THE ECOLOGY AND PARASITOLOGY OF SMALL MAMMALS FROM SELECTED SITES IN SWAZILAND

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THE ECOLOGY AND PARASITOLOGY OF SMALL MAMMALS FROM SELECTED SITES IN SWAZILAND

by

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DEDICATION

This thesis is dedicated to my mother Ethie Mantindane and to the memory of my father Caetano April.

PREFACE

The field work described in this thesis was conducted in Mlawula Nature Reserve, eKundizeni Farm, University of Swaziland Luyengo Campus and Vuvulane Irrigated Farms in Swaziland. Laboratory work was carried out at the University of Swaziland, Kwaluseni Campus and at the University of KwaZulu-Natal, Pietermaritzburg Campus from 2002 to 2007, under the supervision of Professor M. R. Perrin.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any university. Where use has been made of the work of others it is duly acknowledged in the text.

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T.A.M. Mahlaba

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Professor M. R. Perrin

DECLARATION

I hereby declare that the work presented in this thesis is my own, unaided work and has never before been submitted for any degree at this or any other university.

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T.A.M. MAHLABA

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PROFESSOR M. R. PERRIN

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ABSTRACT

The study was initially a long term study of the ecology of small mammals at Mlawula Nature Reserve in the eastern part of Swaziland. Due to the drought and dwindling numbers of rodents in the reserve the study was redirected to determining the factors resulting in the low numbers. The impacts of food and cover and grazing by the larger ungulates were studied. In addition, the age class distribution and gastro-intestinal parasites of small mammals were studied.

A study of the small mammals in the Siphiso Valley of Mlawula Nature Reserve was conducted over four years from August 2000. The population density, biomass and composition of the small mammal community in the area were studied. The community comprised of *Mus minutoides* A. Smith, 1834, *Mastomys natalensis* (A. Smith, 1834), *Lemniscomys rosalia* (Thomas, 1904), *Crocidura hirta* Peters, 1952, *Steatomys pratensis* Peters, 1846 and *Graphiurus murinus* (Desmarest, 1822). *Mus minutoides* was the dominant species with pregnant females caught from November to May. Species richness varied significantly with the time of the year. The biomass, density and numbers of small mammals were low and by the end of the second year of the study, small mammal density was close to zero.

Mastomys natalensis from a Middleveld study site, Luyengo, Swaziland were used to study the age structure of the population by means of eye lenses. The eye lens to age (in days) curve determined by Leirs (1994) was applied. A large percentage of *M. natalensis*

in winter (June) were 2 months old while in spring/summer (October to March) the population consisted mainly of 3 month old specimens. A very low number of specimens were older than 4 months. This suggests a high mortality/removal rate of the young especially in the winter months.

The impact of grazing pressure and rainfall on small mammal densities were investigated. High grazing pressure by ungulates rendered the habitat unsuitable for small mammals as it removed cover and encouraged colonization by alien invasive plant species. This effect was exacerbated by diminishing and unpredictable rains, such that mild grazing pressure negatively impacted on small mammal communities and on individual species.

When the small mammals disappeared from the study site, *M. natalensis* was reintroduced to determine the factors that led to the disappearance. Supplementary food resulted in the longest persistence of the reintroduced mice while the impact of additional cover was small. Predation was likely responsible for the rapid decline of the reintroduced mice.

Small mammals were examined for ectoparasites and gut parasites as these were thought to negatively impact on their physiology and reproduction. Ectoparasites collected included the ticks *Ixodes sp.* and *Boophilus sp.*, the mite *Allodermanyssus sp.* and another species of mite. The gastrointestinal tracts contained the helminths *Syphacia sp.*, *Heligmonina sp.*, *Trichuris sp.*, *Protospirura sp.*, two unidentified nematode species and three different cestode species. A new species of heligmosomoid nematode is described and named.

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I thank the members of my family who assisted both in the field and laboratory. These are my wife Khetsiwe, my son Sibanesethu, my daughters Siphosothando and Simamukele, Sanele Gwebu, Linda Mngoma and Samukelisiwe Mahlaba.

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Finally, I would like to convey my sincerest gratitude to my family for bearing with me through my frequent absences and for providing logistic and financial support. Thank you.

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INTRODUCTION

Rodents have had a close relationship with man since his early ancestry and have retained a very important influence up to present day (Leirs 1994). They are pests of agricultural products both in the field and in storage (Leirs 1994) and are vectors of disease and disease-carrying ectoparasites (Arata & Gratz 1975; Chowdhury & Aguire 2000; Skinner & Chimimba 2005). The greater part of mankind's interactions with rodents have been directed at eradicating them. Many efforts have failed because of a lack of understanding of their general biology and particular aspects of their ecology (Leirs 1994). Rodents have some benefits for mankind as in many Asian and African societies rodents are an important part of his diet. Ecologically, rodents have a significant impact on the environment as grazers, seed-eaters and occasionally insectivores, and as prey of carnivores (Kern 1981; Perrin 1982; Linzey & Kesner 1997a; 1997b; Hagenah 2006). They are indicators of environmental condition as their populations respond rapidly to environmental change (Linzey & Kesner 1997a; 1997b) underlining the value of long-term studies of small mammals.

Although rodents are an ecologically and economically important group of mammals (Bond *et al.* 1980; Kerley 1992; Linzey & Kesner 1997a; 1997b), there have been too few studies of them in Swaziland to yield sufficient information to understand and manage their populations. Natural rodent populations (not feral or urban) in Swaziland remained unstudied until the research of Monadjem which was conducted in a Middleveld grassland (Monadjem 1997; 1998a; Monadjem 1998b; Monadjem & Perrin 1998; Monadjem 1999,) and in the Lubombo region (Monadjem 1998b). However, there is still much to learn about the biology and ecology of small mammals in the greater part of the country, particularly in the Lowveld.

Small mammal population changes and their underlying causes are the subject of fundamental ecological research (Elton 1924; Krebs & Myers 1974; Happold & Happold 1991, 1992, Yoccoz *et al.* 2001; Lima *et al.* 2003). Often these fluctuations are seasonal (Happold & Happold 1989; Leirs *et al.* 1990; Wirminghaus & Perrin 1993; Firquet *et al.* 1996) and seasonal differences in the productivity of the habitat can result in differences in reproduction, physiological condition and abundance (Stenseth *et al.* 2003). The impact of rainfall on cover and food availability determines the density of small mammal communities (FitzGibbon 1995). Small mammal communities are negatively affected by large mammal grazing pressure, whether domestic (Nyako-Lartey & Baxter 1995) or wild (Delany 1964; Bowland & Perrin 1989; Hagenah 2006). Small mammal populations fluctuate in tandem with fluctuations in their predators (Begon *et al.* 1990; Šálek *et al*. 2004). Infection by parasites can cause major reductions in rodent populations (Dobson 1988; Jaenike 1996).

This project was aimed at long term monitoring of a small mammal community at Mlawula Nature Reserve in the eastern part of Swaziland. There is only one recorded study of rodents extending to three years in Swaziland (Monadjem & Perrin 2003) and this was in Middleveld grassland. Research on rodents in the Lowveld up to now has been over a year or less (this study). Studies in other parts of southern Africa have shown inter-yearly variations in population dynamics and breeding seasons of rodents (Nel 1978; Chidumayo 1984; Perrin & Swanepoel 1987). The disappearance of several species and the numerical decline of rodents in the study site prompted the second aim which was to investigate the causes of these disappearances. The influence of grazing by ungulates and drought were investigated as well as the availability of food and cover. Lastly, the study aimed at determining what ectoparasites and gut parasites infest the small mammals because of the possibility that the densities were declining because of the physiological consequences of parasite infestation. In addition to death, parasite infestation has been shown to reduce mating in rodents (Edwards & Barnard 1987) which could result in population decline.

Swaziland is located between the South African plateau (reaching over 1500 m) and the coastal plains of Mozambique. Thus the western part of the country lies in escarpment area, and the eastern part in the zone of the coastal plains. Separating the Swaziland coastal plains from the Mozambique coastal plains, is the Lubombo Mountain Range.

With its divergent geology, climate and subsequent landforms, the physiographic regions within the country's boundaries are very distinct. Although the country has historically been divided into four regions (Highveld, Middleveld, Lowveld, and Lubombo), it has now been more appropriately reclassified into six physiographic zones, taking into account elevation, landforms and geology (Remmelzvaal 1993; Sweet & Khumalo 1994). These six zones are discussed below.

The Swaziland Highveld (33%) is the upper part of an escarpment, consisting of a complex of steep slopes between low and high levels, dissected plateaux, plateau remnants, and associated hills, valleys and basins. The Upper Middleveld (14%) consists of a strongly eroded plateau, remnants and hills at an intermediate level of the overall escarpment. It also contains structurally defined basins in relatively protected positions, which are weakly eroded. The Lower Middleveld (14%) is basically the piedmont zone of the escarpment, characterised by generally strongly eroded foot slopes. The slopes are predominantly moderate and the zone classifies at the first level as a plain.

The Lowveld consists of sedimentary and volcanic Karoo beds as opposed to the igneous and metamorphic rocks of the Highveld and Middleveld. The Lowveld is subdivided into the higher Western Lowveld (20%) on sandstone or claystone, and the lower Eastern Lowveld (11%) on basalt. The sixth zone is the Lubombo Range (8%), a cuesta with a steep escarpment bordering the Eastern Lowveld and having a gradual dip slope of about 1:20 descending east. As a major landform the Lubombo qualifies as a plateau.

The study was carried out in four areas, Mlawula Nature Reserve, Vuvulane, eKundizeni and Luyengo Campus. Mlawula Nature Reserve and Vuvulane are in the Eastern Lowveld while eKundizeni and Luyengo Campus are found in the Upper Middleveld. The main study area was Mlawula Nature Reserve while EKundizeni in Malkerns and the Luyengo Campus of the University of Swaziland (near Malkerns) were used to provide data on grazing in comparison with data from Mlawula Nature Reserve and specimens for age class study respectgively. Vuvulane was the source of *Mastomys natalensis* for release into Mlawula Nature Reserve in the reintroduction study. More detailed descriptions of the study areas are given in Chapters 1 and 3 while Figure 1 shows the location of these areas.

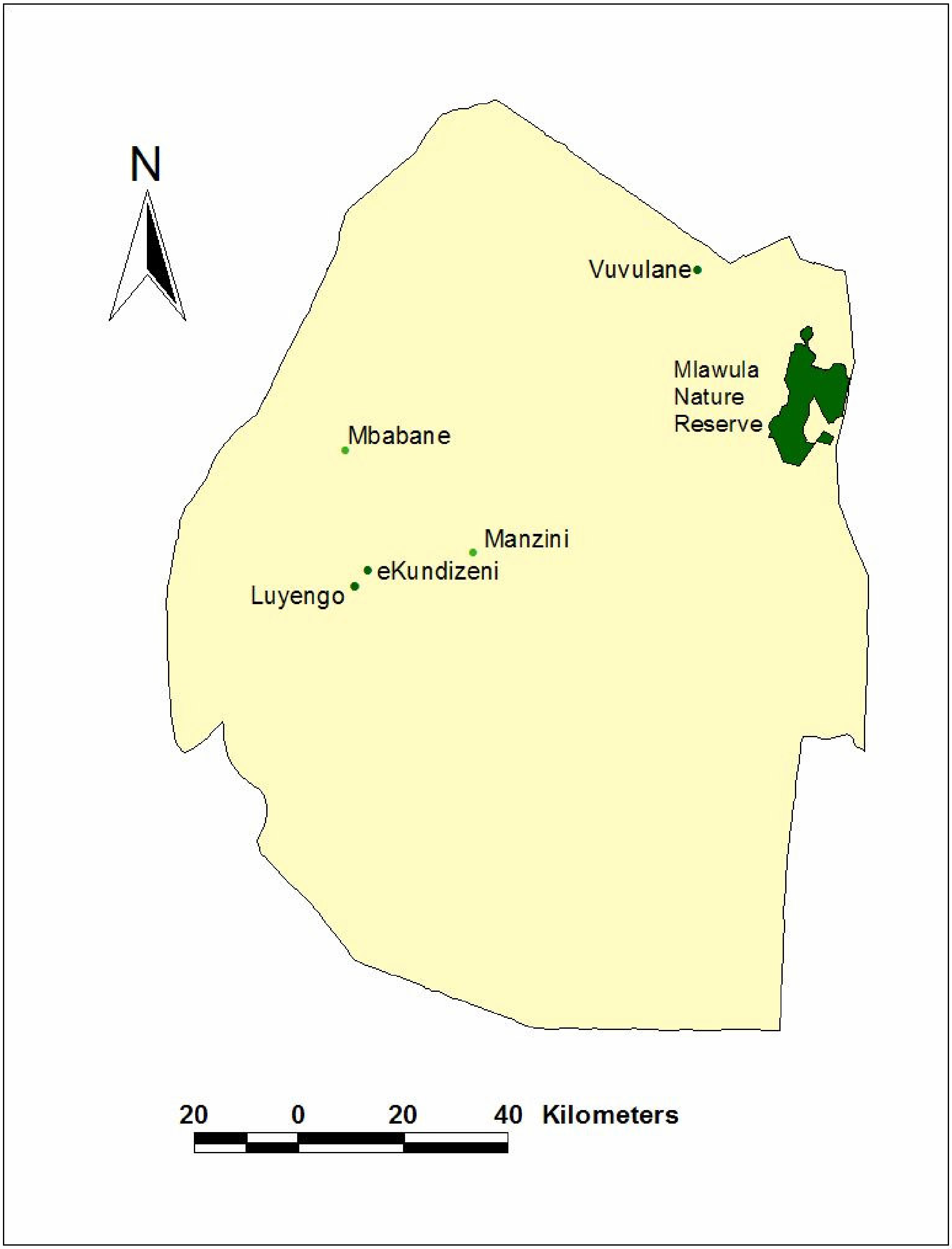


Figure 1: Map of Swaziland showing Mlawula Nature Reserve, Vuvulane, eKundizeni and Luyengo.

Small mammal monitoring was carried out at Mlawula Nature Reserve using the capture-mark-release method over a period of five years. Eight permanent grids were set up in similar vegetation in the Siphiso Valley and animals caught in Sherman live traps (H.B. Sherman Traps Inc., Tallahassee, Florida) were marked by unique toe clipping. Small mammal populations were estimated using the minimum number alive method (Krebs 1966).
To access grazing impacts, road transect counts (Braun 1992) were used to estimate ungulate abundance. For the reintroduction study, *Mastomys natalensis* were collected from Vuvulane using Sherman live traps (H.B. Sherman Traps Inc., Tallahassee, Florida) placed along line transects. Trapped mice were marked by unique toe-clipping before they were released onto the grids. Released animals were monitored by means of live trapping and numbers remaining were estimated using the minimum number alive method (Krebs 1966). A line transect was set up in Mlawula Nature Reserve and the rodents caught were examined for gut parasites.

The study investigated the composition and characteristics of the small mammal community in the Siphiso Valley of Mlawula Nature Reserve. The numbers of species and changes in abundance were determined. Community traits including relative densities of the different species and species diversity were examined in addition to the reproductive biology of the constituent species. Causes determining fluctuations in the populations of small mammals were investigated. In previous studies, *Mus minutoides*, *Mastomys natalensis*, *Lemniscomys rosalia*, *Saccostomus campestris*, *Aethomys chrysophilus* and *Crocidura hirta* were recorded in the area (Monadjem 1998b). Results showed that *Mus minutoides* was present at a greater density than the other species which disappeared over time from the area. This study aimed to determine the possible causes of the disappearances and their impact on the dominance by *M. minutoides*.

The impact of grazing by ungulates and rainfall on rodent abundance was investigated. The study site is occupied by large numbers of impala (*Aepyceros melampus*), warthog (*Phacochoerus africanus*) and blue wildebeest (*Connochaetes taurinus*). Large numbers of ungulates in an area are known to negatively impact on small mammal abundance (Hagenah 2006), however, this study aimed at quantification in another area with a different grazing regime and different species of ungulates.

Rainfall at Mlawula has declined and become irregular as well, and is known to determine the onset and duration of the reproductive season in rodents (Happold & Happold 1989; Firquet *et al.* 1996). The impact of habitat factors, particularly cover and of food availability, was explored. This was done by reintroducing *M. natalensis,* a species that was common and abundant in the area previously (Monadjem 1998b) but which disappeared. Mice were collected from an adjacent area and released onto grids and monitored. The eight grids received different treatments, additional cover only, supplemental food and additional cover, additional food only and no food or cover manipulation. The occupancy of these grids by the released mice showed which factors contribute most to the disappearance of mice from the area.

The last part of the study determined the infestation rates of ectoparasites and digestive system parasites of the small mammals in the study area. Parasites may have contributed to the factors causing the population declines by direct negative physiological impacts on condition and indirect effects on the fecundity of the rodents (Edwards & Barnard 1987). Gut parasites of rodents have not been well studied in southern Africa and new species of parasite has been described.

Two of the chapters, Chapter 1 and Chapter 6 have been published in refereed journals (Mahlaba & Perrin 2003; Durette-Desset *et al.* 2007). The remaining chapters are either being prepared for submission or have been submitted for publication in refereed scientific journals.

References

ARATA, A.A. AND GRATZ, N.G. 1975. The structure of rodent faunas associated with arenaviral infections. *Bulletin of the World Health Organization* **52**: 621-627.

BEGON, M., HARPER, J.L. AND TOWNSEND, C.R. 1986. *Ecology, individuals, populations and communities.* Blackwell Scientific Publications, Oxford.

BOND, W., FERGUSON, M. AND FORSYTH, G. 1980. Small mammals and habitat structure along altitudinal gradients in the southern Cape mountains. *South African Journal of Zoology* **15**(1): 35-43.

BOWLAND, A.E. AND PERRIN, M.R. 1989. The effect of overgrazing on the small mammals in Umfolozi Game Reserve. *Z. Saugetierkunde* **54**: 251-260.

BRAUN, K. 1992. *Road transect count of impala, Mlawula Nature Reserve*. Swaziland National Trust Commission. Lobamba.

CHIDUMAYO, E.N. 1984. Observations on populations of multimammate mice at Livingstone, Zambia. *Journal of Zoology, London.* **48**: 363-376.

CHOWDHURY, N. AND AGUIRE, A.A. 2000. *Helminths of wildlife: A global perspective*. Science Publishers.Chicago.

DELANY, M.J. 1964. An ecological study of the small mammals in the Queen Elizabeth Park, Uganda. *Revue de Zoologie et de Botanique Africaines.* **70**: 129-147.

DOBSON, A.P. 1988. Restoring island ecosystems: the potential of parasites to control introduced mammals. *Conservation Biology* **2** (1): 31-39.

DURETTE-DESSET, M.C., DIGIANI, M.C., MAHLABA, T. AND BEHNKE, J.M. 2007. Description of a new species of *Heligmonina* Baylis, 1928 (Nematoda: Heligmonellidae) a parasite of *Mastomys natalensis* (Rodentia: Muridae) from Swaziland and new data on the synlophe of *Heligmonina chabaudi* (Desset, 1966). *Parasite* **14**: 271-280.

EDWARDS, J.C. AND BARNARD, C.J. 1987. The effects of *Trichinella* infection on intersexual interactions between mice. *Animal Behaviour* **35**: 533-540.

ELTON, C. 1924. Fluctuations in numbers of animals. *British Journal of Experimental Biology* **2**: 119-163.

FIRQUET, E., LEIRS, H. AND BRONNER, G. 1996. Germinating grasses and reproductive seasonality of *Mastomys*-species (Rodentia, Muridae). *Mammalia* **60**(4): 775-779.

FITZGIBBON, C.D. 1995. Distribution, population dynamics and habitat use of the lesser pouched rat, *Beamys hindei*. *Journal of Zoology*, London **236**: 499-512.

HAGENAH, N. 2006. *Among rodents and rhinos: Interplay between small mammals and large herbivores in a South African savanna.* Department of Environmental Sciences. Wageningen University. Wageningen**:** 138.

HAPPOLD, D.C.D. AND HAPPOLD, M. 1989. Biogeography of montane small mammals in Malawi, Central Africa. *Journal of Biogeography* **16**: 353-367.

HAPPOLD, D.C.D. AND HAPPOLD, M. 1991. An ecological study of small rodents in the thicket-clump savanna of Lengwe National Park, Malawi. *Journal of Zoology, London* **223**: 527-547.

HAPPOLD, D.C.D. AND HAPPOLD, M. 1992. The ecology of three communities of small mammals at different altitudes in Malawi, Central Africa. *Journal of Zoology, London*. **228**: 81-101.

JAENIKE, J. 1996. Population level consequences of parasite aggregation. *Oikos* **76**: 155-160.

KERLEY, G.I.H. 1992. Trophic status of small mammals in the semi-arid Karoo, South Africa. *Journal of Zoology, London* **226**: 563-572.

KERN, N.G. 1981. The influence of fire on populations of small mammals of the Kruger National Park. *Koedoe* **24**: 125-157.

KREBS, C.J. 1966. Demographic changes in fluctuating populations of Microtus californicus. *Ecological Monographs* **36**(3): 239-273.

KREBS, C.J. AND MYERS, J.H. 1974. Population cycles in small mammals. *Advanced Ecological Research* **8**: 267-399.

LEIRS, H. 1994. *Population ecology of Mastomys natalensis (Smith, 1834).* Belgian Administration for Development Cooperation. Brussels.

LEIRS, H., STUYCK, J., VERHAGEN, R. AND VERHEYEN, W. 1990. Seasonal Variation in growth of *Mastomys natalensis* (Rodentia: Muridae) in Morogoro, Tanzania. *African Journal of Ecology* **28**: 298-306.

LINZEY, A.V. AND KESNER, M.H. 1997a. Small mammals of a woodland-savannah ecosystem in Zimbabwe. I. Density and habitat occupancy patterns. *Journal of Zoology, London* **243**: 137-152.

LINZEY, A.V. AND KESNER, M.H. 1997b. Small mammals of a woodland-savannah ecosystem in Zimbabwe. II. Community structure. *Journal of Zoology, London* **243**: 153-162.

LIMA, M., STENSETH, N.C. LEIRS, H AND. JAKSIC, F.M. 2003. Population dynamics of small mammals in semi-arid regions: a comparative study of demographic variability in two rodent species. *Proceedings of the Royal Society of London B.* **270**: 1997-2007.

MAHLABA, T.A.M. AND PERRIN, M.R. 2003. Population dynamics of small mammals at Mlawula, Swaziland. *African Journal of Ecology* **41**: 317-323.

MONADJEM, A. 1998a. Biomass of rodents at Mlawula Nature Reserve, Swaziland. *Uniswa Journal of Agriculture, Science and Technology* **2**(1): 117-120.

MONADJEM, A. 1998b. *Mammals of Swaziland*. The Conservation Trust & Big Game Parks. Mbabane.

MONADJEM, A. AND PERRIN, M.R. 1998. Effects of supplemental food on the habitat selected by *Mastomys natalensis* (Muridae: Rodentia) in a subtropical grassland in Swaziland. *South African Journal of Zoology* **33**(3): 172-177.

MONADJEM, A. AND PERRIN, M.R. 2003. Population fluctuations and community structure of small mammals in a Swaziland grassland over a three-year period. *African Zoology* **38**(1): 127-137.

NEL, J.A.J. 1978. Habitat heterogeneity and changes in small mammal community structure and resource utilization in the southern Kalahari. *Bulletin of Carnegie Museum of Natural History* **6**: 118-131.

NYAKO-LARTEY, Q. AND BAXTER, R.M. 1995. The effects of different grazing regimes on the population dynamics of small mammals in the Eastern Cape. *Transactionsof the Royal Society of South Africa* **50**: 143-151.

PERRIN, M.R. 1982. Prey Specificity of the barn owl, *Tyto alba*, in the Great Fish valley of the Eastern Cape Province. *South African Journal of Wildlife Research* **12**: 14-25.

PERRIN, M.R. AND SWANEPOEL, P. 1987. Breeding biology of the bushveld gerbil *Tatera leucogaster* in relation to diet, rainfall and life history theory. *South African Journal of Zoology* **22**(3): 218-227.

ŠÁLEK, M., SVOBODOVÁ, J., BEJČEK, V. AND ALBRECHT, T. 2004. Predation on artificial nests in relation to the numbers of small mammals in the Krušné hory Mts, the Czech Republic. *Folia Zoologica*. **53**(3): 312-318.

