Comparing small mammal assemblages between communal and commercial rangelands within a region of the Succulent Karoo, South Africa.

by

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Submitted in partial fulfilment for the degree of Master of Science (Conservation Ecology)

at

Stellenbosch University

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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.

Date: 25 November 2008

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Acknowledgements

I would like to thank my supervisor, Dr. Cornelia Krug, and co-supervisor, Dr. Sonja Matthee, for giving me the chance to come to this breathtaking country and allowing me to carry out this work. Thank you for all advice and help throughout the entirety of this study.

I am also grateful for the help of Timm Hoffman, with whom I first met prior to fieldwork, for his advice and suggestions on potential study sites, and Marius Kieck for translating the Abstract. A thank you also goes to Professor Nel of the Centre of Statistical Consultation for help with statistical analyses. For financial support during the fieldwork phase of the project, I would like to thank BIOTA and DS&T (GUN 2070538 to Dr. C.B. Krug). This study was approved by the animal ethics committee of the University of Stellenbosch (reference number: 2006B01005).

Many thanks go to the people of Paulshoek and the farmers of the commercial rangelands for permitting access to their lands. From Paulshoek, I would like to thank Mariana Lot, Susanna, Maria and Anna for assisting me in the field. Additional thanks go to Jenny Jackson and Darren Houniet for also providing assistance in the field, and especially 'Makebitsamang Nchai who was always there to help check traps for animals, no matter what time.

I would particularly like to thank my parents for being behind me throughout all stages of my studies, and being a phone call away. A very special thank you also goes to Kevin Hopkins for assistance in the field and being available to talk to 24/7.

Abstract

The widespread ecological impacts of overgrazing by livestock within the Succulent Karoo have received considerable attention. Literature shows communal and commercial rangelands have been thoroughly studied, and vegetation responses have been investigated in an attempt to understand the effects of overgrazing. Regarding animal species, literature is in short supply. In a one-year study of small mammal assemblages, the effect of the rangelands, and subsequently vegetation, on small mammal assemblages was examined, as well as the effects on number of occupied, unoccupied and collapsed burrows.

This study shows that vegetation composition differs between rangelands, with a greater perennial shrub cover on the communal rangelands and a greater perennial succulent cover on commercial rangelands, consequently creating different habitats for animal assemblages. This study supports the notion of small mammal composition relating to vegetation structure, with certain species being impacted by heavy grazing. Four small mammal species were found in greater abundances on commercial rangelands, with one being exclusive, while communal rangelands were exclusively occupied by three nocturnal species. Diet and habitat requirements are the most important factors regarding species occurrence. With small mammal species composition differing between rangelands, and species richness not being affected by rangeland type, this study illustrates that the disappearance of certain species may arise without these different rangelands. This could result in reduced species richness, and thus diversity being lost.

Regarding species present on both rangelands, no differences were observed in body mass, body size or body condition. Despite no differences found in body condition, calculating a body condition index is a good method for investigating how a species is coping within an environment. The proportion and number of occupied and collapsed burrows can be seen as a measure of trampling effect. It was expected for grazing intensity, as well as vegetation changes, to affect the occurrence of such burrows. This study showed differences between the communal and commercial rangelands as negligible. As expected, numbers of burrowing small mammal species were

negatively correlated with numbers of collapsed burrows. However, a lack of consistency deemed this result unimportant.

Results show that the effects of overgrazing on small mammal populations are complex and require more attention if to be fully explained. This study provides insights into the effects of land use on small mammals and burrow numbers, which have implications for the conservation of these species within arid regions.

Opsomming

Die ekologiese implikasies van oorbeweiding in die Sukkulente Karoo is 'n onderwerp van baie belangstelling in bewaringskringe. Die effete van oorbeweiding op plantegroei is in beide kommersiële en gemeenskaps weivelde telkemale in die literatuur ondersoek. Die respons van Sukkulente fauna is egter nie só 'n algemene tema nie. In dié betrokke studie is die effekte van oorbeweiding en plantegroei versteurings op die klein-soogdier gemeentskappe en populasies bevraagteken en ondersoek.

Die huidige studie toon daarop dat kommersiële en gemeenskaps weivelde verskil in hulle plantegroei samastellings en dat kommersiële weivelde 'n hoër plantegroei bedekking het waar vervolgens die klein-soogdier samestelling beïnvloed. Die bevinding is telkens in die literatuur opgeteken met klien-soogdier samestelling wat negatief deur oorbeweiding geassosieer word. Die klein-soogdier samestellings in die gemeenskaps weivelde was, soos in ander studies, 'n onderverdeling van dié van die kommersiële weivelde. Vier spesies was in groter hoeveelhede in kommersiële weivelde gevind met 'n enkele spesie wat eksklusief was tot dié weivelde. Gemeenskaps weivelde het ekslusief drie nagtelike spesies gehuisves. Dieet en habitat voorkeure was die belangrikste faktore wat tot spesie verspreiding bygedra het. Die verskil in spesies samestelling in die twee betrooke weiveldtipes en die onveranderde spesies rykheid tussen dié twee weivelde dui daarop dat die behoud van verskillende weiding praktyke tot spesies rykheid kan bydra. Die weglating van een tipe weiveld kan moontlik tot die verlies in spesies rykheid en diversiteit kan lei.

Spesies wat op beide weivelde gevind was het sommige verskille getoon. Byvoorbeeld, individue was vroëer seksueel aktief op gemeenskaps weivelde. Laasgenoemde is weens die feit dat die liggaams gewig geslagsrypheid van volwasse individue op die kommersiële weivelde hoër was as dié op gemeenskap weivelde. 'n Verdere verklaring kan te doen hê met die hoër plantbedekkening op kommersiële weivelde wat predasie risiko kan verminder en vervolgens lewensduur verleng. Met betrekking toon weiveld tipe het geslagsryp inidividue het egter geen verskil in liggaams kondisie getoon nie.

Vertrapping is aan die hand van aantal ineengestorte gate gemeet. Daar is geen vergelykbare ooreenkoms tussen klein-soogdier hoeveelheid en aantal gate gevind nie. In die gemeenskaps weivelde is daar wel groot hoeveelhede ineengestorte gate gevind, 'n aanduiding van die hoër intensiteit beweiding. Die hoeveelheid besetde en onbesetde gate was nie van weiveld tipe afhanklik nie.

Die studie toon daarop dat oorbeweiding in die Sukkulente Karoo 'n komplekse interaksie het met klein-soogdier populasies, gemeenskappe en ook seksuele en voorplantings status. Die tema verlang meer navorsing om dié prossesse beter te verstaan. Die studie lewer wel insae in die effekte van oorbeweiding en weiveld tipe op klein-soogdier samestellings en versaf die wetenskap met belangrikke bewarings besluite.

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Chapter 1

General Introduction

1.1 Introduction

Livestock grazing within Namaqualand dates back circa 2,000 years. To date, the management practices employed have left marked effects on the lands. One practice comprises overstocked lands with severely deteriorated surroundings, whilst the other comprises the appropriate stocking density for the specified area. This consequently results in a comparatively-less degraded surrounding. These two practices are fascinating when examining the differences in both vegetation and animal communities, between the communally- and commercially-managed farmlands.

This study took place in Paulshoek, an area situated in the Leliefontein region of the Kamiesberg Mountain range, Northern Cape. Here, much is known about the effects of overgrazing on the surrounding vegetation, but less is known how this affects the animal species within the area.

1.2 Background

The Succulent Karoo Biome and the history of Namaqualand

The Succulent Karoo Biome covers 111,000km², and is the fourth largest biome in southern Africa (following the Savanna, Nama-Karoo and Grassland Biomes) (Rutherford and Westfall, 2003; Mucina *et al.*, 2006) (Figure 1.1). It is one of 34 biodiversity hotspots and the only entirely arid region classified as such (Myers *et al.*, 2000; Desmet, 2007). The distribution is discontinuous as it passes down the west coast of southern Africa, from Namibia to the southwestern Cape.

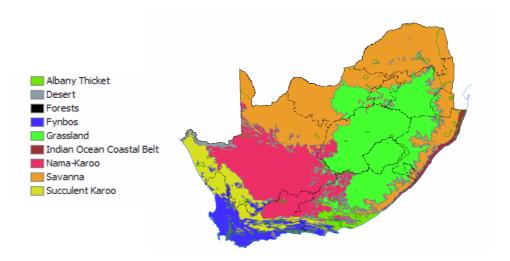


Figure 1.1: The biomes of South Africa, Lesotho and Swaziland, with key (Mucina and Rutherford, 2006).

Namaqualand, where this study took place, falls within the Succulent Karoo. It extends northwards for 325km from the northern section of the Western Cape into the Northern Cape. Namaqualand has passed through many hands over the last four centuries, from the Khoi-khoi herders through to the Trekboers and the British. Prior to the Khoi-khoi herders of Botswana settling as nomadic pastoralists during the 17th century, the impacts of the Khoekhoen were minimal on the land. This changed with the settlement of the Khoi-khoi, as the introduction of domestic animals arose in regions previously uninhabited by humans. As a consequence livestock farming become the main subsistence method (Cowling and Pierce, 1999; Hoffman and Ashwell, 2001).

The end of the 17th century saw the occupation of the Trekboers (Dutch pastoralists), who forced the Nama herders and San (Bushmen) out of habitable areas (Hoffman and Ashwell, 2001; Webley, 2007). Such colonial growth and development further reduced remaining populations of Nama herders and San populations by the end of the 18th century. The early 19th century saw the British take over the land, imprisoning and driving many San into uninhabitable areas, with many others eventually being forced into slavery on colonial farmlands or restricted to areas such as the Kamiesberg (Cowling and Pierce, 1999). During the late 19th century, land was given to the nomadic pastoralists, which today are known as 'Coloured Rural Areas' (Hoffman and Ashwell, 2001). This act began the communal and commercial management systems, with areas such as the Kamiesberg and Richtersveld today being classified as communal rangelands. During the 19th century, more farmers colonized areas with reliable water supplies, and soon signs of land degradation through occupancy and overstocking were apparent. The introduction of a fencing act (early 20th century) made it mandatory for farmers, who owned land and livestock, to erect fences separating their land. This begun a rotational land management practice (employed by some of the settlers) as seen today on commercial rangelands (Dean et al., 1995).

Land management practices in Namaqualand

With more than 80% of land within southern Africa described as grazing lands, livestock farming is the main land-use type (Seymour and Dean, 1999; Hoffman and Ashwell, 2001). Across Namaqualand, two land management practices are employed. Firstly, there are the communal systems which are essentially centred on the kraaling

of livestock. Secondly, there are the commercially-managed systems, also known as 'private' farms. Kraaling is a traditional method where livestock are grazed throughout the year, herded daily across unfenced lands, and returned to stock posts nightly (Lebert and Rohde, 2007). These lands hold high human populations and have stock densities 1.5 to 2.5 times higher than those recommended by the Department of Agriculture (Hoffman *et al.*, 1999; Lebert and Rohde, 2007). Despite the Department of Agriculture issuing recommended densities to ensure sustainable livestock production, farmers operating such systems continue to maintain high livestock numbers (Hoffman and Ashwell, 2001), with densities seen to fluctuate yearly. Available land within commercially-managed areas is minimal and a steady income is hard to come by. Many of the farmers often resort to multiple methods to increase personal income (Benjaminsen *et al.*, 2006). Many income methods are not secure, so livestock ownership can act as a 'bank account'. This means that if/when other monetary sources fluctuate or fail, the livestock can act as a 'safety net'.

Commercial rangelands on the other hand, also known as camp systems, hold lower human populations and have stock densities below those recommended. Farm sizes range from 4,000 to 12,000ha, with livestock roaming unattended through fenced paddocks, day and night, as well as being rotationally grazed (Todd and Hoffman, 1999; Benjaminsen *et al.*, 2005; 2006). Rotational grazing controls the density of animals kept, with the aims of increasing vegetation cover and retaining high soil productivity levels, thus resulting in a high animal quality (Jürgens *et al.*, 2001; Hahn *et al.*, 2005).

In recent years, the communal systems have been under scrutiny and labelled 'economically inefficient and environmentally degrading' (Benjaminsen *et al.*, 2006), making them the centre of attention of government planners and scientists.

Effects of grazing intensity on vegetation and faunal communities

Land use and human encroachment into undisturbed areas can have profound effects on animal populations. Different grazing intensities of livestock and other herbivorous grazers are known to affect surrounding vegetation and soil properties (Valone and Sauter, 2005; Kraaij and Milton, 2006; Anderson and Hoffman, 2007), as

well as vertebrates' communities (Rosenstock, 1996; Mathis et al., 2006; Muck and Zeller, 2006).

Land degradation is present throughout the Succulent Karoo, but more so on communally-managed rangelands, where researchers have labelled overstocking, over-cultivation and poor land management to be contributing factors towards the degree of degradation seen today (Hoffman and Ashwell, 2001; Lebert and Rohde, Communal rangelands are under increasing examination as husbandry 2007). techniques employed threaten the surrounding biodiversity. While light grazing intensities often positively influence surrounding vegetation, with reports of increases in species richness and diversity (Ayyad and Elkadi, 1982; West, 1993), responses to heavy grazing intensities within low-lying areas are more diverse. Responses can range from a loss in vegetation cover, species richness, diversity and productivity (Todd and Hoffman, 1999; Simons, 2005) to complete compositional shifts in vegetation species (Milton and Hoffman, 1994; Anderson and Hoffman, 2007). Such shifts include from perennial to annual species (Steinschen et al., 1996) and to systems dominated by unpalatable species owing to selective grazing (Hoffman and Cowling, 1990; 1991; Riginos and Hoffman, 2003).

While the Kamiesberg region is an area noted for its biodiversity and conservation concern, only 3.2% of the area of Namaqualand is under formal conservation (Jonas, 2004). Within regions of Namaqualand, livestock grazing has potentially major ecological implications, with particular attention being placed upon the effects of the farming practices. Small mammal species have been identified as prime indicators when detecting environmental changes (Zeller et al., 2002). Short-lived small mammal species often exhibit high reproductive turnover rates compared to larger species, making them more prone to the effects of changing environments (Delany, 1972; Saetnan and Skarpe, 2006). This subsequently makes small mammal species ideal candidates for studying the impacts of grazing intensities and environmental changes. Many faunal species are impacted by differing grazing intensities (Zeller *et al.*, 2002; Torre *et al.*, 2007), which results in alterations in species richness and diversity, as well as changes in community structure, composition and abundance (Muck and Zeller, 2006; Smit *et al.*, 2001; Spencer *et al.*, 2005).

The conservation of small mammals is vital, as they play both important and non-ecologically redundant roles within ecosystems (Kotliar, 2000; Reichman and Seabloom, 2002). This is because they have fast reproductive turnover rates, are part of the food chain (prey and a predator), and are key mechanisms in seed dispersal (Campos and Ojeda, 1997; Hongjun and Zhang, 2007). Small mammal species are little studied within the Paulshoek region. Subsequently this study is required in order to examine small mammal community structure, composition and abundance between the communally- and commercially-managed farms.

Previous work investigating the impacts of heavy grazing intensities within Namaqualand showed significant decreases in large palatable perennial shrubs and leaf-succulents, and increases in unpalatable vegetation species, annual cover (Todd and Hoffman, 1999), and dwarf perennial cover (Anderson and Hoffman, 2007). Research investigating grazing impacts on small mammal species through numerous arid regions of the world (Heske *et al.*, 1991; Muck and Zeller, 2006; Tabeni and Ojeda, 2007) showed grazing intensity, and alterations to ecosystems, to play a key role in changing faunal community structure and abundances. Through examining the effects of overgrazing, more insight can be gained on the effects on small mammal communities.

1.3 Objectives of the Study

This study, which has the central aim of expanding our understanding of the impacts of grazing in semi-arid regions on small mammal communities, addresses the following objectives:

- to examine whether there is a difference in vegetation composition, species richness and diversity, and the abundances of bare ground and rock between communal and commercial rangelands;
- ii. to establish if there is a difference in small mammal community structure, composition and abundance between rangelands;
- iii. to assess if vegetation species richness, diversity and composition affects small mammal communities;
- iv. to ascertain if small mammal abundance relates to burrow numbers, and if burrow proportions differ between rangelands.

1.4 Thesis Structure

This thesis consists of six chapters that focus on providing answers regarding how small mammal communities vary between two land management practices within Namaqualand. Chapter 1 introduces the context and need for this study, while Chapter 2 centres on previous literature of particular relevance to this work. Together, these chapters provide a backbone so hypotheses and predictions could be formulated. Chapters 3 to 5 focus on providing answers to the given hypotheses and predictions through analysed data, while chapter six pulls together results from previous sections and puts them in context.

The applied reference style follows that of the African Journal of Ecology.

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Chapter 2

Literature Review

2.1 Background and introduction to research problem

Widespread ecological impacts, due to overgrazing within arid regions, have been a hot topic over past decades and studied thoroughly (see Castellano and Valone, 2006; Mathis *et al.*, 2006). Many have examined the effects of grazing, from impacts on the soil and vegetation (Anderson and Hoffman, 2007; Steffens *et al.*, 2008) through to impacts on the animal species present (Grant *et al.*, 1982; Eccard *et al.*, 2000; Tabeni *et al.*, 2007). Overgrazing results in changes in plant species composition (Ayyad and Elkadi, 1982; Perkins and Thomas, 1993), vegetation cover (Allsopp, 1999) and diversity (Shaltout *et al.*, 1996). Overgrazing not only affects biodiversity, but also the associated ecological processes such as pollination (Mayer *et al.*, 2006; Sjödin, 2007), seed dispersal and germination, and nutrient dispersal.

