1
Tatera afra	6	(1)	-		1	(0)	-		7	(1)	2.27	2
Mysorex varius	1	(0)	-		-		1	(0)	2	(0)	0.65	2
Total	**161**		**67**		**39**		**41**		**308**		**100.0**	
No. of species	**7**		**3**		**5**		**2**					

Table 3. 4 Small mammal species Shannon diversity (H), richness (S) and evenness (H/ log S) indices for transformed and natural habitats at Elandsberg and Riverlands and Pella.

Site	Spp richness (S)	Shannon diversity (H)	Shannon evenness	Brillouin diversity	Brillouin evenness	Abundance per trap night	Total unique captures (N)
Elandsberg natural	4	0.232	0.167	0.210	0.156	0.0276	199
Elandsberg transformed	3	0.836	0.761	0.700	0.743	0.0029	21
Riverlands & Pella natural	6	1.246	0.695	1.141	0.687	0.0217	78
Riverlands & Pella transformed	2	0.693	1	0.553	1	0.0028	10
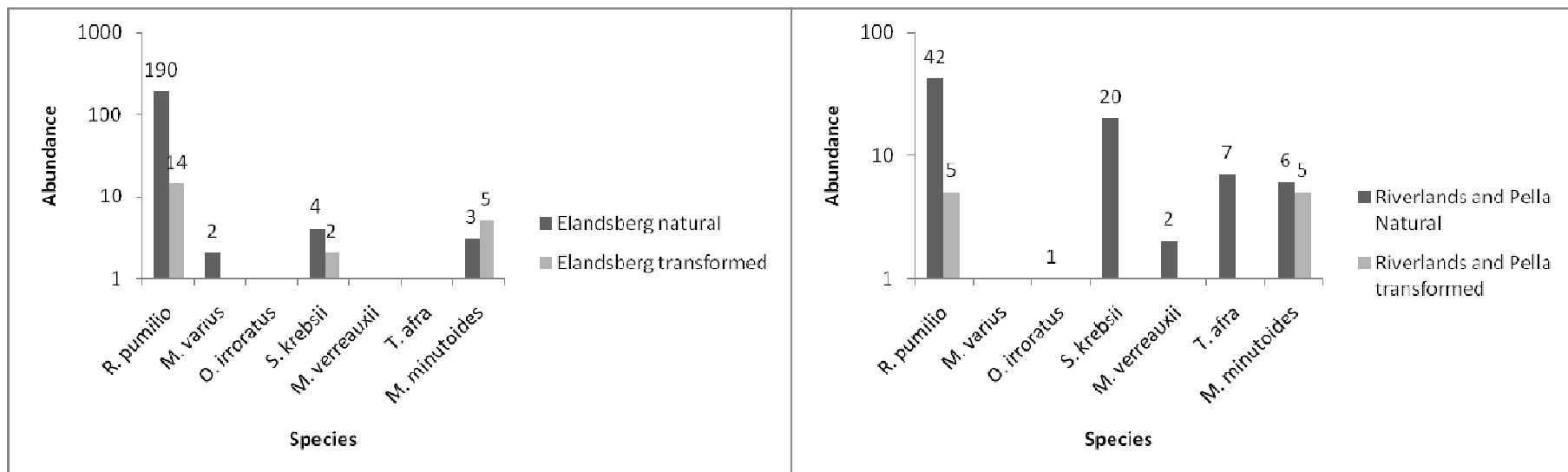
Fig 3. 5 A comparison between the abundances of species captured in the natural and transformed habitats (a) at Elandsberg and (b) at Riverlands and Pella. The abundance axis is plotted on a log10 scale.
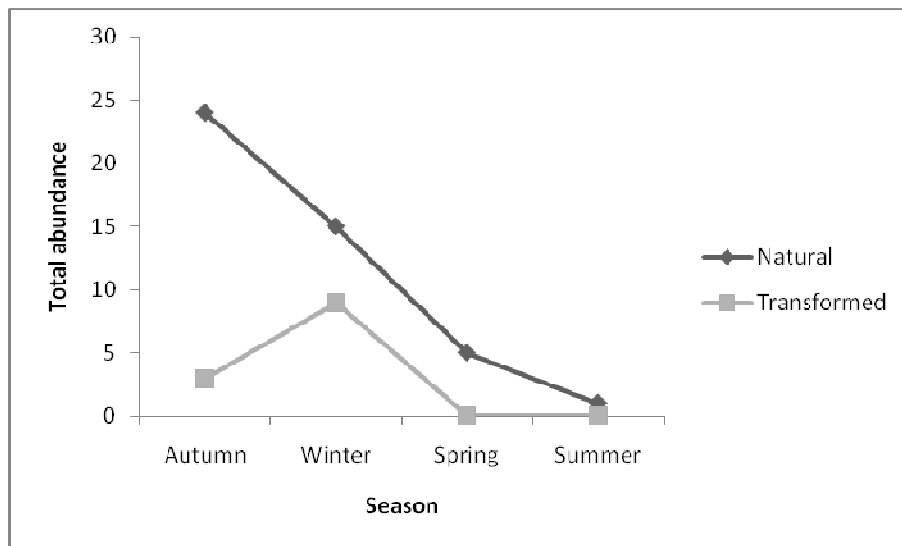
Fig 3. 6 Graph comparing the abundances of small mammal species (with the exception of *Rhabdomys pumilio*) captured in the natural and transformed habitats at Elandsberg, and Riverlands and Pella sites.
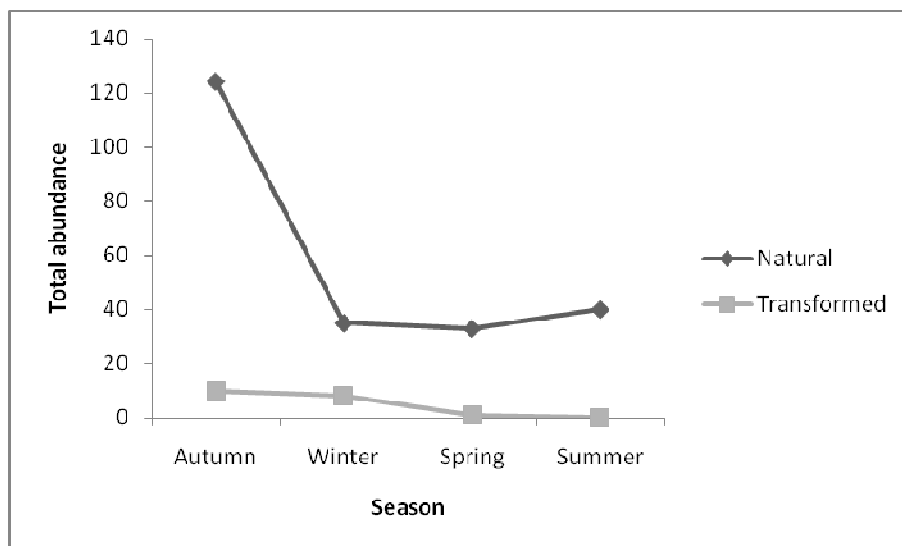
Fig 3.7 Graph showing the abundances of all the *Rhabdomys pumilio* captured in the natural and transformed habitats at the Elandsberg and Riverlands sites.

3.3.4   Reproductive activity in *R. pumilio*

Adult rodents in breeding condition were found throughout the year (Fig 3.8). Nevertheless, reproductive activity was found to differ significantly between seasons ($F = 9.869$, $df = 3$, $p = 0.000$). Summer had the highest proportion of reproductively active adults constituting 91.4% of all the adult rodents (93.3% adult males and 90% adult females) whilst autumn had the lowest proportion of reproductively active adults (47.7% and 76.9% of the adult males and females, respectively) (Fig 3.8). In all seasons except for summer, a higher proportion of

males were reproductively active than females. Reproduction in females was significantly higher in summer than autumn, spring and winter, ($F = 4.581$, $df = 3$, $p = 0.004$), but the differences between autumn, spring and winter were not significant. Even though reproduction in males was highest in summer, the difference between summer, winter and spring was not significant (Fig 3.8). However, reproductive activity was significantly lower in autumn than three other seasons ($F = 5.529$, $df = 3$, $p = 0.001$). Reproductive activity did not differ significantly between natural habitats at Riverlands and Pella ($F = 0.06858$, $df = 1$, $p = 0.795$), and at Elandsberg ($F = 0.606$, $df = 1$, $p = 0.437$). There was no correlation between vegetation cover and reproductive activity in the Elandsberg natural habitats ($R^2 = 0.023$, $p = 0.572$, $F = 0.335$, $df = 14$), Elandsberg transformed ($R^2 = 0.092$, $p = 0.249$, $F = 1.447$, $df = 14$), Riverlands and Pella natural ($R^2 = 0.007$, $p = 0.842$, $F = 0.434$, $df = 14$) and the Riverlands and Pella transformed habitats ($R^2 = 0.172$, $p = 0.307$, $F = 1.246$, $df = 14$).
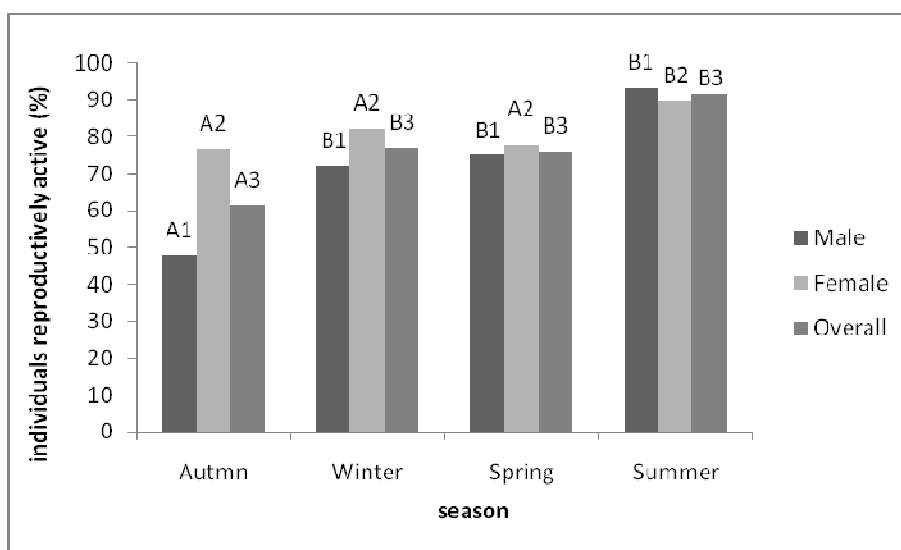
Fig 3. 8 Percentage *Rhabdomys pumilio* adults (mice with body mass over 40 g) that were potentially reproductively active (i.e. individuals having a scrotal sac for males and females with an open vagina or pregnant) during the four sampling seasons. Different letters denote significant differences between seasons.