SKINNER, J.D. AND CHIMIMBA, C.T. 2005. *The mammals of the Southern African Subregion*. Cambridge University Press Cambridge.

WIRMINGHAUS, J.O. AND PERRIN, M.R. 1993. Seasonal changes in density, demography and body composition of small mammals in a southern temperate forest. *Journal of Zoology, London* **229**: 303-318.

YOCCOZ, N.G., STENSETH, N.C., HENTTONEN, H.AND PREVOT-JULLIARD, A. 2001. Effects of food addition on the seasonal density dependent structure of bank vole Clethrionomys glareolus populations. *Journal of Animal Ecology* **70**: 713-720.

CHAPTER 1

Population dynamics of small mammals at Mlawula, Swaziland

Abstract

Population density, biomass and composition of a small mammal community in an *Acacia nigrescens* savanna were studied over 12 months from August 2000. The community consisted of *Mus minutoides* (A. Smith, 1834), *Mastomys natalensis* (A. Smith, 1834), *Lemniscomys rosalia* (Thomas, 1904), *Crocidura hirta* (Peters, 1952), *Steatomys pratensis* (Peters, 1846) and on one occasion *Graphiurus murinus* (Desmarest, 1822) was caught. *M. minutoides* was the dominant species on the site. Species richness was found to vary significantly with the time of the year. The density of *M. minutoides* was significantly high in winter and low in the other seasons. The ratio of males to females was equal and pregnant females were caught from November to May. The biomass of small mammals in the area (also density and numbers) was generally low (mean biomass 212g/ha). The occurrence of new individuals in catches remained high throughout the study suggesting a high mortality or emigration rate or a combination of the two.

Introduction

Although small mammals are an important group of organisms (Bond *et al.* 1980; Kerley 1992; Linzey & Kesner 1997a; 1997b), there have been insufficient studies to yield information to manage small mammal populations in Swaziland. They are important pests of agricultural products both in the field and in storage (Leirs 1994) and are vectors of disease (Skinner & Chimimba 2005). Ecologically, small mammals have a significant impact on the environment as grazers, seed-eaters and insectivores, and as prey for some carnivores (Kern 1981; Linzey & Kesner 1997a; 1997b). Small mammals are also useful indicators of environmental condition as their populations respond rapidly to environmental change (Linzey & Kesner 1997a; 1997b), underlining the value of long-term studies of small mammals. Small mammals in Swaziland remained unstudied until the studies by Monadjem in a Middleveld grassland (Monadjem 1997a; 1997b; 1998a; Monadjem 1998b; Monadjem & Perrin 1998; Monadjem 1999) and in the Lubombos (Monadjem 1998b). This study was carried out in low-lying savanna.

Small mammal populations in woodland savanna are known to respond to environmental change especially habitat quality i.e., food, cover and indirectly rainfall (Gliwicz 1985; Perrin 1986; Kerley 1992; Eshelman & Cameron 1996; Linzey & Kesner 1997a, 1997b; Monadjem & Perrin 1998). Long-term studies in a grassland showed that populations of *L. rosalia*, *M. minutoides* and *M. natalensis* had wide aseasonal fluctuations (Monadjem & Perrin 2003).

Studies on populations of small mammals have generally concentrated on the larger or the more numerous in the catches (Gliwicz 1985; Armstrong & van-Hensbergen 1996; Linzey & Kesner 1997a; 1997b; Monadjem 1997b; Monadjem & Mahlaba 2000). In Swaziland, only one study of *Mus minutoides* is on record (Monadjem 1999). Consequently, very little is known about populations of this species. Furthermore, within the country, there is only one known study on the community structure and populations of small mammals in lowveld Acacia savanna (Monadjem 1998a). However, here sampling was conducted only once every three months.

The aims of this study were, to determine the species composition of the small mammal community in an Acacia savanna at Mlawula Nature Reserve. Second, to study the population dynamics and ecology (feeding, habitat preferences, space use, reproductive biology) of the small mammal species over a twelve-month period. Lastly, to seek an explanation for the community dominance by *Mus minutoides.*

Study Area

The study was carried out in the Mlawula Nature Reserve (26°11'S, 31°59'E, 160 m a.s.l.), in northeastern Swaziland (Fig. 2). The 16500 ha reserve encompasses part of the Lubombo Mountains, Lowveld plains and the Mlawula and Siphiso rivers. It is bounded by Mozambique to the east, Shewula Game Reserve to the north, Mbuluzi and Hlane Game Reserves to the west and Royal lands to the south. Altitudes within Mlawula range from 76 m in the Mbuluzi gorge to around 500 m on the Ndzindza plateau. Mean monthly temperatures range from 17 to 27 °C and the annual rainfall 600 to 650 mm. The vegetation comprises Acacia woodland in lower areas and combretaceous woodland on the slopes of the Lubombo Mountains.

The study site was located in Acacia woodland in the Siphiso valley with the commonest trees being knobthorn (*Acacia nigrescens*), tree wisteria (*Bolusanthus speciosus*) and leadwood (*Combretum imberbe*) (T. Mahlaba pers. obs.). The area was burnt in August 2000 and within three months was covered by the alien invasive herb feverfew, *Parthenium hysterophorus*, and the alien invasive bush triffid weed, *Chromolaena odorata*, occurring in patchy clumps. The area is grazed by large numbers of medium to large sized mammals, in particular the warthog (*Phacochoerus africanus*), impala (*Aepyceros melampus*), blue wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*).

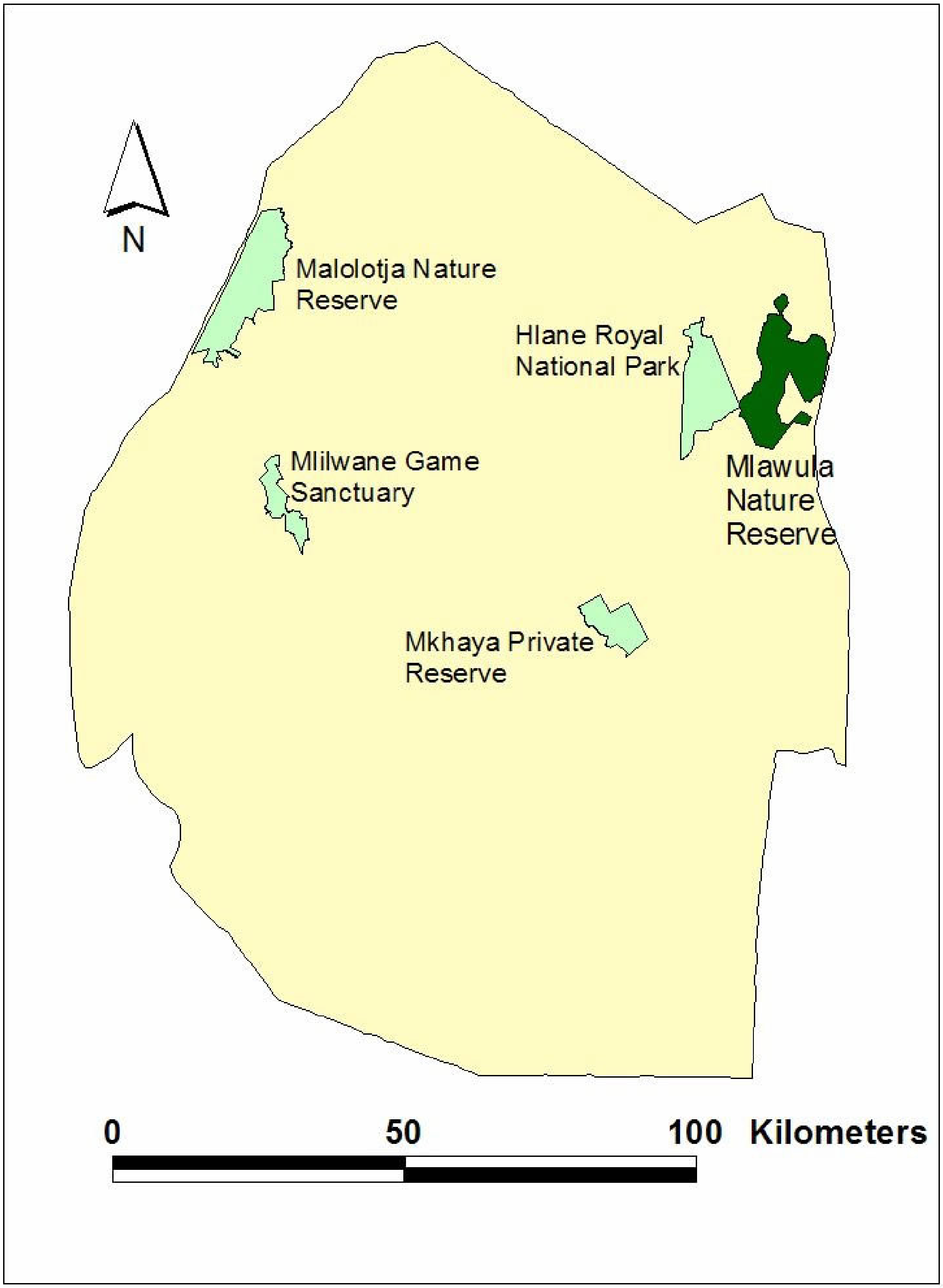


Figure 2. Map of Swaziland showing Mlawula Nature Reserve

Materials and Methods

Rodents were caught in Sherman live traps (H.B. Sherman Traps Inc., Tallahassee, Florida) baited with oats. Sampling was monthly or more frequently with the exception of two months, which were not sampled. Traps were set 10m apart on six permanent grids (7 X 7) more than 100m apart. A total of 294 traps were set for 3 nights on each occasion from August 2000 to July 2001, a total of 14 112 trap-nights. Traps were checked early in the morning, left closed during the day (to prevent unnecessary mortality of animals) and then opened and re-baited in the late afternoon.

Animals caught were identified, weighed and sexed. In addition, length of body; tail; ear and hind foot (c/u) measured. These measurements provided an indication of physiological condition (together with weight) and were also used to confirm identifications. Reproductive condition was noted, the condition of the animal, its teats and the opening into the vagina were studied in females, while in males the scrotum was inspected for the presence or absence of testes (Leirs 1995). Females were classified as imperforate, perforate, pregnant or lactating. Males were classed as scrotal or non-scrotal. Each animal was uniquely toe-clipped and released at the point of capture. The minimum number alive (MNA) method (Krebs 1966) was used to estimate the number of animals present. These data were used to estimate population size, biomass and other demographic parameters.

Analyses of species-specific data were only done for *Mus minutoides,* as it was the only species with a large sample size. The year for the seasonality analysis was divided into four seasons, summer, autumn, winter and spring (see Table 3). Below is shown the months in each season.

Summer:	November	Winter:	May
	December		June
	January		July
Autumn:	February	Spring:	August
	March		September
	April		October

Species richness was defined as the number of small mammal species occurring in the study area. Data was analyzed using the Chi-squared and Students' T tests.

Results

Data from the six grids were grouped. Although the number of animals was significantly different between the grids (χ^2 = 33.88; d.f. = 5, $P < 0.001$), the trends in the populations were the same between the grids (unpublished data). Furthermore, there was no difference in treatments between the grids.

Six species of small mammals were captured. *M. minutoides* (pygmy mouse), *Mastomys natalensis* (multimammate mouse), *Lemniscomys rosalia* (single-striped mouse), *Steatomys pratensis* (little fat mouse), *Graphiurus murinus* (woodland dormouse) and the Insectivora *Crocidura hirta* (lesser red musk shrew) (Table 1).

Mus minutoides was the most numerous small mammal sampled (Fig. 3). By the end of July 2001 the other species of small mammals had emigrated or died out. The density of *Mus minutoides* was high and contributed most to community composition (Fig. 4). However, because of its small size its contribution to the biomass of the area was very small such that total biomass fell when the larger species like *Lemniscomys rosalia* were absent (Fig 4). *Graphiurus murinus* was caught only once. Species richness in the study area varied significantly with the time of the year (month) (χ^2 = *2.45, d.f. = 9, P < 0.975*). Trapping success ranged from 2% to 34% (mean = 13%).

Table 1. Total numbers of each species of small mammal caught at Mlawula Nature Reserve with standard anatomical measurements ± standard deviation.

Species	Sex	Number	Weight (g)	Body Length (mm)	Tail Length (mm)	Ear Length (mm)	Foot Length (mm)
Mus minutoides	M	186	5.8 ± 2.14	50.3 ± 6.37	34.6 ± 6.38	8.7 ± 5.55	12.1 ± 1.22
	F	179	5.7 ± 2.44	50.9 ± 7.96	35.1 ± 5.04	8.2 ± 1.50	12.2 ± 1.22
Lemniscomys rosalia	M	2	77.5 ± 2.12	123.2 ± 5.16	120.5 ± 3.25	10.4 ± 4.95	25.2 ± 5.51
	F	2	63.5 ± 3.53	121.4 ± 0.64	131.8 ± 5.23	16.2 ± 0.35	25.8 ± 1.63
Mastomys natalensis	M	10	23.6 ±11.70	84.4 ± 21.99	80.0 ± 9.16	14.5 ± 3.54	20.2 ± 1.37
	F	12	19.8 ± 10.47	83.9 ± 9.80	76.2 ± 9.87	13.0 ± 2.10	19.8 ± 0.65
Steatomys pratensis	M	1	25.5	93.7	44.2	12.6	16.7
	F	1	19.0	80.1	32.0	10.0	15.4
Crocidura hirta	M	9	14.2 ± 4.30	78.5 ± 7.93	38.9 ± 1.76	8.3 ± 1.14	14.1 ± 1.98
Graphiurus murinus	F	1	27.5	100.0	77.4	11.6	15.0

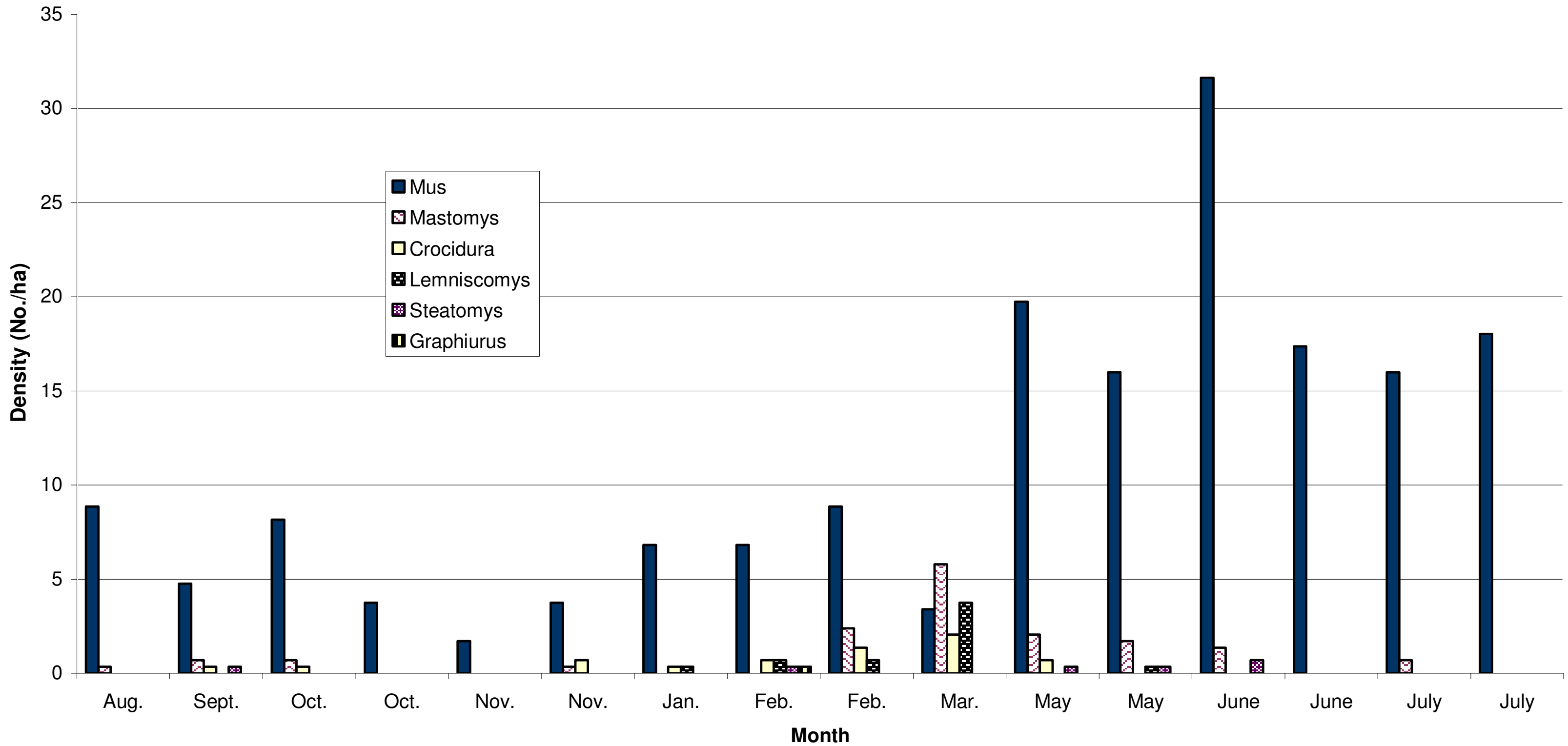


Figure 3. The density of *Mus minutoides* and other small mammals between August 2000 and July 2001 in Acacia savanna at Mlawula Nature Reserve.

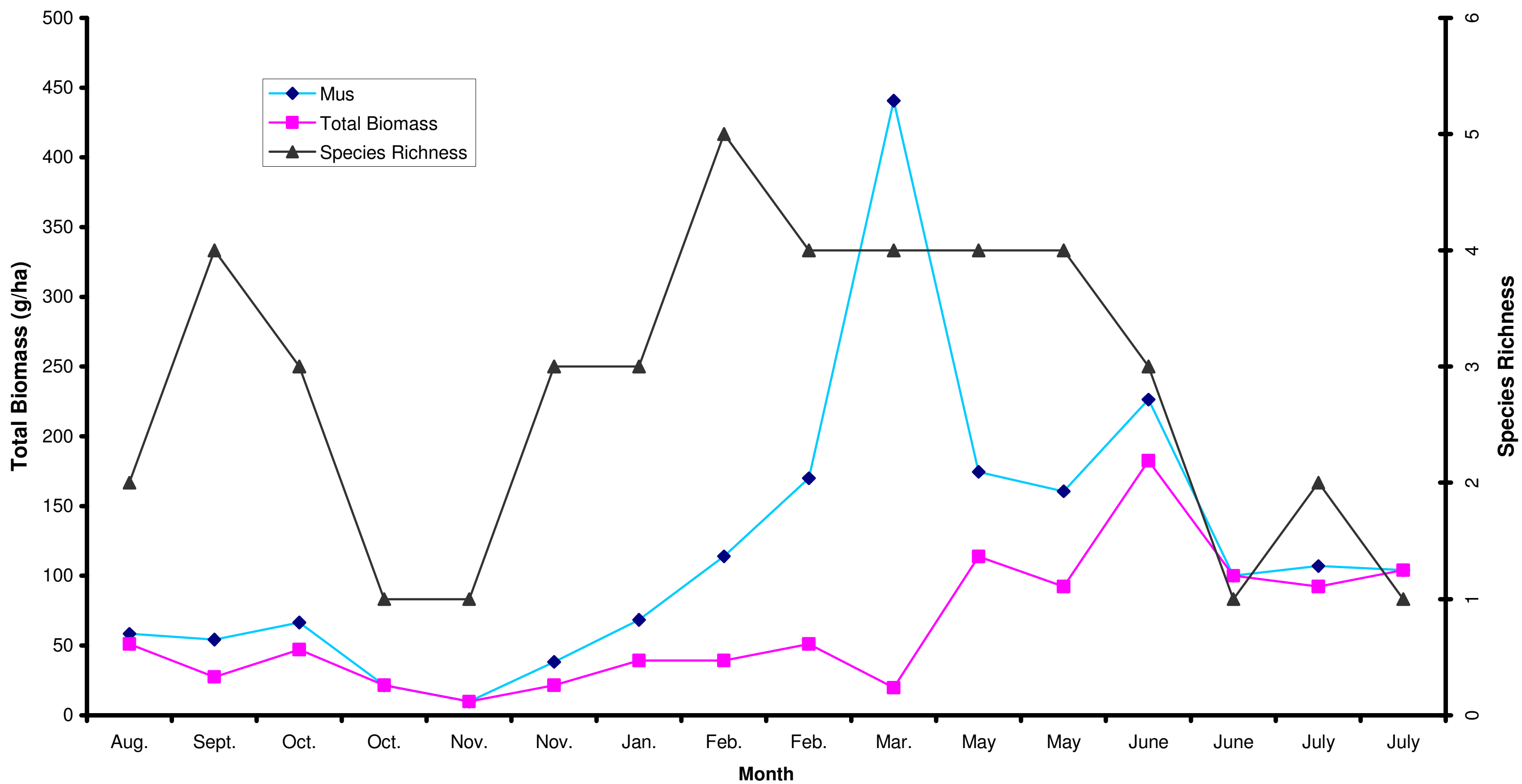


Figure 4. Monthly species richness and biomass of the small mammal community at Mlawula Nature Reserve between August 2000 and July 2001. Also shown is the monthly biomass of *Mus minutoides*.

Anatomical measurements are given in Table 1; Analyses were only done for *Mus minutoides*. There was no significant difference in the number of male and female *Mus minutoides* (χ^2 = *0.134, d.f. = 1, P > 0.05*). There were no significant differences between sexes in body weight (*t = 0.530, d.f. = 179, P > 0.05*), body length (*t = -0.459, d.f. = 179, P > 0.05*), tail length (*t = -0.950, d.f. = 179, P > 0.05*), ear length (*t = 0.640, d.f. = 179, P > 0.05*) and hind foot length (*t = -1.055, d.f. = 179, P > 0.05*). *Mus minutoides* does not exhibit sexual dimorphism.

Because of the very low numbers of large rodents the rodent biomass was low, least in November (9.81 g/ha) and highest in February (440.69 g/ha); mean biomass was 119.64 g/ha (Table 2).

Table 2. Density(D) numbers per hectare and biomass (B) grams per hectare of small mammals in Acacia savanna at Mlawula Nature Reserve between August 2000 and July 2001. Shown in bold are the months in which pregnant *Mus. minutoides* females were caught.

Month.	***Mus minutoides***		***Mastomys natalensis***		***Crocidura hirta***		***Lemniscomys rosalia***		***Steatomys pratensis***		***Graphiurus murinus***	
	D	**B**	**D**	**B**	**D**	**B**	**D**	**B**	**D**	**B**	**D**	**B**
Aug.	8.8	51.0	0.3	7.4	2.5	34.5	0.0	0.0	0.0	0.0	0.0	0.0
Sept.	4.8	27.5	0.7	14.7	5.0	68.9	0.0	0.0	0.3	7.2	0.0	0.0
Oct.	8.2	47.1	0.7	14.7	5.0	68.9	0.0	0.0	0.0	0.0	0.0	0.0
Oct.	3.7	21.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nov.	1.7	9.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Nov.	**3.7**	**21.6**	0.3	7.4	2.5	34.5	0.0	0.0	0.0	0.0	0.0	0.0

Table 2 continued

Month.	*Mus minutoides*		*Mastomys natalensis*		*Crocidura hirta*		*Lemniscomys rosalia*		*Steatomys pratensis*		*Graphiurus murinus*	
	D	**B**	**D**	**B**	**D**	**B**	**D**	**B**	**D**	**B**	**D**	**B**
Jan.	**6.8**	**39.3**	0.0	0.0	0.0	0.0	0.3	24.4	0.0	0.0	0.0	0.0
Feb.	**6.8**	**39.3**	0.0	0.0	0.0	0.0	0.7	48.7	0.3	7.2	0.3	1.0
Feb.	**8.8**	**51.0**	2.4	51.5	17.5	241.2	0.7	48.7	0.0	0.0	0.0	0.0
Mar.	**3.4**	**19.6**	5.8	125.1	42.5	585.8	3.7	267.9	0.0	0.0	0.0	0.0
May.	**19.7**	**113.8**	2.0	44.1	15.0	206.8	0.0	0.0	0.3	7.2	0.0	0.0
May	**16.0**	**92.2**	1.7	36.8	12.5	172.3	0.3	24.4	0.3	7.2	0.0	0.0
Jun.	31.6	182.5	1.4	29.4	10.0	137.8	0.0	0.0	0.7	14.4	0.0	0.0
Jun.	17.3	100.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Jul.	16.0	92.2	0.7	14.7	5.0	68.9	0.0	0.0	0.0	0.0	0.0	0.0
Jul.	18.0	104.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Variation in density of *M. minutoides* through the year is presented (Table 3 & Fig. 4). Density was generally low during summer, increased in autumn, peaked in winter and declined in spring. Seasonal changes in density were significant ($\chi^2 = 25.04$, *d.f.* = 3, $P < 0.001$). *M. minutoides* reproduced seasonally. Pregnant females were caught from November to May. *M. minutoides* showed no significant deviation from a 1:1 sex ratio (186 males, 179 females; $\chi^2 = 0.13$, *d.f.* = 1, $P < 0.50$)

Table 3. Mean number and density of *Mus minutoides* in the study area through the seasons of the year.