Studies examining changes in vegetation community structure, in response to farming within the Succulent Karoo (Anderson and Hoffman, 2007; Simons and Allsopp, 2007), outweigh those of animal communities (see Joubert and Ryan, 1999; Eccard *et al.*, 2000). There has recently been increased interest in animal responses to grazing-induced vegetation changes. Small mammals have been studied thoroughly, as species react widely to ecosystem alterations. Both community structure and abundance frequently fluctuate within differing grazing intensities, as well as within various stages of vegetation succession/maturity of habitat (Fox, 1990; Fox and McKay, 1990; Monamy and Fox, 2000).

There is a large amount of literature focussing on the complex mechanisms of relationships between environment and small mammals. With reports on the physiological, nutritional, social, and anti-predator requirements (i.e. Birney *et al.*, 1976; Kerley, 1992), as well as on how small mammals have been used as indicators of habitat integrity and quality (Avenant, 2000; 2005). Through observing the impacts of grazing pressures, it is possible to forecast effects on communal and commercial rangelands.

2.2 Impact of grazing on vegetation

The effects of grazing on vegetation community structure and composition in arid and semi-arid environments have been widely documented (Shaltout *et al.*, 1996; van de

Koppel et al., 1997; Hoffman and Ashwell, 2001 among others). Excessive grazing leads to vegetation trampling, reduction in vegetation height and cover (Muck and Zeller, 2006), declines of large woody and succulent shrub species (typically palatable) and the establishment and increase of dwarf shrubs, as well as unpalatable perennial and annual species (Olsvig-Whittaker et al., 1993; van der Westhuizen et al., 1999). Other modifications include changes in vegetation complexity and changes in soil properties. These, in turn, result in infertile soils (Dormaar and Willms, 1998; Allsopp, 1999), increased erosion and compaction (Chanasyk and Naeth, 1995; Snyman and du Preez, 2005), reduced seedling establishment and reduced seedling survival and growth (Simons and Allsopp, 2007). Similar occurrences have been documented for land management systems worldwide, with the alteration of vegetation also being associated with an increase in grazing intensity within southwestern USA, the Russian Federation, Australia, and the American salt marshes (van der Koppel et al., 1997). Increases in unpalatable and unwanted vegetation species bring about an increase of bare ground. This is a sign of 'system' dysfunction' primarily due to the reduction in the soil's efficiency to trap vital organic nutrients and water (Simons and Allsopp, 2007).

Over past years, the need for rangeland rehabilitation has raised concern and an enlarged public awareness regarding the decline in veld condition (Todd and Hoffman, 1999). While many (Witbooi and Esler, 2004; Simons and Allsopp, 2007) suggest opportunistic management approaches (involving stock removal and reseeding) could optimize the restoration potential of rangelands, few (Friedel, 1991; O'Connor, 1991) believe the answer to rehabilitation is not straightforward or within a realistic time-scale. It is therefore imperative that the study of the effects of grazing, and subsequently veld deterioration, on other components (i.e. animal species) of the surrounding ecosystem are examined on a timely basis in order to identify the total severity that overgrazing is having on ecosystems.

2.3 Small mammal responses to grazing pressures

Many studies of small mammals' grazing responses have focussed on comparisons between grazed and ungrazed sites or high and low grazing intensities, reporting on changes in population (density) (Jones and Longland, 1999; Muck and Zeller, 2006) and community structure (Keesing, 1998; Mathis *et al.*, 2006; Muck and Zeller,

2006). Small mammal community structure is associated with biotic and abiotic factors, such as habitat complexity and composition (Rosenweig and Winakur, 1969; Dueser and Brown, 1980), grazing and trampling (Muck and Zeller, 2006; Torre *et al.*, 2007), size of area (Abramsky *et al.*, 1985), predation (Abramsky *et al.*, 2001; Avenant, 2005) and the succession of vegetation (van Hensbergen *et al.*, 1992; Monamy and Fox, 2000).

Livestock grazing can have unfavourable repercussions on the surrounding biodiversity, with the impacts that grazers have on the environment affecting small mammal communities (Heske and Campbell, 1991; Saetnan and Skarpe, 2006). Species differ in their capability to adapt to modified environments, and when areas are disturbed and vegetation replaced by something other than the original vegetation life, small mammal community structure and composition may change (Pearson, 1959; Sly, 1976; Grant et al., 1977). Many species are capable of enduring changes, however alterations to vegetation through simplification (reductions in vegetative layers or increases in bare soil) or increased complexity of habitat structure are commonly associated with changes in small mammal diversity, species richness and abundances (Bock et al., 1984; Eccard et al., 2000; Mathis et al. 2006). Vegetation cover offers shelter for small mammals, and is thus a key habitat characteristic in reducing the risk of predation. Supporting studies have illustrated that predation occurs at higher rates within sparsely covered and open areas when compared to areas with dense cover (Flowerdew and Ellwood, 2001; Torre and Díaz, 2004; Torre et al., 2007). Often, species with specific habitat requirements are directly affected by the structural changes of vegetation, as predator exposure increases and food resources alter (Eccard et al., 2000; Torre et al., 2007). In addition to the simplification of vegetation structure, grazing may increase soil compactness. Such a factor may furthermore affect the burrowing ability of belowground dwelling species, which dig and seek shelter to avoid predation and extreme temperatures (Walsberg, 2000; Muck and Zeller, 2006).

Plant species, diversity, height and cover are all important factors in the persistence of species within a habitat. Small mammal species richness, diversity and abundance increase with a decrease in grazing intensity (Rosenstock, 1996; Hayward *et al.*, 1997; Joubert and Ryan, 1999). Rosenstock (1996) showed a 50% and 80% increase in

species richness and abundance, respectively, within ungrazed sites when compared to grazed sites. Joubert and Ryan (1999) and Saetnan and Skarpe (2006) both showed a higher species richness in sites with a lowered grazing intensity/ungrazed sites, with Heske and Campbell (1991) additionally showing abundance increases.

The impacts of grazing may rely on the species of small mammals present, as well as their habitat preferences (Saetnan and Skarpe, 2006). However, a species may adapt to an environment, resulting in community structure and composition alterations. Species may still be capable of surviving within certain habitats despite them not being completely suited to these species. For example, small mammal species that prefer habitats with high vegetation cover will be more abundant in ungrazed sites (Hayward et al., 1997; Bock et al., 1984), often being affected more by grazing pressure (Grant et al., 1982). Similarly, animals preferring open habitats will be more abundant in grazed sites compared to areas of high percentage cover (Jones and Longland, 1999), with species being affected to a lesser degree by reductions in cover. Such adaptations to this type of habitat can enhance survival, as grazing typically increases annual grass abundance, which in turn are capable of producing greater quantities of seeds than perennial grasses do (Grant et al., 1982; Milton et al., 1994). Activity pattern could also be a factor why small mammal species are more susceptible to alterations in habitat structure. Species active during daylight hours favour and are typically dependent on vegetation cover (Christian, 1980; Joubert and Ryan, 1999). This is due to diurnal activity exposing them to increased predation (see Joubert and Ryan, 1999). Nocturnal species, on the other hand, are not so dependant on cover as nocturnal predators (i.e. jackals) rely chiefly on hearing and olfactory senses to locate prey (Perrin et al., 1999).

Changes in small mammal species composition have been established within areas recovering from disturbance (Fox, 1990; Jones *et al.*, 2003), with strong associations between small mammal assemblages and the successional changes of the vegetative habitat (Fox, 1990). Such associations result from the differences between the requirements of the small mammal species, which generally require different vegetation cover and density (Birney *et al.*, 1976; Grant and Birney, 1979), such as that in the transition from early to late succession. Succession within rotationally grazed or rested areas can occur on both a short- and long-term scale. In turn, this

may supply animal species with a varying habitat which they then can occupy. The habitat accommodation model developed by Fox (1990) relates the entry of a species into the stage of succession which best suits its requirements and suggests that dominant species are lost when competitive species, better suited to a particular successional stage, enter the sequence (Pearson, 1959; Sly, 1976; Schweiger *et al.*, 2000). Many also suggest that animal succession is capable of mirroring shifts in vegetation species composition and structure (Huntly and Inouye, 1987; Sietman *et al.*, 1994). Considering vegetation succession, this could be an underlying factor as to why small mammal species composition differs within areas under differing grazing intensities, as well as grazed and ungrazed areas (Rosenstock, 1996; Flowerdew and Ellis, 2001; Mathis *et al.* 2006).

2.4 Habitat requirements and life history strategies of small mammals

A species' existence within an environment is a result of preferences, and the reproductive strategies implemented (Zeller et al., 2002). Habitat quality (i.e. resource availability) can be influential of several aspects. Such aspects include population dynamics, reproduction, body condition, and body mass of the small mammal species in that habitat. For example, species inhabiting arid regions must be capable of enduring unpredictable and irregular rainfall patterns, extreme temperatures, and a high variability in food resources (Krug, 2007). Diet is important when determining whether a species can exist within an environment. insectivorous species is unable to survive in areas without insects, for instance, while an omnivorous species is able to alter its diet when certain food items are in short supply (Tabeni and Ojeda, 2005) or seasonal. Concerning reproductive strategies, individuals undergo seasonal shifts in reproductive patterns and changes in dietary patterns. Such changes may be implemented by female individuals, so to supply individuals with sufficient energy to produce and nurture offspring (Bronson, 1985; Zeller et al., 2002). If present within areas with different environmental attributes, species often have differing population dynamics, such as differences in the proportions and numbers of certain age classes and sexes. As diet and other environmental variables affect the condition of an individual, one can assume that when comparing individuals from two different habitats there will be differences in condition, and even body mass.

Environmental factors like food availability, social cues, photoperiod, temperature, humidity and rainfall are important in initiating reproduction (Bronson, 1985; Krug, 2002). Elements acquired from food like, vitamins, minerals and amino acids are crucial if an individual is to reproduce successfully and survive. Food restriction during various phases of pregnancy may have various outcomes. Restriction during early stages may have little effect on the young, however restriction later on may result in unborn young being aborted. If food restrictions occur during lactation, the female may consume her young to make up for the lack of nutrients (Bronson, 1989). Millar (1977) stated that small mammal species are usually capable of breeding more or less throughout the year as well as seasonally, with environmental factors occasionally acting as constraints, as demonstrated by Krug (2007). Some species have specified breeding periods; classed as seasonal breeders. Such species are capable of identifying and reacting to environmental indicators like photoperiod and the availability of specific vegetation compounds, thus enabling breeding success in suitable seasons (Bronson, 1985; 1989; Jackson and Bernard, 2001).

Reductions in vegetation, owed to overgrazing, lead to long-lasting changes in soil nutrients and food quality, subsequently causing poor reproduction within rodent populations. When favoured and preferred food items are plentiful, *Rhabdomys pumilio* individuals have been noted to increase body mass prior to times when food was short supply, with this method enabling individuals to survive with a limited food supply (Schradin and Pillay, 2005). If certain food items become unavailable for extended periods, this strategy would certainly fail due to essential foraging taking place during unsuitable periods. Habitat use by different species allows utilisation of the surrounding area, and through behavioural and ecological flexibility, different populations are capable of persisting throughout a range of habitats. This relates to the communal and commercial rangelands of the Succulent Karoo, as one rangeland type may have more suitable and preferred food items, thus enabling occupation of certain species.

2.5 Grazing impacts on burrowing small mammals

To date, not much research has been conducted on the topic of burrow numbers in relation to the effects of grazing. Under high grazing intensities, there is typically a

loss of vegetation cover (Beukes and Ellis, 2003; Anderson and Hoffman, 2007) which in turn increases predator visibility. Furthermore grazing may reduce food availability and decrease refuge possibilities for small faunal species. Trampling caused by grazing may cause burrows to collapse, but also cause the ground to become compacted so species are unable to burrow.

Muck and Zeller (2006) examined the differences between two areas grazed by cattle and wild ungulates. Used and unused burrow numbers were used as indicators of trampling. A pattern emerged when looking at burrow numbers and small mammal individuals caught. Small mammal abundances were lower within wild ungulate grazed areas, while species richness was similar between both areas. Burrow densities declined 20% between March and May in both sites, and it was suggested by Muck and Zeller (2006) that the decline of small mammals was not linked to trampling and the unavailability of burrows.

2.6 Predictions and Hypotheses

In response to conclusions from the reviewed literature, predictions are as follows:

- i. plant species richness and percentage plant cover will differ between communal and commercial rangelands, and it is predicated that the percentage cover will be lower in heavily-grazed areas compared to areas exposed to light grazing
- ii. small mammals will respond to grazing intensity, with alterations in species presence, abundances, reproductive status and demography occurring due to the changes in vegetation community structure and cover;
- iii. changes in burrow proportions should occur due to different grazing intensities, with a focus on burrowing small mammal abundance.

The null-hypothesis of this study is that small mammal community structure, composition and abundance will ultimately not differ between the communal and commercial rangelands.

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Small mammal communities in communal and commercial rangelands

3.1 Introduction

Land-use and human encroachment into undisturbed areas can have profound effects on animal populations (Mathis *et al.*, 2006; Muck and Zeller, 2006). The presence of domesticated livestock and indigenous herbivorous grazers can alter vegetation composition and animal communities (Thompson *et al.*, 1998). Many animal populations have suffered the consequences of disturbance, whether through overgrazing (Bowland and Perrin, 1989; Bock *et al.*, 1990; Eccard *et al.*, 2000; Flowerdew and Ellwood, 2001), fragmentation (Pattanavibool and Dearden, 2002; Cushman, 2006), vegetation succession through anthropogenic disturbance (Pearson, 1959; Sly, 1976; Fox, 1990), or natural factors such as fire (Christian, 1977; Ford *et al.*, 1994; Briani *et al.*, 2004) and climatic variations (Godoy-Bergallo and Magnusson, 1999; Castellarini *et al.*, 2002). Overgrazing impacts on the environment affects animal communities in many ways, with both positive and negative responses (see Heske and Campbell, 1991; Eccard *et al.*, 2000; Smit *et al.*, 2001; Schmidt *et al.*, 2005; Saetnan and Skarpe, 2006).

With more than 80% of the land within southern Africa described as grazing lands, livestock farming is the main land-use type (Seymour and Dean, 1999; Hoffman and Ashwell, 2001). In Namaqualand, where livestock grazing dates back circa 2,000 years, two land management practices are employed (Cowling and Pierce, 1999). Communally-managed rangelands are centred on the kraaling of livestock, whereby animals are grazed throughout the year, continuously herded across the lands, and returned to stock posts nightly (Lebert and Rohde, 2007). In contrast, rotational grazing using a camp system, whereby livestock roam unattended throughout fenced paddocks, is employed on commercially-managed rangelands. Such rangelands are, in general, privately owned (Hoffman *et al.*, 1999; Todd and Hoffman, 1999; Benjaminsen *et al.*, 2006).

Many studies (Hoffman and Ashwell, 2001; Lebert and Rohde, 2007) have labelled overstocking, over-cultivation and poor land management of the communal rangelands as contributing factors towards the degree of land degradation seen today. Stocking densities of communal rangelands typically stand at 1.5 to 2.5 times higher than the Department of Agriculture's recommended densities, in comparison to the commercial rangelands where densities do not exceed recommendations (Hoffman *et*

al., 1999). Communal rangelands are under increasing scrutiny, as the husbandry techniques currently employed threaten the surrounding biodiversity. For example, excessive grazing by livestock can alter vegetation structure and composition (Valone and Sauter, 2005; Kraaij and Milton, 2006; Anderson and Hoffman, 2007) and animal communities (Bock et al., 1990; Joubert and Ryan, 1999; Seymour and Dean, 1999; Saetnan and Skarpe, 2006).

Vegetative responses to grazing vary from a loss in cover, species richness, diversity and productivity (Todd and Hoffman, 1999; Simons, 2005; Valone and Sauter, 2005), to complete compositional shifts (Milton and Hoffman, 1994; Todd and Hoffman, 1999). In the Succulent Karoo, this is typically from perennial to annual species (see Todd and Hoffman, 1999) and to systems dominated by unpalatable species owing to selective grazing (Hoffman and Cowling, 1990; 1991; Riginos and Hoffman, 2003). Numerous researchers (see Beukes and Ellis, 2003; Anderson and Hoffman, 2007) have found the changes comparable within the Succulent Karoo, with higher species richness, vegetation cover and taller vegetation in areas under moderate grazing intensity compared to those under high intensities (Eccard *et al.*, 2000; Valone and Sauter, 2005).

Short-lived rodent species often exhibit high reproductive turnover rates in comparison to larger species, making them more prone to the effects of rapid and unexpected changes (Saetnan and Skarpe, 2006). Grazing herbivores are known to impact small mammal species directly and indirectly; e.g. through grazing and burrow trampling (Bowland and Perrin, 1989; Hayward *et al.*, 1997; Muck and Zeller, 2006) or by increasing predation risk (Grant *et al.*, 1982; Abramsky *et al.*, 2001; Avenant, 2005). Habitat preferences, activity patterns and diet limit a species to certain environments. Grant *et al.* (1982) suggested species inhabiting areas with greater vegetation cover would be more susceptible to habitat changes than those inhabiting areas with less cover. Previous research in arid regions (Zeller *et al.*, 2002; Torre *et al.*, 2007) showed a higher grazing intensity, coupled with a loss of vegetation cover, negatively affected numerous small mammal species. Ungrazed sites harbour more small mammal species and greater abundances when compared to grazed sites (Joubert and Ryan, 1999; Valone and Sauter, 2005). Vegetation cover, structure and composition are important factors for small mammals, and increases in both may be

preferable as predation risk decreases and foraging opportunities increase (Flowerdew and Ellwood, 2001; Torre and Díaz, 2004; Saetnan and Skarpe, 2006; Torre *et al.*, 2007).