3.3.5 Body mass and condition index

The data showed evidence of a generally higher mean body weight at Elandsberg compared to Riverlands and Pella. Most of the captured rodents were adults weighing between 40-49 g (Fig 3.9). Juveniles weighing less than 20 g and large gravid females weighing up to 60 g were also captured in all trapping seasons. Even though males (mean weight = 40.47 g) were generally heavier than females (mean weight = 38.96 g), their mean weight did not differ significantly at both Elandsberg ($F = 0.150$, $df = 1$, $p = 0.699$) and Riverlands and Pella ($F = 0.264$, $df = 1$, $p = 0.610$). Body weight in both male and female *R. pumilio* varied significantly

over different seasons at Elandsberg (Table 3.5). Average body weight of captured striped mice differed significantly between seasons for females ($F = 8.665$, $d = 3$, $p = 0.000$) and males ($F = 4.732$, $df = 3$, $p = 0.004$) at Elandsberg (Table 3.5). Autumn and spring had significantly lower mean body mass than winter and summer ($F = 6.764$, $df = 3$, $p = 0.010$). At Riverlands and Pella, average body mass did not differ significantly between seasons for males ($F = 0.729$, $df = 3$, $p = 0.550$) and females ($F = 1.934$, $df = 3$, $p = 0.404$) (Table 3.5). Observed versus expected body weights across all the habitats differed significantly for *R. pumilio* ($\chi^2 = 303.006$, $df = 240$, $p = 0.004$). However, when sexes were treated separately there was no significant difference between the observed and expected weights in either males ($\chi^2 = 128.0$, $df = 125$, $p = 0.409$ or females ($\chi^2 = 126.091$, $df = 114$, $p = 0.207$).
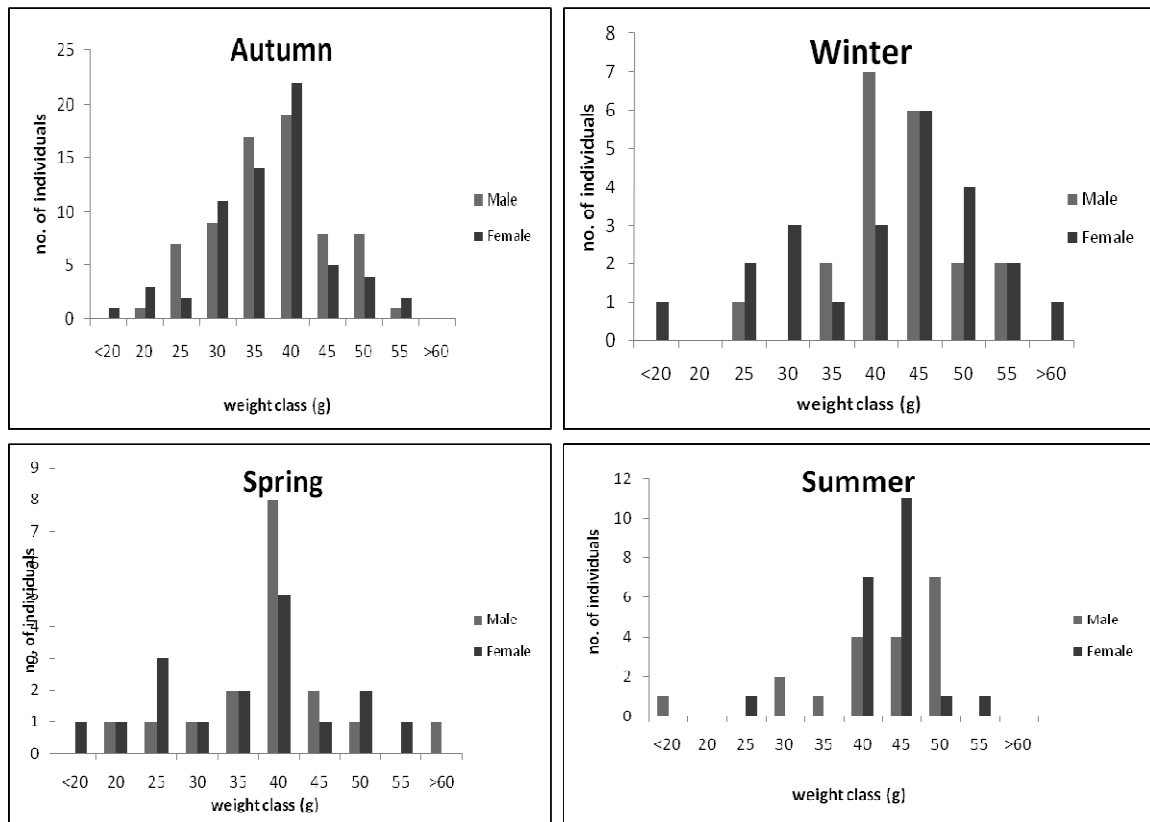
Fig 3. 9 Seasonal differences in mass distribution of *Rhabdomys pumilio* (males and females) trapped in the study sites. Data are presented in weight classes of 5 g each beginning with <20 g up to >60 g.

Table 3. 5 Average body mass and body condition index (BCI) for male and female *Rhabdomys pumilio* at Elandsberg and Riverlands and Pella. Different letters in superscript denote significant differences and the sample sizes are shown in brackets.

Site		Elandsberg				Riverlands and Pella			
Season		Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer
	Female	37.37^{a}	40.55^{b}	40.50^{ab}	45.43^{b}	42.50	41.89	28.25	36.50
Mass (g)		($n = 51$)	($n = 11$)	($n = 12$)	($n = 14$)	($n = 12$)	($n = 9$)	($n = 4$)	($n = 4$)
	Male	39.12^{a}	46.19^{b}	41.20^{ab}	45.41^{b}	42.27	38.50	41.50	33.50
		($n = 59$)	($n = 16$)	($n = 15$)	($n = 17$)	($n = 11$)	($n = 4$)	($n = 2$)	($n = 2$)
	Female	0.937^{a}	0.986^{ab}	0.985^{ab}	1.060^{b}	1.054	1.044	0.833	0.810
BCI		($n = 51$)	($n = 11$)	($n = 12$)	($n = 14$)	($n = 12$)	($n = 9$)	($n = 4$)	($n = 4$)
	Male	0.990	1.031	0.981	1.073	1.052^{a}	1.026^{ab}	0.993^{b}	0.764^{ab}
		($n = 59$)	($n = 16$)	($n = 15$)	($n = 17$)	($n = 11$)	($n = 4$)	($n = 2$	($n = 2$)

Fig 3 10 Relationship between body length (nose to anus) and body mass in the stripped mouse (*Rhabdomys pumilio*) at Elandsberg and Riverlands and Pella (body mass = -10.63 + 0.562×body length). All pregnant females were omitted from the analysis. The dotted lines represent 95% confidence limits.

A simple linear regression model (*body mass = -10.63 + 0.562 × body length*) (Fig 3.10) gave a better fit (R^2 = 0.467, n = 241) compared to a second-degree polynomial or log-log regression for the calculation of the body condition index. The average individual should have an index of condition of 1.0. There was no significant difference in body condition between males and females (Mann-Whitney U test: U= 6426, p = 0.130: n = 241). Both males and females had a mean index of condition of 1.0 and standard deviations of 0.148 (n = 126) and 0.362 (n = 115) respectively. The indices of condition also did not show any significant difference between natural and transformed habitats (U = 1760, p = 0.518: n = 241), and between study plots at Elandsberg and Riverlands and Pella (U = 4017, p = 0693: n = 241). Body condition, however, varied according to season at both the Elandsberg and Riverlands and Pella localities. At Elandsberg, mean index of condition increased from autumn to summer whereas at Riverlands and Pella body condition showed an opposite trend, declining over time from autumn to summer (Table 3.5).

3.4   Discussion

3.4.1   Small mammal responses to seasonal changes in vegetation composition

Previous studies have suggested that small mammal species richness and diversity are positively correlated with vegetation cover (e.g. Olson & Brewer 2003; Monadjem 1997). In our study, vegetation cover correlated with small mammal species diversity and abundance, particularly in the transformed habitats in which there was significant seasonal changes in vegetation cover. For example, the presence of high vegetation cover in transformed habitats

in winter at Elandsberg corresponded with an increase in species richness and abundance in those habitats. Studies in desert habitats have also provided similar evidence, with an increase in small mammal diversity with increasing vegetation cover (Abramsky & Rosenzweig 1984; Kerley 1992). Vegetation cover has been shown to reduce predation levels (Keesing, 1998) and intraspecific confrontation (Birney *et al.* 1976). This is because good vegetation cover is important in a number of small mammal species such as *R. pumilio* and *Otomys sp.* that require dense cover for runways and predator avoidance.

The absence of rodents in the wheat fields (transformed habitat at Elandsberg) during the wheat growing and post-harvest seasons was thus a surprising result. Sampling in the field was done when the wheat was still green with no ripe corn kernels that rodents could utilize as food, and after the harvest period when there was minimal vegetation cover. The wheat crop was expected to provide food and cover for rodents and thus rodents from the Vlei natural fragment (Vlei A) were expected to move into the wheat field to utilize these resources. The absence of rodents in this transformed habitat may be directly linked to the unavailability of simultaneous food and cover. In addition to providing protection from predation, vegetation should also provide a food source (Parmenter & MacMahon 1983; Fuller & Perrin 2001; Cavia *et al.* 2005; Bilenca *et al.* 2007) for the rodents for it to be utilized as a habitat. Lower vegetation cover inevitably leads to reduced protection from predation and the availability of food for small mammals is reduced (Cassini & Galanthe 1992). For example in the canola field, rodents could feed on the vegetative parts of the canola crop (pers. obs.) and thus they could utilize the cover provided by the vegetation in addition to the food, making it a preferable habitat.

3.4.2   Transformed versus natural habitats

Fragmented landscapes often consist of two kinds of habitat. The first is the transformed habitats such as the cultivated fields, where agricultural practices and the size and structure of the farmland are major components explaining the fate of biodiversity (Selmi & Boulinier 2003). The other is made up of the surroundings such as patches of natural vegetation, hilly fragments etc. These non-agricultural patches have been shown to strongly affect farmland faunal communities by providing breeding sites, food supplies, cover or by potentially allowing the colonization by individuals and species (Woodhouse *et al.* 2005; Buckingham *et al.* 2006). When we exclude sporadic species (species not captured more than twice), the natural habitats in our study had just four rodent species compared to three in the transformed

habitats. The low species abundance and richness observed in transformed habitats concurs with results from other studies which demonstrated a causal relationship between disturbance in habitats and species diversity (Wooton, 1998; Trojan 2000; Hastwell & Huston 2001; Avenant & Kuyler 2002). On the other hand, it has been shown that fragments of natural habitat may be important refuges especially in agricultural areas where the surrounding matrix is harvested (Fitzgibbon 1997; Clergeau *et al.* 2001; Krauss *et al.* 2004). Doyle (1990) suggested that such habitats existing as pockets between adjacent crop lands appear to be important in sustaining diverse small mammal communities because the heterogeneous nature of their vegetation composition which usually comprises grasses, herbs, geophytes and shrubs provides a range of food sources for small mammals throughout the year.