Season	Months	Mean Number	Mean Density
Summer	November December January	14	4.76
Autumn	February March April	17	5.78
Winter	May June July	58	19.73
Spring	August September October	19	6.46

Discussion

In most studies of African small mammal communities *M. minutoides* is usually present in low numbers compared with other rodents (Kern 1981; Gliwicz 1985; Armstrong & van-Hensbergen 1996; Linzey & Kesner 1997a, 1997b; Monadjem 1998b; Monadjem 1999; Monadjem & Perrin 2003). In this study, other species of small mammals were present in unusually low numbers. Even the density of *M. minutoides* was significantly lower than that found by Monadjem (1998a) in the same area in 1993/94 ($t = 2.850$, $d.f. = 6$, $P < 0.05$, 21.25 animals/ha versus 9.15 animal/ha). The same observation was made when the total density of rodents in the area was considered ($t = 3.877$, $d.f. = 6$, $P < 0.05$, 57 animals/ha versus 19.33 animals/ha). It is thought that *M. minutoides* in this study was more tolerant of the conditions than the other small mammal species that had emigrated or died. These conditions likely included low food quantity and quality (Lauckhart 1957), habitat variables such as vegetation structure and cover (Bond *et al.* 1980; Linzey & Kesner 1997b). No correlation was found between species richness and density of *M. minutoides* ($r_{606} = -0.045$, $P > 0.05$). The population density of *M. minutoides* in this area was probably determined by interactions between this species and its habitat and not by competitive interactions between *M. minutoides* and the presence-absence of other species, although in a middleveld grassland it was observed that species richness had an inverse relationship with density of *M. natalensis* (Monadjem & Perrin 2003). The low trapping success is further indicative of low populations. Trapping success ranged from 2% to 34% with a mean of 13%, lower than the 25.8% recorded by Monadjem (1998a).

The low biomass of small mammals was caused, in part, by the absence of the 'larger' grassland rodents e.g., *L. rosalia*. When present, even in low numbers, the overall biomass increased. Compared with another study in the same area (Monadjem 1998b) the biomass of small mammals here was low. Monadjem (1998a) recorded a mean biomass of 1442 g/ha, Happold and Happold (1990) recorded a mean biomass of 842 g/ha in similar habitat in Liwonde National Park (Malawi), while in this study, mean biomass was 212g/ha. This is thought to be the result of the combined effects of alien weed infestation, which excluded competing local grasses, shrubs and forbs, and the overgrazing, by the medium to large sized ungulates that were numerous in the area. The negative impact of overgrazing on small mammal reproduction and communities has been demonstrated (Bowland & Perrin 1989).

The anatomical measurements of the *Mus minutoides* from this area are similar to those recorded in previous studies (Monadjem 1998d; Monadjem 1999; Skinner & Chimimba 2005).

The seasonality of breeding of *M. minutoides* observed in this study was also observed by Monadjem (1998b; 1999) and concurs with other reports (Smithers & Wilson, 1979). It is this summer breeding that results in the high winter densities. However, it is suspected that winter mortality if fairly high because by spring the densities were observed to have dropped markedly.

This study has highlighted the paucity of information on *M. minutoides* and its ecology. More in-depth work on the ecology of this species needs to be done. Such research should also explore the relationships between *M. minutoides* populations and those of the other mammal species.

References

ARMSTRONG, A.J. AND VAN-HENSBERGEN, H.J. 1996. Small mammals in afforestable montane grasslands of the northern Eastern Cape Province, South Africa. *South African Journal of Wildlife Research* **26**(1): 11-18.

BOND, W., FERGUSON, M. AND FORSYTH, G. 1980. Small mammals and habitat structure along altitudinal gradients in the southern Cape mountains. *South African Journal of Zoology* **15**(1): 35-43.

BOWLAND, A.E. AND PERRIN, M.R. 1989. The effect of overgrazing on the small mammals in Umfolozi Game Reserve. *Zeitschrift Säugetierkunde* **54**: 251-260.

ESHELMAN, B.D. AND CAMERON, G.N. 1996. Experimentally induced habitat shifts by hispid cotton rats (*Sigmodon hispidus*): response to protein supplementation. *Journal of Mammalogy* **77**(1): 232-239.

GLIWICZ, J. 1985. Rodent community of dry African savanna: population study. *Mammalia* **49**(4): 509-516.

HAPPOLD, D. C. D., & HAPPOLD, M. 1990. An ecological study of small rodents in the woodland savanna of Liwonde Natinal Park, Malawi. Journal of Zoology, London, 221, 219-235

KERLEY, G.I.H. 1992. Trophic status of small mammals in the semi-arid Karoo, South Africa. *Journal of Zoology, London* **226**: 563-572.

KERN, N.G. 1981. The influence of fire on populations of small mammals of the Kruger National Park. *Koedoe* **24**: 125-157.

KREBS, C. J. (1966). Demographic changes in fluctuating populations of *Microtus californicus*. Ecological Monographs, 36(3), 239-273.

LAUCKHART, J.B. 1957. Animal cycles and food. *Journal of Wildlife Management* **21**(2): 230-234.

LEIRS, H. 1994. Population ecology of *Mastomys natalensis (Smith, 1834).* Implications for rodent control in Africa. Brussels: *Belgian Administration for Development Cooperation.Brussels Nr. 35.*

LINZEY, A.V. AND KESNER, M.H. 1997a. Small mammals of a woodland-savannah ecosystem in Zimbabwe. I. Density and habitat occupancy patterns. *Journal of Zoology, London* **243**: 137-152.

LINZEY, A.V. AND KESNER, M.H. 1997b. Small mammals of a woodland-savannah ecosystem in Zimbabwe. II. Community structure. *Journal of Zoology, London* **243**: 153-162.

MONADJEM, A. 1997a. Habitat preferences and biomasses of small mammals in Swaziland. *African Journal of Ecology* **35**: 64-72.

MONADJEM, A. 1997b. Stomach contents of 19 species of small mammals from Swaziland. *South African Journal of Zoology* **32**(1): 23-26.

MONADJEM, A. 1998a. Biomass of rodents at Mlawula Nature Reserve, Swaziland. *Uniswa Journal of Agriculture, Science and Technology* **2**(1): 117-120.

MONADJEM, A. 1998b. *Mammals of Swaziland*. The Conservation Trust & Big Game Parks. Mbabane.

MONADJEM, A. 1999. Population dynamics of *Mus minutoides* and *Steatomys pratensis* (Muridae: Rodentia) in a subtropical grassland in Swaziland. *African Journal of Ecology* **37**: 202-210.

MONADJEM, A. AND MAHLABA, T.A.M. 2000. A mammal survey of the Lower Usuthu Basin, Swaziland. *Uniswa Journal of Agriculture, Science and Technology* **4**(1): 55-61.

MONADJEM, A. AND PERRIN, M.R. 1998. Effects of supplemental food on the habitat selected by *Mastomys natalensis* (Muridae: Rodentia) in a subtropical grassland in Swaziland. *South African Journal of Zoology* **33**(3): 172-177.

MONADJEM, A. AND PERRIN, M.R. 2003. Population fluctuations and community structure of small mammals in a Swaziland grassland over a three-year period. *African Zoology* **38**(1): 127-137.

PERRIN, M.R. 1986. Some perspectives on the reproductive tactics of southern African rodents. *Cimbebasia(A)* **8**(8): 63-77.

SKINNER, J.D. AND CHIMIMBA, C.T. 2005. *The mammals of the Southern African Subregion*. Cambridge University Press Cambridge.

SMITHERS, R. H. N. AND V. J. WILSON, 1979. Not seen cited in Skinner, J. D. and R. H. N. Smithers, 1990. *The Mammals of the Southern African Subregion*. University of Pretoria. Pretoria.

CHAPTER 2

Seasonal change in the age distribution of *Mastomys natalensis* at Luyengo, Swaziland

Abstract

Mastomys natalensis from a Middleveld study site, Luyengo, Swaziland were used to study the age structure of the population by means of eye lenses. The eye lens to age (in days) curve determined by Leirs (1994) was applied. A large percentage of *M. natalensis* in June (winter) were 2 months old while in October to March (spring/summer) the population consisted mainly of 3 month old specimens. A very low number of specimens were older than 4 months. This suggests a high mortality/removal rate of the young especially in the winter months.

Introduction

One of the most important characteristics of a species population is its age structure (Leirs 1994). Recognising this fact ecologists have used a number of means to determine the age of wild caught animals (Lord 1959; Martinson *et al.* 1961; Carstairs 1976; Perrin 1979; Wheeler & King 1980; Leirs 1994; Stockrahm *et al.* 1996; Vukicevic-Radic *et al.* 2005). Each of the methods tried requires a measurable physical attribute of the animal that changes over time and the rate of change of this attribute must be known. Body weight, body length and eye lens weight have been used for this purpose but eye lens weight has been found to be superior to the others (Carreno *et al.* 1990; Leirs 1994). All of these are based on the fact that the larger heavier animals with heavier eye lenses are the older ones. Although body weight and body length increase over time, their increase is subject to other influences besides time such that the small animals may not always be the young (Mills *et al.* 1992). Eye lens weight has been shown to be and is generally accepted as the best available estimator of age in small mammals (Martinson *et al.* 1961; Perrin 1979; Mills *et al.* 1992;Leirs 1994; Jacob *et al.* 2007). Consequently, eye lens weight curves have been developed for species such as *Microtus pennsylvanicus* (meadow vole) (Thomas & Bellis 1980), *Mus musculus* (wild house mouse) (Rowe *et al.* 1985) and *Mastomys natalensis* (multimammate mouse) (Leirs 1994). By means of these curves the ages of wild caught rodents can be estimated with reasonable confidence. However, because of the log-linear relationship between age and eye lens weight, these curves estimate with better accuracy the ages of young animals (Perrin 1979). These curves work well in all the areas where the species occurs though there maybe minor variations (Wheeler & King 1980). Body length is also a good estimator of age and has greater accuracy than other body parameters (Carreno *et al.* 1990). However, age estimation using eye lens weights are superior in the case of animals whose body length or weight is not growing ‘regularly’, for example, anoestrus corn mice (*Calomys musculinus*) (Carreno *et al.* 1990).

This study aimed to use the eye lens weight curve determined by Leirs (1994) to estimate the age distribution of *M. natalensis* caught in Swaziland. This enabled the comparison of the age structure of *M. natalensis* populations caught in summer and winter. In Swaziland the high density at the beginning of winter and the extremely low density of small mammals has been observed (Monadjem 1998). A study of the age structure would show any changes in age distribution as a result of differential mortality. It is suspected that there is high winter mortality of both juveniles and adults but there are more young adults at the onset of spring due to the higher numbers of juveniles at the onset of winter. The animals were caught at Luyengo because exploratory trapping here had resulted in high catches of *M. natalensis*. This species has shown a similar trend to that observed in *M. minutoides,* i.e. high numbers at the onset of winter and very low numbers by the beginning of spring (Monadjem & Perrin 2003).

Material and Methods

Study Site

The rodents were trapped at the Luyengo Campus of the University of Swaziland, Luyengo. The campus is situated in the Middleveld of Swaziland at an altitude of 650-700 m a.s.l.. The mean annual rainfall recorded over 30 years (by the University of Swaziland Meteorological Station) is 928 mm. Most of this rain falls between September and April. The mean minimum temperature for July is 7.6°C, while the mean maximum temperature for February is 27.3°C.

Trapping

The mice were trapped in Sherman live traps (H.B. Sherman Traps Inc., Tallahassee, Florida) baited with rolled oats arranged in a line transect made up of 100 traps with 5m between trap points. The line transect went through maize and sorghum fields and uncultivated land. Trapping was carried out in June 2005 for one week and from the last week of 27 October 2006 to 6 March 2007. The second trapping session was made longer because the number of animals caught at each instance was low. Animals caught were euthanized using chloroform then weighed and lengths of body, tail, hind legs and ears taken. Their reproductive state was noted. The teats and opening into the vagina were studied in females, while in males the scrotum was inspected for the presence or absence of testes (Leirs 1995). Females were classified as imperforate, perforate, pregnant or lactating. Males were classed as scrotal or non-scrotal. Animals were then frozen until they were needed for other studies.

Eye lenses were removed and placed in small vials and dried for 7 days at 80°C. Paired lenses were weighed to the nearest 0.1mg on a microbalance (Cahn Instrument Co., California). The age of the animals was estimated using the formula of the standard curve from Leirs (1994), given below:

$$a = e^{\frac{(10.46088+w)}{4.35076}}$$

where a = estimated age in days, e = the natural logarithm and w = eye lens weight. The estimated age (in days) was used to group the population into monthly groups.

Regression and correlation analyses were done to test the relationship between the eye lens weight and body length. This relationship was further tested for significance using the analysis of variance (ANOVA) (Zar 1999). These analyses were carried out using the statistical package GenStat (9th Edition).

Results

One hundred specimens of *M. natalensis* were caught in June 2005 (June sample) while only 69 were trapped in the October 2006 to March 2007 (October sample). There was a significant correlation between total body length and eye lens weight. For the October sample the Pearson's correlation co-efficient was 0.737 (*d.f. = 1,68,* $P < 0.001$) and for the June sample it was 0.594 (*d.f. = 1,98,* $P < 0.001$). Figures 1 and 2 show the scatter plots with the 90% confidence intervals. From the regression analysis eye lens weight accounted for 53.7% of the variation in body length in the October sample and 34.6% in the June sample, this relationship was significant in both cases (*ANOVA* $F_{calc}=53.47$, *d.f. = 1,98,* $P < 0.001$ and $F_{calc}=79.75$, *d.f. = 1,67,* $P < 0.001$ respectively).

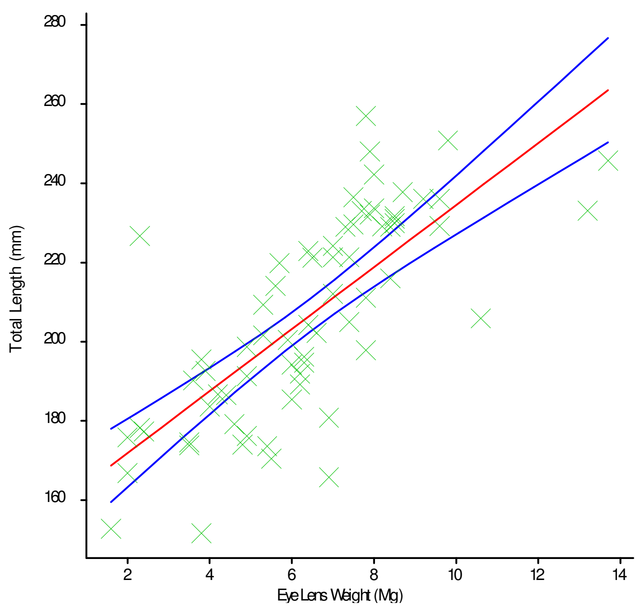


Figure 5. Plot of eye lens weight (mg) versus total body length with 95% confidence intervals shown for *Mastomys natalensis* caught in Luyengo in October-March.

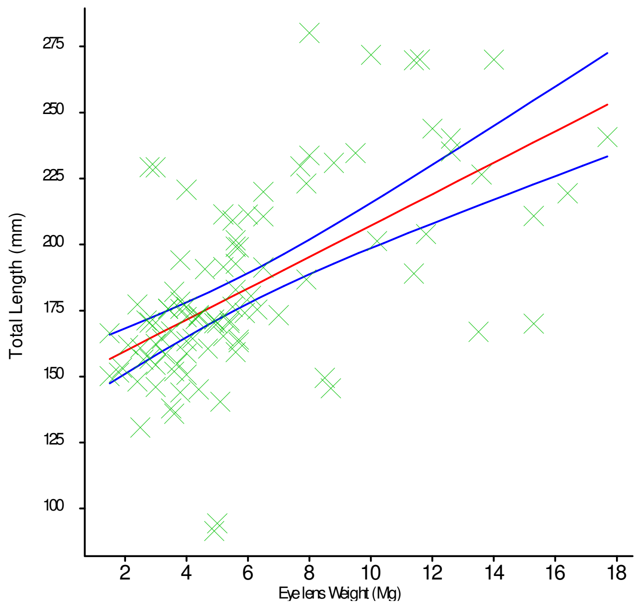


Figure 6. Plot of eye lens weight (mg) versus Total body length with 95% confidence intervals shown for *Mastomys natalensis* caught in Luyengo in June.

The plots of eye lens weight versus total body length (Figures 5 & 6) show the linearity of the relationship between the two. However, because of the great variability in eye lens weight and body length most of the points fell outside the 95% confidence interval.

In the October sample the majority of the animals were 2-3 months old with only 4% older than 4 months (Figure 7). In the June sample the greatest number of mice were 0-1 month old with 14% being older than 4 months (Figure 8). However, in the latter sample there were animals that had lived a year and longer (4 animals).

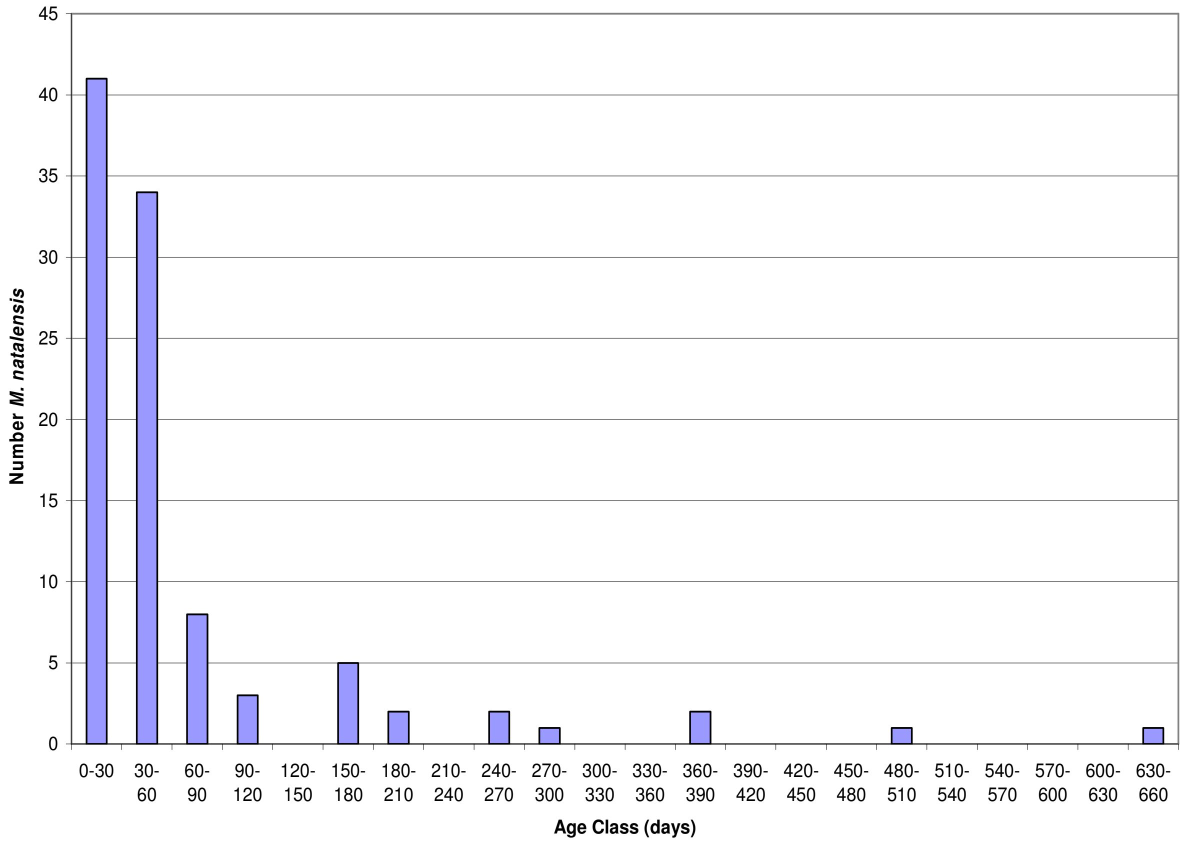


Figure 7. Age classes of *Mastomys natalensis* caught in Luyengo in June.

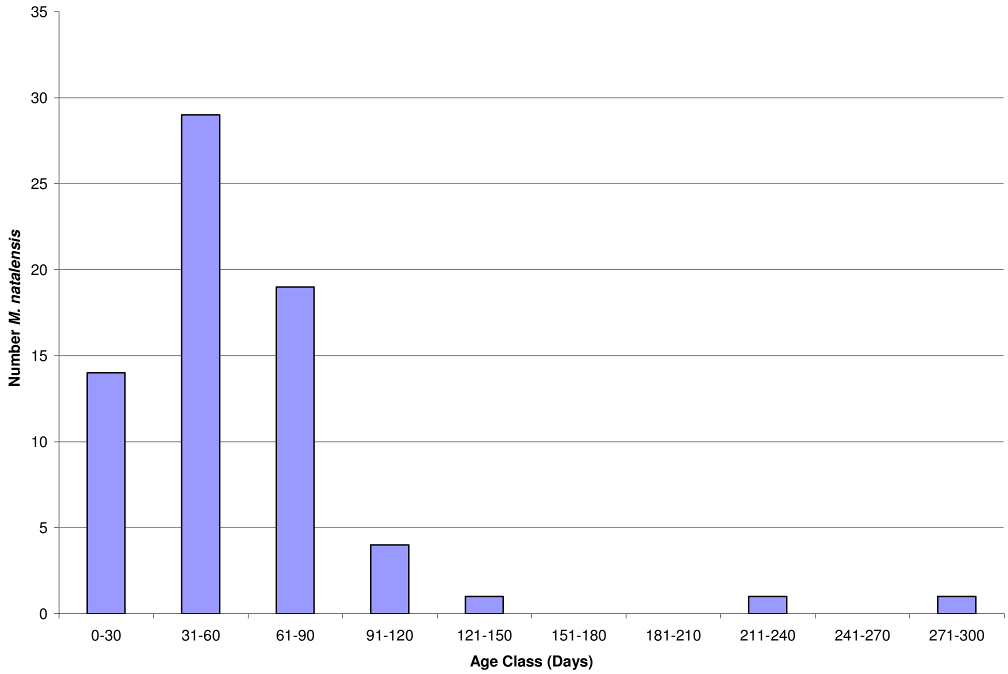


Figure 8. Age classes of *Mastomys natalensis* caught in Luyengo in October - March.

Discussion

Based on the correlation and regression analyses the equation calculated by Leirs (1994) was applicable to mice from this study site. The June sample showed that the population consisted mainly of 1-2 month old animals. The low numbers of the other age classes suggests a high rate of removal from the area of the young animals by mortality or emigration. It is suspected that the cause was a combination of mortality due to scarce food resources (Monadjem & Perrin 2003) and possibly the low winter temperatures. The large number of mice at the end of June and the rapid decline in abundance has been observed previously in Swaziland (Monadjem 1998; Mahlaba & Perrin 2003). The young animals are those born in April-May as the breeding season of *M. natalensis* in the Middleveld of Swaziland is September-May (depending on climatic factors) (Monadjem & Perrin 2003; Skinner & Chimimba 2005). Predation may also contribute to the rapid decline. The age structure of a small mammal population varies with factors in their physical environment (Edwards 1964) such as grazing (Retzer 2007), cover and disturbance (Chapman & Ribic 2002) and predation (Schmidt *et al.* 2005).

Eye lens weight understandably co-varies with total body length, but this study indicates that there maybe other factors that determine total body length besides age. These other factors were more prominent in the sample that had a greater number of older animals. The relationship between eye lens weight and age is more predictable in juvenile animals that are still growing and becomes less precise in older animals (Perrin 1979). In older animals, other factors, particularly reproduction, have a confounding impact on the relationship between age and eye lens weight (Janova *et al.* 2007).