This study assesses the effects of different grazing intensities on both vegetation and small mammal communities within the Succulent Karoo Biome, South Africa. Vegetation and small mammal assemblages were compared between two rangeland types, separated by fence-lines. The hypotheses tested are that:

- small mammal species composition on communal rangelands differs from that of commercial rangelands
- ii. small mammal species richness and diversity are negatively affected by higher grazing intensities seen on communal rangelands;
- iii. abundance of small mammal individuals is affected by grazing intensities.

3.2 Study Site

i. Location

This study took place in Paulshoek (30°22'S, 18°16'E), Namaqualand, one of ten villages located in the southern section of the Leliefontein communal area within the Kamiesberg region of the Northern Cape Province (Allsopp, 1999; Joubert and Ryan, 1999; Todd and Hoffman, 1999; Hahn *et al.*, 2005). Namaqualand, an arid region of the Succulent Karoo Biome within the western section of South Africa, covers approximately $50,000 \, \text{km}^2$ and holds as much as 10% of the world's succulent plant species (Cowling *et al.*, 1999; Lebert and Rohde, 2007; MacKellar *et al.*, 2007). Paulshoek lies approximately $980 - 1,400 \, \text{m}$ above sea level, with an area of $\pm 20,000 \, \text{h}$ and approximately $1,000 \, \text{people}$ (Hahn *et al.*, 2005; Lebert and Rohde, 2007).

ii. Topography and vegetation

The Kamiesberg Mountain range is positioned within the Great Escarpment, approximately 50km in width, between the Sandveld (west) and the Bushmanland plateau (east) (Cowling *et al.*, 1999; Todd and Hoffman, 1999; Anderson and Hoffman, 2007). Topography comprises sandy lowland flats, characterized by leaf-and stem-succulents, and rocky uplands, characterized by non-succulent shrubs (Todd

and Hoffman, 1999, Hoffman and Ashwell, 2001). However, as a whole, the vegetation comprises mostly perennial succulents, deciduous and evergreen dwarf-shrubs, geophytes and annuals (Allsopp, 1999; Seymour and Dean, 1999; Anderson and Hoffman, 2007).

iii. Climate

Namaqualand is a winter (May to September) rainfall region. The total rainfall per annum received is \pm 180 - 230mm, and temperatures range from sub-zero during winter months to temperatures in excess of 37°C during summer (Mucina *et al.*, 2006; MacKellar *et al.*, 2007; Simons and Allsopp, 2007).

iv. Livestock densities

While stock densities on commercial farms have remained relatively steady over past decades, those of the communal farms have shown a tendency to increase (Hoffman and Ashwell, 2001). The Department of Agriculture issue recommended stock densities to ensure sustainable production of livestock, but the communal rangelands continue to experience high stocking numbers (Hoffman and Ashwell, 2001; Benjaminsen *et al*, 2005). Recommended stock densities for Paulshoek commons, an area of 20,000ha, are estimated at 1,667 animals, or 12ha per small stock unit (SSU) (Samuels *et al.*, 2007). For the past 30-years, stock numbers within Paulshoek have been between 1.5 to 2.5 times higher than the recommendations (Hoffman *et al.*, 1999; Todd and Hoffman, 1999).

3.3 Methodology

This study took place during March 2006 (early autumn), July 2006 (late winter), September 2006 (early spring) and January 2007 (mid-summer) at three sites (Kuile, Remhoogte and Kleinfontein) within Paulshoek, South Africa. For Clarity, in each chapter these periods have been referred to as autumn, winter, spring and summer. At each individual site, trapping grids were established on a communal rangeland and a neighbouring commercial rangeland.

i. Trapping of small mammals

Fixed paired trapping grids were set up in a 9 by 10 formation at each of the 3 sites, with two grids in place simultaneously, one on the communal and one on the commercial side of the fence-line. Grids contained 90 Sherman-like live-traps comprising 45 small (4.5 x 4.5 x 15cm) and 45 large (8 x 8 x 25cm) traps baited with a mixture of peanut-butter and oats (after Beer, 1964; Patric, 1970; Krug, 2002). Small and large traps were alternated through grids, spaced 15m apart (1.62ha with no boarder zone included) and filled with straw intending to reduce heat- and coldinduced mortalities (Kerley, 1990; Krug, pers. comm.). The trap layout followed previous studies investigating the impacts of land use on small mammal communities along the BIOTA transect (Hoffmann and Zeller 2005; Muck and Zeller 2006). Traps were set for four nights and checked daily at 06h00, 10h00, 15h00 and 19h00, with one trapping session per site per season. Each session comprised 720 trap nights per site (90 traps on communal rangeland + 90 traps on commercial rangeland x 4 nights = 720 trap nights). Straw and bait present were removed, and then replaced for subsequent trapping sessions. This reduced any potential odour-induced biases occurring in subsequent sessions (Boonstra and Krebs, 197; Drickamer, 1995). Species other than small mammals trapped (i.e. tortoise and bird species) were released immediately.

Upon capture, the time, date, trap number and GPS coordinates of trap location were recorded. Trapped individuals were identified to species-level (using descriptions by Skinner and Chimimba (2005)). Mass (recorded to nearest gram using a Pesola spring balance), head/body length, tail length, left hind foot length (as suggested by Barnett (1992)) including claws, and ear height were measured using callipers. Additional information was recorded regarding sex, age class (juvenile, sub-adult or adult) and reproductive status (male: abdominal, inguinal (moving) or scrotal (when possible); female: imperforate or perforate), and whether the individual was newly or had previously been captured. McCravy and Rose (1992) suggest that external reproductive characteristics (i.e. testes position) of male individuals are relatively accurate predictors (87% - 94%) of reproductive condition. Male reproductive condition was thus distinguished by noting testes position as abdominal, inguinal or scrotal (after Gurnell and Flowerdew, 1990; McGravy and Rose, 1992; Krug, pers. comm.). Such classifications were used for all species except elephant shrew species

as testes remain internal even during reproductive periods. Despite this, as Withers (1983) states, elephant shrews are capable of breeding throughout the year, so only female data were relied upon when determining reproductive status in this species. While male reproductive condition is rather accurate and can be distinguished by the use of testes position, reproductive condition of female individuals (i.e. nipple size and vaginal condition) is less accurate (58% - 85%) and far less constant, with nipple size being the best indicator of sexual condition. Due to this factor, McGravy and Rose (1992) suggest the combination of body weight and certain external characteristics (i.e. nipple size) to enable a more accurate method of distinguishing reproductive condition, and subsequently age, in females. Furthermore, female reproductive condition was distinguished as either imperforate or perforate. The vagina of immature females is characterized as being covered with a thin membrane, whilst this membrane perforates upon the onset of first oestrus when individuals can then be classed as perforate. That said, during pregnancy or the non-breeding season, a thin layer of scar tissue can cover the vagina, and as Gurnell and Flowerdew (1990) state, this may cause some confusion in identification of reproductive condition. In addition, a mucus plug may be present subsequent to recent copulation, further confusing identification though this does disappear within a few hours (McGravy and Rose, 1992). In order to increase efficiency in recording data, abbreviations specified by Gurnell and Flowerdew (1990) and Krug (pers. comm.) were modified and applied (Table 3.1).

Table 3.1: Scientific nomenclature follows Gurnell and Flowerdew (1990) and Krug (pers. comm.).

Observation	Abbreviation
Small mammal species:	
Desmodillus auricularis (Smith, 1834)	DEAU
Elephantulus edwardii (Smith, 1839)	ELED
Gerbillurus paeba (Smith, 1836)	GEPA
Macroscelides proboscideus (Shaw, 1800)	MAPR
Micaelamys namaquensis (Ellerman, 1941)	MINA
Mus minutoides (Smith, 1834)	MUMI
Rhabdomys pumilio (Sparman, 1784)	RHPU
Sex:	,
Female	F
Male	M
Age:	,
Juvenile	JUV
Sub-adult	SA
Adult	A
Reproductive status:	
Imperforate / Perforate	IP / PF
Pregnant	PG
Lactating	LCT
Nipple size (measured only in females)	S, M <u>or</u> L
Scrotal	SC
Inguinal	IN
Abdominal	AB

A capture-mark-recapture method was used, and new individuals were marked by ear notching (Figure 3.1). Unique marks were given to new individuals to enable recognition upon short- and long-term recaptures. Alternative marking strategies include fur-dyeing, fur-clipping and toe-clipping, however such techniques are often unsuccessful in practice with fur dying and fur-clipping rarely remaining present until the next molt (see Manville, 1949). Ear notching is a method frequently used for marking rodents, as is considered the safest and most humane permanent marking method (Krug, pers. comm.). Twigg (1975) additionally added that the incisions created in the ear are less likely to reform (unlike fur clipping – see above), thus making the mark available over longer periods. Furthermore, toe clipping is classed as the least desirable permanent marking method, hampering movement and the climbing ability of species (Krug, pers. comm.).

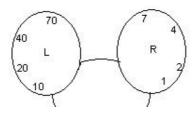


Figure 3.1: Diagrammatical representation of notching method (taken from Krug, pers. comm.).

ii. Vegetation Surveying

A line intercept method was employed whereby two sets of ten-line transects, each measuring 120m, were set up at each site (one set on the communal and one on the commercial side of the fence). Transects corresponded to the rows within each small mammal trapping grid. Each transect was walked and at 5m intervals the vegetation present was measured in height, and identified to growth form (i.e. grass, shrub or succulent) and life cycle (i.e. perennial or annual) (Krug, pers. comm.; Schmiedel, 1999). In the absence of live vegetation, presence of bare ground or rock was noted.

iii. Climatic data

Weather data were supplied by Dr. Klaus Berger of the University of Hamburg, Germany (BIOTA South Africa, 2007), from the Paulshoek BIOTA weather station; situated in close proximity to Kuile and Remhoogte. The parameters used for analysis in this study were minimum air temperature (°C), relative humidity of the air (%), solar radiation (MJ/m²), wind speed (m/s), and rainfall (mm). Mean monthly minimum and maximum temperatures (°C) for the study period are depicted in Figure 3.2, mean monthly rainfall and relative humidity in Figure 3.3.

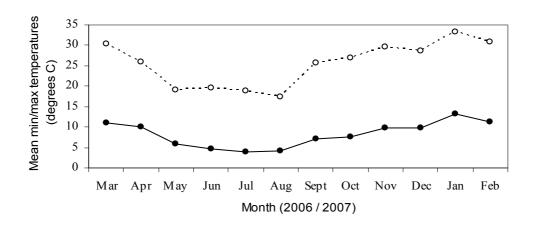


Figure 3.2: Mean monthly maximum (dashed line, open circles) and minimum temperature (°C) (solid line, closed circles) (data supplied by BIOTA South Africa, 2007).

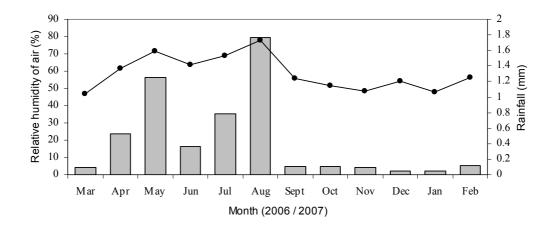


Figure 3.3: Mean monthly rainfall (closed bars) and relative humidity (solid line, closed circles) (data supplied by BIOTA South Africa, 2007).

iv. Non-metric multidimensional scaling

In non-metric multidimensional scaling (NMS) and correspondence analysis ordination diagrams, both site and rangeland types will be referred to as the following: Kuile communal and commercial (SITE 1a and SITE 1b); Remhoogte communal and commercial (SITE 2a and SITE 2b); and Kleinfontein communal and commercial (SITE 3a and SITE 3b).

Seasonal vegetation data were pooled for each site and rangeland type, and rangelands were characterised by classifying vegetation according to life cycle (i.e. perennial or annual) and growth form (i.e. grass, shrub or succulent). Non-metric multidimensional scaling (NMS) ordination identified vegetation composition of the communal and commercial rangelands of the three sites sampled. The communal and

commercial rangelands of each site were enveloped (communal: black solid line; commercial: green solid line), thus enabling identification of the rangeland types and sites based on their vegetation composition. The environmental variable arrows pointing in roughly the same direction (i.e. perennial grass and annual succulent) indicate positive correlations, arrows crossing at right angles indicate low correlations (i.e. perennial shrubs and bare ground), while arrows pointing in opposite directions indicate negative correlations (i.e. perennial shrubs and perennial succulents). The longest arrows are the most important and the longer the arrow, the surer one can be about an inferred correlation.

v. Correspondence Analysis

A correspondence analysis was used to explore the abundances of the different small mammal species in connection with rangeland type and the environmental attributes. Similar to the non-metric multidimensional scaling shown previously, vegetation life cycles (i.e. perennial or annual) and growth forms (i.e. grass, shrub (forb) or succulent), as well additional information regarding the abundance of the small mammal species captured, were included. The correspondence analysis is a descriptive ordination technique that identifies the most important trends in the variation of the data, and thus distributes the variables along continuous axes in accordance with these trends.

The position of the environmental variables indicates that the species points are nearest to the sample points in which they occur with the highest abundance, and the sample points are scattered near the positions of species that tend to occur in those samples. The arrows belonging to the environmental variables show which species largely occur in the areas with the greater cover of perennial grasses or annual succulent, for example. To explain the environmental variable arrows in relation to the small mammal species, one must picture each arrow being extended in both directions. Each species point must then be dropped perpendicularly onto each environmental variable axes. By doing this, the points where the species and environmental variable lines meet indicate the relative positions of the species distributions along each variable axis, or as Ter Braak (1986) defines it, 'it is indicative of the relative value of the weighted average of each species with respect to the environmental variable in question'.

3.4 Data Analysis

i. Species Richness, Abundance and Diversity

Species richness, abundance and diversity of small mammal and vegetation communities were determined for both the communal and commercial rangelands, at each of the three sites during each season over one year. Species richness was calculated by counting the number of species captured, while species abundances were quantified as total number of individuals captured per species. Species diversity was calculated using both Shannon diversity and Brillouin indices.

The Shannon index was primarily selected as it is frequently used in other studies concerning small mammal communities (see Joubert and Ryan, 1999; Tabeni and Ojeda, 2005; Mathis *et al.*, 2006), and as it is the most widely-used diversity index due to its high discriminatory ability. The disadvantages of using this index are that it is sensitive to sample size, and is based on the assumptions that all species are equally represented in the sample and that individuals sampled stem from an 'indefinitely large' population (Magurran, 1988). The Brillouin index was additionally selected despite frequently being criticized for having a low discriminatory power, as it is a more accurate measure in cases where randomness of a sample cannot be guaranteed, as is the case with using traps to survey small mammals. Whilst the Shannon index estimates the diversity of the unsampled as well as the sampled portion of the community, the Brillouin index describes known collections (Magurran, 1988). By comparing both diversity indices, it may be possible to identify a correlation (see Magurran, 1988), thus ensuring that the biases associated with the Shannon index are indeed negligible.

The Shannon index (H) value was calculated using $-\sum p_i \ln p_i$ where p_i is the abundance of a particular species in a sample, which is then multiplied by the natural logarithm of itself. H is then calculated by summing the product for all of the species in the given sample (Fowler *et al.*, 2002). The Brillouin index (HB) value was calculated using: $\ln N! - \sum \ln n_i! / N$ where N is the total number of individuals, n_i is the number of individuals in each species, the factorial of which is then multiplied by the natural logarithm of itself and summed (see Magurran, 1988).

ii. Statistical Analysis

Non-metric multidimensional scaling (NMS) ordination biplots were used to determine the configuration of samples in the ordination space so that the distance of samples correspond best to the dissimilarities of their species composition. Ordination by correspondence analysis (CA) was additionally used to determine the species-environment relationships, where patterns of variation in the environmental data were analysed and then the species variation were superimposed onto the distribution. This relates the measured environmental variables indirectly to the species data, thus providing a diagram showing the most important patterns of variation in species distribution and the environmental variables. These analyses, with climatic and vegetation parameters as environmental variables, were conducted using the program package CANOCO (version 4.5) (Ter Braak, 1987)

Vegetation data were normally distributed and Independent samples T-tests were applied, using the SPSS statistical package, for comparisons between groups of vegetation life and growth forms. To test that the biases associated with the Shannon index were negligible, both diversity indices were compared to identify possible correlations using a Pearson's product-moment correlation, data used were normally The Shannon T-test was used to determine differences in species diversity between communal and commercial rangelands for both vegetation and small mammals; it was not necessary to transform data. This was not necessary for the Brillouin indices, as they are significantly different from one another without statistical testing. A G-test was used to determine homogeneity in species richness between communal and commercial rangelands for both vegetation and small mammals, as well as for small mammal abundances; it was not necessary to transform data. A Pearson's product-moment correlation was carried out post square root transforming small mammal abundance data, using the SPSS statistical package, to establish relationships between small mammal species richness, diversity and total small mammal abundances, nocturnal abundances, diurnal abundances, and vegetation height and cover.

A best subsets multiple regression analysis was performed, using the Statistica 7.0 statistical package, to evaluate how well specific predictor variables (i.e. climatic variables, vegetation variables (cover of different growth forms, and heights of growth

forms), and vegetation species richness and diversity) influenced the three most abundant small mammal species. Abundance data were square-root transformed. Seasonal data, for each rangeland type at each site, were pooled due to small sample sizes. A p value of <0.05 indicates significance.