When these habitat patches and their rodent species communities are not isolated in the landscape, movements of individuals within landscapes are a possible mechanism for enabling efficient utilization of these habitats by rodents. This can be explained by phenomenon known as the 'neighbourhood effects' (Dunning *et al.* 1992) where the biodiversity of a given habitat is also dependent upon the surrounding matrix. Though habitat quality may be the most important factor determining the presence of a species at a given site (Duelli 1997), diversity within a patch additionally depends on the structure of the surrounding landscape (Dauber *et al.* 2003). These so-called matrix-effects have been demonstrated by various authors (e.g. Burel *et al.* 1998; Weibull *et al.* 2000). Transformed habitats such as the canola field could be utilized, not only as secondary habitats but also as corridors for movement between surrounding natural habitats. For example some rodents captured at the Slang kop site were also captured after the winter season in a plot within the nature reserve (Krug, unpublished data) and at the Vlei fragment (pers. obs.). The winter crop of canola provided a more or less continuous vegetation cover between Slang kop and the Nature Reserve which could be used as a corridor for passage and movement by small mammals. This, in turn, could also explain the presence of *M. minutoides* on the Slang kop natural habitat during and after the winter season when none had been captured there in autumn.

Even though in this study we did not measure fragment sizes, the fragments sizes at Elandsberg were generally smaller than the remnants at Riverlands and Pella (pers. obs.). However, higher abundances of small mammals were found at Elandsberg sites compared to the Riverlands and Pella site. This observation is consistent with the suggestion that small

isolated habitat patches often support higher densities of small mammals than larger contiguous habitats (Adler & Levins 1994; Krug 2005). The reason for this phenomenon is unclear though it has been suggested that disturbed habitats serve as important refugia for small mammals (Doyle 1990) depending on the biological needs of the species present, spatial distribution of resources and permeability of the landscape itself (Butet *et al.* 2006). Conversely, habitats of uniform structure and plant form support tiny small mammal communities. Our data suggest that more intensive habitat transformation favours the abundance of small mammals especially generalist rodent species such as *R. pumilio* whilst less transformed habitats habour smaller, but more diverse small mammal communities. This trend is consistent with studies such as Malcolm (1997), that have found increased species richness and total abundances in smaller remnants.

3.4.3   Seasonal abundance and species richness

Rodent populations are also known to exhibit great seasonal (Leirs *et al.* 1989) and year to year variation (David & Jarvis 1985). A similar pattern was found in the present study with more rodents being captured in autumn than in winter, spring and summer. As there was no significant changes in vegetation structure and composition in most of the study sites, seasonal changes in small mammal abundances may have been due to other factors such as predation, death, or changes in the availability of alternative food sources e.g. canola and herbs in winter and seeds in summer. In a study to quantify habitat characteristics that provide suitable small mammal habits, Fuller & Perrin (2001) found that small mammal species richness in the Umvoti Vlei Conservancy in KwaZulu Natal increased with the approach of winter. However, Avenant (2000) observed an opposite trend in the Willem Pretorius Nature Reserve in the Free State, with the highest species, diversity and richness found in autumn. This result is compares favourably to our study where abundances peaked in autumn and declined in winter. Kern (1981) also found lowest diversity indices in winter in the Kruger National Park. Small mammal abundance in our study was highest in autumn. This is comparable to Fuller & Perrin (2001) in KwaZulu Natal and Avenant (2000) in the Free State. Autumn peak abundances have been attributed to juvenile recruitment following late summer breeding (Mendelson 1982).

3.4.4   Species-specific responses to habitat transformation

Small mammal responses to habitats transformation may be strongly dependent on species-specific properties (Wiegand *et al.* 2005). Many studies have shown that species vary in their responses to fragmentation (Malcolm 1997; Terborgh *et al.*, 1997; Cosson *et al.* 1999). The striped mouse is described as a generalist and opportunistic omnivore with a broad niche that exploits transient nutritious food sources including seeds (Smithers 1983; Kerley 1989; Nowack 1991; Krug 2002). In addition, the great adaptability of the species to a variety of habitats explains its presence in the different habitat types in our study, ranging from stands of alien *A. saligna*, natural fynbos and fields of canola crop. Eccard and coworkers (2000), whilst studying the effects of livestock grazing on small mammals in the Karoo also found *R. pumilio* to be the most dominant of all the captured species. Therefore the dominance of this species in the study was not surprising. *Rhabdomys pumilio* was captured in all but two sites during the study and constituted more than 80% of the total rodent captures. Similarly, the presence of *M. minutoides* in a variety of habitats is also not surprising. This species is sufficiently small to avoid predators by making use of any available vegetation cover and refuges which would otherwise be inadequate for larger species (van Wyk 1995). *Mus minutoides* is omnivorous and this places it in a broad feeding niche making it capable of surviving in a variety of habitats. In a study by Monadjem (1997), *M. minutoides* exhibited no obvious habitat preferences, being absent only at sites devoid of grass cover. A diverse habitat preference favours survival by making a species more pliable to environmental change (Brooks 1974). The canola crop was only in the field for a limited period of time and the presence of *M. minutoides* and *R. pumulio* provides further evidence of their opportunistic nature. These two species were also found in most of the sites where trapping was done. These findings appear to corroborate the findings of previous workers. *Mus minutoides* and *R. pumilio* have been reported as occurring in almost any habitat (De Graaff 1981, Rowe-Rowe & Meester 1982; Monadjem 1997)

In contrast, the Vlei rat (*O. irroratus*), is known to be a narrow niche species (Fuller & Perrin 2001), with well defined habitat preferences and specialized feeding habits. It is a specialist herbivore (Wandrag *et al.* 2002), feeding predominantly on green plant material and does not readily eat seeds or insects (van Wyk 1995). *Otomys irroratus* is found mainly where there is dense grass cover (De Graaff 1981; Bond *et al.* 1980). Individuals from genera such as *Tatera* and *Mysorex* are more restricted in their habitat preferences (De Graaff 1981). Such species are likely to be affected most by environment change and habitat transformation. This

probably explains the low abundance of *O. irroratus, M. verreauxii*, and *T, afra. Mysorex varius* is linked with moist grassland (Rautenbach 1982) even though in KwaZulu-Natal province of South Africa, it was found to occupy a wide variety of vegetation types (Fuller & Perrin 2001). The low numbers observed in our study are thus surprising. The dominance of *R. pumilio* and *Mus minutoides* and the low abundance of specialist species such as *O. irroratus*, and *M. verreauxii* suggest that transformation of natural habitats favours opportunistic and generalist rodents whilst discriminating against specialist rodents. Studies have shown the dominance of a few species in disturbed habitats (e.g. Olson & Brewer 2003; Heroldova *et al.* 2007). This observation corresponds to Schropfer (1990) who inferred that more than 75% of individuals in European small mammal communities inhabiting a given locality belong at most to three species.

3.4.5   Body mass, condition index and reproductive activity in *R. pumilio*

Our study did not show significant differences in body weights, and body condition between males and females. This is unusual, as small mammals are known to exhibit sexual dimorphism (Heske & Ostfeld 1990; Schulte-Hostede *et al.* 2001; Schradin & Pillay 2005). In a study by Schradin & Pillay (2005) in the Succulent Karoo, males were significantly heavier than females. Our study also revealed that reproductive activity was positively correlated to the body condition index. Female mammals' reproductive success is known to be correlated with body condition (Atkinson & Ramsay 1995). Body mass and body condition index fluctuated seasonally as did reproductive activity in *R. pumilio* which peaked in winter and summer when the index of condition also peaked. In our study, body mass, condition and reproductive activity were high in the winter season and declined in spring. Krug (2007) observed a similar trend with body mass. The average decline in body mass may reflect an influx of young mammals being born into the population (Krug 2007).

High body mass and a high proportion of adults in breeding condition are indicative of the suitability of habitats for animal species (Doyle 1990). Natural habitats were expected to provide better food and cover resources for small mammals, and thus body condition index, body mass and reproductive activity were be expected to be higher than in the transformed habitats. In our study sites body condition index, body mass and reproductive activity did not differ between natural and transformed habitats. One possible reason for this would be that the small mammals captured in the transformed habitats were not separate populations from

those captured in the natural habitats and thus there would be no differences in their characteristics.

Previous studies on *R. pumilio* recorded seasonality in reproductive activity in the Western Cape (Krug 2002; Schradin & Pillay 2005). However, our study shows evidence of year-round reproductive activity. The presence of juveniles weighing less than 20 g and gravid females weighing more than 60 g during all the seasons suggests year round reproductive activity. High densities during the wet season are typical since rainfall results in food being abundant which in turn increases breeding (Taylor & Green 1976). In our study, winter together with summer showed significantly high reproductive activity. This, in part contrasts David & Jarvis (1985) and Krug (unpublished data) who suggest scant reproductive activity during the cool, wet winter months. Their explanation was that since the Western Cape is a winter rainfall region, the resultant low temperatures may not be conducive for reproduction and may in fact result in deaths. Our study, in part, confirms the assertion by these workers that the main breeding season of *R. pumilio* is the summer months. There was no significant seasonal change in vegetation structure and composition in the natural habitats and this continuity may be instrumental in providing a more or less stable environment that rodents can utilize for reproduction throughout the year. Also, the provision of transformed habitat resources such as cover and food items such as insects, vegetative plant matter, and seeds especially in winter may be important factors in enabling *R. pumilio* to breed throughout the year.