References

CARRENO, N.B., BRIGADA, A.M., ROSI, M.I. AND CASTRO-VAZQUEZ, A. 1990. Estimating ages of corn mice (*Calomys musculinus*). *Journal of Mammalogy* **71**(3): 468-470.

CARSTAIRS, J.L. 1976. Population dynamics and movements of *Rattus villosissimus* (Waite) during the 1966-69 plague at Brunette Downs, N.T. *Austral Wildlife Research* **3**: 1-9.

CHAPMAN, E.W. AND RIBIC, C.A. 2002. The impact of buffer strips and stream-side grazing on small mammals in southern Wisconsin. *Agriculture, Ecosystems and Environment* **88**: 49-59.

EDWARDS, W.R. 1964. Evidence for a Normal Age Composition for Cottontails. *The Journal of Wildlife Management* **28**(4): 738-742.

JACOB, J., HINDS, L.A., SINGLETON, G.R., SUTHERLAND, D.R. AND YLONEN, H. 2007. Is the reproductive potential of wild house mice regulated by extrinsic or intrinsic factors? *Austral Ecology* **32**: 202-209.

JANOVA, E., HAVELKOVA, D. AND TKADLEC, E. 2007. Does reproduction accelerate growth of eye lens mass in female voles? *Belgian Journal of Zoology* **137**(1): 85-88.

KREBS, C.J. AND MYERS, J.H. 1974. Population cycles in small mammals. *Advanced Ecological Research* **8**: 267-399.

LEIRS, H. 1994. *Population ecology of Mastomys natalensis (Smith, 1834).* Belgian Administration for Development Cooperation Brussels.

LORD, R.D., Jr. 1959. The Lens as an Indicator of Age in Cottontail Rabbits. *The Journal of Wildlife Management* **23**(3): 358-360.

MAHLABA, T.A.M. AND PERRIN, M.R. 2003. Population dynamics of small mammals at Mlawula, Swaziland. *African Journal of Ecology* **41**: 317-323.

MARTINSON, R.K., HOLTEN, J.W. AND BRAKHAGE, G.K. 1961. Age criteria and population dynamics of the swamp rabbit in Missouri. *The Journal of Wildlife Management* **25**(3): 271-281.

MILLS, J.N., ELLIS, B.A., CHILDS, J.E., MAIZTEGUI, J.I. AND CASTRO-VAZQUEZ, A. 1992. Seasonal changes in mass and reproductive condition of the corn mouse (*Calomys musculinus*) on the Argentine pampa. *Journal of Mammalogy* **73**(4): 876-884.

MONADJEM, A. 1998. Reproductive biology, age structure, and diet of *Mastomys natalensis* (Muridae: Rodentia) in a Swaziland grassland. *Zeitschrift fur Saugetierkunde* **63**: 347-356.

MONADJEM, A. AND PERRIN, M.R. 2003. Population fluctuations and community structure of small mammals in a Swaziland grassland over a three-year period. *African Zoology* **38**(1): 127-137.

PERRIN, M.R. 1979. Ageing criteria and population age structure of co-existing populations of *Rhabdomys pumilio* and *Otomys irroratus*. *South African Journal of Wildlife Research* **9**(3/4): 84-95.

RETZER, V. 2007. Forage competition between livestock and Mongolian pika (*Ochotona pallasi*) in Southern Mongolian mountain steppes. *Basic and Applied Ecology* **8**: 147-157.

ROWE, F.P., BRADFIELD, A., QUY, R.J. AND SWINNEY, T. 1985. Relationship betwen eye lens weight and age in the wild house mouse (*Mus musculus*). *The Journal of Applied Ecology* **22**(1): 55-61.

SCHMIDT, N.M., OLSEN, H., BILDSOE, M., SLUYDTS, V. AND LEIRS, H. 2005. Effects of grazing intensity on small mammal population ecology in wet meadows. *Basic and Applied Ecology* **6**: 57-66.

SKINNER, J.D. AND CHIMIMBA, C.T. 2005. *The mammals of the Southern African Subregion*. Cambridge University Press Cambridge.

STOCKRAHM, D.M.B., DICKERSON, B.J., ADOLF, S.L. AND SEABLOOM, R.W. 1996. Aging Black-Tailed Prairie Dogs by Weight of Eye Lenses. *Journal of Mammalogy* **77**(3): 874-881.

THOMAS, R.E. AND BELLIS, E.D. 1980. An eye-lens weight curve for determining age in *Microtus pennsylvanicus*. *Journal of Mammalogy* **61**(3): 561-563.

VUKICEVIC-RADIC, O., JOVANOVIC, T.B., MATIC, R. AND KATARANOVSKI, D. 2005. Age structure of yellow-necked mouse (*Apodemus flavicollis* Melchior, 1834) in two samples obtained from live traps and owl pellets. *Archives of Biological Science, Belgrade* **57**(1): 53-56.

WHEELER, S.H. AND KING, D.R. 1980. The use of eye-lens weights for aging wild rabbits, *Oryctolagus cuniculus* (L), in Australia. *Australia Wildlife Research* **7**: 79-84.

ZAR, J.H. 1999. *Biostatistical Analysis.* Prentice Hall, New Jersey.

CHAPTER 3

The impact of rainfall and grazing pressure on small mammal populations in Swaziland

Abstract

The impact of grazing and rainfall on small mammal densities was investigated at two sites in Swaziland, Mlawula Nature Reserve (MNR), and eKundizeni Farm. At MNR small mammals were caught on permanently marked grids while data on ungulate populations were sourced from the Ecology Section of the reserve. At eKundizeni Farm, small mammals were trapped on two grids one in which cattle were excluded and one of which was grazed. High grazing pressure by ungulates rendered the habitat unsuitable for small mammals as it removed cover and encouraged alien invasive plant species. This effect was exacerbated by diminishing and unpredictable rains. Small mammal numbers fell from 19.33 animals per hectare to zero. Although there were no pronounced changes in vegetation greenness and cover between the grazed and ungrazed grids there were differences in small mammal community structure and densities between the two areas at eKundizeni Farm. This showed that mild grazing pressure impacts on small mammal communities and on individual species. *Lemniscomys rosalia* and *Crocidura hirta* preferred the ungrazed area.

Introduction

Fluctuations in small mammal populations and their underlying causes are the subject of fundamental ecological research (Elton 1924; Krebs & Myers 1974; Happold & Happold 1991, 1992, Yoccoz *et al.* 2001; Lima *et al.* 2003). Often these fluctuations are seasonal (Happold & Happold 1989; Leirs *et al.* 1990; Wirminghaus & Perrin 1993; Firquet *et al.* 1996) and seasonal differences in the productivity of the habitat can result in differences in reproduction, physiological condition and abundance (Stenseth *et al.* 2003). FitzGibbon (1995) working on *Beamys hindei* in Tanzania found that the suitability of the habitat was a critical factor in driving population density. Density was determined by the impact of rainfall on cover and food availability (FitzGibbon 1995).

Terrestrial small mammal communities in Africa are negatively affected by large mammal grazing pressure, whether domestic (Nyako-Lartey & Baxter 1995) or wild (Delany 1964; Bowland & Perrin 1989). There is a greater biomass and species diversity of small mammals in areas with reduced grazing pressure (Delany 1964; Bowland & Perrin 1989, Hagenah 2006). Areas grazed by goats support fewer rodents than those grazed by cattle or undergoing rotational resting (Nyako-Lartey & Baxter 1995). Few studies have documented the effects of ungulate grazing pressure on terrestrial small mammal communities in southern Africa (Nyako-Lartey & Baxter 1995; Bowland & Perrin 1989; Hagenah 2006). Nyako-Lartey & Baxter's (1995) study was primarily concerned with the comparative effects of grazing by cattle and goats on rodent demography but suffered from very small sample sizes (induced by drought). Bowland & Perrin's (1989) study employed four trapping grids but these were far apart (at least 2 km) which may have caused subtle changes in the microhabitat which may have confounded the effects of grazing pressure.

Severe grazing leads to a change in plant species composition and basal cover (O'Connor 1985). In the Queen Elizabeth National Park in Uganda, long term exclusion of herbivores resulted in higher density and cover in the grass and thicket layer, lower plant biodiversity in the above layers and higher root biomass (Lenzi-Grillini *et al.* 1996).

As the distribution and abundance of many species of small mammals is dependent on grass cover (Bond *et al.* 1980; Monadjem 1997), severe grazing pressure is thought to affect the community structure of small mammals (Monadjem 1999). The effects of moderate grazing pressure, however, have not yet been investigated in southern Africa. Little is known about the factors affecting the community structure and population dynamics of Swaziland's small mammals. Recent experimental work, however, has shown that vegetation cover influences the distribution and abundance of some species (Monadjem & Perrin 1998); a reduction in cover leading to a decline in total biomass and species richness.

The effects of unpredictable and variable annual rainfall on small mammal populations in Swaziland have not been elucidated. Small mammal population densities on Zomba Plateau in Malawi and Swaziland's MNR are lowest at the end of the dry season and highest at the end of the wet season (Happold & Happold 1989; Mahlaba & Perrin 2003). Neither of these studies, however, explored the impacts of the onset of the rainy season, and variations in monthly rainfall, on the small mammal population densities. Rainfall in Tanzania has a big impact on the growth and reproduction of the multimammate mouse *Mastomys natalensis* (Leirs *et al.* 1990; Firquet *et al.* 1996). The additional impact of large numbers of grazing ungulate herbivores on populations of rodents has also not been studied.

The key questions of this study are: what is the impact of rainfall (timing and quantity) on the small mammal population demography? Does moderate grazing pressure affect the population dynamics of rodents and insectivores? And, if grazing does reduce population density, is this change mediated by changes in vegetation structure? Large ungulates are suspected to have a negative impact on small mammal populations.

Study Sites, Materials and Methods

Mlawula

The first part of the study was carried out in the MNR, in north-eastern Swaziland (26°11'S, 31°59'E, 160 m a.s.l.). The 16500 ha reserve encompasses part of the Lubombo Mountains, Lowveld plains and the Mlawula and Siphiso rivers. It is bounded by Mozambique to the east, Shewula Game Reserve to the north, Mbuluzi and Hlane Game Reserves to the west and Royal lands to the south. Altitudes within Mlawula range from 76 m in the Mbuluzi gorge to around 500m on the Ndzindza plateau. Mean monthly temperatures range from 17°-27ºC and the annual dependable rainfall 450-700 mm. The vegetation comprises Acacia woodland in lower areas and combretaceous woodland on the slopes of the Lubombo Mountains (Sweet & Khumalo 1994).

The study site was located in Acacia woodland in the Siphiso valley with the commonest trees being *Acacia nigrescens*, *Bolusanthus speciosa* and *Combretum imberbe*. The area was burnt in August 2000 and within three months was covered by the alien invasive herb *Parthenium hysterophorus* and the alien invasive bush *Chromolaena odorata*, occurring in patchy clumps

(T. Mahlaba, pers. obs.). The area is grazed by large numbers of medium to large sized mammals, in particular zebra (*Equus burchelli*), impala (*Aepyceros melampus*), blue wildebeest (*Connochaetes taurinus*), kudu (*Tragelaphus strepsiceros*) and warthog (*Phacochoerus africanus*).

Methods

Trapping was usually conducted monthly from August 2000 to March 2003. Rodents were caught in Sherman live traps (H.B. Sherman Traps Inc., Tallahassee, Florida) baited with rolled oats. Traps were set 10 m apart on six permanent grids (7 x 7) spaced more than 100 m apart. A total of 294 traps were set for 3 nights on each occasion. Traps were checked early in the morning, left closed during the day (to prevent unnecessary mortality of animals) and then opened and re-baited in the late afternoon.

Animals caught were identified, weighed and sexed. Length of body, tail, ear and hind foot (*cum unguis*) measurements were recorded and provided an indication of physiological condition. Reproductive condition was noted: females were classified as imperforate, perforate, pregnant or lactating while males were classed as scrotal or non-scrotal. Each animal was uniquely toe-clipped and released at the point of capture. The minimum number alive (MNA) method (Krebs 1966) was used to estimate the number of animals present. These data were used to estimate population size, biomass and other demographic parameters (Mahlaba & Perrin 2003).

Monthly rainfall data were obtained from the Mlawula Weather Station (National Meteorological Service). In the analysis of rainfall data, the year was divided into four seasons: spring (September-November), summer (December-February), autumn (March-May) and winter (June-August).

Data on ungulate abundance were obtained from the Ecology Section of MNR. The large mammals were counted using road count transects. In these transects a 4 x 4 vehicle was driven at a maximum speed of 20 km/hr with two observers in the back. The following data were recorded: species, number of groups, number of individuals, distance from the observer, angle from the transect, distance from the start of the transect, time of observation, estimated age (adult or sub-adult) and sex ratios.

The reserve was covered evenly in distance and in time. The total number of each species of ungulate was estimated using an adaptation of the strip transect sampling equation:

$$N = DA$$
$$D = n / 2wL$$

Where D is the density of the individuals i.e., number sighted (n) in an area of length (L) and width (W = 2w, where w is sampling distance on each side of the road) (Buckland et al. 1993). The total number of individuals (N) was estimated by the density (D) multiplied by the area (A). For the area under study (Siphiso Valley), A was estimated to be 3200 ha and w to be 75 m on either side of the road (W=150 m) (Braun 1992). Although this application of the formula and the manner of counting are rough and imprecise, the data provided an index of the numbers of ungulates (Braun 1992).

EKundizeni

Two permanently marked grids were established in a natural grassland on eKundizeni Farm (26°33'S, 31°16'E) on the outskirts of Malkerns (Figure 1). The two grids were approximately 100 m apart, but were located on the same slope with the same topographical position, had identical aspects and the top soils appeared to be the same. Grid 1, however, was situated in an area supporting cattle at a stocking rate of 5.9 ha/cow. The stocking rate recommended by the Swaziland Ministry of Agriculture is 3 ha/cow indicating that this area was being moderately grazed at the time of the study. Cattle have been grazing this area for at least a decade (probably much longer), but past stocking rates are unknown. Grid 2 was situated in a fenced-off area (of approximately 20 ha) from which cattle had been excluded for at least seven years (W. Allan pers. comm.).

This region receives most of its rainfall between October and March, but the rains do not begin at a set time each year. The mean annual rainfall recorded over 30 years by the University of Swaziland Meteorological Station, located 8 km to the east of the study site (at a similar altitude of 650-700 m a.s.l.), is 928 mm. Mean minimum temperature for July was 7.6°C , while mean maximum temperature for February was 27.3°C. The vegetation was very similar on the two grids. *Hyparrhenia hirta* was the dominant grass species on both grids. The only other common grass species was *Hyperthelia dissoluta*. No trees were present on or near any of the grids, while a few *Lippia javanica* shrubs (up to 1.5 m tall) occurred irregularly on each grid.

The following rainfall and habitat data were collected monthly: total monthly rainfall for eKundizeni Farm was recorded using a rain gauge placed 200 m from the grids, grass cover on each grid was estimated in 20 randomly placed 1 m^2 quadrats each month. The 20 readings were averaged to give an estimate of grass cover on the grid. Grass height was measured using a meter ruler. For each quadrat, an average grass height was estimated. This estimate presented few problems since the grass was generally thick and a “canopy” was usually obvious. The percentage of the grass that was green was estimated for each quadrat and averaged for each grid. The dominant grass species was recorded for each quadrat. Finally, all plant species present in each quadrat were recorded.

Small mammals were trapped monthly on the two grids from June 1997 to March 1998. Between June and October, inclusive, 100 Elliot (Elliot Scientific Equipment, Upwey, Victoria) and Sherman (H.B. Sherman Traps Inc., Tallahassee, Florida) live-traps, baited with rolled oats, were set 10 m apart on each grid (10 x 10) on three consecutive days per month. Between November and March, 36 Sherman live-traps were set at 10 m intervals on each of the same grids (6 x 6). The reduction from 100 to 36 traps was unfortunate but was due to logistic reasons out of the researchers’ control. The traps were set in the afternoon and checked within two hours of dawn. Each trapped rodent was uniquely toe-clipped, sexed, weighed and its reproductive condition assessed.

The number of individuals on each grid was estimated using the minimum number known alive method (MNA) (Krebs 1966). Since the number of traps used varied through the study, the estimated densities were standardized to animals per hectare. Biomasses were estimated by multiplying the density of each species by the average weight of that species for a particular month, and then summing the biomass figures for all of the species. All biomass figures are quoted as g/ha. Species richness was the total number of species recorded. The Shannon index of species diversity (H') was calculated based on the proportional distribution of biomass among species using the following formula (Grant *et al.* 1982; Monadjem & Perrin 1998):

$$H' = - \sum Pi \log Pi$$

where Pi represented the proportion of the total small mammal biomass contributed by the ith species. Evenness (J'), which measures the equatability of the spread of biomass among species, was calculated using the following formula (Begon *et al.* 1986):

$$J' = H'/\log S$$

where S represented the total number of species in the community. Values for J' range from 0 to 1, with J' = 1 describing a group of species each of which contributes an equal amount to total biomass.

Differences between the two grids were tested using the Mann-Whitney rank test, Spearman's rank correlation and the chi-square test (Zar 1999). The statistical programme GenStat (9^{th} Edition) was used to perform these analyses.

Results

Mlawula

Rainfall

Between September 1998 and August 2003, a yearly average of 914.7mm of rain was recorded at Mlawula Nature Reserve (MNR) (Figure 5). Most rain fell between October and March although there is wide variation between years (Figure 3). Rainfall in MNR is clearly seasonal with very little, if any, rain falling in the winter season (June-August). Most rainfall was recorded in 1999 - 2000 (September-August) while much lower amounts were recorded for all the other years with total rainfall decreasing from 1999 - 2003. For 1999 - 2000 (September-August) the rainfall had two peaks, one in summer and another one in autumn.

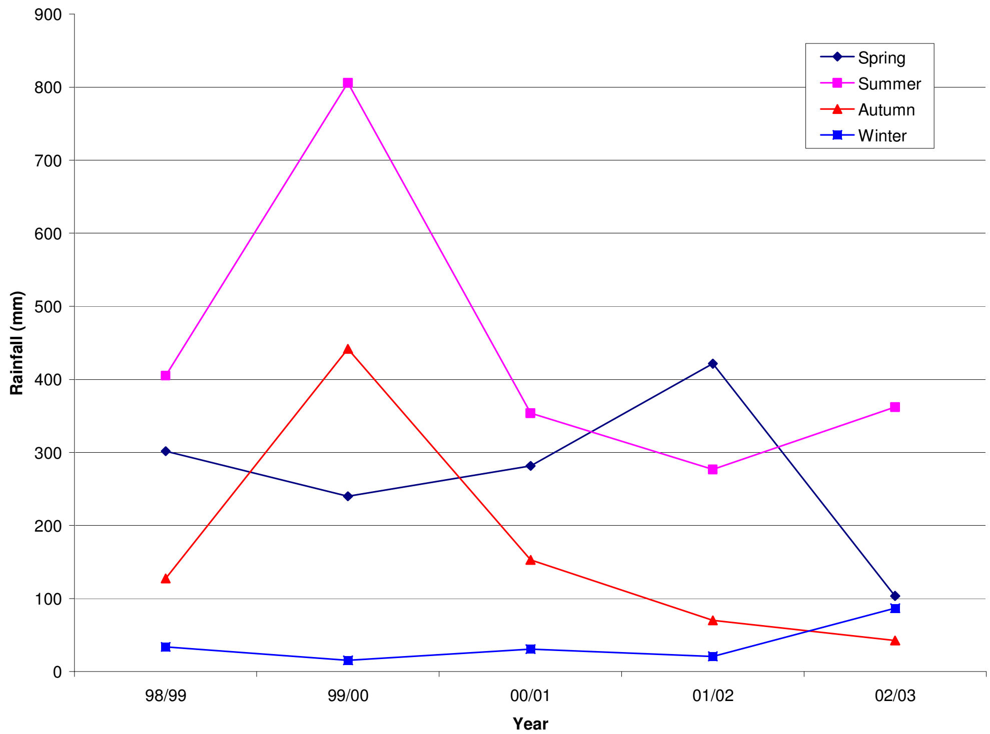


Figure 9. Total seasonal rainfall in Mlawula from 1998-2003

The rainfall pattern in Mlawula was irregular for the period under study (Figures 9 & 10). In the 1999-2000 period the greatest amount of rain fell in summer while in 2001-2002 it fell in spring. For 2000-2001 and 2002-2003 there was generally very little summer rainfall and some rainfall fell in winter. The total rainfall for the twelve month period starting in spring (September-August) was greatest in the 1999-2000 period (1503.2 mm), 2000-2001 received about half of this amount and this continued decreasing until the 20002-2003 period which received a mere 594.8 mm of rainfall.

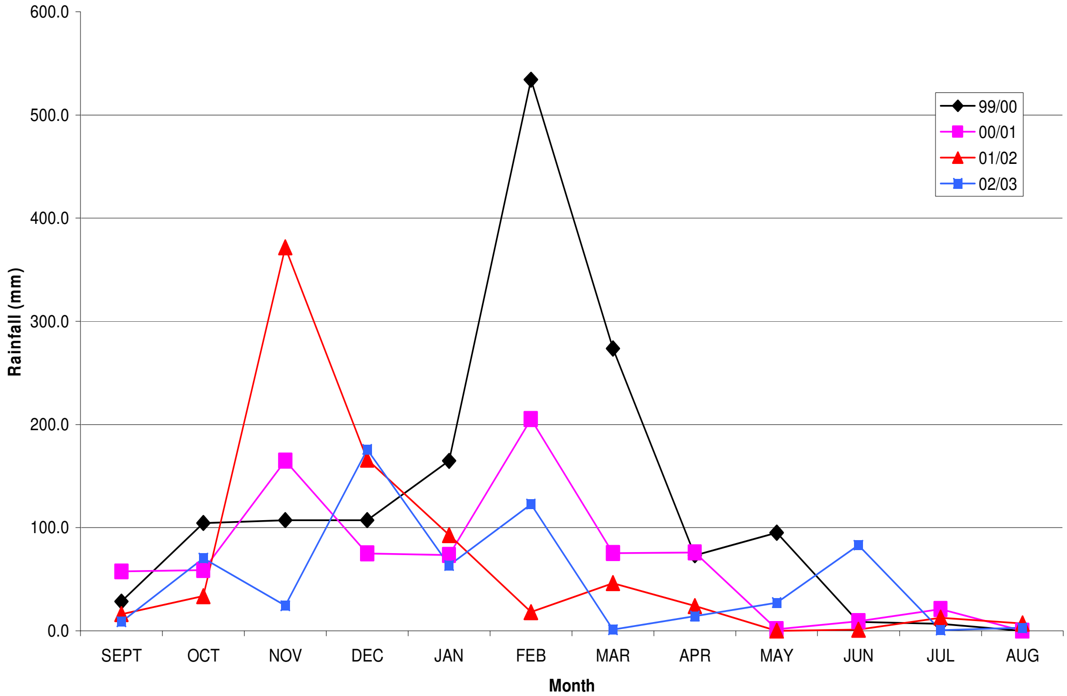


Figure 10. Monthly rainfall for Mlawula (1998-2003).

Ungulates

Data on ungulate populations was sketchy and irregular. Four counts were recorded in 2000-2003 (June 2000, June 2001, September 2002 and November 2003). The number of ungulates in the study area was estimated between 1400 and 1700 individuals (density ranged from 0.44-0.55 animals/ha) during this period (Figure 11).

Small mammals

The number of rodents in the study area fluctuated from zero to 19.33 animals/hectare. The population generally was highest in March-July (autumn) and lowest in October-February (spring and summer). The density of small mammals decreased from 19.33 animals/ha in June 2001 to zero by June 2003. Because of the incomplete data on ungulate populations the impact of ungulates on small mammal populations could not be adequately explored.

Rainfall and small mammals

Rainfall was found to have a significant but delayed impact on small mammal population density (*Spearman's* $r = 0.455$, $P < 0.05$) (six months). This impact was less but still significant for a delay of 4 months (*Spearman's* $r = 0.407$, $P < 0.05$) to 8 months (*Spearman's* $r = 0.411$, $P < 0.05$). Therefore, the amount of spring rainfall predicts the number of small mammals in summer. Figure 11 compares rainfall, number of *Mus minutoides*, total number of rodents and ungulates for 2000–2003.