3.5 Results

i. Correlation between Shannon index and Brillouin index

There were significant positive correlations between the Shannon diversity index and the Brillouin diversity index regarding small mammal diversity (r $_{0.05(2), 24} = 0.98$, p < 0.001) and vegetation diversity (r $_{0.05(2), 24} = 0.99$, p < 0.001), indicating that the biases associated with the Shannon index were negligible.

ii. Environmental features of each site

Perennial shrubs, perennial succulents and bare ground were the most important variables separating the rangelands (Figure 3.4). The first axis (left to right) reflects the difference between perennial succulent dominated areas (on the left side) and areas dominated by perennial shrub areas (on the right side), while the second axis (top to bottom) correlates negatively with the amount of bare ground, and to a lesser extent, with rock. In terms of dissimilarities between the rangelands, Remhoogte communal rangeland was different from the other two communal rangelands, and was more similar to the commercial rangelands, in particular Kuile commercial (Figure 3.4). Results from the non-metric multidimensional scaling (NMS) ordination were supported by results obtained from Independent samples T-tests (Appendix 1; Table 1.1; Figures 3.5 and 3.6).

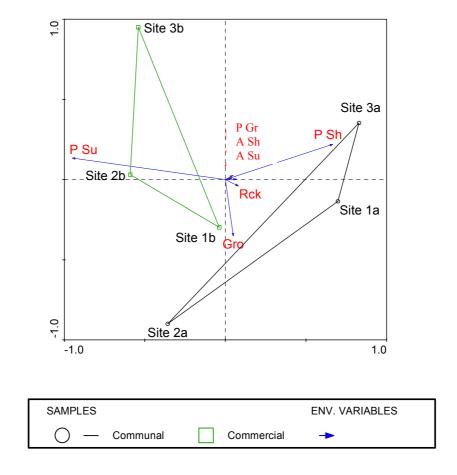
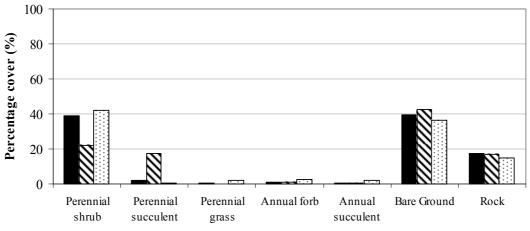


Figure 3.4: Non-metric multidimensional scaling (NMS) ordination biplot of dissimilarities [of pooled environmental variables] between communal (black open circles, solid lines) and commercial (green open squares, solid lines) rangelands of the three sites sampled. Sample points indicate site and rangeland type (see section: 3.3 Methodology), with distance between points approximating the dissimilarity of the composition. Length and direction of environmental variable arrows indicate relative importance of the variables (A Sh = annual forb, A Su = annual succulent, P Gr = perennial grass, P Sh = perennial shrub, P Su = perennial succulent, Rck = rock, Gro = bare ground), where the angles between arrows indicate correlations (or covariance) between variables. Final stress = 0.00002.



Percentage cover of the different life/growth forms

Figure 3.5: Graphical representation of percentage of life/growth forms within Kuile (solid bars), Remhoogte (diagonal striped bars) and Kleinfontein (dotted bars) communal sites.

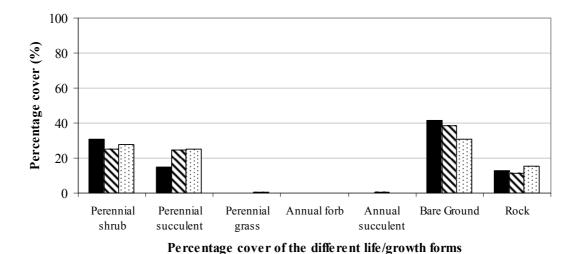


Figure 3.6: Percentage cover of the different life/growth forms within Kuile (solid bars), Remhoogte (diagonal striped bars) and Kleinfontein (dotted bars) commercial sites.

Plant species richness (Table 3.2) was greater on the commercial rangelands than on the commercial rangelands, except at Kuile and Remhoogte during spring, and at Kleinfontein during winter.

Table 3.2: Temporal variation in plant species richness and species richness average (±s.e.) at the communal and commercial rangelands. March 2006 to January 2007.

-	Kuile		Reml	noogte	Kleinf	ontein
Season	communal	commercial	communal	commercial	communal	commercial
Autumn	2	7	5	7	6	7
Winter	8	10	6	7	11	8
Spring	11	9	13	10	11	12
Summer	9	10	9	10	6	9
Average	30 (± 1.94)	36 (± 0.71)	33 (± 1.80)	34 (± 0.87)	34 (± 1.44)	36 (± 1.08)

At Kuile, plant diversity was significantly greater on the commercial rangeland during all seasons (Table 3.3). At Remhoogte, the same was true for all seasons apart from spring. There were significant differences in diversity between the rangelands of Kleinfontein during autumn, spring and summer, with diversity during autumn and summer being greater on the commercial rangeland (Table 3.3). There were significant negative correlations between vegetation cover and both rock cover (r $_{0.05(2), 24}$ = -0.88, p <0.001) and bare ground (r_s $_{0.05(2), 24}$ = -0.41, p <0.05.

Table 3.3: Plant diversity (Shannon index) and diversity average (\pm s.e.) at the communal and commercial rangelands. March 2006 to January 2007. † Significance tested using Shannon T-tests: NS = not significant; * p <0.05; ** p <0.01; *** p <0.001.

Kuile			Remhoogte				Kleinfontein					
Season	communal	commercial	Value	DF p^{\dagger}	communal	commercial	Value	DF p^{\dagger}	communal	commercial	Value	DF p^{\dagger}
Autumn	0.34	1.77	2.69	118 **	1.06	1.62	4.32	86 ***	1.32	1.55	2.34	185 *
Winter	0.76	1.64	5.89	235 ***	1.12	1.46	3.02	198 **	1.92	1.79	1.31	6 NS
Spring	1.23	1.54	2.14	259 *	2.06	1.89	1.7	276 NS	1.93	1.87	0.7	318 ***
Summer	0.67	1.55	6.09	258 ***	1.47	1.54	0.57	235 ***	1.46	1.77	3.49	246 ***
Average	$3 (\pm 0.18)$	$6.5 (\pm 0.05)$	$16.81 (\pm 1.04)$		$5.71 (\pm 0.23)$	$6.51 (\pm 0.09)$	$9.61 (\pm 0.81)$		$6.63 (\pm 0.16)$	$6.98 (\pm 0.07)$	$7.84 (\pm 0.61)$	

iii. Small mammal assemblages

The abundance of *Macroscelides proboscideus* at Remhoogte was significantly higher at the commercial rangeland than at the communal rangeland ($\chi^2_{6, 21} = 1.02, p < 0.001$), while the difference in abundances on the rangelands at Kuile were not significant ($\chi^2_{6, 21} = 1.47, p > 0.05$; Table 3.4). Abundances of *Gerbillurus paeba* were significantly higher on the commercial rangelands both at Kuile ($\chi^2_{6, 21} = 4.91, p < 0.05$) and Remhoogte ($\chi^2_{6, 21} = 11.41, p < 0.001$), while the differences in abundances between the two rangeland types at Kleinfontein were not significant ($\chi^2_{6, 21} = 1.45, p > 0.05$). The higher abundances of these two species on the commercial rangelands

coincide with a greater plant species richness (Table 3.2) and greater plant diversity (Table 3.3) on these sites.

Differences in small mammal species richness were negligible, with the number of species only differing by one or two species between rangelands (Table 3.5). Given the limited trapping area (1.6ha) used within each rangeland and that small mammal sample sizes were very small it can be argued that it is most probable that not all of the species present were sampled during each season at each site.

Table 3.4: Small mammal species and total abundances at the communal and commercial rangelands. March 2006 – January 2007. † Significance tested using G-test: NS = not significant; p < 0.05; *** p < 0.001. Degrees of freedom = 1 with Yates' correction for continuity.

Kuile			Remhoogte			Kleinfontein						
Species	communal	commercial	χ2	p†	communal	commercial	χ2	p†	communal	commercial	χ2	p†
Desmodillus auricularis	6	0	-	-	0	0	-	-	3	0	-	
Elephantulus edwardii	7	0	-	-	0	0	-	-	0	0	-	-
Macroscelides proboscideus	13	20	1.47	NS	6	21	1.02	***	3	3	0	NS
Micaelamys namaquensis	0	2	-	-	0	0	-	-	0	1	-	-
Mus minutoides	1	0	-	-	0	0	-	-	0	0	-	-
Gerbillurus paeba	7	18	4.91	*	4	20	11.41	***	6	11	1.45	NS
Rhabdomys pumilio	0	0	-	-	1	4	1.75	NS	0	0	-	-

Seven small mammal species were captured in total over a 1-year period (Table 3.4). Five species were captured during autumn, winter and summer, and four species were captured during spring. One species (*Mus minutoides*), present only during winter, was represented by a single individual on the communal rangeland of Kuile, whilst two species (*Elephantulus edwardii* and *Rhabdomys pumilio*) were only captured each within one site, Kuile and Remhoogte respectively. *Elephantulus edwardii* was only found on the communal rangeland, while *R. pumilio* was captured at both rangeland types (Table 3.4). *Micaelamys namaquensis* was captured within the commercial rangelands of Kuile and Kleinfontein, but only during the summer season (Appendix 2; Table 1.1), while *E. edwardii* (during autumn and spring) and *M. minutoides* (during winter) were both exclusive to Kuile communal rangelands. In comparison *Desmodillus auricularis* was only captured on the communal rangelands of Kuile and Kleinfontein (Table 3.4). *Rhabdomys pumilio* was only captured, at Remhoogte and in small numbers, during autumn, winter and summer. This species occurred on both rangeland types, with five in total being captured (Table 3.4): two on the commercial

rangeland during autumn and winter, and one on the communal rangeland during summer (Appendix 2; Table 1.1).

Table 3.5: Temporal variation in small mammal species richness and species richness average (±s.e.) at the communal and commercial rangelands. March 2006 – January 2007.

	K	uile	Rem	hoogte	Kleinfontein		
Season	communal	commercial	communal	commercial	communal	commercial	
Autumn	2	1	2	3	2	1	
Winter	4	2	1	1 3		1	
Spring	3	2	0	2	2	2	
Summer	3	3	3	2	3	3	
Average	$12 (\pm 0.41)$	8 (± 0.41)	$6 (\pm 0.65)$	$10 (\pm 0.29)$	$8 (\pm 0.41)$	$7 (\pm 0.48)$	

Seasonal small mammal data were combined for each rangeland at each site. Only Kuile showed a significant difference in Shannon diversity between rangeland types, with a greater diversity on the communal rangeland (Table 3.6).

Table 3.6: Small mammal diversity (Shannon index) at the communal and commercial rangelands. March 2006 to January 2007. † Significance tested using Shannon T-tests: NS = not significant; *** p < 0.001.

	Rangel				
Site	communal	commercial	Shannon index (H)	DF	p^{\dagger}
Kuile	1.43	0.86	5.23	56	***
Remhoogte	0.92	0.93	0.09	12	NS
Kleinfontein	1.04	0.73	1.54	24	NS

iv. Small mammal abundances, environmental and climatic variables

Small mammal species diversity positively correlated with vegetation height but not plant cover (r $_{0.05(2), 24} = 0.44$, p < 0.05; r $_{0.05(2), 24} = 0.14$, p > 0.05, respectively). Small mammal species richness was also positively correlated with vegetation height (r $_{0.05(2), 24} = 0.55$, p < 0.01), but not plant cover (r $_{0.05(2), 24} = 0.08$, p > 0.05). The total (pooled) abundance of small mammal species, from all sites and rangelands, was positively correlated with vegetation height (r $_{0.05(2), 24} = 0.61$, p < 0.001), but not plant cover (r $_{0.05(2), 24} = -0.22$, p > 0.05). Both the pooled abundances of nocturnal and diurnal small mammal species (classified following Skinner and Chimimba, 2005) were positively correlated with vegetation height (r $_{0.05(2), 24} = 0.66$, p < 0.001; r $_{0.05(2), 24} = 0.000$; r $_{0.000(2), 24} = 0.000$;

= 0.45, p <0.05), while neither correlated to plant cover (r $_{0.05(2), 24}$ = -0.23, p >0.05; r $_{0.05(2), 24}$ = 0.15, p >0.05, respectively).

Three small mammal species (G. paeba, M. proboscideus and D. auricularis) were captured in sufficient numbers to analyse the relationship between small mammal abundance and environmental variables. There was a significant relationship between G. paeba abundance and annual forb (p < 0.001) and bare ground cover (p < 0.05) (from vegetation cover factor), as well as perennial shrub height (p < 0.01). From the R^2 values, it can be inferred that 40% and 32%, respectively, of the variance of G. paeba abundance in the sample can be accounted for by the mentioned predictor variables (Table 3.7).

Table 3.7: Environmental variables best explaining variations in *Gerbillurus paeba* abundance, as identified using a best subsets multiple regression; ** p < 0.01; *** p < 0.001.

Factor	Adj. R ²	р	Predictor Variable	<i>T</i> -value	р	Sig
Climate	0.08	0.092				
Vegetation cover	0.40	0.003	Annual Forb Bare Ground	-3.80 -2.61	0.001 0.016	***
Height of growth forms	0.32	0.013	Perennial Succulent	2.91	0.008	**
Vegetation species richness; diversity	0.06	0.120				

There was a significant relationship between M. proboscideus abundance and solar radiation (p < 0.01) and wind speed (p < 0.01) (from climatic factors) and plant species diversity (p < 0.01). From the R^2 values, it can be inferred that 44% and 23%, respectively, of the variance of M. proboscideus abundance in the sample can be accounted for by the mentioned predictor variables (Table 3.8). While the vegetation cover factor showed that it accounted for 22% of the variance of M. proboscideus abundance in the sample, none of the predictor variables were significant.

Table 3.8: Environmental variables best explaining variations in *Macroscelides proboscideus* abundance, as identified using a best subsets multiple regression; ** p < 0.01.

Factor	Adj. R ²	р	Predictor Variable	<i>T</i> -value	р	Sig
Climate	0.44	0.001	Solar radiation	3.10	0.005	**
			Wind speed	3.28	0.003	**
Vegetation			-			
cover	0.22	0.025				
Height of						
growth forms	0.35	0.008				
Vegetation species						
richness; diversity	0.23	0.009	Species Diversity	-2.83	0.009	**

The only significant relationship found was between D. auricularis abundance and perennial succulent cover (from the environmental attributes factor) (p < 0.001). From the R^2 value, it can be inferred that 48% of the variance of D. auricularis abundance in the sample can be accounted for by such a predictor variable (Table 3.9).

Table 3.9: Environmental variables best explaining variations in *Desmodillus auricularis* abundance, as identified using a best subsets multiple regression; *** p < 0.001.

Factor	Adj. R ²	р	Predictor Variable	T-value	р	Sig
Climate	0.02	0.511				
Vegetation cover	0.48	0.000	Perennial Succulent	-4.70	0.000	***
Height of growth forms	0.01	0.247				
Vegetation species richness; diversity	0.00	0.342				

A correspondence analysis was used to explore the abundances of the different small mammal species in connection with rangeland type and the environmental attributes. In contrast to the NMS ordination based on the vegetation data alone, a correspondence analysis based on small mammal abundances and correlated environmental variables shows a clear distinction of the two rangeland types, with the exception of Remhoogte, where communal and commercial rangelands appeared more similar to one another than the other rangeland pairs.

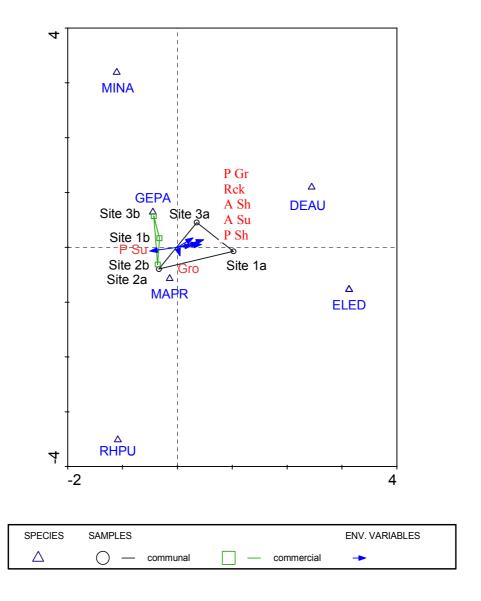


Figure 3.7: Correspondence analysis (CA) biplot showing pooled seasonal small mammal abundances (DEAU: Desmodillus auricularis; ELED: Elephantulus edwardii; MAPR: Macroscelides proboscideus; MINA: Micaelamys namaquensis; GEPA: Gerbillurus paeba; RHPU: Rhabdomys pumilio) relative to the communal (black open circles, solid lines) and commercial (green open triangles, solid lines) rangelands, as well as the vegetation attributes (A Sh = annual forb, A Su = annual succulent, P Gr = perennial grass, P Sh = perennial shrub, P Su = perennial succulent, Rck = rock, Gro = bare ground). The distance between species points approximates the dissimilarity of distribution of relative abundance of those species across the samples, while the distance between sample points approximates the dissimilarity of their species composition. The environmental variable arrows point in the expected direction of the steepest increase of values, while the angles between arrows show correlations between individual variables.

Elephantulus edwardii has the lowest weighted average with respect to perennial succulents, as they tend to occur in areas with a lower cover of perennial succulents and a greater cover of rocks, grass, annual forbs and succulents, and perennial shrubs.

Rock cover, on the other hand, shows the order of small mammal species to be exactly opposite to that of perennial succulents, with *E. edwardii* being associated with a greater cover of rock (as mentioned above), and *R. pumilio* being associated with a lesser rock cover. Concerning perennial succulents, *D. auricularis* holds the second lowest value, and so on to *R. pumilio*, which has the highest weighted average (occurring in sites where perennial succulent cover is greater). Using bare ground as another example from Figure 3.7, one can see that *R. pumilio* has the highest weighted average, followed by *E. edwardii*, *M. proboscideus*, and lastly by *D. auricularis*, *G. paeba* and *M. namaquensis* (lowest weighted average thus occurring in sites with less bare ground).