In most mammals, reproduction is timed such that birth coincides with the time that maximizes growth and survival of the offspring (Fitzgerald & McManus 2000). In species with short life spans such as small mammals, however, reproduction may be timed to coincide with favourable environmental conditions (Muteka *et al.* 2006). The timing of female reproduction in a population of small mammals appears to be shaped by the availability of high quality food and availability of moisture (Krug 2007). This opportunistic breeding stratergy is known to be employed by a number of rodent species. For example, even though house mice (*Mus domestica*) normally breed seasonally (Bronson & Perrigo 1987) they have also been shown to breed from spring to autumn (Twig & Kay 1994). In our study both male and female striped mice were reproductive throughout the year even though during three out of the four seasons, a larger proportions of males than females was reproductively active. A higher proportion of females were reproductively active in summer,

the season with the highest breeding rates, giving further evidence that the actual reproductive period is determined by females who react to specific cues. Krug (2007) observed the same trend in the Kalahari, a hyper-arid region, and this reveals how *R. pumilio,* which is widely distributed throughout Southern Africa, exhibits plasticity and adaptability in life history. The fluctuations in reproductive effort by the rodents may explain the observed abundance patterns in the small mammal populations. For example, high reproductive activity in summer might have caused the resultant increased rodent abundance in autumn. On the other hand, even though reproductive activity in winter was high, the decline in small mammal abundance might be a result of winter deaths caused by rainfall and very cold temperatures. In some studies, very high winter mortalities have been recorded e.g. 74% in Krug (2004) and 73% in Schradin & Pillay (2005).

Limited food resources has been widely accepted as one of the most important factors affecting life history strategies in birds (Martin 1987) as well as in mammals (Sikes & Ylonen 1998). Studies investigating the relationship between food resources and reproduction in mammals (e.g. Boutin 1990; Singleton *et al.* 2001; Ylonen *et al.* 2003) have demonstrated that food quality and quantity are important factors driving changes in rodent numbers. In addition, rainfall might also be an essential factor affecting reproductive changes (Ylonen *et al.* 2003) as the lack of water might potentially hinder mice from exploiting available high quality (but dry) food resources. Even though in our study we did not evaluate the availability of food sources and their effect on reproductive activity in the striped mouse, food supplies in the form of ripening grain have been shown to trigger the onset of breeding and the provision of high quality food can extend the breeding season (Bomford & Redhead 1987).

3.4.6   Conclusion

In conclusion, highly fragmented landscapes such as those present at Elandsberg Private Nature Reserve and Farms favour opportunistic, broad-niche species such as *R. pumilio* and *M. minutoides* whilst discriminating against those with specific habitat requirements. Less fragmented landscapes support smaller, species rich small mammal communities than highly fragmented ones. Transformed habitats are useful in mitigating the dangers faced by these small mammal communities and are useful as secondary habitats, corridors for dispersal and movement and for the provision of food and cover resources. High species richness and abundance of small mammals in vegetation remnants among cropping systems support the idea that these relatively natural habitats may serve as refugia for wildlife (Ellis *et al.* 1998)

and so they should be interconnected to form corridors throughout agricultural landscapes (Bilenca *et al.* 2007). This in turn helps populations maintain energy reserves and body condition necessary to ensure continuous and successful breeding throughout the year, as in the case of *R. pumilio*. The role of transformed habitats as dispersal sinks thus requires further investigation. Dispersal sinks are refuge areas that may be marginal, or even unsuitable, habitats to which surplus individuals from the primary habitats can disperse (Doyle 1990). Use of dispersal sinks by small mammals was suggested by Van Horne (1982). Doyle (1990) also demonstrated the use of upland habitats as dispersal sinks by small mammals juveniles.

Whilst fragments of natural habitats especially at Riverlands and Pella may be playing an important role in harbouring rare and possibly endangered small mammal species, transformed habitats are also important as secondary habitats providing both cover as well as seasonal food resources. It is also possible that the growing season in the fields, particularly in winter, makes the transformed habitats useful refuge and corridors of movement of some species, thus enhancing the connectivity within the fragmented landscapes. The winter season usually coincides with the highest mortalities of small mammals due to the very low temperature, rainfall and general reduction in food supplies. However, in this study, the availability of the winter canola crop as food and cover resources in provides some mitigation and cushion for the small mammals and winter mortalities in the study sites may not be very severe.

3.5   References

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Chapter 4

Alien invasion into a fynbos remnant: the role of small mammals

Abstract

The Australian shrubs *Acacia saligna* and *Acacia cyclops* are among the most successful invasive alien plant species within the Cape Floristic Region (CFR) threatening the conservation of fynbos. Their success is, in part, attributed to their production of copious amounts of small hard-shelled seeds and well-established soil seed banks. At Riverlands Nature Reserve in the CFR, the natural sand fynbos is under intensive pressure from Port Jackson Willow (*A. saligna*), which forms dense stands in the lands adjacent to the nature reserve. These stands have been encroaching into the fynbos vegetation within the nature reserve. The aim of this study was to investigate the effect of alien invasion on the resident small mammal communities and to determine the role of small mammals in the removal and predation of *A. saligna* seeds. Rodent species abundance and diversity was very low in the alien stands compared to the adjacent fynbos vegetation. Only two species, *R. pumilio* and *M. minutoides* were present in the acacia stands. The interaction of rodents with seeds (removal or predation) was dependent upon seed size and seed abundance in the habitats. Whilst rodents may play an important role in dispersing the seeds of acacias, it is possible that they will be playing a significant role as seed predators, limiting invasion by the acacias into fynbos.

Key Words: alien invasives, *Acacia saligna*, seed predation, removal, rodents, fynbos

4.1 Introduction

Invasive alien species are one of the greatest threats to natural ecosystems worldwide (Cronk & Fuller 1995) and are regarded as the second most pressing threat to biodiversity after direct habitat transformation (Mooney & Hobbs 2000). The Australian shrubs, *Acacia saligna* (Labill.) Wendl. and *A. cyclops* A. Cunn ex G. Don are problematic plants which have invaded the South African fynbos biome, typically forming dense thickets, suppressing the indigenous vegetation and reducing plant species richness (Richardson *et al.* 1989) and thus threatening its conservation (Rebelo 1992). *Acacia saligna* was introduced into South Africa around 1845 (Shaughnessy 1980) and has since been able to outcompete the indigenous vegetation completely in some areas in the Cape Floristic Region (CFR) (Macdonald & Jarman 1984).

Alien plants, in addition to having escaped from most of their co-evolved natural enemies (pests and predators), need to develop new seed dispersal mechanisms in order to successfully invade new habitats. Key factors in the success of *A. saligna* and *A. cyclops* include the efficient seed dispersal and the copious production of hard-coated seeds, which accumulate in the soil (Dean *et al.* 1986; Holmes 1990a). Annual seed production by *A. saligna* and *A. cyclops* is about 10 000 and 3 000 seeds m^{-2} of canopy cover, respectively (Milton & Hall 1981). Most of the seeds fall directly to the ground and a large proportion of these remains dormant, because of a water-impermeable testa (Rolston 1978), resulting in the accumulation of large seed banks in the soil. In Australia, *A. saligna* is ant dispersed, whilst both ants and birds disperse *A. cyclops* (O'Dowd & Gill 1986). In the fynbos, these seeds are believed to be removed and buried by ants belonging to the genera *Anoplepsis* and *Pheidole*, which are widespread in the fynbos (Bond & Slingsby 1983). These ants seldom carry the seeds a distance exceeding 2-3 m and thus are more important in maintaining *Acacia* soil seed banks than in extending their invasive front (Holmes 1990b). On the other hand, the amount of seed recruited into the seed bank can be greatly reduced due to seed predation by rodents (principally the striped mouse, *Rhabdomys pumilio*), which may consume a large proportion of the seeds (Holmes 1990a). Studies in *A. cyclops* invaded habitats (e.g. David 1980; David & Jarvis 1985) have shown that seeds form about 50% of the diet of *R. pumilio*. This, together with population density estimates, translates to a minimum consumption of 3 001–2 336 seeds $m^{-2}y^{-1}$ (Holmes 1990a).

Rodents show seed preferences in their natural habitats where they are exposed to differing physical and nutritional environments (Kerley & Erasmus 1991). Whilst seed selection is correlated to net energy gain (Kerley & Erasmus 1991), granivorous rodents must also take into account other costs such as locating and harvesting seeds and exposure to predation. Seeds vary in both their distribution and abundances (Henderson *et al.* 1985) and this in turn will influence granivore behaviour.

Granivory by vertebrate and invertebrate seed predators can have profound effects on development of plant communities (Reader 1997), affecting the survival and recruitment of plants (Kerley & Erasmus 1991). Rodents have been shown to be the most important granivores in the northern hemisphere deserts (e.g. Mares & Rosenzweig 1978; Abramsky 1983) and are also regarded as important seed predators in mesic environments (Bayne & Hobson 1998). The discovery that rodents in an acacia savannah in Southern Africa consume up to 25% of the annual seed crop of *Acacia* sp. suggests that they also play a role in influencing plant communities in less arid sites in the southern hemisphere (Miller 1994). Seedpods of *Acacia arioloba* form a major part in the diet of *R. pumilio* in the Namib Desert (Krug 2002). A major cause of recruitment failure is seed predation (Bond & Slingsby 1984; Bond & Breytenbach 1985). These authors have also shown that seed predation by rodents is significant in a number of different fynbos communities and that ants reduce seed predation by quickly burying the seeds away from the reach of these rodent predators. However, all these observations were on large seeded Proteaceae and no information is available for *Acacia* species invading fynbos ecosystems.

Scatter hoarding, which refers to the burying of food items in many depots for later recovery (Vander Wall 1990), has been shown to be widespread behaviour among small mammals (Forget & Vander Wall 2001). Granivores disperse seeds by scatter-hording and such seed dispersal by animals is one of the most important mechanisms in the ecology and evolution of mutualistic systems (Bronstein 1994). It is, however, a newly discovered phenomenon in the fynbos of the south Western Cape, South Africa (Midgley *et al.* 2002), as it was previously thought that there were no seed-caching rodent species in fynbos (Slingsby & Bond 1985). Even though following the movements and fates of all dispersed seeds is difficult (Wang & Smith 2002), to generate a thorough understanding of the role of seed dispersal by animals and rodents in particular, it is important to be able to determine the ultimate fate individual

seeds (Xiao *et al.* 2006). A detailed assessment of the spatial and temporal dynamics of seed dispersal and predation systems of both alien invasive plants and native vegetation, and the role small mammals play in the invasion of the fynbos is needed to inform effective alien management and conservation planning for the fynbos. Animal seed dispersal has the potential to accelerate forest regeneration and restoration (Wunderle 1997); thereby making it possible that animal seed dispersal may aid the invasiveness of the *Acacia* species in the fynbos ecoregion. Alternatively, seed bank reduction because of seed predation by rodents may provide a potential key to successful control of invasive alien acacias (Holmes *et al.* 1987).

In many studies seed predation has been documented through studies of rodents' diets rather than through the perspective of its potential on recruitment in plant communities. Few if any, studies have investigated the effect of these invasions on small mammal assemblages, and the role that small mammals play in the removal (predation or dispersal) of alien seed after seed fall. The aim of the study was thus to determine the importance of rodents in the removal of alien seed in the invaded fynbos systems. More specifically, the objectives were to determine the proportions of seeds predated upon, moved and left alone. We also sought to determine the effect of seed availability, size and nutrient content on seed utilization (predation or removal) by rodents. The study also sought to determine the effect of invasion on small mammal species diversity, abundance and richness in comparison with uninvaded fynbos habitats.