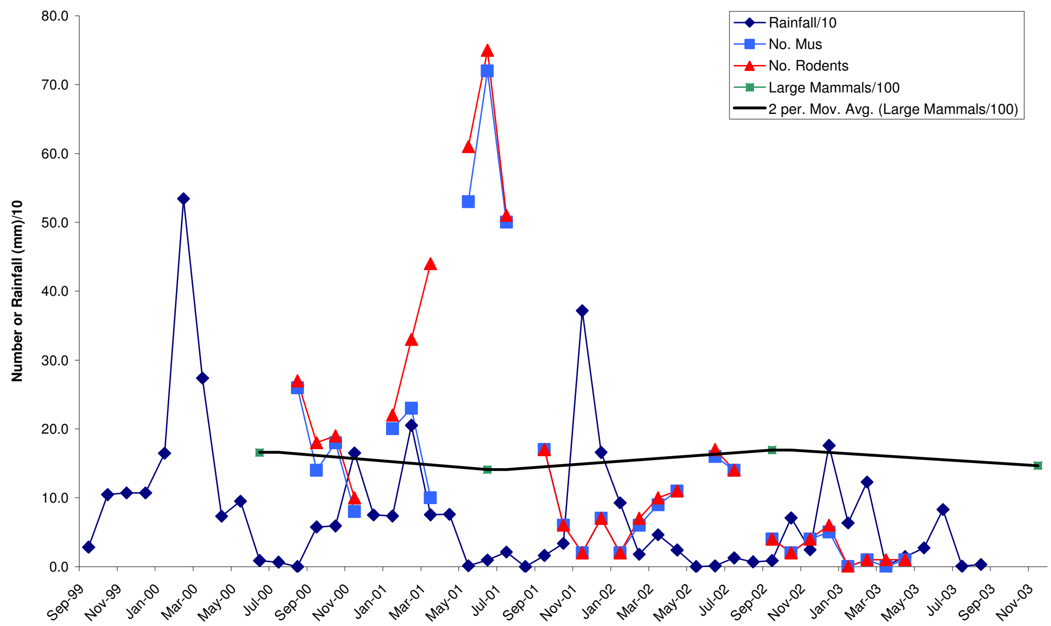


Figure 11. Numbers of large mammals, numbers of small mammals (*Mus minutoides* and total number of rodents caught) and rainfall in Mlawula Nature Reserve.

EKundizeni Farm

Between June 1997-March 1998, 931 mm of rain was recorded at this study site, with a clear summer peak (Figure 12). The vegetation characteristics of the two grids are shown (Figure 13). Grass greenness increased to a peak in February-March and grass cover in October–March, however, there were no significant differences in grass cover or greenness on the two grids (*Mann-Whitney U*, $P > 0.05$). There were no differences in plant species richness between the two grids (*Mann-Whitney U*, $P > 0.05$) but there were significant differences in grass height (*Mann-Whitney U* = 90, $P < 0.005$) (June 1997–March 1998).

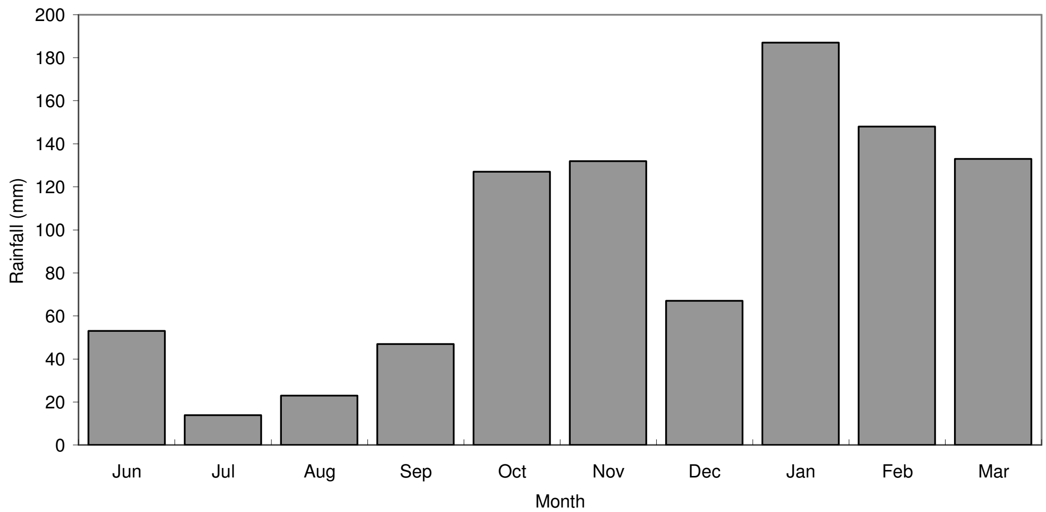
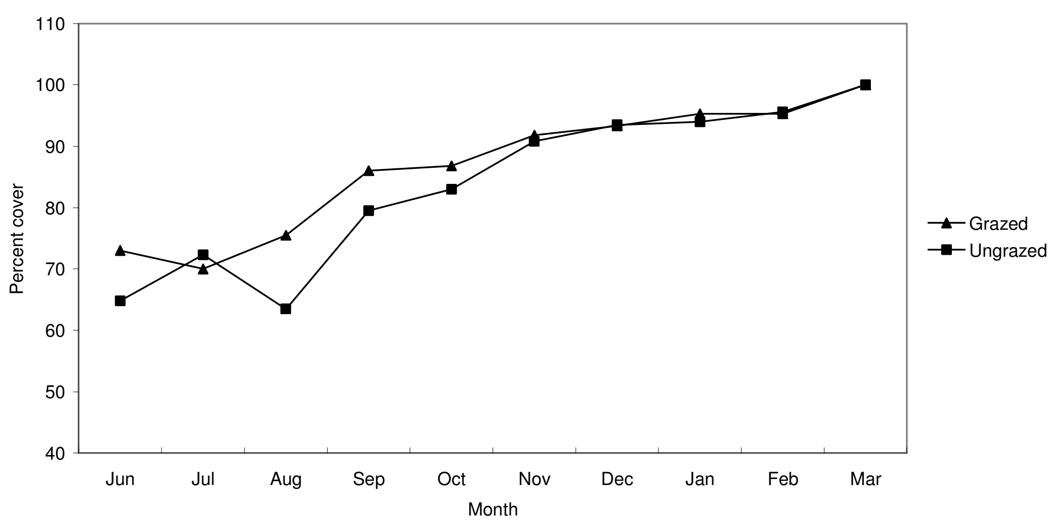
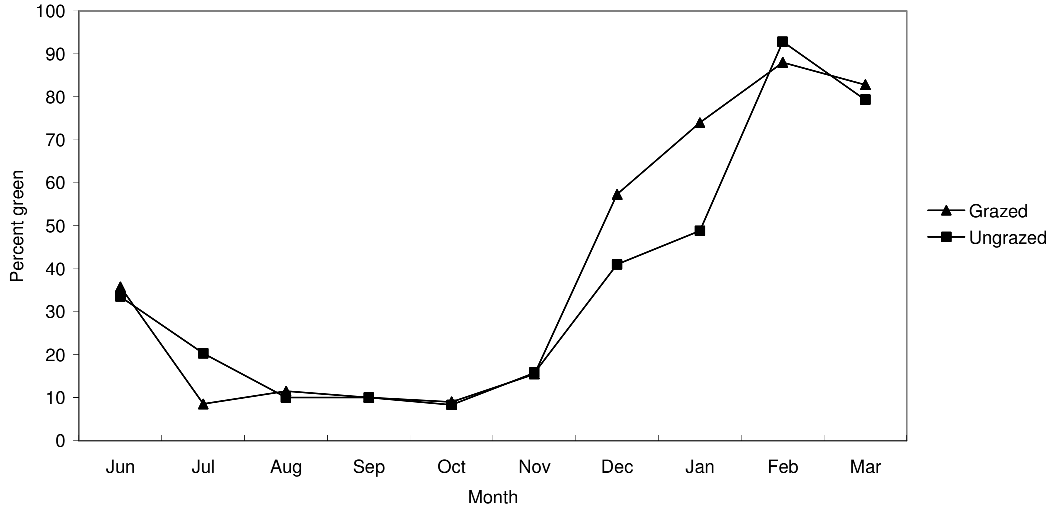


Figure 12. Total monthly rainfall at eKundizeni Farm, Swaziland from June 1997 to March 1998.

(a)



(b)



(c)

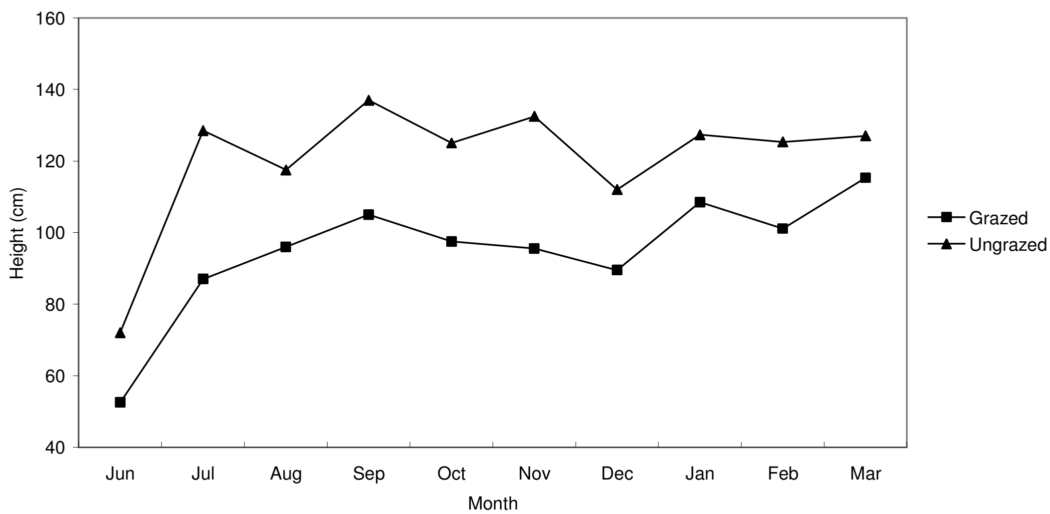


Figure 13. Mean monthly grass cover (a), grass greenness (b) and grass height (c) on grid 1 (grazed) and grid 2 (ungrazed) at eKundizeni Farm.

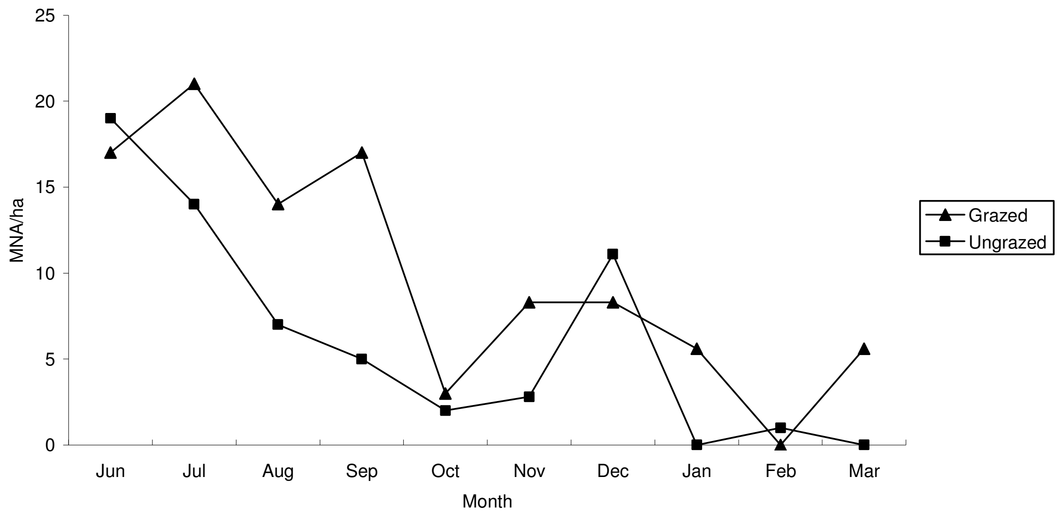
Five species of rodents and one species of insectivore were captured on the two grids with the capture of a seventh species (*Otomys angoniensis*) on grid 1 (Table 4). The total number of *Mastomys natalensis* and *M. minutoides* captured did not differ between the two grids (χ^2, $P >$

0.05). More *Lemniscomys rosalia* were captured on grid 2 than on grid 1 and this difference approached significance ($\chi^2 = 3.330, P < 0.1$). Significantly more *Crocidura hirta* were captured on grid 2 than on grid 1 ($\chi^2 = 9.432, P < 0.01$). Small sample sizes of the other species precluded statistical analysis. Monthly densities of *L. rosalia*, *M. natalensis*, *C. hirta* and *M. minutoides* are shown (Figure 14).

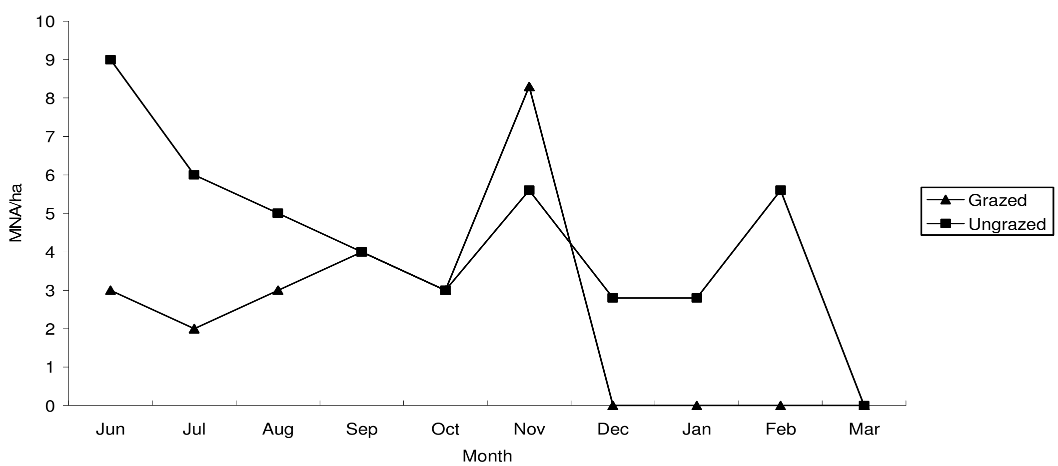
Table 4. Mean body weight and total numbers of small mammals captured between June 1997 and March 1998 on grazed and ungrazed grids at eKundizeni Farm, Swaziland. (The numbers presented are the actual numbers of individuals captured and have not been corrected for the reduction in size of trapping grids after October)

Species	Mean weight (g)	Grid	
		Grazed (1)	Ungrazed (2)
Rodentia			
Mastomys natalensis	32.8	34	26↓
Mus minutoides	5.8	22	16↓
Lemniscomys rosalia	48.2	7	13↑
Dendromus mystacalis	9.1	6	7
Steatomys pratensis	26.0	1	2
Otomys angoniensis	64	2	0
Insectivora			
Crocidura hirta	12.0	4	15↑

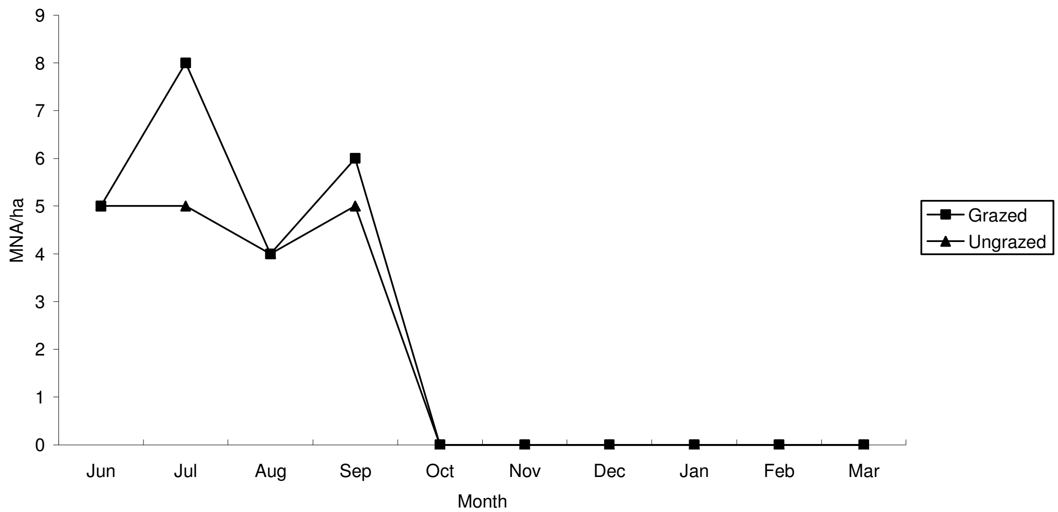
(a)


25
20
15
10
5
0
MNA/ha
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Month
Grazed
Ungrazed

(b)


10
9
8
7
6
5
4
3
2
1
0
MNA/ha
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Month
Grazed
Ungrazed

(c)



(d)

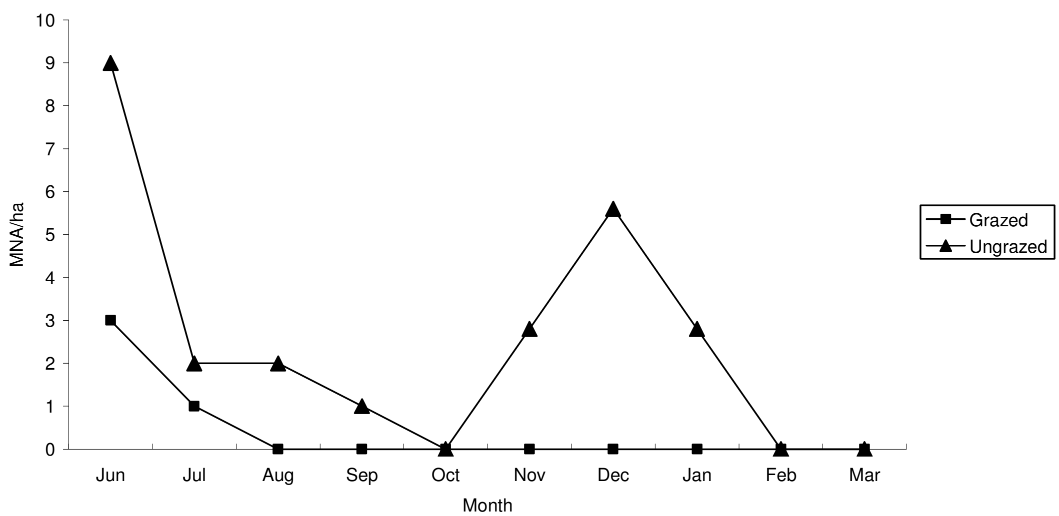


Figure 14. Monthly densities of *Mastomys natalensis* (a), *Lemniscomys rosalia* (b), *Mus minutoides* (c) and *Crocidura hirta* (d) on grid 1 (grazed) and grid 2 (ungrazed) at eKundizeni Farm.

Mus minutoides disappeared from both grids in October, while *L. rosalia* disappeared from grid 1 in December and *C. hirta* in August. *M. natalensis* was present on both grids for the duration of the study, albeit at reduced densities after September on grid 1 and after July on grid 2. There were significantly higher monthly densities of *C. hirta* (*Mann-Whitney* $U = 78.5$, $P < 0.05$) on grid 2 than on grid 1. Similarly, monthly densities of *L. rosalia* were higher on grid 2, this difference approached significance (*Mann-Whitney* $U = 73.0$, $P < 0.1$). There were no significant differences in monthly densities of *M. natalensis* on the two grids (*Mann-Whitney U*, $P > 0.05$).

Figure 15: A typical view of the study area in winter showing lack of cover.

Mean monthly biomass was not significantly different between the two grids (Table 5). However, the total biomass of *M. natalensis*, *L. rosalia*, *M. minutoides* and *C. hirta*, was significantly higher in the dry season (June – September) than in the wet season for both the grazed and ungrazed grids ($t = 2.62$, $P<0.05$ and $t = 2.32$, $P<0.05$; respectively). This effect was more significant for the grazed grid. Species richness was higher, but species diversity and evenness were lower, on grid 1 than on grid 2 (Table 5).

Table 5. Habitat and small mammal community characteristics on grazed and ungrazed grids at eKundizeni Farm.

Grid	Plant community			Small mammal community			
	Cover[1] (%)	Height[1] (cm)	Green[1] (%)	Richness*	Diversity	Evennes s	Biomass [1] (g/ha)
Grazed	86.7	94.8	39.2	7	0.50	0.59	219.8
Ungrazed	83.9	120.4	36.0	6	0.56	0.71	235.7

Figure 16. A typical view of the study area in summer. Note the *Parthenium* in the foreground and the grass only growing where its protected by thorns.

Discussion

Mlawula

The rainfall falling in MNR has decreased since 2000 to levels close to the lowest value of the annual dependable rainfall range (450 mm – 700 mm). The impact of this decrease in rainfall was in the vegetation which was scant in many areas for a greater part of the year. The lack of cover is a major factor contributing to the low density of small mammals. Previous studies have emphasized the importance of cover for small mammal species (Monadjem & Perrin 1997; Monadjem 1997; Hagenah 2006). Cover is a critical habitat factor for *L. rosalia* and *S. campestris* and these species do not occupy areas with low cover that offer no nesting sites or protection from predators and unfavourable climatic conditions (Monadjem & Perrin 1997).

The transect strip method used to estimate numbers of ungulates has some serious shortcomings (Braun 1992) but the main one is peculiar to MNR. Because culling is customarily done by shooting animals from the back of a vehicle, animals, especially impala, run and hide on sighting a slow moving vehicle (N. Dlamini pers.com.). This likely caused a gross underestimation of the ungulate populations in the area. However, the relative densities may reflect real trends and relationships in the mammal communities of the area. The greater Mlawula area (which includes the study area) is classified mainly vegetation unit L3 (Lubombo Plateau Broadleaf Savanna) (Sweet & Khumalo 1994) for which they recommended a stocking rate of 2.9-3.6 ha/LSU (LSU = livestock unit). The current stocking rate ranges from 1.82-2.27ha/LSU. Thus the area has a carrying capacity of ungulates beyond that recommended for continued productivity of the veld. Monadjem (1999) and Hagenah (2006) showed an inverse relationship between grazing pressure and abundance of small mammals. This density of ungulates above the carrying capacity likely caused the low grass cover and dominance of the alien invasive *Parthenium hysterophorus* (Figures 11 & 12). Densities of small mammal species were negatively correlated with *P. hysterophorus* and this was possibly mediated through the loss of the normal grass cover of the area. The few stands of grass that survived suffer from trampling and heavy grazing pressure. This result concurs with the observations of Saetnan and Skarpe (2006) who showed that in areas with large ungulates at high density there is a reduction in the species richness and density of small mammals caused by a reduction in graze and litter cover. Grazing pressure and loss of cover was exacerbated by the low rainfall in the area since it slowed down the recovery, production and germination of the grass and forb species.

The irregular unpredictable rainfall favoured the fast germinating, fast growing weed species particularly *Parthenium* which out-competed the grass and forb species. Scant rains also deprive small mammals of predictable food resources that negatively impact on local populations (Leirs *et al*. 1990). This could explain the near absence of the larger herbivorous rodents such as *Otomys* species.

EKundizeni

The preference of *L. rosalia* for areas with dense vegetation cover is well known (Bowland & Perrin 1988; Monadjem 1997; Monadjem & Perrin 1997). However, since ungulate grazing did not reduce grass cover in this study, some other factor must have been at play. Both grids had been burnt at the same time in September 1996 and therefore the age and amount of moribund grass was presumably similar. It is highly unlikely that grass height *per se* would have influenced the distribution of *L. rosalia* as, although grass was taller on the ungrazed grid, it was also tall (mean height almost 1 m) on the grazed grid. Grass species composition was the same on the two grids and was unlikely to have influenced the distribution of *L. rosalia*. Similarly, the reasons for the higher density of *C. hirta* on the ungrazed are unknown but may be correlated with subtle differences in cover, since it selects areas with dense grass and litter cover (Skinner & Chimimba 2005). *Crocidura hirta* populations are severely affected by overgrazing (A. Monadjem pers. com.). Moderate grazing may result in a reduction in cover with a concomitant decrease in *C. hirta* numbers.