3.6 Discussion

Communal rangelands were characterised by a greater perennial shrub cover. Perennial grasses and annual forbs were present on both rangelands. A greater perennial succulent cover however characterised the commercial rangelands. These findings were similar to those by Milton et al. (1994), Todd and Hoffman (1999) and Anderson and Hoffman (2007). The ordination diagram did show that, unlike Kleinfontein, where the communal rangeland was dissimilar to the commercial rangeland, Kuile commercial rangeland was most similar to the communal rangeland of Remhoogte. No particular rangeland showed any trend for plant species richness. Differences in species richness were negligible between rangelands, with most cases showing only a difference of one or two species. This finding supports that of Anderson and Hoffman (2007) whereby there was no significant difference overall in the number of species within the communal and commercial rangelands, for both lowland and upland habitats. However vegetation diversity showed significant differences between the rangelands of Kuile (all seasons), Remhoogte (autumn, winter and summer), and Kleinfontein (autumn, spring and summer), with diversity being greater on the commercial rangelands barring Kleinfontein during autumn and summer.

Higher grazing intensities of the communal rangelands did not affect small mammal species richness (Hypothesis 1 – rejected). As with plant species richness, the differences here were also negligible, with the communal and commercial rangelands showing a difference of one or two species. Whilst Joubert and Ryan (1999) showed

similar results, with differences in species richness between rangelands also being minimal, the study carried out here showed no consistent pattern of greater species richness on any one particular rangeland type. Joubert and Ryan (1999) however found slightly greater species richness within areas under lower grazing intensities when compared to those under higher intensities. Studies of small mammal species and land disturbance will often show diminished species richness, diversity and abundance within heavily grazed areas (Joubert and Ryan, 1999; Eccard et al., 2000; Tabeni and Ojeda, 2005; Valone and Sauter, 2005; Tabeni et al., 2007; Torre et al., 2007). This would suggest that small mammal species are strongly associated with certain environments, and that plant life and growth forms will be influential to not only the presence of a species, but also to its abundance as Joubert and Ryan (1999) and Fox (1990) demonstrated. Associations result from differences between requirements of the small mammal species, which generally require different vegetation cover and density (Birney et al., 1976; Grant and Birney, 1979). Although small mammal species richness and diversity did not differ between rangelands, the species captured differed between rangelands. Desmodillus auricularis and E. edwardii were only present on communal rangelands, while others (i.e. M. proboscideus and G. paeba) were present across both rangelands (Hypothesis 2 – accepted). In these latter species, abundance seemed negatively affected by the increased grazing intensity on the communal rangelands (Hypothesis 3 – accepted for M. proboscideus and G. paeba). Species present only on the communal rangelands in high numbers, D. auricular and E. edwardii, suggest a strong favouritism towards this rangeland type and the more open, lower vegetation with more annuals and rocks. Rhabdomys pumilio, a diurnal species, was found on both rangelands in addition to M. proboscideus and G. paeba, although small sample sizes in this study make it difficult to support these findings.

Joubert and Ryan (1999) suggested that species active during daylight hours become negatively affected by a reduced vegetation cover and height, thus becoming dependent on cover to escape diurnal predators (see also Woodall *et al.*, 1989; Torre *et al.*, 2007). The same is likely to be true for crepuscular species, such as *M. proboscideus* (pers. obs., but see Woodall *et al.*, 1989; Roxburgh and Perrin, 1994; Skinner and Chimimba, 2005). In contrast, nocturnal species tend to be capable of inhabiting areas where vegetation is not so abundant, i.e. gerbilline species. Both

nocturnal and diurnal groups were positively correlated with vegetation height but not vegetation cover, thus leading to the conclusion that vegetation height, rather than cover, may be essential when avoiding predation both during day and night. One explanation may be that taller vegetation may have the complexity, in their height, to protect a small mammal species better than shorter vegetation. However, despite that it might equally seem advantageous for species to be associated with a greater vegetation cover, so moving from plant to plant would not be as hazardous on an individual scale (i.e. increased predation risk), this study disproved this potential advantage.

Nocturnal species are not as vegetation cover-dependent as species active during daylight hours, dawn and dusk inclusive (Christian, 1980; Joubert and Ryan, 1999), as predators rely chiefly on hearing and olfactory senses to locate prey (Perrin et al., 1999). Nevertheless, reductions in cover of specific vegetation growth forms could be detrimental to certain species. The nocturnal G. paeba is an omnivorous species, feeding on foliage, seeds and insects (Kerley, 1989). It flourishes in and exploits open habitats with low vegetation diversity, and areas with a thin grass/scrub cover (Kerley, 1992; Perrin et al., 1999; Skinner and Chimimba, 2005). Through using its welladapted eyes and ears, predator detection and avoidance are utilized within such habitats (Perrin et al., 1999). From descriptions of the 'ideal' habitat, and as Kerley (1992) documented, one would expect abundance negatively associated with an increase in canopy height and vegetation diversity, and preferences shown for an increase in bare ground (Kerley et al., 1990). Here, the main determinant for the abundance of the nocturnal G. paeba within this semi-arid system appears to be annual forb and bare ground cover, along with an increasing height of perennial This result was unpredictable, based upon and contradicting other succulents. findings (Kerley, 1992; Perrin et al., 1999; Skinner and Chimimba, 2005), as such a species favours open habitats with little vegetation (Kerley et al., 1990). This abundance of G. paeba thus seems to result in part, from the need for some cover to escape predation. There was one other gerbil species captured in this study, D. auricularis. Unlike G. paeba, D. auricularis abundance was greater on the communal rangelands. Such an increased faunal abundance within areas under heavy grazing applies to other granivorous species in addition to the selected small mammal species discussed above; like the southern large-billed lark (Galerida magnirostris),

redcapped lark (Calandrella cinerea) and Cape sparrow (Passer melanurus) according to Joubert and Ryan (1999), as well as harvester ants (Messor capensis) as shown by Milton and Dean (1993). Unlike G. paeba, D. auricularis abundance was not determined by annual forbs or bare ground cover, but by perennial succulent cover. Despite this, perennial succulent cover accounted for only 48% of the variance of abundance. Due to this species being a granivore, one would expect a relationship with annual plants, as such species are commonly associated with increased seed production, which in turn would make seeds more abundant (Milton et al., 1994; Seymour and Dean, 1999). Rodents within southern hemisphere semi-arid environments are mostly herbivorous, while those within northern hemisphere environments are largely granivorous (Kerley, 1991; 1992). Despite D. auricularis being predominantly granivorous, it does feed on other items. Joubert and Ryan (1999) stated that perennial vegetation cover is important to this small mammal species as it contributes as a large proportion of the animals' diet. It seems rather odd though, that such a species was present only on communal rangelands where there was a lower cover of perennial succulents, yet the best subsets multiple regression showed such a growth form to influence abundance. As perennial succulent cover only accounted for 48% of the variance, there may be other environmental factors that could explain a species choice of a particular habitat area. One factor not measured here was soil compactness. As both species are burrowers, soil property could be important since vegetation structure affects the compactness of the soil, and an increase in livestock numbers may further increase soil compactness through trampling. Desmodillus auricularis is generally associated with more compacted soils (e.g. gravel plains of the Namib Desert), while G. paeba prefers areas with looser, sandier soils. Therefore, this factor may be a large determining factor in why there was a greater abundance of G. paeba on the commercial rangelands, and a greater abundance of D. auricularis on communal rangelands, and warrants being measured in other studies.

Macroscelides proboscideus was the only species where climatic variables influenced abundance. The main climatic determinants were solar radiation and wind speed. Despite such variables being determinants of abundance, together they only accounted for 44% of the variance in abundance, so such predictors can only be classed as mild predictors of abundance. One of the few essential habitat requirements for this

crepuscular species is a sparse rock or bush/grass cover (Skinner and Chimimba, 2005), and it is understandable why such requirements are essential when looking at activity patterns and the need to escape predation. Despite the expected importance of canopy height of particular growth forms, based on reasons outlined previously, none of the tested variables proved to be so. Vegetation species richness and diversity account for only 23% of the variance in abundance, and climatic factors account for 44% variance, one would suggest there are other factors that need to be tested. Looking at insect and invertebrate abundances may reveal an insight into why the omnivorous M. proboscideus [principally insectivorous but additionally feeds on foliage and seeds (Skinner and Chimimba, 2005)] was found in greater abundances on the commercial rangelands. Despite this being a plausible explanation and a good area on which to focus and that Nchai (unpublished data) showed termite and ant abundance greater on commercial rangelands, Kerley (1995) suggested that the contribution of insects to the diet of M. proboscideus was not an influencing factor in the abundance of such a species. Furthermore, Laakkonen et al. (2001) showed Sorex ornatus and Notiosorex crawfordi not affected by ant abundance.

Joubert and Ryan (1999) previously studied the effects of rangeland type on small mammal and bird assemblages at Kuile and Kleinfontein, as well as an additional site [Slootijiesdam] in 1999. Faunal species richness, diversity and composition were examined within rangelands and conclusions suggested that vertebrate diversity would continue to decrease unless steps were taken to conserve the perennial vegetation cover. The study was only conducted during the spring of 1997, meaning that only one season was studied and the effects of factors such as climatic variations throughout the year were not incorporated into the conclusions. Milton (1994) noted that seed production is highly related to rainfall, so in years or even seasons where rainfall was higher than usual, seed abundance should be greater therefore perhaps appealing to granivorous species. This would increase granivore abundance and result in higher species diversity within such plots. However seed production is not the only abundance factor related to rainfall. Todd and Hoffman (2000) showed stock density also to be related, which could be detrimental to burrowing small mammal species due to soil compaction and/or burrow trampling. Despite many small mammal species showing preferences for commercial rangelands, both in this study (4 of 7: M. proboscideus, M. namaquensis, G. paeba and R. pumilio) and Joubert and Ryan's study (1999) (5 of 6: *M. proboscideus, M. namaquensis, R. pumilio, Otomys unisulcatus* and *Suncus varilla*), it became apparent there were two species absent from the commercial rangelands and three which appeared only in communal rangelands during this study when compared to the study of Joubert and Ryan (1999). This disappearance and appearance of such species could be a vital indicator of rangeland quality, as the two species (*O. unisulcatus* and *S. varilla*) absent from this study may have found not only communal rangelands uninhabitable, but also commercial rangelands, subsequent to the study by Joubert and Ryan (1999). The three species captured in this study but not in that of Joubert and Ryan (1999), may have found communal rangelands more inhabitable now than they were a decade ago, allowing occupancy by such species.

To obtain completely accurate data regarding abundances, one must consider the potential sample sizes needed, and decide whether additional action needs to be taken to increase sample sizes for suitable analyses. Throughout this study, a number of flaws were apparent. Given the limited trapping area (1.6ha) within each rangeland, and that the small mammal sample sizes were small, one can argue that it is most probable that not all the small mammal species present were sampled. The problem of the small sample sizes collected was not the result of too few traps being laid out, or that more than 50% of the traps were occupied at any one time. If this was the case, as Gurnell and Flowerdew (1990) suggest, then (i) more traps should have been placed at each 'station', or (ii) the trapping grid should have be increased in size. If more traps were necessary, then more should have been set up at each station so an individual is less likely to come across an occupied trap, but on the other hand traps could have been added to the grid, resulting in a larger area being covered. Furthermore, the period of trapping could be increased from 4 nights (Kerley and Erasmus, 1992; Hayward et al., 1997) to five (see Joubert and Ryan, 1990) or even six, depending on the success of trapping within initial nights. Gurnell and Flowerdew (1990) suggest three trapping days (see Shenbrot and Krasnov, 2001; Bergström, 2004) and nights is ample if one aims to simply catch, mark and recapture individuals. One major drawback of increasing trapping period is that it could potentially increase the quantity of trap-happy individuals, who become reliant on the bait and straw provided. However, increasing the period of trapping could increase the chances of capturing a trap-shy individual, which would give some insight of the

'true' species composition within the sample area. The distance between trapping stations and lack of replications may have been the major downfalls of this study's design. It is agreed that trapping grids should be used over trap lines when studying population size/density, but the correct spacing between the stations needs to be thought out carefully prior to sampling. The correct spacing between stations depends partly on the distances between pairs or groups of stations, which the study species typically moves. Factors such as habitat type and time of year should also be considered. Gurnell and Flowerdew (1990) suggest traps be spaced 5m apart in grassland, 10m to 15m apart in deciduous or coniferous woodland, and 20m apart in arable (agricultural) habitats. Concerning desert environments and trap spacing, Shenbrot and Krasnov (2001) used 50 Sherman traps placed on a 5 by 5 grid (2 traps at each station, and each station 20m apart), Kerley and Erasmus (1992) used 100 traps set for 4 nights, 10m apart, on 10 by 10 grids, while Hayward *et al.* (1997) used 49 traps on a 7 by 7 grid, spaced 15m apart. Despite this, station distances seem to be a combination of success of past research and personal choice.

The number of small mammals trapped depends not only on the factors outlined above (concerning altering trapping method), but on several other factors. Conditions when trapping and thus the activity of the animals, the size of the population sampled, the size of the average territory, and population cycle, among others conditions, play important roles in the trapability of animals (Krug, pers. comm.). Trapping success is greatest when traps are set during new moon or quarter moon phases (Daly et al., 1981; Vicker and Bider, 1981; Stokes et al., 2001), and when temperatures and climatic conditions are ideal (i.e. not too cold or hot) (Gentry and Odum, 1957; Getz, 1961; Stokes et al., 2001). In these periods, animals will be most active and are most likely to be caught. The greater the population, the more likely individuals are to be captured, as more animals encounter traps. Similarly, if territory sizes are small, there will be a greater number of individuals on a particular site. Female activity is somewhat limited during breeding/lactating periods, while males are more active and are searching for females. At the end of the breeding season, more individuals may be encountered, as animals disperse from former groups and are thus more active. Food availability also influences trapping success (Schradin and Pillay, 2006), and animals may be more enticed into traps when food resources are limited.

To resolve the problem of the lack of replications, perhaps setting up three grids within each rangeland would have been more beneficial and produced larger sample sizes, so that suitable statistical analyses could have been used. However, the grids would have had to be spaced a suitable distance from one another so to exclude any crossing-over of individuals from one grid to the other, it would have been necessary to assess species' home ranges prior to sampling. The number of replications could also have been increased by continuing use of only one grid (90 traps) per rangeland, but instead of repeating sampling once per season, repeat 3 times per season (12 individual sampling sessions in total). This would have also given a large sampling size with which to work.

Livestock grazing has potentially major ecological implications, with particular attention focussing upon the effects of the overgrazing seen on communal rangelands. If overstocking and increasing agricultural pressures continue to pressurise such rangelands, then the stresses placed upon the current vegetation may lead to alterations in structure being more severe than those today. Despite none of the small mammal species captured here being classified by the IUCN or CITES as threatened or endangered, changes in vegetation do have repercussions on the surrounding biodiversity, additionally having the ability to influence faunal species. Continual follow-ups are necessary to ensure a constant surveillance for areas under such regimes and the impact of their changes in vegetation on the surrounding environment to prevent localised extinctions, in the extreme case. Further studies are needed to elucidate the influence of grazing on small mammals and other faunal species within heavily-grazed areas when compared to areas with excluded livestock (see Smit et al., 2001; Valone and Sauter, 2005). It is important to recognize not only whether natural vegetation can re-establish (see Milton, 1992; 1994; Simons and Allsopp, 2007), but also whether certain faunal species can re-establish thriving populations (see Schwartz and Whitson, 1987; van Aarde et al., 1996; Ferreira and van Aarde, 1996). Furthermore, studies on small mammal population fluctuations can be valuable and should be documented, as declines in species can have disadvantageous direct and indirect impacts on both predator and prey species.

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Chapter 4

Population demography and breeding status in small mammal species present on communal and commercial rangelands

4.1 Introduction

Livestock grazing has drastic effects on the surrounding environment. This leads to alterations in vegetation composition and structure (Beukes and Ellis, 2003; Hahn *et al.*, 2005; Anderson and Hoffman, 2007), which in turn result in changes in faunal assemblages (Seymour and Dean, 1999; Jones *et al.*, 2003; Valone and Sauter, 2005; Mathis *et al.*, 2006).

Larger herbivores, such as cattle and wild ungulates, can affect small mammals indirectly and directly, and results are well-documented (e.g. Hayward *et al.*, 1997; Eccard *et al.*, 2000; Tabeni *et al.*, 2007; Torre *et al.*, 2007). Indirect effects include compacting surrounding soils, eventually resulting in stony shallow soils prone to crusting (Beukes and Ellis, 2003), as well as reducing vegetation cover and height, plant diversity and composition. This affects the fitness, reproduction, and predator avoidance of small mammal species (Schmidt *et al.*, 2005). The direct effects include competition for food resources (Krueger, 1986; Mishra *et al.*, 2004; Retzer, 2005), and the trampling of burrows, which is detrimental to belowground dwelling species (Van Rooyen *et al.*, 1991; Muck and Zeller, 2006).