4.2   Methods

4.2.1   Study Area

Riverlands Nature Reserve is located 63 km north of Cape Town, (approximately 18° 37′ E and 33° 29′ S) at an altitude of 190 m in the Malmesbury Magisterial district of the Western Cape Province. The native vegetation is classified as Atlantis sand fynbos (Musina & Rutherford 2006). The climate is Mediterranean, with hot dry summers and cool wet winters (Yelenic *et al.* 2004). It lies on quaternary sand and receives an average annual rainfall of 400 mm. The nature reserve was set aside for the conservation of locally endemic and endangered fynbos species and the dominant fynbos species include *Protea scolymocephala, Eligia Filacea, Ischyrolepis paludosa and Leucadendron corymbosum* (Kongor, pers. comm.). The conservation status of the Atlantis sand fynbos has been recognized as vulnerable (Mucina &

Rutherford 2006). Whilst some 40% has been transformed, inherent threats include cultivation (agricultural small holdings and pastures), and gum and pine plantations. The nature reserve covers an area of about 1300 ha and hosts about 400 native plant species, (Killian 1995). It consists of a landscape mosaic composed of invasive alien vegetation, fallow fields, and uninvaded indigenous fynbos communities. By 1995, 300 ha within the reserve were covered in dense alien vegetation, mostly *A. saligna* (Yelenik *et al.* 2004). Through the work being done by the Working for Water programme, a significant amount of these aliens has been cleared. However, the dense alien stands on the neighboring lands still pose problems of potential invasions in the future and subsequent significant alterations to the fire regimes and subsequent vegetation structure in the nature reserves.

Fig 4. 1 Dense stand of flowering *Acacia saligna* plants adjacent to Riverlands Nature reserve.

Seed removal experiments were carried out in the stands of alien acacias adjacent to the reserve (Fig 4.1), whilst small mammals were trapped in both the alien stands and the fynbos vegetation (Fig 4.2). The vegetation in the alien stands was composed mainly of *A. saligna* shrubs growing to an average height of over 3 m. Canopy cover was at least 90% and litter

underneath the stands was composed of leaves, seed pods and other dead plant material (see chapter 3 for more results on vegetation cover).

Fig 4. 2 Photograph of the Atlantis sand fynbos vegetation at Riverlands Nature Reserve in the foreground bordered by a stand of the alien *Acacia saligna* in the background.

4.2.2   Key rodent species affecting seed disappearance

In order to identify the rodent species involved in seed removal small mammal sampling was carried out in the alien stands as well as in the adjacent fynbos vegetation. The sampling was conducted over four seasons and methods and results are described in detail in Chapter 3.

4.2.3   Seed removal experiments

Acacia saligna sheds seed in early summer (November-December; Holmes, 1990a) and most of the seeds fall directly to the ground. Three seed availability seasons were identified as follows: high – season immediately after *A. saligna* sets seeds; low- season just before the next seed fall; moderate- the season in between high seed availability and low seed availability. We assumed that the largest amount of seed on the ground would be immediately after seed fall and we also assumed that the amount of the seeds on the ground would generally decline until the next seed fall. The study was carried out in September 2006 (low seed availability), November-December 2006 (high seed availability) and April-May 2007 (intermediate seed availability). Experiments to investigate the role of small mammals in the removal of seeds were carried out using seeds of *A. saligna* and the sunflower, *Helianthus annuus. Helianthus annuus* does not occur naturally in the study site but we introduced it in the study to provide size comparison on the effect of seed size as this has been shown to have an impact on seed fate (Xiao *et al.* 2006).

The location of cafeteria plots was determined by initially placing 20 groups of 50 seeds (25 *A. saligna*, 25 *H. annuus*), each group at a randomly selected site (cafeteria plot) within the *A. saligna* stands. Seeds were placed either in trays or on the ground and observations were made over the next two days. Once sites were found where the seeds disappeared i.e. were moved or eaten, cafeteria plots were established at these sites. Further groups of 50 *A. saligna* and 50 *H. annuus* seeds were placed at each cafeteria plot and five cafeteria plots were used in all the seasons. The cafeteria plots were placed at least 50 m apart. A 15 cm length of colourful fly-fishing line was attached to each seed using quick setting super glue to enable detection of the seeds if they were moved or buried (Midgley & Anderson 2005). Checks were carried out every day after the initial day for at least five days to observe if any seeds were consumed *in situ* or moved from the cafeteria plots. Removed seeds were traced and found again by locating the fly-fishing lines. Cafeteria plots were observed over a five day period and all the seeds remaining at the original cafeteria plot were collected and counted. Seed fate was classified as "predated *in situ*" if husks or bits of seed were recovered at origin; "remaining" if whole seeds were recovered at the origin after 5 days. Seeds that could not be accounted for as either eaten or remaining were considered to have been "moved". All husks that were found at the cafeteria plot and within 0.5 m of the origin were collected and counted

to determine the number of seeds predated upon *in situ*. Visual observations together with tooth marks on the remaining husks and foot prints on the ground around the cafeteria plots were used to try and determine the taxa responsible for predation or removal (Krug pers. comm.). The ground around the cafeteria plots was inspected everyday for the next five days by intensively searching a radius of 15 m around each cafeteria plot to recover all the seeds that were moved. Buried seeds would be found by locating the fly fishing line.

4.2.4   Data Analysis

Data was summarized and analyzed using Statistica 7 © (Statsoft. Inc. 2007). Proportions of seed for each seed size (species) were calculated as the total number of seeds facing a particular fate (i.e. removed, eaten *in situ* or remaining) divided by the total number of seeds set out in the cafeteria plots. In order to analyze the differences between the different seed sizes in the different seed availability seasons, we first grouped the data according to the seasons and used to one way ANOVA and Post hoc Bonferronni comparisons to test for significant difference in the different seed fates for the two seed types. We then grouped the data according to the seed species (size) in order to investigate within seed-size variation in seed fate over the different seasons. Differences between proportions of seeds that were predated upon, removed and remaining were also analyzed using one way ANOVAs and Post hoc Bonferronni comparisons to test for significant differences.

4.2.5   Nutrient profile analysis

To determine the nutritional content of both seed types, samples of *A. saligna* and *H. annuus* seeds were taken to the Nutrition Laboratory (Department of Animal Science) for a nutrient profile (feed analysis). The feed analysis done calculated the percentage constituents, in each seed type, of moisture content, dry matter, ash, nitrogen, crude protein, fibre and fat. The percentage composition of the nitrogen-free extract (NFE) was calculated by subtracting all the nitrogen containing components from 100%. The NFE is considered to be the available carbohydrate (Maynard 1940) and may be composed of starch, lignin and hemicelluloses (van Soest & McQueen 1973). The data were not sufficient to carry out statistical analyses such as regression correlations with predation/ removal rates thus the feed analysis values were compared with the predation/ removal rates to investigate relationships.

4.3 Results

4.3.1 Rodents

Only six individuals from two species (*Rhabdomys pumilio* and *Mus minutoides*) were captured in the alien stands in the four trapping sessions during the study period compared to 42 individuals from six species (*R. pumilio, M. minutoides, Myomyscus verreauxii, Tatera afra, Steatomys krebsii* and *Otomys irroratus*) captured in the adjacent fynbos vegetation (Fig 4.3). Of the rodents captured in the stands of *A. saligna,* none were recaptured in the natural fynbos and vice versa. Some active burrows were also found in both the fynbos vegetation and in the alien stands. Although it could not be ascertained, which rodent species the burrows belonged to, a few *R. pumilio* individuals were observed near one of the cafeteria plots. At the cafeteria plots, small mammals appeared to be the seed predators. Small mammal activity could be easily identified by the opened or crushed husks and by footprints at or near the cafeteria plots. No ants or granivorous birds were observed at or near the cafeteria plots during the study.
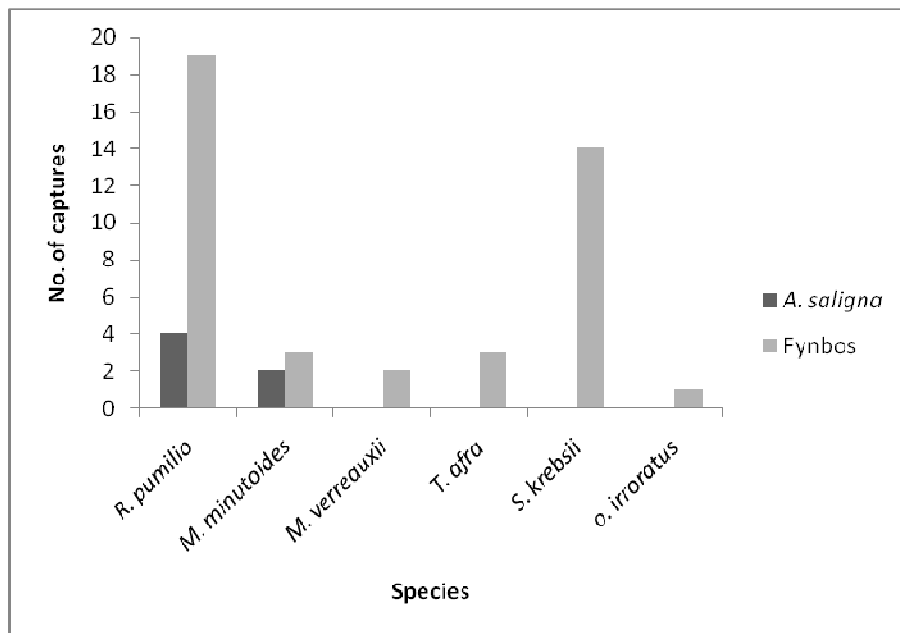
Fig 4. 3 A comparison of the rodent captures in the study site (*A. saligna stand*) and the adjacent fynbos vegetation at Riverlands Nature Reserve. Trapping effort was equal in both plots.

Fig 4. 4 Opened husks of (a) *Helianthus annuus* **and (b)** *Acacia saligna* **seeds provided evidence of rodent predation on seeds in cafeteria plots. Photos by James Mugabe.**

4.3.2   Seed removal

Seeds placed in cafeteria plots were either removed, eaten *in situ*, or remain untouched. Small mammal activity could be easily identified by the opened or crushed husks at or near the cafeteria plots (Fig 4.4). Even though rodent foot prints could be seen at the cafeteria plots, it was difficult to follow them due to the high littler levels on the ground and also because most rodent trails follow the covered areas (Gurnell & Flowerdew 1990) as these provide cover from predation (Kotler 1984). Some of the fly fishing lines were bitten off before the seeds were either carried away or eaten. No buried seeds were found within the 15 m radius thus the fate of the removed seeds could not be ascertained.