The significantly higher biomass during the dry season (beginning of the study) is thought to be a result of the higher than normal rainfall during the preceding two years. The higher biomass in the grazed grid is similar to observations made by Nyako-Lartey & Baxter (1995) i.e., that there was higher biomass and lesser species diversity in areas grazed by cattle or undergoing rotational resting than areas grazed by goats. Species like *M. natalensis* and *M. minutoides* seemed to prefer the slightly shorter grass of the grazed area.

At many southern African savanna localities, rainfall has had an over-riding influence on vegetation cover (O'Connor 1985). Rainfall, therefore, likely influences community structure of small mammals in the region. Unfortunately, few long-term population studies of small mammals have been conducted in southern Africa, and none have investigated the combined effects of rainfall and grazing pressure. The present study was conducted during a year which experienced average rainfall but was preceded by two years of above-average rainfall. The good rains of the preceding two years may have reduced observable differences in vegetation structure on the two grids resulting in insignificant differences in the populations and community structure of the small mammals.

It appears that grazing does not have to be severe to affect small mammal abundance. A detailed investigation into the effects of grazing intensity on small mammals of southern Africa is highly desirable considering the extent of land dedicated to stock- and game-farming in this region.

References

BEGON, M., HARPER, J.L. AND TOWNSEND, C.R. 1986. *Ecology, individuals, populations and communities.* Blackwell Scientific Publications, Oxford.

BOND, W., FERGUSON, M AND FORSYTH, G. 1980. Small mammals and habitat structure along altitudinal gradients in the southern Cape mountains. *South African Journal of Zoology* **15**(1): 35-43.

BOWLAND, A.E. AND PERRIN, M.R. 1988. The effect of fire on the small mammal community in Hluhluwe Game Reserve. *Zeitschrift für Säugetierkunde* **53**: 235-244.

BOWLAND, A.E. AND PERRIN, M.R. 1989. The effect of overgrazing on the small mammals in Umfolozi Game Reserve. *Zeitschrift für Säugetierkunde* **54**: 251-260.

BRAUN, K. 1992. Road transect count of impala, Mlawula Nature Reserve. Unpublished Report. Swaziland National Trust Commission, Lobamba.

BUCKLAND, S.T., ANDERSON, D.R. BURNHAM, K.P. AND. LAAKE, J.L. 1993. *Distance sampling. Estimating abundance of biological populations.* Chapman and Hall, London.

DELANY, M.J. 1964. An ecological study of the small mammals in the Queen Elizabeth Park, Uganda. *Revue de Zoologie et de Botanique Africaines.* **70**: 129-147.

ELTON, C. 1924. Fluctuations in numbers of animals. *British Journal of Experimental Biology* **2**: 119-163.

FIRQUET, E., LEIRS, H. AND BRONNER, G. 1996. Germinating grasses and reproductive seasonality of *Mastomys* species (Rodentia, Muridae). *Mammalia* **60**(4): 775-779.

FITZGIBBON, C.D. 1995. Distribution, population dynamics and habitat use of the lesser pouched rat, *Beamys hindei*. *Journal of Zoology*, London **236**: 499-512.

GRANT, W.E., BIRNEY, E.C., FRENCH, N.R. AND SWIFT, D.M. 1982. Structure and productivity of grassland small mammal communities related to grazing-induced changes in vegetative cover. *Journal of Mammalogy* **63**: 248-260.

HAGENAH, N. 2006. *Among rodents and rhinos: Interplay between small mammals and large herbivores in a South African savanna.* Wageningen University. Wageningen.

HAPPOLD, D.C.D. AND HAPPOLD, M. 1989. Biogeography of montane small mammals in Malawi, Central Africa. *Journal of Biogeography* **16**: 353-367.

HAPPOLD, D.C.D. AND HAPPOLD, M. 1991. An ecological study of small rodents in the thicket-clump savanna of Lengwe National Park, Malawi. *Journal of Zoology, London* **223**: 527-547.

HAPPOLD, D.C.D. AND HAPPOLD, M. 1992. The ecology of three communities of small mammals at different altitudes in Malawi, Central Africa. *Journal of Zoology, London*. **228**: 81-101.

KREBS, C.J. 1966. Demographic changes in fluctuating populations of Microtus californicus. *Ecological Monographs* **36**(3): 239-273.

KREBS, C.J. AND MYERS, J.H. 1974. Population cycles in small mammals. *Advanced Ecological Research* **8**: 267-399.

LENZI-GRILLINI, C.R., VISKANIC, P. AND MAPESA, M. 1996. Effects of 20 years of grazing exclusion in an area of the Queen Elizabeth National Park, Uganda. *African Journal of Ecology* **34**: 333-341.

LEIRS, H., STUYCK, J., VERHAGEN, R. AND VERHEYEN, W. 1990. Seasonal Variation in growth of *Mastomys natalensis* (Rodentia: Muridae) in Morogoro, Tanzania. *African Journal of Ecology* **28**: 298-306.

LIMA, M., STENSETH, N.C. LEIRS, H AND. JAKSIC, F.M. 2003. Population dynamics of small mammals in semi-arid regions: a comparative study of demographic variability in two rodent species. *Proceedings of the Royal Society of London B*. **270**: 1997-2007.

MAHLABA, T.A.M. AND PERRIN, M.R. 2003. Population dynamics of small mammals at Mlawula, Swaziland. *African Journal of Ecology* **41**: 317-323.

MONADJEM, A. 1997. Habitat preferences and biomasses of small mammals in Swaziland. *African Journal of Ecology* **35**: 64-72.

MONADJEM, A. 1998. Effects of food supplementation and fire on small mammal community structure in a Swaziland Grassland. *South African Journal of Science* **94**: 89-93.

MONADJEM, A. 1999. Geographic distribution patterns of small mammals in Swaziland in relation to abiotic factors and human land-use activity. *Biodiversity and Conservation* **8**: 223-237.

MONADJEM, A. 1998. Effects of food supplementation and fire on small mammal community structure in a Swaziland Grassland. *South African Journal of Science* **94**: 89-93.

MONADJEM, A. 1999. Geographic distribution patterns of small mammals in Swaziland in relation to abiotic factors and human land-use activity. *Biodiversity and Conservation* **8**: 223-237.

MONADJEM, A. AND PERRIN, M.R. 1997. Population dynamics of Lemniscomys rosalia (Muridae: Rodentia) in a Swaziland grassland: effects of food and fire. *South African Journal of Zoology* **32**(4): 129-135.

MONADJEM, A. AND PERRIN, M.R. 1998. Effects of supplemental food on the habitat selected by Mastomys natalensis (Muridae: Rodentia) in a subtropical grassland in Swaziland. *South African Journal of Zoology* **33**(3): 172-177.

NYAKO-LARTEY, Q. AND BAXTER, R.M. 1995. The effects of different grazing regimes on the population dynamics of small mammals in the Eastern Cape. *Transactionsof the Royal Society of South Africa* **50**: 143-151.

O'CONNOR, T.G. 1985. A synthesis of field experiments concerning the grass layer in the savanna regions of southern Africa. *South African National Scientific Programmes Report 114.* CSIR. Pretoria.

ROGERS, L.M. AND GORMAN, M.L. 1995. The population dynamics of small mammals living in set-aside and surrounding semi-natural and crop land. *Journal of Zoology, London* **236**: 451-464.

SAETNAN, E.R. AND SKARPE, C. 2006. The effect of ungulate grazing on a small mammal community in southeastern Botswana. *African Zoology* **41**(1): 9-16.

SKINNER, J. D., & CHIMIMBA, C. T. 2005. *The mammals of the Southern African Subregion*. Cambridge: Cambridge University Press..

STENSETH, N.C., LEIRS, H., SKONHOFT, A., DAVIS, S.A., PECH, R.P., ANDREASSEN, H.P., SINGLETON, G.R., LIMA, M., MACHANG'U, R.S., MAKUNDI, R.H., ZHANG, Z., BROWN, P.R., SHI, D. AND WAN, X. 2003. Mice, rats, and people: the bio-economics of agricultural rodent pests. *Frontiers in Ecology and the Environment* **1**(7): 367-375.

SWEET, R.J. AND KHUMALO, S. 1994. *Range resources and grazing potentials in Swaziland*. Government of Swaziland/United Nations Development Programme. Mbabane.

WIRMINGHAUS, J.O. AND PERRIN, M.R. 1993. Seasonal changes in density, demography and body composition of small mammals in a southern temperate forest. *Journal of Zoology, London* **229**: 303-318.

YOCCOZ, N.G., STENSETH, N.C., HENTTONEN, H.AND PREVOT-JULLIARD, A. 2001. Effects of food addition on the seasonal density dependent structure of bank vole Clethrionomys glareolus populations. *Journal of Animal Ecology* **70**: 713-720.

ZAR, J.H. 1999. *Biostatistical Analysis.* Prentice Hall, New Jersey.

CHAPTER 4

The effects of cover and supplemental food on the re-introduction of the multimammate mouse (*Mastomys natalensis*) to Mlawula Nature Reserve, Swaziland

Abstract

The aim of this study was to investigate the causes of the failed establishment of reintroduced *Mastomys natalensis* in the Siphiso Valley of Mlawula Nature Reserve where rodent densities were very low. The low density in the study area was thought to have resulted from overgrazing by ungulates which reduced food availability and habitat quality. Two hundred and seventy-two mice trapped from Vuvulane were released on to eight grids on two occasions in 2004, 144 in October and 128 in December. The eight grids represented two sets of replicates with one pair receiving extra cover, or supplemental food and additional cover, or additional food only, or no cover or food manipulation (controls). The reintroduced populations declined rapidly on all the grids. Disappearance rates differed significantly between the treatments as evidenced by regression equations fitted to the data sets. Populations that received supplementary food persisted the longest while the impact of additional cover was small. Other unknown factors and possibly predation were likely responsible for the rapid decline in reintroduced mice.

Introduction

Habitat factors such as cover, food and nest site availability are very important for the viability of small mammal populations and define habitat quality. A number of studies have demonstrated the importance of habitat factors in determining the structure of small mammal communities and the population dynamics of individual species (Kern 1981; Grant *et al.* 1982; Montgomery *et al.* 1991; Canova *et al.* 1994; Edge *et al.* 1995; Oguge 1995; Monadjem 1997a; 1998b; Keesing 2000; Hagenah 2006). The population dynamics of a species is indicative of the conditions of existence in the habitat (Bernshtein *et al.* 1989). At high densities, rodents have small home ranges and occupy secondary (less favourable) habitats lacking cover, nesting sites or adequate food supplies which may cause emigration or increased mortalities (Murray 1979). Cover is very important for rodents (Bond *et al.* 1980) as it offers protection from predators (Kotler *et al.* 1991; Dickman 1992), influences microclimate, and the level of intra- and inter- specific confrontation, thus reducing behavioural stress (Birney *et al.* 1976). In the vole, *Microtus arvalis,* nest site unavailability and other resource limitations result in dispersal (Boyce & Boyce 1988; Gliwicz 1988).

The hispid cotton rat, *Sigmodon hispidus*, utilizes habitat with insufficient cover when sufficient food is obtainable suggesting that food may be more important than predator avoidance and that there is an equilibrium between the risk of exposure and the reward of food (Eshelman & Cameron 1996; Monadjem & Perrin 1998). Food availability determines the amount of time spent foraging, diet composition and quality, and density and home range size in woodmice (*Apodemus sylvaticus*) (Gorman & Zubaid 1993; Zubaid & Gorman 1993a; 1993b). In the same species, food availability and quality influences physiology, range size and mortality. Rodent populations respond to variations in primary production and fluctuations in food availability (Brown & Zeng 1989; Mallorie & Flowerdew 1994) and their distribution is correlated with the distribution of food (Montgomery *et al.* 1991). Increased habitat complexity leads to occupancy by many small mammal species because it offers different microhabitats in terms of availability of cover, food and other habitat factors (Rowe-Rowe & Meester 1982). The importance of food in the reproduction of African small mammals has been well demonstrated (Happold 1975; Perrin 1980; Perrin & Swanepoel 1987; Leirs *et al.* 1990; Wirminghaus & Perrin 1992; Firquet *et al.* 1996). In the multimammate mouse *Mastomys natalensis* the female is responsible for the timing of breeding which is moderated through food availability (Bronner & Rautenbach 1988).This is because reproduction involves the commitment of a large amount of physiological resources that would be unavailable if there was insufficient food or the food was not of good quality.

The role played by habitat factors in small mammal ecology has been the subject of a number of studies in Swaziland (Monadjem 1997a; Monadjem & Perrin 1997; Monadjem 1998c Monadjem & Perrin 1998). These studies, however, did not cover the fascinating case of Mlawula Nature Reserve (Mlawula) which seems to have lost its once vibrant small mammal community. Earlier studies in the same area recorded small mammal densities of 57 rodents/ha (Monadjem 1998c) and 19 rodents/ha (Mahlaba & Perrin 2003). By 2003, the rodent density in the area had fallen to zero, even the pygmy mice *Mus minutoides* which were common in 2000/2001 had disappeared from a study site although a few single striped mice *Lemniscomys rosalia* remained. This study, therefore, was aimed at evaluating the role played by cover and food availability in the disappearance of small mammals from the site. The primary hypothesis was that the provision of supplemental food and additional cover will result in re-introduced animals establishing and remaining in the grids.

Reintroduction refers to establishing or attempting to establish a species in an area in which it formerly occurred (McCleery *et al.* 2005). Reintroduced animals face a number of challenges upon release which include those that resulted in the initial extinction and lack of familiarity with the area and therefore difficulties in locating food sources and safe areas, for example. Wild caught animals often establish quicker than captive bred ones (Bright & Morris 1994). Removing some of the obstacles should lead to reintroduced animals settling in and remaining in the area (van Dierendonck *et al.* 1996).

Study Areas, Materials and Methods

Mlawula Nature Reserve

The study was carried out in Mlawula Nature Reserve (Mlawula), in north-eastern Swaziland (26°11'S: 31°59'E, 160 m a.s.l.). The 16500 ha reserve encompasses part of the Lubombo Mountains, Lowveld plains and the Mlawula and Siphiso rivers. It is bounded by Mozambique to the east, Shewula Game Reserve to the north, Mbuluzi and Hlane Game Reserves to the west and Royal lands to the south. Altitudes within Mlawula range from 76 m a.s.l. in the Mbuluzi gorge to around 500 m a.s.l. on the Ndzindza plateau. Mean monthly temperatures range from 17°C-27ºC and the annual dependable rainfall 450-700 mm. The vegetation comprises Acacia woodland in lower areas and combretaceous woodland on the slopes of the Lubombo Mountains (Sweet & Khumalo 1994).

The study site was located in Acacia woodland in the Siphiso valley with the dominant trees being *Acacia nigrescens*, *Bolusanthus speciosa* and *Combretum imberbe*. The area was burnt in August 2000 and within three months was covered by the alien invasive herb *Parthenium* *hysterophorus* and the alien invasive bush *Chromolaena odorata*, which occurred in clumps. The area had large numbers of zebra (*Equus burchelli*), impala (*Aepyceros melampus*), blue wildebeest (*Connochaetes taurinus*), kudu (*Tragelaphus strepsiceros*) and warthog (*Phacochoerus africanus*) (T. Mahlaba pers. obs).

Vuvulane

The area is located in north-eastern Swaziland (31°50':26°03', 500 m a.s.l) in the Lubombo region to the north of Mlawula. The mean annual dependable rainfall ranged from 450-550 mm, whilst the mean temperature range was 5-32°C. The natural vegetation is classified as Eastern Lowveld *Acacia nigrescens* savanna (Sweet & Khumalo 1994). As a consequence of intensive agricultural activity it has lost much of its natural vegetation except in isolated patches.

The rodents for re-introduction were trapped from two sites. Site 1 is located proximal and to the east of Vuvulane High School premises. It is a fallow sugar cane field last cultivated about two years ago (T. Mahlaba pers. obs.), presently, it is covered by tall grasses, including stands of sugarcane, and small Acacia trees. Site 2 is to the west of the school adjacent to an irrigation dam. It is rank grassland with occasional Acacia and marula trees, *Sclerocarya birrea*. Vuvulane was chosen from a number of sites because of its proximity to Mlawula and the large numbers of *M. natalensis* that were caught during pre-trapping regimes.

Methods

Collection of Mastomys. natalensis

The *Mastomys natalensis (sensu lato)* for release into Mlawula were trapped from two sites in Vuvulane. At each site, a 150 m transect line with 10 m between trap points was set up with one Sherman trap at each point. Traps were baited with oats and were set in the late afternoon and checked at dawn. They were left closed during the day to avoid mortalities due to heat. Animals caught were weighed, sexed and uniquely identified before being placed in transport cages, taken to Mlawula and kept in large cages. The period between collection and release was 21 days for the first round and 29 days for the second round. During this period the male and female mice were kept in separate cages. When sufficient numbers of male and female mice had been collected they were divided into eight groups (each group comprising equal numbers of males and females) before release onto the eight study grids at Mlawula.

Releases

Eight permanent grids (70 x 70 m) on which trapping had been carried out since 2000 were prepared. The grids, set 100 m apart, were located in the Siphiso valley and all appeared to have similar vegetation and microhabitats. For the treatment, the grids were randomly selected. Grids 1, 3, 5 and 6 received extra cover (+cover) in the form of cut *Dicrostachys cinerea* bushes. These were placed in a 6 x 6 network regularly within the grid, with a bunch of bushes placed at the centre of each set of four trap-points with 10m spacing between bushes. Existing cover, which was scant, in each grid was not removed. Grids 2 and 8 had all the cover removed (-cover) while grids 4 and 7 had no cover manipulation or additional food (controls). Because the study area was bare of vegetation for the duration of the study, these two grids were not much different from those that had cover removed. Grids 2, 3, 5 and 8 were further prepared by scattering oats as evenly as possible (2 kg/ha once a week) (+food) while grids 1 and 6 had no additional food. Eighteen adult *M. natalensis* (9 ♂and 9 ♀) were released in each of the eight grids at 17h00 on 23 October 2004. Immediately after the release, Sherman traps were set in each of the grids with 10 m between trap points and one trap per point. Traps were closed during the day, set in the late afternoon, and checked at dawn each morning. Animals caught were identified using their unique toe clip number and then released. This was continued for three weeks or until all marked mice had disappeared.

The collection and release exercise was repeated. On 14 December 2004, 16 *M. natalensis* (8♂ and 8♀) were released in each of the eight grids. Because of increasing difficulty in getting animals to be released, the exercise could not be repeated a third time, as initially planned.

Statistical analysis

For each repetition the data from each pair of similarly treated grids was averaged and analyzed using the statistical software ‘GenStat 9’. Non-linear regression and accumulated analysis of variance (Zar 1999) were performed using the software. In the ‘regression analysis’ mode, the ‘standard curves’ option was selected with ‘treatment’ as the grouping factor, ‘day after release’ as the explanatory variable and number of animals remaining in the grid as the response variable. Data from the two repetitions were analysed separately as preliminary analysis of the data (basic statistics) showed that they were disparate.

An analysis of the area under the curve (AUC) was calculated using the trapezoidal rule (in GenStat 9). The AUC provides a measure of the persistence of the animals in each of the treatments. If animals persisted for a long time in a grid then the AUC (in animal-days) was larger in comparison with the case where the animals did not persist for a long time. The AUCs were tested using analysis of variance to determine the impact of the treatments (Zar 1999) on persistence of the *M. natalensis* in each of the grids.

Results

A plot of the decline in the populations of the *M. natalensis* introduced into the study area generated a reversed (negative) exponential curve in all the habitats under study. The population declined rapidly in the beginning with very few individuals surviving for an extended period of time.

In all of the treatments, the released *M. natalensis* disappeared very rapidly so by the end of the first week after release, less than a third of the released animals remained in any of the grids (Figures 17 & 18). The populations, in all the habitats, declined rapidly with a mean half life of 2.3 days.

There was a logarithmic relationship between the number of animals remaining versus days after release. The formula for the best fit in each case was of the type:

$$y = A + BR^x$$

where y = number of animals remaining, A = y intercept, B = slope of curve, R = a constant and x = number of days after release

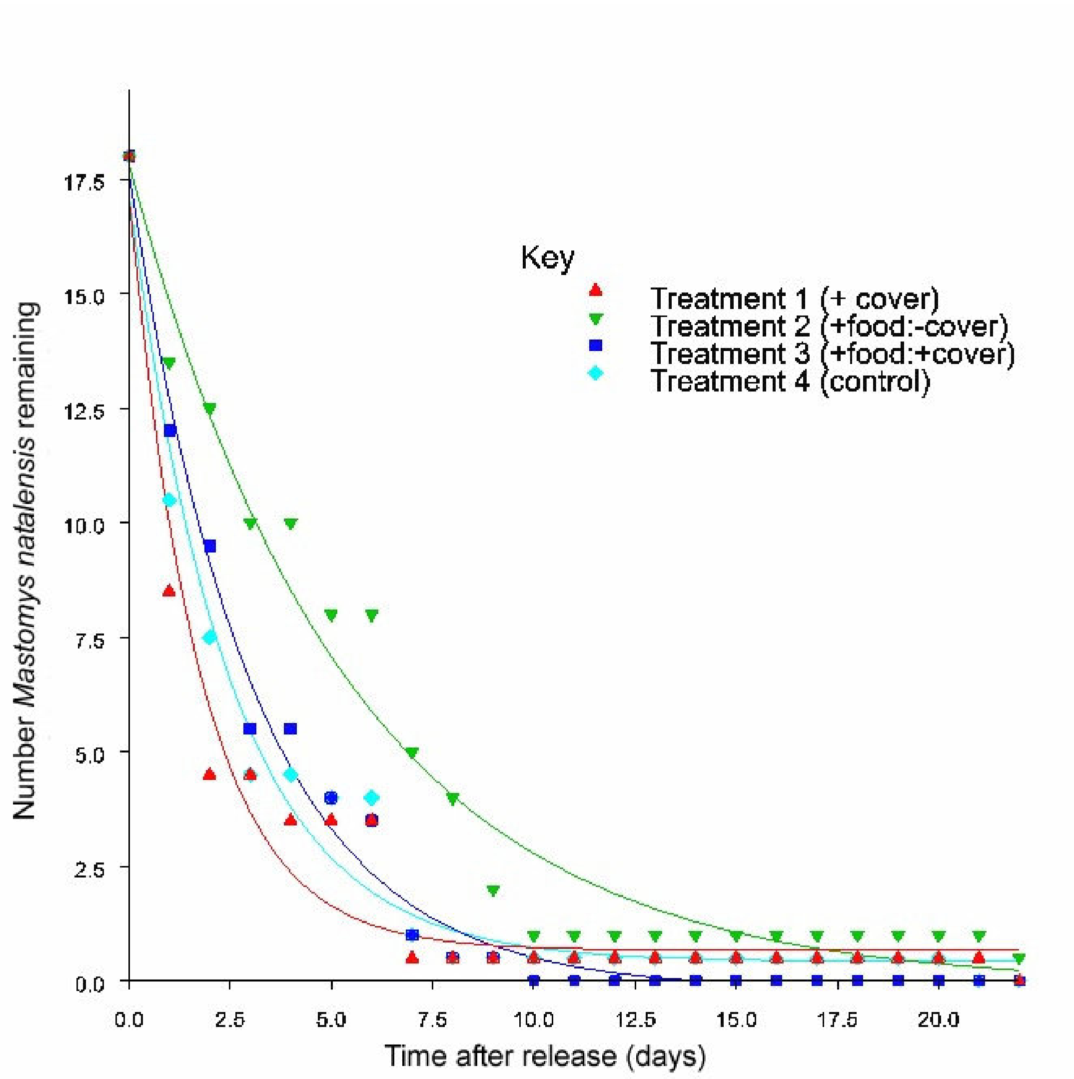


Figure 17: Number of *Mastomys natalensis* remaining versus day after release in October (with fitted curves).