The relationships between the environment and small mammal species are complex, shaped by physiological, nutritional, social, and anti-predator requirements of the species (see Birney et al., 1976; Kerley, 1992; Kerley and Erasmus, 1992). Based on these, small mammals can be used as indicators of habitat integrity and quality (Avenant, 2000; 2005), and to distinguish environmental alterations (Zeller et al., 2002). Short-lived rodent species are highly prone to the effects of changes (and respond quickly) because of their high reproductive turnover rates (Saetnan and Skarpe, 2006). Past research has shown that a higher grazing intensity will often negatively affect small mammal communities (Eccard et al., 2000; Zeller et al., 2002; Torre et al., 2007), with ungrazed sites typically holding greater species richness, as well as increased abundances compared to sites subjected to extensive grazing (Grant et al., 1982; Joubert and Ryan, 1999; Saetnan and Skarpe, 2006). Habitat and food preferences, as well as activity period and reproductive strategy determine in which region/climate a species can exist (Zeller et al., 2002). Species inhabiting arid regions must be capable of enduring unpredictable and irregular rainfall patterns, extreme temperatures, and a high variability in food resources in order to survive (Krug,

2007). Environmental controls of small mammal reproduction are of primary importance when establishing the timing and extent of breeding (White *et al.*, 1997). The high seasonal fluctuations of food availability, photoperiod, minimum temperature and rainfall are important factors concerning the survival and reproductive success of an individual (Bronson, 1985; Jackson and Bernard, 2001; Krug, 2002; Krug, 2007). Temperature fluctuations may cause extended foraging times during seasons where favoured food items are available, while extended foraging during cold and wet months may be hazardous for small species, as they carry little excess body fat and have a large surface area to volume area ratio (Krug, 2007). Vital elements acquired from food (i.e. vitamins and minerals) are crucial if an individual is to remain healthy and reproduce successfully (Bronson, 1985). A deprivation from such items may have detrimental repercussions on the reproductive system, as seen in laboratory rats (see Glass and Swerdloff, 1980) and other rodent species (Jackson and Bernard, 2001).

To survive during periods with unfavourable environmental conditions, individuals have been recorded to increase and decrease body mass accordingly (Schradin and Pillay, 2005). Due to preferred food being in short supply throughout summer months within the Succulent Karoo, some small mammal species store excess fat during spring and early summer months. Increasing body mass, and storing enough fat to last through summer, is advantageous to individuals as mortality rates are low despite body mass having decreased (Schradin and Pillay, 2005). Within stable environments, the age at which sexual maturity begins is noted as considerably delayed compared to individuals occupying unstable habitats. Individuals are also recorded smaller in size in East Africa (Neal, 1980). Due to the unpredictable nature of unstable habitats, individuals may seek refuge when vegetation provides sufficient cover but when environments become modified individuals may experience a loss of available food because reduced vegetation may reduce food availability. Additionally, cover-dependent individuals, especially diurnal species may become susceptible to increased predation because of the reduced vegetation cover (Cassini and Galanthe, 1992; Flowerdew and Ellwood, 2001).

By looking at the effects of varying grazing intensities on small mammal communities, more insight can be generated into the impacts on issues like

reproduction and sex ratios. Small mammal data were compared within and between communal and commercial rangelands in the Succulent Karoo, separated by fencelines. The hypotheses tested are that:

- i. small mammal female and male abundances differ within and between rangeland types;
- ii. small mammal body size differs between the communal and commercial rangelands;
- iii. small mammal body condition index of the communal rangelands differs from that of the commercial rangelands;
- iv. small mammal reproductively / non-reproductively active proportions, and age class proportions, differ between the communal and commercial rangelands.

4.2 Methodology

Methodology on the trapping of small mammals and vegetation surveying are as described in Chapter 3.

4.3 Data Analysis

i. Body Condition Index

Body condition index (BCI, after Krug, 2002) of adult animals was used to compare sexual maturity of female and male individuals between communal and commercial rangelands. Body condition index integrates total mass and head/body length of an individual; with a small light individual having a lower BCI in comparison to a large heavy individual (Krug, 2002). This gives indications of condition, with the latter being in a 'better' condition. When measuring individuals, it was occasionally difficult to obtain precise head/body length measurements as individuals arched their backs, thus appearing smaller. Taking accurate measurements of the left hind foot (after Barnett, 1992) and plotting them against head/body length allowed a linear regression to be used for species within each site. This produced predicted values for head/body length, enabling a BCI to be determined using the following formula:

BCI =
$$\frac{\text{body mass (g)}}{\text{head/body length (cm)}}$$
 x 10

Females were identified as sexually mature when perforate vaginas were noted, while sexually-mature males were identified when testes were inguinal or scrotal (but see Chapter 3, section 3.3i, for more detail). Due to drastic changes in body mass of pregnant females, only non-pregnant female individuals were measured.

ii. Statistical Analysis

Small mammal body mass, body measurements and body condition data were distributed normally. Independent samples T-tests were applied, using the SPSS statistical package, for comparisons between individuals and groups (i.e. body masses, body measurement and body conditions). A binomial test was used, using the SPSS statistical package, to determine differences in female and male abundances on communal and commercial rangelands, as well as for differences between female and male abundances between the rangelands. A χ^2 test was used to determine differences in reproductively-active and -inactive individual proportions, as well as differences in juvenile/sub-adult and adult individual proportions between the communal and commercial rangelands, using the SPSS statistical package. A p value of p <0.05 indicates significance.

4.4 Results

i. Differences in female and male abundances within rangelands

As sample sizes were small, female and male seasonal abundance data were grouped for each study site. Small mammal species with too little data were not used in analysis; therefore only *Gerbillurus paeba* and *Macroscelides proboscideus* were used. Differences in abundance of female and male *G. paeba* were significant, with both Kuile and Kleinfontein showing greater abundances of males on the communal rangeland (p < 0.05), while differences on the commercial side of the fence line were not significant (p > 0.05). The communal rangeland at Remhoogte had equal numbers of females and males, while the communal rangeland had a significantly greater abundance of males (p < 0.01). Differences between female and male *M. proboscideus* varied marginally, with the only significant difference recorded at the commercial site at Remhoogte.

Table 4.1: Abundances of female and male *Gerbillurus paeba* and *Macroscelides proboscideus* on communal and commercial rangelands. † Significance tested using binomial test: NS = not significant; *p <0.05; ** p <0.01.

		Con	nmunal		Commercial			
Species	Site	Females	Males	p^{\dagger}	Females	Males	p^{\dagger}	
Gerbillurus paeba	Kuile	0	7	*	6	12	NS	
-	Remhoogte	2	2	NS	2	14	**	
	Kleinfontein	0	6	*	4	6	NS	
Macroscelides proboscideus	Kuile	7	6	NS	11	9	NS	
-	Remhoogte	2	4	NS	15	5	*	
	Kleinfontein	2	1	NS	1	2	NS	

ii. Differences in female and male abundances between rangelands

Similar to the section above, individual female and male seasonal abundance data were combined for only G. paeba and M. proboscideus. In both G. paeba and M. proboscideus, males were more abundant on commercial than on communal rangelands (Table 4.1), although these differences were only significant for G. paeba at Remhoogte (p < 0.01).

Female *G. paeba* were significantly more abundant on the commercial side of the fenceline at Kuile (p < 0.05) (Table 4.1). The difference at Remhoogte and Kleinfontein was not significant. Female abundance for *M. proboscideus* was higher on the commercial rangelands of Kuile and Remhoogte, with only the differences at Remhoogte being significant (p < 0.01) (Table 4.1).

iii. Body size differences between rangelands

Only adult female *M. proboscideus* were included in the analysis, as the testes of males remain internal and the reproductive status is thus difficult to distinguish. Adult, non-pregnant *M. proboscideus* females on commercial rangelands were slightly heavier and larger than those on communal rangelands (Table 4.2). However, the differences were not significant.

Table 4.2: Mean body mass and size of communal and commercial adult non-pregnant female *Macroscelides proboscideus*. Mass: body mass; HB: head-body length; T: tail length; HF: hind foot length. N_1 and N_2 denote number of individuals caught on communal and commercial rangelands. †Significance tested using Independent samples T-test: NS = not significant.

		Rangel	and type				
Measurement	Unit	Communal	Commercial	N_1	N_2	<i>T</i> -value	p^{\dagger}
Mass	g	44.50	46.30	8	25	-0.818	NS
HB	mm	94.50	101.50	8	24	-0.834	NS
T	mm	98.00	100.00	8	25	0.379	NS
HF	mm	34.50	35.30	8	25	-0.417	NS

No adult *G. paeba* females were captured within the communal rangelands and only data for males were analysed (Table 4.3). Adult *G. paeba* males on commercial rangelands were slightly heavier than those on communal rangelands. However, there was no significant difference in the mass, or head-body, tail or hind foot length between the two rangeland types (Table 4.3).

Table 4.3: Mean body mass and size of communal and commercial adult male *Gerbillurus* paeba. Mass: body mass; HB: head-body length; T: tail length; HF: hind foot length. N_1 and N_2 denote number of individuals caught on communal and commercial rangelands. †Significance tested using Independent samples T-test: NS = not significant.

		Rangel	and type	-			
Measurement	Unit	Communal	Commercial	N_1	N_2	<i>T</i> -value	p^{\dagger}
Mass	g	27.80	30.00	6	17	-0.978	NS
HB	mm	85.70	80.29	6	17	-0.405	NS
T	mm	97.50	91.24	6	17	0.036	NS
HF	mm	24.00	24.41	6	17	1.076	NS

iv. Body condition index

The body condition of sexually-mature and -immature *M. proboscideus* females did not differ between the two rangeland types (Table 4.4). For *G. paeba*, body condition of sexually-immature females and males did not differ between the two rangeland types, but body condition of sexually-mature males was higher on commercial rangelands than on communal rangelands (Table 4.5).

Table 4.4: Body condition index of sexually-mature and -immature *Macroscelides proboscideus* females within communal and commercial rangelands. Number in brackets indicates number of individuals (caught). †Significance tested using Independent samples T-test: NS = not significant.

	body cond			
reproductive status	communal	commercial	T-test	p^{\dagger}
perforate	4.7 (8)	4.6 (24)	0.41	NS
imperforate	4.1(2)	5.0(2)	-0.72	NS

Table 4.5: Body condition index of sexually-mature and -immature *Gerbillurus paeba* females and males within communal and commercial rangelands. Number in brackets indicates number of individuals (caught). † Significance tested using Independent samples T-test: NS = not significant; * p < 0.05.

	body cond			
reproductive status	communal	commercial	T-test	$oldsymbol{p}^{\dagger}$
perforate	-	3.8 (5)	-	-
imperforate	4.1(1)	3.6 (4)	0.74	NS
scrotal	3.3 (6)	3.8 (17)	-2.35	*
abdominal	3.6 (9)	3.7 (15)	-0.39	NS

v. Proportions of reproductively-active individuals

While proportions of reproductively-active *M. proboscideus* females did not differ significantly between rangelands, those of non-reproductively-active *M. proboscideus* females and non-reproductively-active *G. paeba* females did (Table 4.6). A higher proportion of *G. paeba* males were reproductively-active on the commercial rangelands, while the proportion of non-reproductively-active males was higher on the communal rangelands. Differences were not significant.

Table 4.6: Proportion of reproductively-active and non-reproductively-active *Macroscelides* proboscideus and Gerbillurus paeba on communal and commercial rangelands. Number in brackets indicates number of individuals (caught). † Significance tested using χ^2 : NS = not significant; *p < 0.05; ***p < 0.001. Degrees of freedom = 1.

			% pro	portion		
species	sex	reproductive status	communal	commercial	χ^2	p^{\dagger}
Macroscelides proboscideus	female	perforate	81.82 (9)	92.31 (24)	0.63	NS
•		imperforate	18.18 (2)	7.69 (2)	4.25	*
Gerbillurus paeba	female	perforate	-	55.56 (5)	_	_
•		imperforate	100.00(1)	44.44 (4)	21.4	***
	male	scrotal	40.00 (6)	53.13 (17)	1.85	NS
		abdominal	60.00 (9)	46.88 (15)	1.61	NS

vi. Recruitment within the population

As recruitment in small mammals is generally seasonal, data were not pooled so to keep seasons separate, although sample sizes were undesirably small. Instead, to increase sample sizes, female and male data from communal and commercial rangelands were combined to produce pooled data for both rangeland types. Juvenile and sub-adult data were also combined to increase data points.

On the communal rangeland, proportions of juvenile/sub-adults in the populations of *D. auricularis* and *G. paeba* were highest during spring and autumn respectively. The commercial rangelands show different results, with both *M. proboscideus* juvenile/sub adults being present across two seasons (spring and summer) (Table 4.7). While proportions of juvenile/sub-adult *G. paeba* individuals were not significantly different between the rangelands during autumn, summer showed a highly-significant difference (Table 4.7). Differences in the proportions of adult individuals present however showed that, however, for the majority of the time there were significant differences between the rangelands. *M. proboscideus* showed significant differences in all seasons except summer, while *G. paeba* showed differences in proportions between the rangelands during winter and spring (Table 4.7).

Table 4.7: Proportion of juvenile/sub-adult and adult *Macroscelides proboscideus*, *Gerbillurus paeba* and *Desmodillus auricularis* individuals on communal and commercial rangelands. Number in brackets indicates number of individuals (caught). †Significance tested using χ^2 : NS = not significant; ** p < 0.01; *** p < 0.001. Degrees of freedom = 1.

		Proportion juv	eniles/sub adults			Proport	ion adults		
Species	Season	communal	commercial	χ2	$p\dagger$	communal	commercial	χ2	p^{\dagger}
Macroscelides proboscideus	autumn	-	-	-	-	35.29 (12)	64.71 (22)	8.74	**
	winter	-	-	-	-	28.57 (2)	71.43 (5)	18.88	***
	spring	-	25.00(2)	-	-	12.50(1)	62.50 (5)	36.15	***
	summer	-	13.33 (2)	-	-	46.67 (7)	40.00 (6)	0.51	NS
Gerbillurus paeba	autumn	44.44 (4)	33.33 (3)	1.58	NS	11.11 (1)	11.11 (1)	0.00	NS
•	winter	-	8.33 (1)	-	-	8.33(1)	83.33 (10)	70.85	***
	spring	-	20.00(3)	-	-	20.00(3)	60.00 (9)	20.79	***
	summer	4.76 (1)	23.81 (5)	13.63	***	28.57 (6)	42.86 (9)	2.85	NS
Desmodillus auricularis	autumn	-	-	_	_	100.00(1)	_	_	_
	winter	-	-	-	-	100.00(3)	-	-	-
	spring	100.00(3)	-	-	-	-	-	-	-
	summer	- ` ´	-	-	-	100.00(2)	-	-	-

4.5 Discussion

Variation in activity between females and males will influence the trapability of the individual sexes. Females and males become more active during reproductive months; females will gather food (containing essential vitamins, minerals and amino acids) to supply and sustain her throughout pregnancy (Bronson, 1985), while males will be captured more often, theoretically, as they actively search for females during such periods. Subsequent to females gathering food, they will be less-frequently captured once they become pregnant and/or are nursing new-borns, as they are nesting. Furthermore, there will be periods during winter and, perhaps, summer where both sexes will seldom be captured. Reasons being weather-related, with animals storing food and hiding from the extreme weather conditions during the harsher winter and summer months (Schradin and Pillay, 2005). Additionally, animals take refuge in burrows or under vegetation during the mid-day sun of the summer months, as air temperature and relative humidity differ significantly below ground when compared to those above ground (Bulova, 2002).

To explain the lack of constant pattern regarding sex abundances, one could suggest species behaviour was a responsible factor. Males are frequently under strong competition for mates, so it becomes necessary for them to disperse from their former territory and establish new territories with non-related females. In some species, certain sexes have larger home ranges (see Quimby, 1951: jumping mouse; Beer et al., 1958; Krug, 2002; Schradin and Pillay, 2005: striped mouse). Unlike the Namib, where resources are limited (Krug, 2002), the Succulent Karoo has ample resources to provide occupation to a species and allow access to other individuals. Having an environment with more resources means individuals are more likely to disperse from the maternal territory and form new territories, unlike that of *Rhabdomys pumilio* in the Namib where both sexes remain within the maternal territory. Sex differences of certain species within this study, varied only marginally within rangeland type, with G. paeba showing the main differences between sexes. Gerbillurus paeba males mostly dominated captures at both rangeland types. There was little difference in the number of captured M. proboscideus females and males at any site or rangeland type barring Remhoogte commercial rangeland where females were captured in significantly greater quantities. Individuals with larger home ranges would encounter a greater number of traps than an individual with a smaller home range, and would have a higher probability of entering traps. If this was indeed the case, then the sex ratio would be biased in favour of that sex which has the larger home range (i.e. may explain the greater abundance of male *G. paeba* compared to females). The female dominance of *M. proboscideus* could suggest that this sex may have a larger home range than the males but, as only one case was significant, this is unlikely- otherwise there would have been more widespread occurrence of female dominance. Schradin and Pillay (2006) noted that female *R. pumilio* individuals increase and decrease home range size and shift ranges during seasons. However, it has not been seen in *G. paeba* in this study, but this may be an ordinary occurrence.

Body mass, body size and body condition of *M. proboscideus* females were not affected by rangeland type, and consequently the differing amounts of cover from the growth/life forms present. The same applies to adult *G. paeba* males concerning body mass and body size, while body condition of scrotal *G. paeba* males was different between rangelands, with a greater condition on commercial rangelands. Given that there were no other differences between the rangelands, it is fair to say that if a larger sample were collected then results may have showed a stronger pattern. Body mass and body condition within small mammal populations (Spencer *et al.*, 2005), and body mass within larger mammals (Pepin *et al.*, 1996) can be influenced by juvenile and sub-adult presence and fluctuating population densities. This can be through food reduction and pressures, which affect energy expenditure and food competition (Pepin *et al.*, 1996). Perhaps if the abundance of such age classes within the population would be considered, then one could look deeper into the relationship between body mass/condition and juvenile/sub-adult abundance.

Calculating BCI is a good method of investigating how well a species is coping within a habitat and, by observing this across seasons, it is possible to see how condition changes. Here, sample sizes were too small to perform such an analysis, but by increasing sample sizes, the impacts of climatic variables and length of daylight could be analysed. With temperature fluctuations, foraging times become extended during seasons where preferred food items are available. However, having to forage during cold and wet months may be hazardous for smaller species (Krug, 2007), and a drop in temperature can have detrimental repercussions on survival (Bronson, 1985). Diet

would be another factor to explore, as during certain seasons favoured foods are abundant, resulting in increased condition.