4.3.3   Seed availability

Helianthus annuus

In all the seasons, rodents removed higher proportions of *H. annuus* (large) seeds than those eaten *in situ* or left alone. The highest proportion of removed seeds (about 75%) was at high seed availability though the differences between seasons were not significant ($F = 0.957$, $df = 2$, $p = 0.397$). On the other hand, a significantly lower proportion of large seeds were eaten *in situ* at higher seed availability compared to the low and moderate seed availability seasons ($F = 2.4882$, $df = 4$, $p = 0.003$; Fig 4.5). In all the seasons the proportion

of large seeds remaining at the cafeteria plots was low and differences were not significant ($F = 0.036$, $df = 2$, $p = 0.965$).

Acacia saligna

More seeds were eaten *in situ* rather than removed from cafeteria plots. Seed predation was significantly higher at high seed availability than at low and moderate seed availability ($F = 10.668$, $df = 4$, $p = 0.000$). Inversely, a significantly lower proportion of small seeds were removed at high seed availability with rodents removing less than 10% of small seeds from cafeteria plots (Fig 4.5).
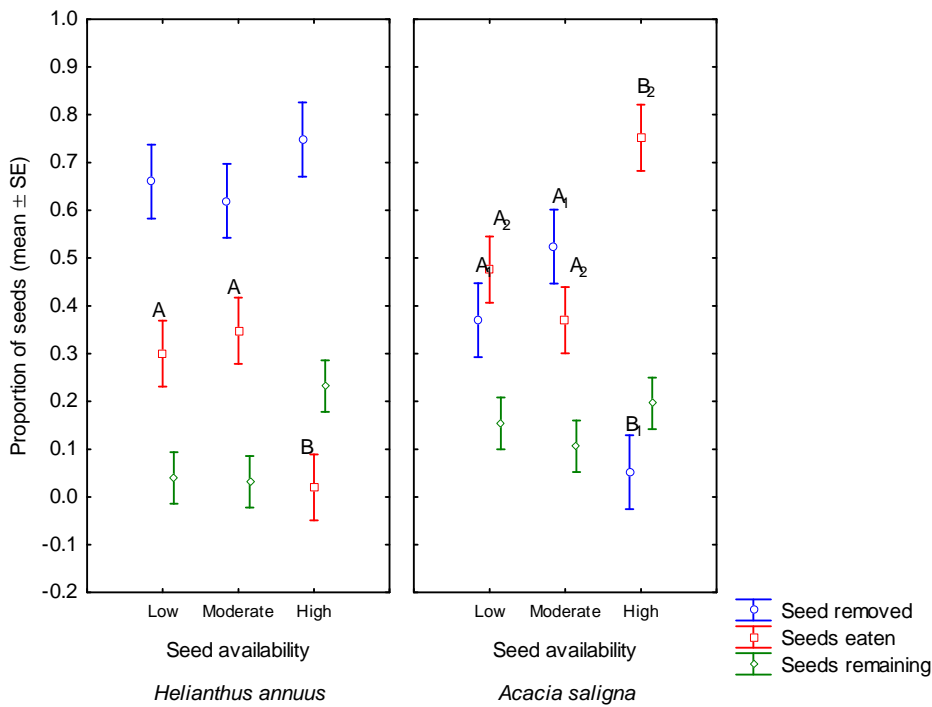
Fig 4. 5 Mean proportions (± SE) of seeds that were removed, eaten or remained during different seed availability seasons. Significant differences are denoted by different letters.

4.3.4 Seed size

Seed size had a significant influence on whether seeds were eaten, removed or left alone. In all the seasons rodents removed more large seeds than small seeds. However, it was only at low and high seed availability that these differences were significant ($F = 6.7065$, $df = 2$, $p = 0.024$ and $F = 2257.3$, $df = 2$, $p = 0.000$ respectively). More small seeds were eaten *in situ* than were removed or left alone, although the differences were not significant (Fig 4.6). When seed availability was moderate, rodents consumed and removed

similar proportions of both small and large seeds. The proportion of remaining seeds was very low for both seed sizes in all the seasons and there was no significant difference between them ($F = 1.083$, $df = 1$, $p = 0.307$). For both seed sizes the remaining seeds (seed survivorship) were less than 20% of the total in all the seasons. Increasing seed availability resulted in increased proportion of remaining seeds even though the differences were not significant.
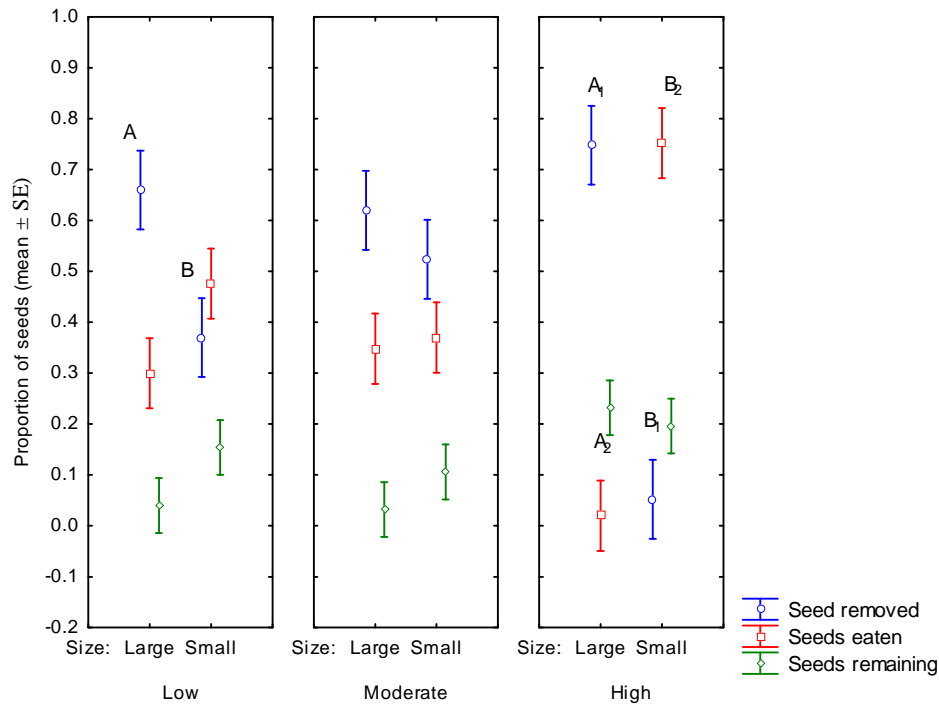
Fig 4. 6 Mean proportions (± SE) of seeds of two different sizes that were removed, eaten or remaining in the cafeteria plots in all the seed removal seasons. *Acacia saligna* represented small seeds and *Helianthus annuus* large seeds. Different letters indicate significant differences

4.3.5   Nutrient composition

The two seed types contained very little moisture. Crude fat, protein and fibre constituted a higher proportion of the seed content in *H. annuus* constituting more than 80% of the seed's dry mass compared to about 46% content in *A. saligna*. On the other hand *A. saligna* seed contained almost three times more carbohydrate than *H. annuus*. The results of the complete nutrient profiles for the two seed types are shown in Table 4.1.

Table 4. 1 Comparison between nutrient content of *Acacia saligna* and *Helianthus annuus* seeds.

Nutrient	*Acacia saligna* (%)	*Helianthus annuus* (%)
Moisture	3.95	5.85
Dry matter	96.05	94.15
Ash	7.26	2.82
Nitrogen	4.14	2.49
Crude Protein	25.85	15.56
Crude fibre	10.37	27.47
Crude fat	10.20	33.75
Nitrogen-free extract (NFE)	42.37	14.55

4.4   Discussion

4.4.1   Rodents

Rodents are known to be important seed predators in various habitat types (e.g. Sullivan 1979; Hulme 1998; Edwards & Crawley 1999) including in fynbos habitats where they feed on, amongst others, seeds of *Leucospermum truncatulum* (Midgley & Anderson 2005) and alien *Acacia* species (Holmes 1990a, b). However, the role of rodents in seed predation may be a function of rodent abundance (Linzey & Washok 2000) and thus understanding processes that determine rodent abundance in ecosystems may be important in understanding the role of small mammals in seed removal and predation. Habitat heterogeneity (Lu & Zhang 2004) and the vegetation structure (Forget *et al.* 1998; Jansen & Forget 2001) in the habitats affect the abundance and diversity of potential seed-eating animal communities. Most studies of the distribution of small mammals have used vegetation structure (cover and diversity) as correlates. However, Midgley & Anderson (2005) argue that distribution has rarely been considered relative to food resources. Rodent abundance in the *Acacia* stand at the study site was lower than within the adjacent fynbos remnant. This supports the notion that *Acacia* invasions may reduce rodent abundance (Holmes 1990a). Even though the mechanism for this observation is not fully understood, it can be suggested here that the low rodent abundance in the *Acacia* stand might, therefore, be the result of a low diversity in food resources available to rodents and generally lower grass and shrub cover compared to the adjacent fynbos. Few African rodents are granivorous (Monadjem 1997) and that may further explain why there are few rodents in *Acacia* stands where food available is mostly *Acacia* seed.

Rodents use elaiosomes as cues for locating seeds (Christian & Stanton 2004) and so elaiosome removal by ants can reduce rodent predation (Slingsby & Bond 1985) by taking seeds and burying them (Heithaus 1981; Bond & Breytenbach 1985). Seeds buried deeply may have greater chance of evading rodent predators (Reichman 1979; Fuchs *et al.* 2000). The reduced small mammal abundances in alien stands may also be a result of intense competition for seeds with ants (Brown & Davidson 1977).

It was previously thought that seed-caching rodent species were absent from the fynbos and thus the efficient dispersal of *Acacia* seeds by rodents was assumed to be unlikely (Slingsby & Bond 1985). Milton & Hall (1981) also suggested that dispersal by ants was relatively unimportant as they only move the seeds for distances not more than 3 m (Bond & Slingsby 1983). No ants or granivorous birds were observed at the study site or cafeteria plots during the study. However, rodent footprints and seed husks remaining at most cafeteria plots indicated rodent activity in seed removal and predation. Only two small mammal species (*R. pumilio* and *M. minutoides*) were captured in the alien stands during the study period. Other known granivores with seed caching tendencies such as *T. afra* (Midgley pers. comm.) were also captured in the adjacent fynbos vegetation. It is possible that the agent responsible for the removal and predation of seeds could be the striped mouse. *Rhabdomys pumilio* is an opportunistic omnivore (Krug 2004) feeding on a variety of food items include vegetative plant parts and seeds (pers. obs.) and insects. The species has been shown to be the principal vertebrate seed predator in *A. saligna* and *A. cyclops* invaded systems consuming large proportions of the seeds (Holmes 1990a). A study in *A. cyclops* stands showed that *Acacia* seeds constitute up to 50% of the *Rhabdomys* diet within *Acacia* stands (David & Jarvis 1985). Although *M. minutoides* is not considered a strict granivore, seeds constitute a third of its diet (Linzey & Washok 2000). No study, however, has shown *M. minutoides* as being involved in granivory in fynbos or stands of alien acacias.