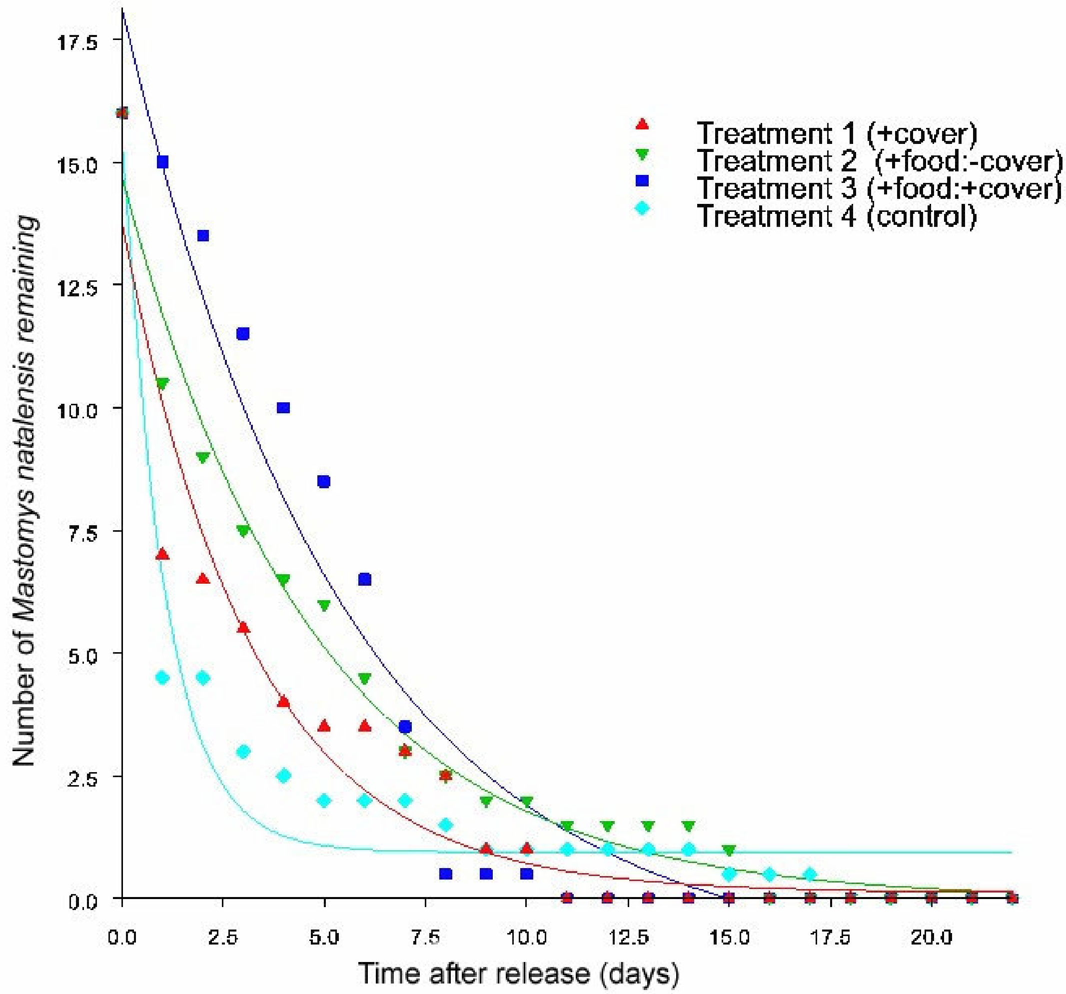


Figure 18: Number of *Mastomys natalensis* remaining versus day after release in December (with fitted curves).

An accumulated analysis of variance of these data showed that the treatments had significantly different impacts on the persistence of the released *M. natalensis* (Figure 18, Table 6). In both repetitions, mice in treatments receiving additional food but no additional cover (+food:-cover) and those receiving additional food and cover (+food:+cover) persisted longest while those on the control grids and those without additional food persisted the least.

The presence of extra cover without additional food in grids 1 and 6 did not result in animals remaining longer on those grids.

Table 6. (a) Accumulated analysis of variance results for Round 1 (October) and (b) accumulated analysis of variance results for Round 2 (December).

(a)

Change	d.f.	m.s.	$F_{calculated}$	P
+ Day	2	855.8553	1305.80	<0.001
+ HABITAT	3	22.9447	35.01	<0.001
+ Day.HABITAT	3	5.5364	8.45	<0.001
+ Separate	3	18.0458	27.53	<0.001
Residual	80	0.6554		
Total	91	20.9201		

(b)

Change	d.f.	m.s.	$F_{calculated}$	P
+ Day	2	710.044	673.44	<0.001
+ HABITAT	3	15.727	14.92	<0.001
+ Day.HABITAT	3	25.646	24.32	<0.001
+ Separate	3	18.136	17.20	<0.001
Residual	80	1.054		
Total	91	18.494		

An analysis of variance for the AUC data showed that there was no significant difference between the four treatments for both instances ($F_{3,7} = 1.07$; P = 0.455 for the October release and $F_{3,7} = 3.70$; P = 0.119 for the December release). However, there was great variability in the individual areas under the curve (Table 7 & Figure 19). In October the grids receiving additional food and no cover had mice with the longest persistence while in December it was the grids receiving food and cover that persisted longest. In October, with the exception of the grids with food and cover, the grids had low AUCs while in December there was variability in AUCs.

Table 7. Areas under the curve (AUC) for the four treatments for October and December are presented. Where 1 = +cover, 2 = +food;-cover, 3 = +food;+cover and 4 = control.

Treatment	**1**	**2**	**3**	**4**
October				
Replicate 1	72	69	31	64
Replicate 2	17	119.5	71	39
December				
Replicate 1	27	70	82	43
Replicate 2	64	67	74	32

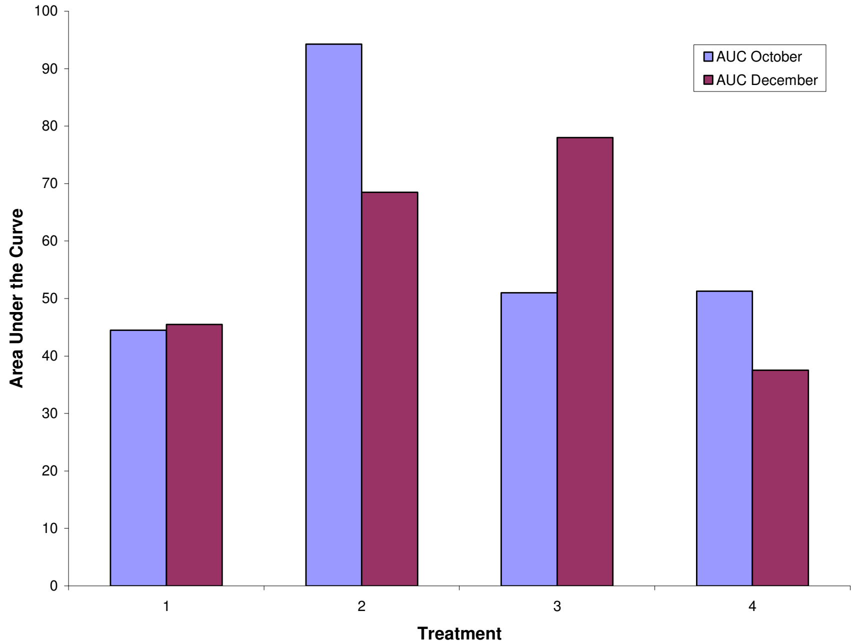


Figure 19: Mean area under the curve (AUC) for the four treatments for October and December. Where 1 = +cover, 2 = +food;-cover, 3 = +food;+cover and 4 = control.

Discussion

The rate of decline of the released *M. natalensis* was very high although no similar studies are reported in the available literature. This rapid disappearance of *M. natalensis* from the study grids is likely the result of predation and emigration. Emigration is probably insignificant at this site as the area is uniformly resource poor and without cover, so the study grids were the only places with food and cover in the greater study area. However, trap-shyness, low densities in the area and other factors may have resulted in the trapping success. The aggregation of warthogs, baboons and birds on the grids with food emphasizes the general lack of food resources in the area. Although adequate food was laid out (the grids were regularly checked for oat pellets), the impact of the presence of the other species on these grids had a confounding effect. Dispensing the oats in the centralized 'feeding areas' attracted baboons, warthogs and birds which interfered with the traps.

The presence of the released mice in the area may have attracted predators that fed on them. The area is known to have barn owls, *Tyto alba*, spotted eagle owls, *Bubo africanus* and other species of owl (Parker 1994) that are known to feed on small mammals (Perrin 1982, Wirminghaus & Perrin 1992). The study area also has a number of mammalian predators such as African striped weasel (*Poecilogale albinucha*), large-spotted genet (*Genetta tigrina*), slender mongoose (*Galerella sanguinea*) (Monadjem 1998b) and non-mammal predators such as snakes and birds of prey. It is suspected that the impact of predation was overlooked in this study. Predators are known to respond very rapidly to increases in prey density (Lin & Batzli 1995) and can have a big impact on small mammal populations leading to declines and local extinctions (Wingate *et al.* 1976). The unfamiliarity of the mice with the territory and burrows meant that these mice were vulnerable to predation. This was exacerbated by the lack of cover in the area and the fact that they came from an area with very dense cover and perhaps fewer predators. The rapid disappearance of the introduced *M. natalensis* may be the result of high predation pressure, which explains why the patchy cover that was provided on some of the grids was ineffective.

The interactions of small mammals and their habitats are very complex. The dissimilarity of the rates of population decline between the two repetitions demonstrates this. However, it is clear that food is a crucial factor in small mammal persistence. In both repetitions, the grids that had animals persisting the longest had supplemental food. This underlines the importance of food to small mammals (Akbar & Gorman 1993a; 1993b; Canova *et al.* 1994; Monadjem 1997a, 1998b). The small influence of cover in this study further emphasizes the importance of food. Small mammals will risk predation by sacrificing cover for food (Kotler *et al.* 1988; Eshelman & Cameron 1996; Monadjem & Perrin 1998). The cover that was used in this study may have been inadequate; providing only insufficient protection.

The rate of disappearance in the area under the curve analysis demonstrates the complexity of animal-habitat interactions. It showed that additional food did result in longer persistence especially on the grids with no cover but additional food. However, the small impact of additional food on the grids with additional food and cover is not understood. This is thought to be the result of other factors such as predation and emigration that were not quantified. The effects of the increased numbers of other rodents in the area are further confounding factors. Although the analyses of AUC were not significant they do, however, suggest the advantage of the food and cover combination over that of additional food. Cover without additional food offered some slight advantage to the *M. natalensis.*

Ungulates as well as rodents at Mlawula were under severe food shortages. As a result of overgrazing and competition with the ungulates the rodents had no cover or food. Ungulates compete with small mammals for food and decrease cover availability for rodents (Hagenah 2006). This resulted in *Mus minutoides* being the dominant species in the area during a previous study (Mahlaba & Perrin 2003) though it is now present at very low densities. Other species including *Saccostomus campestris*, *M. natalensis, Steatomys pratensis* and *Aethomys chrysophilus* which were recorded in previous studies, have disappeared while *Lemniscomys rosalia* are occasionally trapped (T. Mahlaba pers. obs.). The above species are herbivore-granivores and granivore-herbivores (Monadjem 1997b). Since seeds are normally available for only part of the year, these mice rely on plant food for the greater part of the year causing direct competition with the ungulates. The species that disappeared prefer areas with good cover (Skinner & Chimimba 2005).

It is clear that food and possibly cover are among the habitat factors responsible for the very low densities of small mammals at Mlawula. A similar study incorporating more effective cover, predator impacts, and a more even distribution of food is necessary to answer some of the remaining questions.

References

AKBAR, Z. AND GORMAN, M.L. 1993a. The effect of supplementary feeding upon the demography of a population of woodmice *Apodemus sylvaticus*, living on a system of maritime sand-dunes. *Journal of Zoology, London* **230**: 609-617.

AKBAR, Z. AND GORMAN, M.L. 1993b. The effect of supplementary feeding upon the sizes of home ranges of woodmice *Apodemus sylvaticus* living on a system of maritime sand-dunes. *Journal of Zoology, London* **231**: 233-237.

BERNSHTEIN, A.D., ZHIGALSKY, O.A. AND PANINA, T.V. 1989. Multi-annual fluctuations in the size of a population of the bank vole in European part of the Soviet Union. *Acta Theriologica* **34**(30): 409-438.

BIRNEY, E.C., GRANT, W.E. AND BAIRD, D.D. 1976. Importance of vegetative cover to cycles of *Microtus* populations. *Ecology* **57**: 1043-1051.

BOND, W., FERGUSON, M. AND FORSYTH, G. 1980. Small mammals and habitat structure along altitudinal gradients in the southern Cape mountains. *South African Journal of Zoology* **15**(1): 35-43.

BOYCE, C.C.K. AND BOYCE, J.L. 1988. Population ecology of *Microtus arvalis*. II. Natal and breeding dispersal of females. *Journal of Animal Ecology* **57**: 723-736.

BRIGHT, P. W. MORRIS, P.A. 1994. Animal Translocation for Conservation: Performance of Dormice in Relation to Release Methods, Origin and Season. *The Journal of Applied Ecology* **31**, (4): 699-708

BRONNER, G. AND RAUTENBACH, I.L. 1988. Environmental influence on reproduction in the Natal multimammate mouse *Mastomys natalensis* (A. Smith, 1834). *South African Journal of Wildlife Research* **18**(4): 142-148.

BROWN, J.H. AND ZENG, Z. 1989. Comparative population ecology of eleven species of rodents in the Chihuahuan desert. *Ecology* **70**(5): 1507-1525.

CANOVA, L., MAISTRELLO, L. AND EMILIANI, D. 1994. Comparative ecology of the wood mouse Apodemus sylvaticus in two differing habitats. *Zeitschrift für Säugetierkunde* **59**: 193-198.

DICKMAN, C.R. 1992. Predation and habitat shift in the house mouse, *Mus domesticus*. *Ecology* **73**(1): 313-322.

VAN DIERENDONCK, M.C. AND DE VRIES, M.F.W. 1996. Ungulate reintroductions:experiences with the takhi or Przewalski horse (*Equus ferus przewalski*) in Mongolia. *Conservation Biology* **10**(3): 728-740.

EDGE, W.D., WOLFF, J.O. AND CAREY, R.L. 1995. Density-dependent responses of gray-tailed voles to mowing. *Journal of Wildlife Management* **59**(2): 245-251.

ESHELMAN, B.D. AND CAMERON, G.N. 1996. Experimentally induced habitat shifts by hispid cotton rats (*Sigmodon hispidus*): response to protein supplementation. *Journal of Mammalogy* **77**(1): 232-239.

FIRQUET, E., LEIRS, H. AND BRONNER, G. 1996. Germinating grasses and reproductive seasonality of *Mastomys*-species (Rodentia, Muridae). *Mammalia* **60**(4): 775-779.

GLIWICZ, J. 1988. Seasonal dispersal in non-cyclic populations of *Clethrionomys glareolus* and *Apodemus flavicollis*. *Acta Theriologica* **33**(18): 263-272.

GORMAN, M.L. AND ZUBAID, A.B.M.A. 1993. A comparative study of the ecology of woodmice *Apodemus sylvaticus* in two contrasting habitats: deciduous woodland and maritime sand-dunes. *Journal of Zoology, London* **229**: 385-396.

GRANT, W.E., BIRNEY, E.C., FRENCH, N.R. AND SWIFT, D.M. 1982. Structure and productivity of grassland small mammal communities related to grazing-induced changes in vegetative cover. *Journal of Mammalogy* **63**: 248-260.

HAGENAH, N. 2006. Among rodents and rhinos: Interplay between small mammals and large herbivores in a South African savanna. *Department of Environmental Sciences*. Wageningen University. Wageningen**:** 138.

HAPPOLD, D.C.D. 1975. The effects of climate and vegetation on the distribution of small rodents in Western Nigeria. *Sonderdruck aus Zeitschrift für Säugetierkunde Bd.* **40**(H. 4): 221-242.

KEESING, F. 2000. Cryptic consumers and the ecology of an African savanna. *Bioscience* **50**(3): 205-215.

KERN, N.G. 1981. The influence of fire on populations of small mammals of the Kruger National Park. *Koedoe* **24**: 125-157.

KOTLER, B.P., GAINES, M.S. AND DANIELSON, B.J. 1988. The effects of vegetative cover on the community structure of prairie rodents. *Acta Theriologica* **33**(27): 379-391.

KOTLER, B.P., BROWN, J.S. AND HANSSON, O. 1991. Factors affecting gerbil foraging behaviour and rates of owl predation. *Ecology* **72**(6): 2249-2260.

LEIRS, H., STUYCK, J., VERHAGEN, R. AND VERHEYEN, W. 1990. Seasonal variation in growth of *Mastomys natalensis* (Rodentia: Muridae) in Morogoro, Tanzania. *African Journal of Ecology* **28**: 298-306.

LIN, Y.K. AND BATZLI, G.O. 1995. Predation on voles: an experimental approach. *Journal of Mammalogy* **76**(4): 1003-1012.

MAHLABA, T.A.M. AND PERRIN, M.R. 2003. Population dynamics of small mammals at Mlawula, Swaziland. *African Journal of Ecology* **41**: 317-323.

MALLORIE, H.C. AND FLOWERDEW, J.R. 1994. Woodland small mammal population ecology in Britain: a preliminary review of the Mammal Society survey of wood mice

Apodemus sylvaticus and bank voles *Clethrionomys glareolus*, 1982-87. *Mammal Reviews* **24**(1): 1-15.

MCCLEERY, R.A., LOPEZ, R.R., SILVY, N.J. AND GRANT, W.E. 2005. Effectiveness of supplemental stockings for the endangered Key Largo woodrat. *Biological Conservation* **124**: 27–33.

MONADJEM, A. 1997a. Habitat preferences and biomasses of small mammals in Swaziland. *African Journal of Ecology* **35**: 64-72.

MONADJEM, A. 1997b. Stomach contents of 19 species of small mammals from Swaziland. *South African Journal of Zoology* **32**(1): 23-26.

MONADJEM, A. AND PERRIN, M.R. 1997. Population dynamics of Lemniscomys rosalia (Muridae: Rodentia) in a Swaziland grassland: effects of food and fire. *South African Journal of Zoology* **32**(4): 129-135.

MONADJEM, A. 1998a. Effects of food supplementation and fire on small mammal community structure in a Swaziland Grassland. *South African Journal of Science* **94**: 89-93.

MONADJEM, A. 1998b. Biomass of rodents at Mlawula Nature Reserve, Swaziland. *Uniswa Journal of Agriculture, Science and Technology* **2**(1): 117-120.

MONADJEM, A. 1998c. *Mammals of Swaziland*. The Conservation Trust of Swaziland & Big Game Parks Mbabane.

MONADJEM, A. AND PERRIN, M.R. 1998. Effects of supplemental food on the habitat selected by *Mastomys natalensis* (Muridae: Rodentia) in a subtropical grassland in Swaziland. *South African Journal of Zoology* **33**(3): 172-177.

MONTGOMERY, W.I., WILSON, W.L., HAMILTON, R. AND MCCARTNEY, P. 1991. Dispersion in the wood mouse *Apodemus sylvaticus*: variable resources in time and space. *Journal of Animal Ecology* **60**: 179-192.

MURRAY, B.G. 1979. *Population Dynamics: Alternative Models*. Academic Press New York.

OGUGE, N.O. 1995. Diet, seasonal abundance and microhabitats of *Praomys* (*Mastomys*) *natalensis* (Rodentia: Muridae) and other small rodents in a Kenyan sub-humid grassland community. *African Journal of Ecology* **33**: 211-223.

PARKER, V. 1994. *The Swaziland Bird Atlas 1985-1991*. Webster's Mbabane.

PERRIN, M.R. 1980. The breeding strategies of two coexisting rodents, *Rhabdomys pumilio* and *Otomys irroratus*: with a brief review of some pertinent life history ideas. *Acta Oecologica/ Oecologica Generalis* **1**(4): 383-410.

PERRIN, M.R. 1982. Prey Specificity of the barn owl, *Tyto alba*, in the Great Fish valley of the Eastern Cape Province. *South African Journal of Wildlife Research* **12**: 14-25.

PERRIN, M.R. AND SWANEPOEL, P. 1987. Breeding biology of the bushveld gerbil *Tatera leucogaster* in relation to diet, rainfall and life history theory. *South African Journal of Zoology* **22**(3): 218-227.

ROWE-ROWE, D.T. AND MEESTER, J. 1982. Habitat preferences and abundance relations of small mammals in the Natal Drakensberg. *South African Journal of Zoology* **17**: 202-209.

SKINNER, J.D. AND CHIMIMBA, C.T. 2005. *The mammals of the Southern African Subregion*. Cambridge University Press Cambridge.

SWEET, R.J. AND KHUMALO, S. 1994. Range resources and grazing potentials in Swaziland. Government of Swaziland/United Nations Development Programme. Mbabane**:** 60.

WINGATE, C.J., WINGATE, I., LEDUC, J., REDFIELD, J.A., TAITT, M. AND HILBORN, R. 1976. *Microtus* population biology: dispersal in fluctuating populations of *M. townsendii*. *Canadian Journal of Zoology* **54**: 79-95.

WIRMINGHAUS, J.O. AND PERRIN, M.R. 1992. Diets of small mammals in a southern African temperate forest. *Israel Journal of Zoology* **38**: 353-361.

ZAR, J.H. 1999. *Biostatistical Analysis.* Prentice Hall, New Jersey.

ZUBAID, A. AND GORMAN, M.L. 1993a. The effect of supplementary feeding upon the sizes of the home ranges of woodmice *Apodemus sylvaticus* living on a system of maritime sand-dunes. *Journal of Zoology, London* **231**: 233-237.

ZUBAID, A. AND GORMAN, M.L. 1993b. The effect of supplementary feeding upon the sizes of the home ranges of woodmice *Apodemus sylvaticus* living on a system of maritime sand-dunes. *Journal of Zoology, London* **230**: 609-617.

CHAPTER 5

Parasites of small mammals from Mlawula Nature Reserve and Vuvulane, Swaziland

Abstract.

One hundred and thirty nine small mammals collected over a twelve month period, from two areas in Swaziland were examined for digestive system helminths. The gastrointestinal tracts contained the helminths *Syphacia sp.*, *Heligmonina sp.*, *Trichuris sp.*, *Protospirura sp.*, two unidentified nematode species and three cestode species. *Heligmonina sp.* is a new species and *Syphacia sp.* is probably a new species. Infestations by more than one gut parasite species per host were very uncommon in the sample from Mlawula Nature Reserve while a large number of specimens from Vuvulane had more than two gut parasites.

Introduction

Many poorer rural communities in Africa live in fairly close association with rodents, necessitating their studies, especially of their parasites, as they constitute an important reservoir of diseases, and the parasites are transmissible to both humans and their livestock (Arata & Gratz 1975, Abd El-Wahed *et al.* 1999). Rodent ectoparasites may transmit zoonotic diseases such as plague and murine typhus and the rodents harbour helminth parasites that complete their life cycles in other hosts, including man. Small mammals eat and soil crops both in the field and in storage and enter and occupy dwellings (Leirs 1994).

The study of helminths of wild rodents has been widely undertaken in Europe and North America although little is known of the biology of the helminths of African small mammals (Behnke *et al.* 2000). There have been very few studies of these parasites in southern Africa, particularly Swaziland. In South Africa, there have been a number of studies of the helminths of humans, domestic livestock and the larger wild mammals, but few have focused on small mammals (Horak 1999, Louw 1999, Van-Wyk *et al.* 1999, Boomker *et al.* 2000, Matthee *et al.* 2000, Woolhouse *et al.* 2000, Horak & Cohen 2001, Horak *et al.* 2001a, Horak *et al.* 2001b, Minnaar & Krecek 2001, Nsoso *et al.* 2001a, Nsoso *et al.* 2001b). In northern Africa, the 1928 study of nematodes of Nigerian mammals is significant (Baylis 1928). More recently, further studies have been published on the intestinal parasites of small mammals in Nigeria and Egypt (Ugbomoiko & Obiamiwe 1991; Abd El-Wahed *et al.* 1999, Behnke *et al.* 2000).

Very little is known about the occurrence and host specificity of parasites harboured by rodents in southern Africa, particularly Swaziland. Preliminary data suggest that there may be new species and fascinating novel host-parasite relationships to investigate (M. Durette-Desset pers. comm.).

This study was aimed at determining the occurrence, abundance and host specificity of gastro-intestinal parasites infesting small mammals at Mlawula Nature Reserve and Vuvulane in Swaziland.

The Study Area

Mlawula Nature Reserve

Mlawula Nature Reserve (MNR) is in the Lebombo Mountain Range of Swaziland (Sweet & Khumalo 1994). The altitude of this area is 250 - 600m. The vegetation of the study area consists of mixed woodland savanna with grasses, *Acacia* species and *Combretum* species (classified by Sweet & Khumalo (1994) as hillside bush and plateau savanna). Trapping was conducted in the Siphiso valley at eight sites with similar vegetation. The line transect was moved to a new site when no animals were caught. A full description of the study area is given in Mahlaba & Perrin 2003.