The highest proportions of juveniles/sub-adults in this study occurred during spring and summer, resulting in perhaps non-marked individuals being captured even towards the end of the study in summer. Concerning the communal rangelands both D. auricularis and G. paeba individuals had peaks in juvenile/sub-adult abundance, with high proportions clustered around certain times of the year. Juvenile/sub-adult individuals were found more often in the commercial sites compared to the communal sites. This was especially true for G. paeba and M. proboscideus. Macroscelides proboscideus juveniles/sub-adults were present during two seasons, while G. paeba juveniles/sub-adults were present across all seasons compared to only two individuals on communal rangelands. Regarding M. proboscideus juveniles/sub-adults on commercial rangelands, this abundance would imply that individuals were born at the start of spring, continuing throughout spring until the beginning of summer. This pattern is similar to that noted for this species by Skinner and Chimimba (2005), where individuals breed during spring and young are born from spring to summer. Both Gerbillinae species (D. auricularis and G. paeba) captured are capable of breeding throughout the year (Skinner and Chimimba, 2005), so it was interesting to see that G. paeba juvenile/sub-adults were present at the commercial sites during each of the four sampling seasons.

White *et al.* (1997) explained that environmental controls of small mammal reproduction are of primary importance when establishing the timing and extent of breeding. The age at which individuals mature when in stable environments is typically delayed compared to the maturity age of individuals inhabiting changing environments (Krug, 2002). By looking at the proportion of juveniles/sub-adults within the population, one can see that the presence was highest for *G. paeba* during the initial sampling session for the communal rangelands and the last sampling session for both rangelands, in comparison to the other three seasons. It may be the case that within commercial rangelands (classed as the more stable of the rangelands) the age at which individuals become sexually mature is delayed. This has also been found in *Arvicanthis niloticus* (Neal, 1980), and Krug (2002) showed *R. pumilio* individuals to reach maturity at a higher body mass and a later age in the Namib

Desert, when compared to individuals inhabiting other regions (David and Jarvis, 1985).

Exploring the proportions of reproductively-active and non-reproductively-active individuals, one would imagine that indications would be given regarding what may influence reproduction. In total, female G. paeba individuals were found in greater proportions on commercial rangelands, while male G. paeba and female M. proboscideus individuals showed no differences between rangelands. Communal rangelands tended to show greater proportions of non-reproductively-active individuals (female M. proboscideus, and female G. paeba). Given that the proportions of reproductively-active females and males were greater on commercial rangelands (though not significant), larger sample sizes were might then have demonstrated a significant difference on communal rangelands, also. The implication might then be that the reproductively-active individuals were present in greater abundances within commercial rangelands due to the offer of more protection in the form of vegetation cover as well as the offer of more nutritious food items than in communal rangeland. One would imagine that reproductively-active individuals, compared to non-reproductively active individuals, would require an environment which could supply more nutritious food which would result in a better body condition. In support of this suggestion, higher BCI was recorded for reproductivelyactive G. paeba individuals on commercial rangelands. Despite the significant differences, results may suggest that because non-reproductively-active individuals were in significantly greater abundances on the communal rangelands, and reproductively-active individuals were in greater abundances within commercial rangelands, the characteristics of the individual rangelands may better suit different age classes. Thus migration between rangelands occurs at different age classes.

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Chapter 5

The effects of the communal and commercial rangelands on occupied, unoccupied and collapsed burrow proportions

5.1 Introduction

Livestock grazing is known to have major effects on the surrounding vegetation (Steinschen *et al.*, 1996; Hoffman and Ashwell, 2001; Simons, 2005; Kraaij and Milton, 2006) as well as on many animal species (Rosenstock, 1996; Joubert and Ryan, 1999; Seymour and Dean, 1999; Mathis *et al.*, 2006). Vegetation composition and structure are negatively affected by grazing; plant cover and diversity are reduced, leading to compositional and structural shifts (Milton *et al.*, 1994; Anderson and Hoffman, 2007). This, in turn, contributes to changes in ecosystem structure and function. However, substantial variation in the responses of plant and animal communities regarding grazing has been well-documented (van Aarde *et al.*, 1996; Todd and Hoffman, 1999; 2000; Beukes and Ellis, 2003).

The effects of grazing on small mammals are rather variable, and might well be species dependent. Gerbillinae species (i.e. *Gerbillurus paeba*) are typically found in greater numbers within areas with a light grass, scrub or woodland cover (Perrin *et al.*, 1999; Skinner and Chimimba, 2005), while *Rhabdomys pumilio* is generally associated with densely-covered areas, possibly owing to its diurnal nature (De Graaff, 1981). Furthermore, grazing effects depend on which grazers are present, as the grazing techniques of cattle, game and sheep/goats differ significantly from one another. On the one hand, although cattle will have a greater trampling effect, their grazing might benefit small mammal species, retaining some vegetation cover and allowing them to make runways in the vegetation. Wild ungulates, on the other hand, tend to graze more selectively than cattle, but in a similar way when compared to sheep and goats. However, they leave a reduced, and unfavourable, vegetation cover available to small mammal species (Muck and Zeller, 2006).

Many small mammal species inhabiting arid regions have adapted to the type of environment (Perrin *et al.*, 1999; Skinner and Chimimba, 2005). There are morphological and physiological adaptations present (i.e. via thermoregulatory control and the ability to concentrate urine) within such species to enable occupation within arid environments where food and water may be limited. Many small mammal species use burrows to provide shelter from predators, and allow the animal to avoid extreme temperatures. Air temperature and relative humidity differ significantly below ground when compared to those above ground, e.g. relative humidity was

greater inside desert tortoise (*Gopherus agassizii*) burrows than above ground in the late morning (Bulova, 2002). In addition, Soholt (1974) found metabolic activities of Merriam's kangaroo rats (*Dipodomys merriami*) to alter respiratory gas concentration within burrows, increasing burrow temperature to above that of the surrounding soil temperature. The small mammals identified as burrowing in this study include *Desmodillus auricularis*, *G. paeba, Macroscelides proboscideus* and *R. pumilio*. Despite these species residing in burrows, not all will necessarily create their own burrows, but instead will simply take over burrows vacated by other species, as in the case of *M. proboscideus* and *R. pumilio*.

Many burrow-dwelling small species live in burrows with more than one entrance. Concerning burrowing species captured during this study, *M. proboscideus* lives in burrows that have an entrance and an emergency/escape tunnel (De Graaff, 1981), whilst *G. paeba* are often found living in simple burrows, that usually have only a single entrance leading to a blind-ending tube. In some cases, *G. paeba* burrows have numerous entrances, with the additional entrances being blocked by loose substrate. *Rhabdomys pumilio*, like *G. paeba*, also inhabits burrows that rarely have more than one entrance. Burrows are usually in close proximity to one another, and are generally seen as simple formations with entrances characteristically concealed when in occupation. Findings by Pettifer and Nel (1977), looking at burrows dug by *D. auricularis*, showed individual burrows to have additional entrances which not only have no signs of excavated matter or food remnants, but also have a slope almost completely vertical.

Burrow density has been shown to fluctuate between seasons (Muck and Zeller, 2006), and small mammal abundances, grazing intensity and even climatic variables may act as determining factors in such fluctuations. The number of occupied and collapsed burrows can be seen as a measure, and an indicator, of trampling effects by grazing herbivores (Heske and Campbell, 1991; Hayward *et al.*, 1997; Hoffmann and Zeller, 2005). Muck and Zeller (2002) demonstrated that both burrow abundance and percentage of occupied burrows could be linked to small mammal abundances. Owens and Borchert (1975) showed that the quantity of occupied burrows can predict approximate population densities of burrowing ground squirrels, however, results are often variable (see also van Horne *et al.*, 1997). Grazing intensity, as well as vegetation changes, may potentially influence the occurrence of different burrow

states (i.e. occupied or collapsed), with higher grazing intensities expected to produce higher numbers of collapsed burrows. A reduction in rodent numbers was coupled with a lower percentage of occupied burrows, and when small mammal abundance was at its lowest, burrow count was lower due to unoccupied burrows being trampled by grazing animals which resulted in a higher proportion of occupied burrows. Under favourable conditions, one would expect burrowing small mammal abundances to be considerably higher than in areas which have non-favourable conditions.

Burrowing small mammal species and burrow densities within the Paulshoek area of Namaqualand have not been studied before. Abundances of occupied, unoccupied and collapsed burrows were compared between areas under heavy and light grazing intensities, separated by fence-lines, within Kuile, Remhoogte and Kleinfontein over the period of one-year. Relationships between burrow state and burrowing small mammal abundances were analysed. The hypotheses tested are that:

- occupied, unoccupied and collapsed burrow abundance, as a measure of ground perturbation by trampling, differs between the communal and commercial rangelands;
- ii. proportions of occupied, unoccupied and collapsed burrows fluctuate from season to season on both rangelands;
- iii. small mammal abundances show relationships with quantities of occupied, unoccupied and collapsed burrows.

5.2 Methodology

Methodology on the trapping of small mammals and vegetation surveying are as described in Chapter 3.

i. Burrow counts

The number of burrows within the communal and commercial rangelands of Kuile, Remhoogte and Kleinfontein were estimated during autumn, winter and spring 2006, and summer 2007. Within each rangeland of each of the three sites, nine fixed transects, spaced apart by 15m, each measuring 120m in length were walked, and numbers of occupied, unoccupied and collapsed burrows were recorded up to a distance of 1 metre on either side of the transect. Burrows were defined as occupied if

a clean and accessible entrance was present; unoccupied if dirt, vegetation litter and/or spider webs obstructed the entrance; or collapsed if no obvious opening was observed and what previously may have been an entrance was filled with dirt or debris. Diggings larger than 10cm in diameter were considered scratches (Muck and Zeller, 2006) from an animal other than a small mammal occupant and were not recorded.

Ascaray (1986) stated that all *G. paeba* burrow entrances that were less than one metre apart belonged to a single burrow, as past excavations have showed *G. paeba* burrow systems to rarely exceed one metre in length. With this in mind, as well the point made by Nel (1967) regarding the fact that *D. auricularis* burrows have the capability of spanning a distance of 7m² and that individuals will conceal burrow entrances when occupied, all burrow entrances counted were regarded as belonging to a single *D. auricularis* individual. This reasoning was because numerous burrowing species were captured, with such species being a mixture of solitary and non-solitary living individuals, and either dwelling in burrows with more than one entrance or only one entrance. Therefore, it was difficult to determine which burrows belonged to which small mammal species. However, it can be argued that the distance between measuring points was longer that the diameter of the burrow systems of these two species, so it was therefore unlikely that the same burrow was encountered twice.

5.3 Data Analysis

i. Statistical Analysis

Proportional data were arcsine transformed prior to analysis. Independent samples T-tests were applied for comparisons between individuals or groups, using the SPSS statistical package, while for comparisons within groups, a repeated measures ANOVA was used. Post hoc tests were run on any significant results from the repeated measures ANOVA to determine where the differences lay. Rather than using proportions of occupied, unoccupied and collapsed burrows, actual numbers of each burrow type counted were used and correlated with burrowing small mammal abundances (from communal and commercial rangelands separately). Small mammal data were square root transformed and burrow data were log transformed prior to analysis. By using Pearson's correlations, in SPSS, indications as to whether burrow

state (i.e. occupied, unoccupied or collapsed) is related to the abundance of burrowing small mammals may be revealed. A p value of p < 0.05 indicates significance.

5.4 Results

i. Burrowing small mammals

In total, four burrowing small mammal species were captured over a 1-year sample period; D. auricularis; G. paeba; M. proboscideus and R. pumilio. The most abundant small mammal species captured within the communal and commercial rangelands of Kuile and Remhoogte was M. proboscideus (Table 3.4). Gerbillurus paeba was the second most abundant species within Kuile commercial rangeland and Remhoogte communal and commercial, while its abundance was equal with that of Elephantulus edwardii (non-burrowing species) on the communal rangeland of Kuile. Desmodillus auricularis, where present, was in greater numbers on communal rangelands, with no individuals captured on commercial rangelands, while R. pumilio was captured during autumn, winter and summer only at Remhoogte, though in small numbers. Considering all burrowing small mammal species will contribute to the quantity of burrows, counts of all burrowing individuals were pooled for each rangeland type within Kuile, Remhoogte and Kleinfontein, so that a total value of burrowing abundance could be used (Table 5.1). Only Remhoogte showed significant differences in the abundances of burrowing small mammals between communal and commercial rangelands

Table 5.1: Pooled number of burrowing individuals from *Desmodillus auricularis*, *Gerbillurus paeba*, *Macroscelides proboscideus* and *Rhabdomys pumilio*, from the communal and commercial rangelands of Kuile, Remhoogte and Kleinfontein during the sampling year. † Significance tested in homogeneity using G-test: NS = not significant; $^*p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$. Degrees of freedom = 1 with Yates' correction for continuity.

		Kuile			Remhoogte				Kleinfontein				
	communal	commercial	χ2	p^{\dagger}	communal	commercial	χ2	p^{\dagger}	communal	commercial	χ2	p^{\dagger}	Total
Autumn	9	13	0.72	NS	4	12	4.06	*	5	3	0.48	NS	46
Winter	5	9	1.11	NS	1	11	9.36	**	1	1	0.00	NS	29
Spring	5	9	1.11	NS	0	8	-	-	2	4	0.63	NS	28
Summer	7	7	0.00	NS	6	13	2.57	NS	4	6	0.38	NS	43
Total	27	38	1.86	NS	11	44	21.01	***	12	14	0.15	NS	146

ii. Differences in occupied, unoccupied and collapsed burrow proportions between communal and commercial rangelands

There was no trend observed in the proportions of occupied burrows being greater on one rangeland type. Only at Kleinfontein during winter were there significantly greater proportions of occupied burrows on the commercial rangeland (Table 5.2). Proportions of both unoccupied and collapsed burrows were not significantly different between rangeland types, the exception being again Kleinfontein, where a significantly lower proportion of unoccupied burrows was observed on the communal lands during summer, and the proportion of collapsed burrows was significantly higher on the communal rangelands during winter.

Table 5.2: Proportions of occupied, unoccupied and collapsed burrows on the communal and commercial rangelands of the three study sites across the four sampling sessions. † Significance tested between proportions using Independent Samples T-tests: NS = not significant; **p < 0.01. Number in brackets indicates number of burrows

			Occupied				Unoccupied				Collapsed		
Site	Season	communal	commercial	<i>T</i> -value	р†	communal	commercial	<i>T</i> -value	p†	communal	commercial	T-value	р†
Kuile	autumn	53.57 (15)	33.33 (4)	0.26	NS	7.14(2)	8.33 (1)	-0.19	NS	39.29 (11)	58.33 (7)	-0.38	NS
	winter	34.31 (35)	27.91 (12)	1.15	NS	8.82 (9)	6.98 (3)	-1.43	NS	56.86 (58)	65.12 (28)	-0.28	NS
	spring	43.40 (23)	26.67 (4)	0.43	NS	22.64 (12)	26.67 (4)	-1.44	NS	33.96 (18)	46.67 (7)	-1.45	NS
	summer	49.02 (25)	46.67 (7)	0.46	NS	15.69 (8)	13.33 (2)	0.26	NS	35.29 (18)	40.00 (6)	-1.73	NS
Remhoogte	autumn	30.56 (22)	41.67 (25)	-1.78	NS	26.39 (19)	20.00 (12)	0.81	NS	43.06 (31)	38.88 (23)	-1.21	NS
	winter	16.44 (12)	21.15 (11)	-1.48	NS	4.11 (3)	5.77 (3)	-0.54	NS	79.45 (58)	73.08 (38)	0.01	NS
	spring	19.23 (5)	26.92 (7)	-0.03	NS	26.92 (7)	23.08 (6)	1.36	NS	53.85 (14)	50.00 (13)	0.64	NS
	summer	66.67 (8)	64.71 (11)	-1.90	NS	0.00(0)	5.88 (1)	-	-	33.33 (4)	29.41 (5)	-1.00	NS
Kleinfontein	autumn	38.02 (46)	29.63 (40)	0.86	NS	18.18 (22)	22.96 (31)	0.20	NS	43.80 (53)	47.41 (64)	-0.43	NS
	winter	20.54 (53)	48.65 (18)	-3.93	**	12.02 (31)	10.81 (4)	-1.36	NS	67.44 (174)	40.54 (15)	1.51	**
	spring	40.74 (88)	51.61 (16)	-1.63	NS	19.91 (43)	19.35 (6)	-1.14	NS	39.35 (85)	29.03 (9)	-1.68	NS
	summer	30.77 (40)	33.33 (13)	-0.93	NS	11.54 (15)	41.03 (16)	-3.57	**	57.69 (75)	25.64 (10)	0.53	NS

iii. Seasonal differences in occupied, unoccupied and collapsed burrow proportions

Very few seasonal differences in burrow state could be found, with the exception of the proportions of unoccupied burrows on Remhoogte communal rangeland. The proportion of collapsed burrows varied significantly on both Remhoogte and Kleinfontein communal rangelands (Table 5.3), but no seasonal trends were detected.

Table 5.3: Proportions of occupied, unoccupied and collapsed burrows on the communal and commercial rangelands of the three study sites over the period of 1-year. † Significance tested between autumn, winter, spring and summer using repeated measures ANOVA: NS = not significant; * p < 0.05; *** p < 0.001. The sphericity assumption was met in all cases.