4.4.2   Seed predation and removal

Animal-dispersed seeds possess traits that in addition to affecting germination, growth and development, also influence seed predation, removal and dispersal by animals (Xiao *et al.* 2006). This in turn affects seed survival and seedling recruitment (Vander Wall 1990; Forget *et al.* 1998, Jansen & Forget 2001). Seed traits such as seed size, nutrient content, secondary

compounds and seed coat hardness have been long recognized factors affecting seed predation and removal (Price & Jenkins 1986; Vander Wall 1990, 2001; Forget *et al.* 1998; Jansen & Forget 2001, Xiao *et al.* 2003; Zhang *et al.* 2004, Xiao & Zhang 2006). Other factors affecting seed utilization (consumption or removal) by rodents are seed abundance, energy, hardness and defensive chemistry (Shimada 2001; Jansen *et al.* 2002). The decision by granivorous rodents whether to consume seeds *in situ* or remove them is primarily linked to the costs and risks associated with handling the seeds (Xiao *et al.* 2003, 2006). Increased foraging and handling time potentially increases the predation risk for rodents (Jacobs 1992). In this study we thus looked at the effects of seed availability, seed size and nutritional content on seed utilization by the rodents in *A. saligna* stands.

In a study by Li & Zhang (2003), predation rates for acorns of the Liaodong oak averaged 67.59%. A study by Holmes (1990) using *A. saligna* and *A. cyclops* seeds showed predations rates averaging 74% attributed to rodents. This is significantly higher than the predation rates of about 40% observed in our study. Another study on rodent seed predation by Xiao *et al.*, (2004) had 0% of the released seeds surviving. This is very low compared to a mean survival of 13.3% observed in our study. High predation and low seed survival rates have been shown to correspond with low seedling regeneration (Li & Zhang 2003; Xiao *et al.* 2004), which is in contrast with the rapid regeneration and encroachment of the alien acacias within the fynbos. The mean seed removal rate of 47% observed in this study is much lower than that observed in previous studies (e.g. Xiao 2003; Xiao *et al.* 2004).

In fynbos habitats being invaded by acacias, resident rodent populations could potentially consume the entire *Acacia* seed crop, were it not for the presence of ants, which rapidly move the seeds below the ground to their nests (Holmes 1990a,b). In a study by Bond & Breytenbach (1985), rodents removed all the seed from a depot once it had been discovered. In our study, this only happened in two plots whilst in the other plots some seeds actually remained in the plot after five days. As the study was carried out in the *Acacia* stands where seeds were also sometimes readily available on the ground, rodents may have encountered other seeds before getting to the cafeteria plots and thus they didn't need to exhaust the seed stocks in the cafeteria plots.

4.4.3 Seed availability

Variation in seed abundance has important impacts on seed predation and dispersal (Forget 1991; Hulme & Benkman 2002; Xiao *et al.* 2005). In general, high seed availability reduces seed removal and seed caching (Kerley 1994; Jansen 2003). Holmes (1990b) found that highest seed removal by rodents in *A. saligna* and *A. cyclops* stands was at low seed availability and lowest when available seed was abundant. However, the variation was only significant for *A. cyclops*. Our data obtained from an *A. saligna* stand show a similar trend and is consistent with results from other studies (e.g. Theimer 2001; Jansen *et al.* 2004; Lu & Zhang 2004; Xiao *et al.* 2005a). Seed removal and seed caching were lower in seed-rich stands than in seed-poor stands (Xiao *et al.* 2005a). They also found that removal of *Castanopsis fargesii* (Fagaceae) seeds was significantly higher in a low-seed year, than in a high seed year.

There are two possible explanations for these observations. Firstly, with increasing availability of seeds, rodents could encounter seeds more frequently during their foraging trips and thus did not have to reach the cafeteria plots to collect seeds for food. Secondly, high seed availability reduces the need for rodent to carry away seed for storage as it is a readily available resource. However, as seed availability decreases rodents face the challenge of storing up food in ladder- or scatter-hoards to take it away from possible competition and also to store it away for future use. Li & Zhang (2003) observed that when acorn production was very low, rodents consumed more acorns *in situ* facing higher food competition pressure. This is in contrast with our observations, where when seed availability was relatively high more seeds were predated upon *in situ* rather that removed from the cafeteria plots. Decreasing seed availability tended to favour seed removal rather than *in situ* predation.

It has also been suggested that both high seed availability and seed scarcity may increase seed removal and reduces instant seed consumption if the animal harvesting seeds is a seed-hoarder (Xiao *et al.* 2005). This is because mast seeding can facilitate seed harvest (Vander Wall 2002) while seed scarcity can stimulate seed caching. In order to minimize the costs of predation some plants have mast seeding, and this often results in predator satiation, which reduces seed predation by rodents.

The proportions of seeds that remained in the cafeteria plots were generally lower than seeds that were predated upon or removed. The proportion of remaining seeds increased with increasing seed availability and was significantly high when seed availability was high. This may be because when seed availability is high, rodents would reach satiation faster than at low seed densities. High seed densities may cause predator swamping, where there are more seeds available than predators can consume or remove, resulting in more seeds remaining at the sites. Though evidence suggests that predator-swamping seed densities may rarely occur in the field (e.g. Orrock *et al.* 2006), our study suggests that it does occur in the *A. saligna* stands because at high seed availability the amount of seeds that were neither removed nor consumed was significantly higher than at moderate and low seed availability. The production of many seeds by acacias might thus be an adaptation to counter the costs of predation as predators become swamped, leading to more seeds being left for recruitment into the seed bank. Predator swamping might also have occurred at the observed seed availability because of the reduced abundance of rodents.

4.4.4 Seed size

Contrary to the hypothesis that large seeds are expected to have higher seed predation and lower survivorship than small seeds (Moles *et al.* 2003), studies have shown that large seeds are more likely to be removed and cached than eaten *in situ* (Vander Wall 1995; Vander Wall *et al.* 2003; Forget *et al.* 1998). Granivorous rodents are known to prefer removing and caching large seeds or seeds with high fat content (Jansen & Forget 2001, Xiao *et al.* 2003). Large seeds present increased handling time and this may increase predation risks for granivorous rodents. Xiao *et al.* (2005b) found that seed size was the dominant factor to determine seed dispersal. They were using five species from the Fagaceae family and they assumed that seed size represented the dominant factor because nutrient composition and caloric value were similar among the large-seeded species in the same family. Small seeds were rather consumed *in situ* whilst larger seeds were removed and possibly cached for future use. Similarly, in studies using similar species (e.g. Vander Wall 1995; Forget *et al.* 1998; Xiao *et al.* 2006) larger seeds were cached more often than small ones.

Our data provide evidence that seed size is an important characteristic determining seed fate. Small *A. saligna* seeds were more readily consumed *in situ* rather than moved whilst larger

sunflower (*Helianthus annuus*) seeds are more readily moved rather than eaten *in situ*. This may be because of two reasons: firstly the amount of time required to handle and consume smaller seeds is much less than that required for larger seeds, and thus the rodents would rather consume as many small seeds as possible *in situ* rather than carry them away, a single seed at a time. On the other hand greater handling effort is required for larger seeds and this in turn increases the risk associated with longer exposure to predators. Rodents would, therefore, rather fetch the larger seeds and consume them in the safety of their burrows or under sheltered habitats. Secondly, the cost of carrying a single small seeds to a hiding spot by far exceeds the benefits derived from feeding on that single seed. However, with larger seeds, storing them for future use would be more profitable as a single large seed would have more food value than a small one.

4.4.5   Nutrient composition

As already mentioned above, inert seed traits such as nutrient composition plays a vital role in making seeds attractive to seed-eating rodents. It is generally assumed that large seeds have a greater nutritional value (Grubb & Burslem 1998; Zhang *et al.* 2003) and are thus more attractive to seed caching rodents (Vander Wall 1990, 1995, 2001; Jansen & Forget 2001; Jansen *et al.* 2002; Xiao & Zhang 2006). High fat content can potentially increase the food value of seeds (Xiao *et al.* 2005b) and studies have shown that seed-eating rodents prefer to remove and cache seeds with high fat content rather than consume them *in situ* (Kerley & Erasmus 1991; Xiao *et al.* 2003, Xiao *et al.* 2006). Xiao *et al.* (2004) using oil tea (*C. oleifera* nuts, provide further evidence of preference for high fat content seeds and nuts by rodents. *H. annuus* seeds in our study had a higher fat content than *A. saligna*. At the same time, carbohydrate content was higher in *A. saligna* seeds. These results are consistent with Xiao *et al.* (2006) where (carbohydrate) starch content was positively correlated to *in situ* predation of seeds. Dry seed mass was also positively correlated with the proportion of seeds removed (Zhang *et al.* 2003) and this may be because hard seeds can be stored for a long time (Jansen & Forget 2001; Lu & Zhang 2004).

4.5   Conclusion

Seed limitation occurs when either seeds never arrive at a suitable micro-site for germination or predators or pathogens destroy seeds that arrive at suitable micro-sites before they can

establish (Crawley 2000). Predator limitation has been shown to affect the distribution and abundance of plants (e.g. Hulme 1998; Crawley 2000) and thus seed predators may play an important role in shaping the distribution of plants (Orrock *et al.* 2006). Our study shows that rodents can possibly play important and contrasting roles in seed limitation as seed predators or in seed dispersal as removers of seeds. Significant amounts of *A. saligna* seeds are consumed *in situ* and this may contribute to predator limitation of *A. saligna.* Such effects may shape the landscape-level abundance of plants (Orrock *et al.* 2006).

Even though more seeds were lost through removal than predation, the possible fates of removed seeds include predation, germination or rotting. Rotting may be a major process occurring in dense alien thickets, accounting for up to 45% of removed and buried seeds (Holmes 1990b). Some of the removed seeds including those remaining in the cafeteria plots can still survive, escaping from predation and rotting. Many forests regenerate by these few survived seeds (Li & Zhang 2003) and thus even though rodents do play a role in reducing the amounts of seed in the alien invaded stands, some of the seeds that remain or that are moved could still survive and contribute to bush encroachment and spread of the aliens.

Plants that use animal dispersal must balance between the costs of predation and the benefits of dispersal. Production of copious amounts of seeds in *Acacia* species may be an adaptation to provide enough seeds for dispersal, recruitment into the soil seed bank without losing all the seeds to predation. Seed dispersal could override predator limitation if seed densities become great enough to satiate or swamp local seed predators (Crawley 2000). Also plants may form mutualistic associations with invertebrate seed dispersers such as ants. Myrmecochory, the mutualistic dispersal of seeds by ants, is common in the fynbos, and particularly well developed in the large seeded Proteaceae (Slingsby & Bond 1983). Ants have been shown to be important in maintaining seed banks of indigenous Proteaceae (Bond & Slingsby 1984; Bond & Breytenbach 1985).

In our study removed seeds could not be located and we thus could not determine the fate of the removed seeds, whether they were buried or eaten after being carried away. To understand fully whether apart from being predators, small mammals are also important in the secondary dispersal of *Acacia* as well as Proteaceae seeds, more work determining the ultimate fate of the seeds needs to be done in the fynbos and alien stands.

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Chapter 5

Conclusion

5.1   Small mammal communities in transformed habitats

Assessments of small mammal diversity, species richness and evenness in specific vegetation or habitat types provides data and information that is essential for conservation and an understanding of biodiversity in terrestrial ecosystems (Avenant 2000; Avenant & Kuyler 2002). Habitat transformations in the Western Cape lowlands have resulted in the creation of habitat matrices composed of islands of natural vegetation surrounded by crop fields, stands of alien vegetation or other land use types, and in the subsequent changes in the structure and diversity of resident faunal populations. Our study confirms reports of reduced small mammal species richness in transformed landscapes and provides evidence to the notion that increasing habitat transformation in the Western Cape shrublands is leading to a skewed community composition, which favours generalist species at the expense of specialized and niche-specific species. (Chapter 3). It is possible that small mammals only exploit these transformed habitats as secondary habitats during the times when sufficient cover and food resources are available before retreating to the 'permanent' untransformed habitats where there is very little seasonal variation in vegetation characteristics. This in part explains why highly transformed habitats support higher abundances of generalist species such as the striped mouse, *Rhabdomys pumilio* and the pygmy mouse, *Mus minutoides*. These species are able to venture into and utilize temporary habitats as long as food and cover from predators is available.

Most studies correlate abundance and diversity of small mammals to vegetation structure (e.g. Olson & Brewer 2003; Bilenca *et al.* 2007; Heroldova *et al.* 2007). However, Midgley & Anderson (2005) suggest an approach that considers the relative importance of food sources. Even though vegetation cover protects rodents from exposure to predators as well as environmental extremes (Keesing 1998), it might not be as of direct importance as is a food source (Parmenter & MacMahon 1983). For example, in our study when we considered small mammal communities within transformed habitats and natural habitats (Chapter 3), small mammal species presence or absence from habitats was explained according to vegetation cover. However, in Chapter 4, we observed the presence of granivorous rodents (*R. pumilio* and *M. minutoides*) and the absence of other non-granivorous rodents from stands of alien

acacias. This can be explained by the fact that few African rodents are known to be granivorous (Kerley 1989, 1992; Monadjem 1997), and that the most abundant food type in the alien stands were *Acacia* seeds. Thus even though there was ample vegetation cover in the alien stands, the absence of alternative food resources made them unattractive to other rodent species. Fuller & Perrin (2001) and Cavia *et al.* (2005) also conclude that, in addition to the provision of cover, vegetation in habitats should also provide a food source for them to be fully utilized by rodents.

A number of factors, e.g. habitat size and structure, vegetation cover and composition, and availability of food, act synergistically to influence behaviors such as reproduction, foraging, competition and predation (Butet *et al.* 2006) and subsequently influence small mammal species presence or absence, abundance, richness and diversity. Our study has shown vegetation composition and cover to be important factors driving small mammal species presence or absence, abundance, richness and diversity. Reproduction and fitness (body mass and condition) in rodents has also been shown to be dependent of habitat quality in terms of vegetation cover and availability of resources such as food. Small mammals consistently inhabited natural habitats where vegetation structure did not change significantly between different seasons. Even though little is known about the details of food supply in relation to specific requirements for different rodent species within these habitats, the inconsistent structure and composition means the transformed habitats can only be utilized at certain periods during the year, whilst the rest of the time they are a hostile environment to fauna. This means that only rodents that are opportunistic or have got wide niches can utilize these temporary habitats effectively. Where habitat fragments are small and isolated but in close proximity to larger or other fragments, the transformed habitats may serve as corridors and temporary habitats for a number of rodent species and thus contribute to the overall maintenance of biodiversity.

5.2   Seed predation and removal

Small mammals have been shown to play important roles in forest ecology, acting as seed predators and dispersers and changes in their abundances have even been shown to affect forest regeneration and succession (Lambert *et al.* 2006). Our study provided evidence for, and supported the fact that *Rhabdomys* may be important in predator limitation of *A. saligna*, consuming large amounts of seeds (Holmes 1990a, b). In addition, we also provide data that

suggest that rodents may play an important role in dispersing the *Acacia* seeds into the fynbos. Even though no direct evidence was provided in our study showing rodents specifically carrying seeds from the *Acacia* stands into the fynbos, seeds missing from the cafeteria plots were linked to rodent activity (Chapter 4). These rodents have been shown to utilize transformed habitats (including *Acacia* stands) as secondary habitats or on foraging trips before returning to their permanent habitats in the fynbos (Chapter 3). Such movements could be responsible for *Acacia* seed being introduced into the fynbos vegetation.

Production of copious amounts of seeds in *Acacia* species may be an adaptation to counter predator limitation and balance between the costs of predation and the benefits of dispersal by providing enough seeds for dispersal and recruitment into the soil seed back without losing all the seeds to predators. It has already been suggested that seed dispersal could override predator limitation if seed densities become great become great enough to satiate or swamp local seed predators (Crawley 2000). Also plants may form mutualistic associations with invertebrate seed dispersers such as ants. Some studies have looked at the role and importance of ant dispersal of seeds of both alien species and indigenous species in the fynbos ecosystems (e.g. Milton & Hall 1981; Bond & Slingsby 1984; Slingsby & Bond 1985). However, Holmes (1990a) contends that, in the absence of ant dispersal, rodents could potentially consume the entire *Acacia* seed crop.

Wood & Morris (2007) report that the use of the gall-forming rust fungus *Uromycladium tepperianum* on *A. saligna* has resulted in reduced seed production by the invasive alien. Most *A. saligna* plants in the study site are infected with this fungus. The subsequent reduced amounts of *A. saligna* seed stock available to rodent seed-eaters favour increased rodent predation as shown by Holmes (1990a, b) and in our study. Rodents could thus play an important role in limiting the invasive edge if *Acacia* species in the Western Cape lowlands if their populations are not reduced significantly. However, if invasions by acacias continue to cause declines in small mammal abundances (Smithers 1983), this may only serve to aid in the effects of predator satiation/ swamping and thus more they can be able to escape the effects of rodent predation on their seeds. Rodents may thus be complementing the effects of the gull forming fungus by reducing the amount of *Acacia* seed available for recruitment into the seed bank.

5.3   Management recommendations

Given the important role of small mammals in food webs (Eisenberg 1980) and predation and dispersal of seeds (Malcolm 1997) and mycorrhizal fungi (Janos *et al.* 1995), it is appropriate that they be considered in management plans for conservation. However, even though it would be convenient to use studies of mammals in disturbed and undisturbed habitats as a proxy for comparing natural and transformed areas, it is known that responses vary between species (Songer *et al.* 1997; Hayward *et al.* 1999) and according to the time of the disturbance (Caro 2001) and the type of disturbance involved (FitzGibbon 1997). Conservation strategies for sustaining biodiversity must therefore consider that species richness and ecological processes are controlled by parameters operating at a wide array of scales (Baudry *et al.* 2000), giving rise to the need for simple indicators of biodiversity which provide quantitative links between landscape patterns and species richness (Dauber *et al.* 2003).

Diversified cropping systems that promote year round crop production may be able to mitigate the effects of habitat transformation and crop monocultures. In addition, new agricultural, small holder and urban development should attempt to redress the effects of extensive habitat transformation by leaving fragments large enough to sustain viable faunal populations. Butet *et al.* (2006) suggested that maintaining the diversity of field margin linear habitats is crucial for conservation of small mammal communities in agricultural landscapes, as some species may be dependent on one habitat type and others are adapted to a wide range of habitats. In our study transformed habitats were more useful as secondary habitats, providing alternative food and cover during the winter season for small mammals. They also provided corridors for the movement and dispersal of rodents between habitats and natural fragments. However, the usefulness of fragments as secondary habitats or corridors hinges on, amongst other things, their location in the landscape matrix, size and vagility of the resident fauna. Managers in agricultural landscapes should therefore endeavor to maintain canopy density of natural vegetation and other vegetative characteristics associated with these rodent species (Webala *et al.* 2006).

Habitat rehabilitation and restoration of natural vegetation is important for the providing breeding and dispersal habitats in agricultural landscapes. At Elandsberg crop production has been ceased on some old fields and current studies are looking at the restoration of the natural vegetation onto the old field (e.g. Midoko-Iponga 2004). The restoration of these sites will go

a long way in aiding the provision of suitable habitats for both fauna and flora affected by the intensification of agriculture in the area. Dispersal habitat matters most for species with intermediate dispersal abilities living in landscapes composed of small patches of breeding habitat in which dispersal habitat can enhance the occasional exchange of individuals between patches (Wiegand *et al.* 2005). Transformed habitats are useful in mitigating the dangers faced by these small mammal communities and are useful as secondary habitats, corridors for dispersal and movement and for the provision of food and cover resources. This in turn helps populations maintain energy reserves and body condition necessary to ensure continuous and successful breeding throughout the year, as in the case of *R. pumilio*.

The information acquired from the study also does point at rodents playing an important role in the fate of *A. saligna* seeds and possibly other seeds within the fynbos ecosystem. It is possible that large seeded Proteaceae in the fynbos ecosystem will benefit from scatter- or larder-hoarding by rodents. Our study shows that rodents can possibly play an important role in seed limitation as seed predators or in seed dispersal as removers of seeds. Orrock *et al.* (2006) showed that such effects might shape the landscape-level abundance of plants. One of the reasons why progress in seed dispersal and predation research has been very slow is the difficulty in tracking the fate of all the seeds that are dispersed (Sork 1984). In our study removed seeds could not be located and we thus could not determine the fate of the removed seeds, whether they were buried or eaten after being carried away. To fully understand whether apart from being predators, small mammals are also important in the secondary dispersal of *Acacia* as well as Proteaceae seeds, we recommend that more work determining the ultimate fate of the seeds needs to be done in the fynbos and alien stands.

5.4   References

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