				Sea	son			
Burrow state	Site	Rangeland	autumn	winter	spring	summer	F-value	p†
Occupied	Kuile	communal	53.57	34.31	43.40	49.02	0.02	NS
		commercial	33.33	27.91	26.67	46.67	0.32	NS
	Remhoogte	communal	30.56	16.44	19.23	66.67	1.34	NS
		commercial	41.67	21.15	26.92	64.71	2.31	NS
	Kleinfontein	communal	38.02	20.54	40.74	30.77	2.77	NS
		commercial	29.63	48.65	51.61	33.33	1.10	NS
Unoccupied	Kuile	communal	7.14	8.82	22.64	15.69	1.15	NS
		commercial	8.33	6.98	26.67	13.33	1.61	NS
	Remhoogte	communal	26.39	4.11	26.92	0.00	12.27	***
		commercial	20.00	5.77	23.08	5.88	1.47	NS
	Kleinfontein	communal	18.18	12.02	19.91	11.54	2.43	NS
		commercial	22.96	10.81	19.35	41.03	2.24	NS
Collapsed	Kuile	communal	39.29	56.86	33.96	35.29	1.54	NS
		commercial	58.33	65.12	46.67	40.00	2.84	NS
	Remhoogte	communal	43.06	79.45	53.85	33.33	15.36	***
		commercial	38.88	73.08	50.00	29.41	2.94	NS
	Kleinfontein	communal	43.80	67.44	39.35	57.69	4.45	*
		commercial	47.41	40.54	29.03	25.64	2.78	NS

Carrying out post-hoc tests on the significant results from Table 5.3 showed differences between autumn and winter (p < 0.001), autumn and spring (p < 0.05) and autumn and summer (p < 0.001) at Remhoogte communal rangeland for unoccupied burrows. Regarding collapsed burrows, the only difference which was not significant was between winter and spring (p > 0.05). Lastly, Kleinfontein communal rangeland showed differences between winter and spring (p < 0.05), and winter and summer (p < 0.05).

iv. Burrowing small mammal abundance and the relationship to occupied, unoccupied and collapsed burrows

No relationship between small mammal abundance and number of occupied burrows or number of un-occupied burrows could be found. However, small mammal abundance negatively correlated with the number of collapsed burrows within the communal rangelands (Table 5.4).

Table 5.4: Correlations between burrowing small mammal abundances, on communal and commercial rangelands, and burrow state (occupied, unoccupied and collapsed) (n=12). Significance tested using Pearson's correlations: *p < 0.05.

		Burrow state				
	Rangeland	Occupied	Unoccupied	Collapsed		
Burrowing small mammals	communal	-0.276	-0.292	-0.691 *		
	commercial	-0.483	-0.391	-0.226		

5.5 Discussion

Numbers of occupied and collapsed burrows were used as measures of trampling effect by livestock. There was no significant difference between the proportions of occupied, unoccupied or collapsed burrows between the communal and commercial rangelands (Hypothesis 1 – rejected).

In hindsight, one would expect the communal rangelands to have had greater proportions of collapsed burrows because of the greater quantities of livestock and thus greater trampling effect (see Muck and Zeller, 2006). However, as these communal rangelands are typically stocked with sheep and goats, which have a smaller trampling impact than cattle, this could explain why there were no burrow state differences between rangelands. It is possible that sheep and goats have a lower bite: step ratio (see Krueger, 1986) than that of larger grazers like cattle. This would result in larger grazers having a greater trampling effect, supporting the results seen here. Although mostly sheep and goats were grazed on the communal rangelands, there were occasionally donkeys observed wandering around the vicinity of the small mammal trapping grids at Kuile. The commercial rangelands contain sheep, goats and cattle, however for the entirety of this study, no such animals were evident on any of the commercial rangelands. Had cattle been present, they would have undoubtedly

had a greater trampling effect, resulting in the commercial rangelands containing a greater proportion of collapsed burrows. Occupied, unoccupied and collapsed burrow proportions did not fluctuate from season to season, despite original expectations (Hypothesis 2 – rejected). Despite only a handful of cases showing a difference in seasonal fluctuations, the fact that no constant pattern emerged in this study made this result rather negligible and irrelevant to the remaining results.

It was expected that abundances of burrowing small mammals would positively correlate to the number of occupied burrows. Furthermore, it would be expected for the number of unoccupied burrows to be negatively correlated to increasing burrowing small mammal abundance given that, with more small mammals present, the number of occupied burrows would increase and thus the number of unoccupied would decrease. However, there was no correlation between numbers of occupied burrows and abundance of burrowing small mammals on either rangeland; similar to conclusions of van Horne et al. (1997) for Townsend's ground squirrels (Spermophilus townsendii) and Powell et al. (1994) for black tailed prairie dog's (Cynomys ludovicianus). Furthermore, no correlations between burrowing small mammal abundances and unoccupied burrows were identified on any of the 3 rangelands (Hypothesis 3 – rejected). Only the communal rangelands showed a correlation (negative) with burrowing small mammal abundance and collapsed burrows. One reason may be that there is no relationship between the numbers of occupied burrows and burrowing small mammals because the average or optimum number of small mammal burrow occupants is unknown. Despite burrow classifications (see method section; 5.2.i) being consistent throughout all sessions, entrances to small mammal burrows cannot be distinguished reliably from those occupied by other faunal species, as van Horne et al. (1997) suggested, without further investigation and/or excavation (see Ascaray, 1986).

There were a number of flaws throughout this study. Concerning burrowing small mammal abundances, the limited trapping area (1.6ha) did not aid in obtaining adequate sample sizes. As mentioned previously, it can undoubtedly be argued that it is highly probable that not all the burrowing small mammal species present were sampled. In addition to the small mammal species being trapped, one can also assume there were more burrowing species present than those captured. Whether this was

because species were trap shy or just present in small numbers is unknown. From a previous study (see Joubert and Ryan, 1999) which took place within Paulshoek, there were two additional species captured, Otomys unisulcatus and Suncus varilla, with the former being a burrowing species. Additional burrowing species, which may have been present in the study area, include Parotomys brantsii and Parotomys littledalei. Another problem of methodology was that, due to the limited sampling time, the study was not able to investigate burrows any further than taking simple counts of occupied, unoccupied and collapsed burrows. If time had not been an issue, then as Ascaray (1986) did with G. paeba burrows, selected burrows could have been excavated to find out the general characteristics of specific species. This may have allowed an average number of burrow entrances to be determined for each species in question, thus making the burrow sampling more accurate and realistic when relating burrow numbers to burrowing small mammal abundances. Pseudoreplication was another problem when looking at the differences between proportions of burrows across the year. It is extremely likely that the same burrows were counted in consecutive seasons given that the transects was fixed. This then rendered the seasonal data sets non-independent replications.

The number of occupied burrows may have given an overestimation of burrowing small mammals, as there may have been other animal species creating burrows or occupying old small mammal burrows. This would leave the burrows appearing occupied rather than unoccupied, and this may have been one of the reasons why no correlation was identified. Occupied burrows may have also been misidentified and subsequently miscounted, as small mammal individuals may either use additional entrances when there are fewer than normal individuals present; other faunal species may use and occupy burrows when small mammals densities are low; or burrow entrances may be preserved even whilst unoccupied. As burrows may persist without being 'occupied' by an individual, small mammal or otherwise, this could potentially lead to an overestimation of burrowing small mammal abundances. The preservation of burrows may be related to certain habitat characteristics like the vegetation present which is capable of influencing soil stability below ground, because entrances within sandier soils are more likely to collapse or become concealed by sand blown by the wind (van Horne et al., 1997). Furthermore, weather may also affect the preservation of burrows as dryness, heat and wind may decrease preservation.

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Chapter 6

Conclusions

This study sought to investigate the effects of communal and commercial land management practices on small mammal communities within Paulshoek, South Africa. The data presented provides support for other studies, which show vegetation and certain faunal assemblages to be affected by a heavy grazing intensity (Todd and Hoffman, 1999; Beukes and Ellis, 2003; Anderson and Hoffman, 2007). The support is in keeping with expectations from much of the literature (Joubert and Ryan, 1999; Eccard et al., 2000; Torre et al., 2007). Concerning the Succulent Karoo, one could argue that Chapter 1 ultimately shows that communal and commercial rangelands together provide a habitat permitting occupancy of a wide range of small mammal species, all of which have different requirements. In turn, this allows species to thrive as suitable attributes are provided within the rangelands, and permits small mammal species richness as well as diversity within the area to flourish. As many have shown (e.g. Hoffman et al., 1999; Hoffman and Rohde, 2007; Lebert and Rohde, 2007), communal rangelands are severely degraded. Failing to conserve the vegetation present could have detrimental repercussions on the animal assemblages inhabiting such regions. Without communal rangelands, species exclusive to the rangelands such as *Elephantulus edwardii* and *Desmodillus auricularis* may disappear. If the commercial rangelands were to become grazed continuously then species with distinct preferences to the higher vegetation cover present, e.g. Gerbillurus paeba, Macroscelides proboscideus and Rhabdomys pumilio may become locally extinct.

Despite original hypotheses, of how rangeland type affects body mass, size and body condition of small mammal individuals, no differences were determined. This suggests that neither rangeland type supported heavier or larger individuals, ultimately resulting in neither rangeland supporting individuals in better condition. Considering *G. paeba* and *M. proboscideus* showed slight preferences for commercial rangelands, it would have been expected for individuals within communal rangelands to be smaller and lighter but this was not the case. Sex differences of certain species varied only marginally within rangeland type, with *G. paeba* showing the main differences between sexes. There was very little difference regarding the other species analysed. A larger data set might have revealed more pronounced differences between females and males within the rangelands, but only the *G. paeba* data stands to any significance in this study.

This study also investigated the effects of rangeland type on the proportions and numbers of occupied, unoccupied and collapsed small mammal burrows. Greater numbers of collapsed burrows were expected for communal rangelands, due to the increased trampling effect. Proportions of all burrows however, were not affected by rangeland type. Nevertheless, perhaps the presence of only sheep and goats does not influence the quantity of burrows as much as the effects of grazing cattle (Muck and Zeller, 2006) on the proportion and numbers of burrows. It would additionally be expected for some degree of interaction between numbers of occupied, unoccupied and collapsed burrows and burrowing small mammals. This study showed little interaction, supporting similar conclusions obtained for Townsend's ground squirrels (Spermophilus townsendii) (van Horne et al., 1997) and black tailed prairie dog's (Cynomys ludovicianus) (Powell et al., 1994). It could be argued that entrances of small mammals' burrows cannot readily be distinguished from those occupied by other animal species, as van Horne et al. (1997) suggested, without there being any further investigation and/or excavation of the burrows. The continual occurrence of occupied burrow entrances may be a result of (i) individuals using additional entrances when there are fewer than normal individuals present; (ii) use and occupancy of burrows by other faunal species; or (iii) burrow entrances being preserved even when vacant.

The outcomes of this study raise several issues that should be addressed in future research:

- i. The response of small mammal species to habitat type is a complex one. To fully understand the effects of land use on such small mammal species, continual follow-ups are deemed necessary to ensure constant surveillance on areas under such harsh regimes and their impacts on the surrounding environment, to prevent in the extreme case, a localised extinction occurring;
- ii. Assessments within this region are still required so to elucidate the influence of grazing on small mammals, and other faunal species, under heavily-grazed areas in comparison to areas completely excluded from large herbivores and/or livestock (Smit *et al.*, 2001; Valone and Sauter, 2005). It is believed that it is important to identify on only whether vegetation can become re-established (Milton, 1992; 1994 and Simons and Allsopp, 2007), but also whether certain

faunal species can re-establish thriving populations (see Schwartz and Whitson, 1987; van Aarde *et al.*, 1996 and Ferreira and van Aarde, 1996), as small mammal species are known to play important roles within the niche they occupy.

iii. The relationship between occupied, unoccupied and collapsed burrows and small mammal abundances is one that needs to be further investigated. As this study indicates, grazers affect not only the quantities of particular burrows but also the abundances of certain small mammal species. Through burrow excavations, one would be able to detect whether vacant burrows are capable of persisting, while it would also be interesting to discover whether there are other faunal species occupying such abandoned small mammal burrows (Kleeberger and Werner, 1983; Regosin *et al.*, 2003).

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Appendix 1

Appendix 1; Table 1.1: Percentage vegetation, rock and bare ground cover on the communal and commercial rangelands of the 3 study sites from autumn, winter, spring and summer. † Significance tested using Independent sample T-tests: NS = not significant; $^{*}p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

		Kuile			Remhoogte				Kleinfontein				
Season		communal	commercial	T-value	p†	communal	commercial	<i>T</i> -value	p†	communal	commercial	T-value	p†
Autumn	Perennial shrub	18.40	13.20	1.45	NS	10.80	24.40	-3.66	**	32.00	16.40	8.74	***
	Perennial succulent	0.00	16.80	-	-	11.00	24.80	-2.68	*	4.00	22.40	-2.39	*
	Perennial grass	0.00	0.00	-	-	0.00	0.00	-	-	0.00	0.00	-	-
	Annual forb	0.00	0.00	-	-	0.00	0.00	-	-	0.00	0.00	-	-
	Annual succulent	0.00	0.00	-	-	0.00	0.00	-	-	0.00	0.00	-	-
	Rock	22.40	13.20	1.88	NS	12.20	8.80	0.87	NS	20.00	16.00	1.02	NS
	Bare ground	59.20	56.80	0.63	NS	66.00	42.00	4.49	***	44.00	45.20	-0.30	NS
Winter	Perennial shrub	40.40	32.80	2.21	*	22.00	26.80	-0.97	NS	41.20	28.80	3.94	**
	Perennial succulent	4.80	18.80	-5.14	***	15.60	21.60	-1.46	NS	2.00	14.00	-1.59	NS
	Perennial grass	0.00	0.00	-	-	0.00	0.00	-	-	0.00	0.00	-	-
	Annual forb	2.00	0.00	-	-	0.00	0.00	-	-	5.00	0.00	-	-
	Annual succulent	1.00	0.00	-	-	0.00	0.00	-	-	5.00	6.80	-0.62	NS
	Rock	24.00	10.80	3.16	**	19.20	11.20	1.97	NS	9.20	18.00	-2.99	**
	Bare ground	27.80	37.60	-1.11	NS	43.20	40.40	0.73	NS	37.60	32.40	1.23	NS
Spring	Perennial shrub	50.40	37.60	0.77	***	28.80	24.00	0.90	NS	50.00	38.00	2.63	*
	Perennial succulent	3.67	10.80	-4.10	***	23.60	27.20	-0.57	NS	4.00	33.60	-3.02	*
	Perennial grass	0.00	0.00	-	-	0.00	0.00	-	-	7.33	4.00	1.49	NS
	Annual forb	5.00	0.00	-	-	10.00	0.00	-	-	5.50	4.00	0.48	NS
	Annual succulent	1.73	0.00	-	-	5.33	16.00	-4.00	NS	6.00	0.00	-	-
	Rock	12.00	11.60	0.12	NS	18.00	11.20	1.65	NS	15.60	9.60	1.85	NS
	Bare ground	27.20	40.00	-3.95	***	24.00	36.00	2.66	*	23.60	17.60	1.43	NS
Summer	Perennial shrub	44.40	40.00	1.52	NS	26.80	24.00	0.59	NS	42.00	28.40	2.77	*
	Perennial succulent	6.00	12.80	-3.22	**	18.40	25.60	-1.40	NS	-	21.60	-	-
	Perennial grass	5.00	4.00	0.45	NS	0.00	0.00	-	-	5.60	4.00	1.63	NS
	Annual forb	0.00	0.00	-	-	0.00	0.00	-	-	0.00	0.00	-	-
	Annual succulent	0.00	0.00	-	-	0.00	0.00	-	-	0.00	0.00	-	-
	Rock	9.60	14.80	-0.71	NS	18.40	14.80	0.86	NS	14.00	17.20	-0.59	NS
	Bare ground	35.00	32.00	1.12	NS	36.40	35.60	0.16	NS	40.40	28.80	2.45	*

Appendix 2

Appendix 2; Table 1.1: Number of individuals caught per season per species.

-	Species	Kuile		Rem	hoogte	Kleinfontein		
Season		communal	commercial	communal	commercial	communal	commercial	
Autumn	Desmodillus auricularis	0	0	0	0	1	0	
	Elephantulus edwardii	6	0	0	0	0	0	
	Macroscelides proboscideus	9	13	3	9	0	0	
	Micaelamys namaquensis	0	0	0	0	0	0	
	Mus minutoides	0	0	0	0	0	0	
	Gerbillurus paeba	0	0	1	1	4	3	
	Rhabdomys pumilio	0	0	0	2	0	0	
Winter	Desmodillus auricularis	2	0	0	0	1	0	
	Elephantulus edwardii	0	0	0	0	0	0	
	Macroscelides proboscideus	2	1	0	5	0	0	
	Micaelamys namaquensis	0	0	0	0	0	0	
	Mus minutoides	1	0	0	0	0	0	
	Gerbillurus paeba	1	8	1	4	0	1	
	Rhabdomys pumilio	0	0	0	2	0	0	
Spring	Desmodillus auricularis	3	0	0	0	0	0	
	Elephantulus edwardii	1	0	0	0	0	0	
	Macroscelides proboscideus	0	4	0	1	1	2	
	Micaelamys namaquensis	0	0	0	0	0	0	
	Mus minutoides	0	0	0	0	0	0	
	Gerbillurus paeba	2	5	0	7	1	2	
	Rhabdomys pumilio	0	0	0	0	0	0	
Summer	Desmodillus auricularis	1	0	0	0	1	0	
	Elephantulus edwardii	0	0	0	0	0	0	
	Macroscelides proboscideus	2	2	3	6	2	1	
	Micaelamys namaquensis	0	2	0	0	0	1	
	Mus minutoides	0	0	0	0	0	0	
	Gerbillurus paeba	4	5	2	7	1	5	
	Rhabdomys pumilio	0	0	1	0	0	0	