Vuvulane

The area is located to the northeast of Swaziland (31°50'E 26°03'S, 500m a.s.l) in the Lubombo region to the north of MNR. The mean annual dependable rainfall ranges from 450-550 mm, whilst the mean temperature range is 5-32°C. The natural vegetation is classified as Eastern Lowveld *Acacia nigrescens* savanna (Sweet & Khumalo 1994). As a consequence of intensive agricultural activity, it has lost much of its natural vegetation except in isolated patches.

The rodents were trapped at two sites. Site 1 is located to the east of Vuvulane High School premises. It is a fallow sugar cane field last cultivated about two years ago , presently, it is covered by tall grasses, including stands of sugarcane, and small Acacia trees. Site 2 is to the west of the school adjacent to an irrigation dam. It is rank grassland with occasional Acacia and marula, *Sclerocarya birrea*, trees.

Materials and Methods

A 500m line transect was set up with one trap at each trap point set 5m apart. Rodents were caught in Sherman live traps (H.B. Sherman Traps Inc., Tallahassee, Florida) baited with rolled oats. A total of 100 traps were set for three nights on each occasion. Traps were checked early in the morning, left closed during the day (to prevent unnecessary mortality of animals) and opened and re-baited in the late afternoon. The animals caught were identified then taken to the laboratory in individual containers, to prevent cross-contamination of ectoparasites. In the laboratory animals were euthanased using chloroform. Small mammals were then weighed and sexed. Length of body, tail, ear and hind foot (c/u) measurements were recorded and, in relation to body mass, provided an indication of physiological condition. Each animal was dissected to collect gut parasites.

Dissection

The body cavity was opened and inspected for signs of cysts or cestode larvae. The complete digestive system was removed by cutting the oesophagus anterior to the stomach and the terminal end of the rectum. The bile duct was checked for the cestode *Rodentolepis microstoma*.

The gastrointestinal tract was separated into the stomach, the small intestine (duodenum and ileum), caecum and large intestine (colon and rectum). Each part of the gastrointestinal tract and its contents were then carefully examined for parasites under a dissecting binocular microscope. The caecum was carefully searched for *Trichuris* worms and *Syphacia sp.*

All parasites found were carefully removed and placed into labeled storage tubes with 70% ethanol, identified using Baylis (1928), counted and recorded. Where identity was uncertain the helminths were classed into morpho-species and given a code (e.g., cestode 1 (C1), nematode 2 (N2), *etc.*). This code applied to that particular morpho-species consistently. Cestodes were flattened by compression under a cover slip with elastic bands in warm acetic acid-formalin (AFA) overnight, and then carefully peeled away and stored in 70% ethanol.

Gastro-intestinal parasite specimens were sent to the University of Nottingham for identification or confirmation of identification by Prof. J. M. Behnke and through him Prof. M-C. Durette-Desset of the Muséum National d’Histoire Naturelle in France.

Results

Unidentified gut parasite species are reported here as morphospecies. A description of the new species of *Heligmonina* is given in Chapter 6 which has been published (Durette-Desset *et al* 2007). The *Syphacia sp*. is possibly another new species as no description of it exists (J. Behnke pers. comm.).

Mlawula Nature Reserve

Fifty-eight specimens of four rodent species (the Natal multimammate mouse, *Mastomys natalensis*; single striped mouse, *Lemniscomys rosalia*; the little fat mouse, *Steatomys pratensis* and the pygmy mouse, *Mus minutoides*) and one insectivore (the lesser red musk shrew, *Crocidura hirta*), were trapped at MNR (Table 1). Most of the gut parasites collected came from *M. minutoides*. 74.4% were infected with gut parasites. Although higher infestation rates are recorded for some of the other species of small mammals (Tables 1 and 2) the number of rodent specimens examined prevented statistical analysis. For this reason, the greater part of the discussion is based on the results of *M. minutoides*.

Of the fifty-eight rodents caught, 44 (75.9%) were infected; 461 parasites were collected (339 from *M. minutoides*) (Table 2). Parasites found were *Syphacia sp*., *Heligmonina sp*., *Rodentolepis nana* and *Hymenolepis diminuta*. The mean intensity of infestation was 10.5 parasites/animal. Only *Heligmonina sp*. were collected from *C. hirta* while *L. rosalia* had *Heligmonina sp*., *R. nana* and *H. diminuta*. *Mus minutoides* and *S. pratensis* were infested by all three gut parasites. *Mastomys natalensis* was infested by *Syphacia sp*., *R. nana* and

Heligmonina sp. *Heligmonina sp., R. nana* and *H. diminuta* were found in the small intestine while *Protospirura sp*., the nematodes 1 and 2 and the fluke were in the stomach. The habitat of *Trichuris sp*. was the caecum. Seven small mammal specimens had two gut parasite species and none had more than two. Specimens which had cestodes had these in low numbers while those infested by *Heligmonina sp*. and *Syphacia sp*. had high intensities of infestation. One specimen of *M. minutoides* had 27 *Syphacia sp*. while another one had 47 *Heligmonina sp*. There is no evidence of host specificity of the gut parasites found in this study.

Table 8. Numbers and percentage of small mammals from Mlawula Nature Reserve and Vuvulane infested with gut parasites.

	Mastomys natalensis	*Mus minutoides*	*Lemniscomys rosalia*	*Steatomys pratensis*	*Saccostomus campestris*	*Otomys angoniensis*	*Crocidura hirta*	Total
MNR								
No. examined	4	39	7	5	-	-	3	58
Mean mass	38.40	5.96	65.09	26.70	-	-	9.90	
No. infested	2	29	6	5	-	-	2	44
Percentage infested	50	74.4	85.7	100	-	-	66.7	75.4
Vuvulane								
No. examined	31	-	35	2	6	3	-	81
Mean mass	50.80	-	60.70	28.30	78.7	62	-	
No. infested	12	-	13	1	4	2	-	34
Percentage infested	38.7	-	37.1	50	66.7	66.7	-	42

Six rodents were infested by more than one gastrointestinal parasite and none by more than two. Three *M. minutoides* specimens were respectively infested with *R. nana* and *H. diminuta*, *R. nana* and *Heligmonina*, and *H. diminuta* and *Syphacia*. One *S. pratensis* specimen was infested with *H. diminuta* and *Syphacia* and another had *R. nana* and *Heligmonina*. A single *M. natalensis* had *H. diminuta* and *Syphacia* while a *L. rosalia* specimen was infested with *H. diminuta* and *R. nana*.

Vuvulane

Eighty-one specimens of six species of small mammals were caught and examined for gut parasites (Table 8). *M. natalensis*, *L. rosalia*, *S. campestris*, *T. leucogaster*, *O. angoniensis* and *S. pratensis* were caught in this area. Thirty-four (42%) rodents were infested and conclusions were made for *M. natalensis* and *L. rosalia* which were caught in sufficient numbers.

Ten species of digestive system parasites were found in the guts of the small mammals examined. These comprised three species of cestode, six species of nematode and one species of fluke (F1). Four hundred and fourteen helminth specimens were collected and of these *Heligmonina* were the most numerous. *Rodentolepis nana*, *H. diminuta*, cestode 1 and *Heligmonina sp*. were found in most of the small mammal species.

The six species of small mammals found in Vuvulane had a number of parasites in common with the exception of nematode 1 which was only found in *S. campestris*; *Trichuris sp*. and *Syphacia sp*. which were only found in *M. natalensis*; and the fluke F1 which was only found in *L. rosalia*.

Of the *L. rosalia*, 17 had two or more species of gut parasites (ten had three to five) while of *M. natalensis*, nine had two or more (five had three to five). The small mammal specimens that were infested with the greatest number of different parasite species (4 and 5) also had the highest density of parasites.

Compared with *M. natalensis*, a much greater proportion of *L. rosalia* were infected with *R. nana* and *H. diminuta* although the mean number of parasites per animal is similar to that for *M. natalensis*.

Table 9. Infection rate (IR) (number infected/total number examined) and parasite load (PL) (mean numbers of each gut parasite per infected specimen).

Species	***Mastomys natalensis***		***Lemniscomys rosalia***		***Saccostomus campestris***		***Tatera leucogaster***		***Otomys angoniensis***		***Mus minutoides***		***Steatomys pratensis***	
	IR	**PL**	**IR**	**PL**	**IR**	**PL**	**IR**	**PL**	**IR**	**PL**	**IR**	**PL**	**IR**	**PL**
Mlawula Nature R														
Rodentolepis nana											3/39	2.67	3/5	2.0
Hymenolepis diminuta	1/4	2	3/7	1.67							4/39	1.25	3/5	2.33
Heligmonina sp	1/4	**7**	**3/7**	13							14/39	14.93	1/5	14
Syphacia sp	1	4									11/39	10.64	1/5	14
Vuvulane														
Rodentolepis nana	7/31	1.7	11/35	1.4	3/6	1.0	1/4	0.5	1/3	0.3				
Hymenolepis diminuta	6/31	2.5	22/35	2.3	2/6	1.0			1/3	1.3				
Cestode 1	7/31	2.1	7/35	1.6	2/6	0.8	1/4	1.0	2/3	1.7				
Cestode 2													1/2	0.5
Nematode 1					1/6	1.3								
Nematode 2			1/35	1			1/4	1.0						
Protospirura. muricola Mastophorus muris	2/31	19.5	4/35	2.3										
Heligmonina sp.	4/31	18	11/35	9	2/6	0.2			1/3	2.3				
Trichuris sp.	1/31	1												
Syphacia sp.	3/31	4.3												
F1			1/35	1										

Discussion

The high numbers of *M. minutoides* and the low numbers of the other small mammal species caught at MNR has been discussed in detail in Mahlaba & Perrin (2003). The infection rate in this species was much higher than in a study of helminths of small mammals in Nigeria which had an infection rate of 48.6% for *M. minutoides* (Ugbomoiko & Obiamiwe 1991). In this study, a larger percentage of *M. minutoides* were infected by fewer species of gut parasites. The parasite loads, however, were low.

The presence of only one species of gut parasite in each specimen of *M. minutoides* is probably related to the diet of the rodent although other factors maybe involved (Pisanu *et al.* 2001; Morand *et al.* 2006). There is a spatial and nutritional limit on the number of parasites that each rodent can support although some occupy different habitats in the animal (Chowdhury & Aguire 2000).

Recent observations have shown that most species of small mammal gut parasites are only found in one host species (J. Behnke pers. comm.). This is exemplified by the proposed *Heligmonina wakelini* found in *M. natalensis* which is a new species (Durette-Desset *et al.* 2007). It is highly likely that other gut parasite specimens may be undescribed species. This, therefore, means the gut parasites of small mammals in Swaziland require more in depth study.

The parasite species in rodents from both study sites showed specificity for parts of the alimentary canal. The cestodes, unidentified fluke and the nematode, *Heligmonina sp*. were only found in the small intestine; while the two unidentified nematodes and *P. muricola*/*M. muris* were found only in the stomach. *Syphacia sp.* and *Trichuris sp.* were only found in the caecum of the rodents. This needs further exploration as the issue of parasite host-specificity is a very complicated one, determined by the ecology of the host and ecology of the parasite and often confounded by factors such as sampling effort and identification of parasites and their hosts (Pisanu *et al.* 2001; Morand *et al.* 2006).

The infection rate of the rodents from Vuvulane was lower compared with similar studies done elsewhere (Ugbomoiko & Obiamiwe 1991, Abd El-Wahed *et al.* 1999). It was also lower than that observed for *M. minutoides* in MNR. The number of parasite species was much higher here (10) compared with MNR but lower than reported by Ugbomoiko and Obiamiwe (1991) who found 20 parasite species in eight species of rodents. In the latter study, much higher numbers of rodents were examined while in MNR lower numbers of rodents and species of rodents were examined.

The validity of the mean density of parasites per rodent here is difficult to assess as there were far fewer rodent specimens infested with each parasite. Density of parasites per host is related to genotype of the host (Froeschke & Sommer 2005).

The number of rodent specimens that had more than two parasite species was much higher for *M. natalensis* and *L. rosalia* than *M. minutoides.* The reason for this is not understood but habitat, size and diet factors maybe involved (Chowdhury & Aguire 2000).

The small mammals in this study were all within normal limits in terms of mass and other body parameters (Monadjem 1998c, Skinner & Chimimba 2005). This suggests that, in spite of the apparent food and water scarcity at MNR there was enough to ensure normal body condition even with gastrointestinal parasites. Domestic animals with good nutrition do not lose body condition even with a heavy parasite load (Tsotetsi & Mbati 2003, Maichomo *et al.* 2004).

New data are presented on the gut parasites of small mammals in Swaziland, and there is the possibility of some new species being uncovered. Further exploratory research on the gastro-intestinal tract parasites and ectoparasites of small mammals is necessary.

References

ABD EL-WAHED, M.M., SALEM, G.H. AND EL-ASSALY, T.M. 1999. The role of wild rats as a reservoir of some internal parasites in Qalyobia Governorate. *Journal of the Egyptian Society of Parasitology* **29**(2): 495-503.

ARATA, A.A. AND GRATZ, N.G. 1975. The structure of rodent faunas associated with arenaviral infections. *Bulletin of the World Health Organization* **52**: 621-627.

BAYLIS, H.A. 1928. On a collection of nematodes from Nigerian mammals (chiefly rodents). *Parasitology* **20**: 280-304.

BEHNKE, J.M., BARNARD, C.J., MASON, N., HARRIS, P.D., SHERIF, N.E., ZALAT, S. AND GILBERT, F.S. 2000. Intestinal helminths of spiny mice (*Acomys cahirinus dimidiatus*) from St Katherine's Protectorate in the Sinai, Egypt. *Journal of Helminthology* **74**: 31-43.

BOOMKER, J., HORAK, I.G., WATERMEYER, R. AND BOOYSE, D.G. 2000. Parasites of South African wildlife. XVI. Helminths of some antelope species from the Eastern and Western Cape Provinces. *Onderstepoort Journal of Veterinary Research* **67**: 31-41.

CHOWDHURY, N. AND AGUIRE, A.A. 2000. *Helminths of wildlife: A global perspective*. Science Publishers Chicago.

FROESCHKE, G. AND SOMMER, S. 2005. MHC variability and parasite load in *Rhabdomys pumilio*. *Molecular Biology and Evolution* **22**(5): 1254-1259.

HORAK, I.G. 1999. Parasites of domestic and wild animals in South Africa. XXXVII. Ixodid ticks on cattle on Kikuyu grass pastures and in Valley Bushveld in the Eastern Cape Province. *Onderstepoort Journal of Veterinary Research* **66**: 175-184.

HORAK, I.G. AND COHEN, M. 2001. Hosts of the immature stages of the rhiniceros tick, *Dermacentor rhinocerinus* (Acari, Ixodidae). *Onderstepoort Journal of Veterinary Research* **68**: 75-77.

HORAK, I.G., EMSLIE, F.R. AND SPICKETT, A.M. 2001a. Parasites of domestic and wild animals in South Africa. XL. Ticks on dogs belonging to people in rural communities and carnivore ticks on the vegetation. *Onderstepoort Journal of Veterinary Research* **68**: 135-141.

HORAK, I.G., MACIVOR, K.M.D.F. AND GREEFF, C.J. 2001b. Parasites of domestic and wild animals in South Africa. XXXIX. Helminth and arthropod parasites of Angora goats in the southern Karoo. *Onderstepoort Journal of Veterinary Research* **68**: 27-35.

LEIRS, H. 1994. *Population ecology of Mastomys natalensis (Smith, 1834).* Belgian Administration for Development Cooperation Brussels.

LOUW, J.P. 1999. The helminths of ranch calves in the North-eastern Mountain Grassland of South Africa. *Onderstepoort Journal of Veterinary Research* **66**: 335-338.

MAHLABA, T.A.M. AND PERRIN, M.R. 2003. Population dynamics of small mammals at Mlawula, Swaziland. *African Journal of Ecology* **41**: 317-323.

MAICHOMO, M.W., KAGIRA, J.M. AND WALKER, T. 2004. The point prevalence of gastro-intestinal parasites in calves, sheep and goats in Magadi division, south-western Kenya. *Onderstepoort Journal of Veterinary Research* **71**: 257-261.

MATTHEE, S., KRECEK, R.C. AND MILNE, S.A. 2000. Prevalence and biodiversity of helminth parasites in donkeys from South Africa. *Jounal of Parasitology* **86**(4): 756-762.

MINNAAR, W.N. AND KRECEK, R.C. 2001. Helminths in dogs belonging to people in a resource-limited urban community in Gauteng, South Africa. *Onderstepoort Journal of Veterinary Research* **68**: 111-117.

MONADJEM, A. 1998. *Mammals of Swaziland*. The Conservation Trust & Big Game Parks Mbabane.

MORAND, S., KRASNOV, B.R. AND POULIN, R., EDS. 2006. *Micromammals and macroparasites: from evolutionary ecology to management*. Pringer-Verlag. Tokyo

NSOSO, S.J., MACHETE, J.B., MOLATOLE, M., NDEBELE, R.T., LEBANI, N.N., CHABO, R.G., KALAKE, A.M., JACYNA, L., SEGADIMO, B.W. AND MINE, O.M. 2001a. The impact of traditional management on seasonal internal parasite burdens and productivity of indigenous Tswana goats in southern Botswana. *Onderstepoort Journal of Veterinary Research* **68**: 101-104.

NSOSO, S.J., SENKU, M.M. AND MINE, O.M. 2001b. The establishment, composition and severity of infection of gastro-intestinal parasites and their impact on productivity of Tswana kids in southern Botswana. *Onderstepoort Journal of Veterinary Research* **68**: 71-74.

PISANU, B., CHAPUIS, J.L. AND DURETTE-DESSET, M.C. 2001. Helminths from Introduced Small Mammals on Kerguelen, Crozet, and Amsterdam Islands (Southern Indian Ocean). *The Journal of Parasitology* **87**(5): 1205-1208.

SKINNER, J.D. AND CHIMIMBA, C.T. 2005. *The mammals of the Southern African Subregion*. Cambridge University Press Cambridge.

SWEET, R.J. AND KHUMALO, S. 1994. Range resources and grazing potentials in Swaziland. Government of Swaziland/United Nations Development Programme. Mbabane**:** 60.

TSOTETSI, A.M. AND MBATI, P.A. 2003. Parasitic helminths of veterinary importance in cattle, sheep and goats on communal farms in the northeastern Free State, South Africa. *Journal of the South African Veterinary Association* **74**(2): 45-48.

UGBOMOIKO, U.S. AND OBIAMIWE, B.A. 1991. Helminths of small mammals in a forest zone of Southern Nigeria. *Helminthologia* **28**: 19-22.

VAN-WYK, J.A., STENSON, M.O., VAN DER MERWE, J.S., VORSTER, R.J. AND VILJOEN, P.G. 1999. Anthelmitic resistance in South Africa: surveys indicate an extremely serious situation in sheep and goat farming. *Onderstepoort Journal of Veterinary Research* **66**: 273-284.

WOOLHOUSE, M.E.J., MUTAPI, F., NDHLOVU, P.D., CHANDIWANA, S.K. AND HAGAN, P. 2000. Exposure, infection and immune responses to Schistosoma haematobium in young children. *Parasitology* **120**: 37-44.

CHAPTER 6

Description of a new species of Heligmonina Baylis, 1928 (Nematoda, Trichostrongylina) a parasite of *Mastomys natalensis* (Muridae) from Swaziland and new data on the synlophe of Heligmonina chabaudi Desset, 1966

Abstract

A new species of heligmosomoid nematode belonging to the subfamily Nippostrongylinae Durette-Desset, 1970 is described: *Heligmonina wakelini* n. sp., a parasite from the small intestine of the commensal rodent, *Mastomys natalensis* (Smith, 1834) from Swaziland. It differs from the most closely related species *H. boomkeri* Durette-Desset & Digiani, 2005 by the number of the cuticular ridges in the female synlophe (10 vs. 12), the width of the left ala, larger than the body diameter in the male, and the inclination of the axis of orientation of the ridges in both sexes (53° vs. 70°). New morphological data (head and synlophe) on *Heligmonina chabaudi* (Desset, 1964), also a parasite of *M. natalensis* in the Democratic Republic of Congo are provided in order to compare with the new species.

Introduction

The rodent genus *Mastomys* is found throughout Africa, but mostly in Sub-Saharan Africa, where some species are important pests of crops, and regularly show population eruptions that result in significant losses to agriculture (Granjon *et al.* 1997; Lima *et al.* 2003; Stenseth *et al.* 2003). Species such as *M. natalensis* are commensal and regularly invade human habitation whilst others are restricted to the grasslands, fields and the bush (Duplantier & Granjon; 1988; Brouat *et al.* 2007). *Mastomys* is one of the genera comprising the *Praomys* group of murine rodents, but their exact relationships to other genera within this grouping and to each other within the genus, have been the subject of debate (Granjon *et al.* 1997), until recently when the molecular phylogeny has been established (Lecompte *et al.* 2002).

Whilst rodents of the genus *Mastomys* are known to carry a number of important bacterial and viral diseases that are transmittable to humans (Leirs, 1994), and some of their metazoan parasites have been reported (Ugbomoiko & Obiamiwe, 1991), including new species (Diouf *et al.*, 1998, 2005), their helminth communities have only recently attracted attention (Brouat et al., 2007). Such studies are dependent on the accurate identification of the helminths infecting hosts, and in the case of *Mastomys* spp. the full spectrum of helminths from all regions of Africa where these rodents occur, is still poorly documented. *Mastomys* spp. are known to be hosts of several species of the Ethiopian branch of the Nippostrongylinae (Helligmonellidae), which are parasites of the Muridae represented by two genera in particular: *Neoheligmonella* Durette-Desset 1970 and *Heligmonina* Baylis, 1928. To-date, three species of *Neoheligmonella* and one of *Heligmonina*, *H. bignonensis* Diouf *et al.*, 1997 have been described from *Mastomys erythroleucus* (Temminck, 1853). In *Mastomys natalensis* (Smith, 1834), two species of *Heligmonina* have been described: *H. chabaudi*

(Desset 1964) and *H. kotoensis* Diouf *et al.*, 2005, the latter being a co-parasite with *Neoheligmonella lamaensis* Diouf *et al.*, 2005. All of these species originate from West Africa (Benin, Senegal, Democratic Republic of Congo and Central African Republic). Despite the wide distribution of *M. natalensis* throughout Sub-Saharan Africa, and the occurrence of closely related *Mastomys* spp. in specific regions (Leirs, 1994), no other *Heligmonina* species have been recorded so far from this host from either East or South Africa.

In the present chapter, a new species of the genus *Heligmonina* Baylis, 1928, a parasite of *M. natalensis* is described offering the first record of *Heligmonina* from South-East Africa. A description of the head and a re-description of the synlophe of *H. chabaudi* from *M. natalensis* from the Central African Republic are also provided in order to compare with the features of the new species.

Materials and Methods

Capture of rodents and study sites

The identity, distribution and population ecology of wild rodents in Swaziland are all well known (Monadjem 1998; 1999; Monadjem & Perrin 2003) and their demography has been studied intensively in other parts of Africa (Lima *et al.* 2003). Despite the known sympatric occurrence of *M. coucha* (Smith, 1836) in South Africa, from available evidence, only *Mastomys natalensis* is believed to occur in our study sites in Swaziland (A. Monadjem, pers. comm.). Wild rodents were caught in Sherman traps set out in the afternoon and inspected the following morning. The animals for this study were caught at two locations in Swaziland during June 2004. The first site was in the Middleveld region, represented in this case by fields of the Faculty of Agriculture of the University of Swaziland at Luyengo (S 26^{o} 34’, E 0 31^{o} 11’). Here traps were set around the periphery of plots where maize was growing. The second site was in the NE of the country, the Lowveld region, in Vuvulane. The site used was a fallow field immediately adjacent to fields with mature sugar cane on an industrial sugar cane plantation (S 26^{o} 04’, E0 31^{o} 52’). Animals were recovered from traps and transported live to the laboratory at the University of Swaziland within a day or two, where they were culled in chloroform, dissected and the worms were recovered from the small intestine by incubation in Hanks’ saline. Worms were then transferred to 70% ethanol, transported to the University of Nottingham and eventually sent to the Muséum National d’Histoire Naturelle in Paris for examination.

Examination of worms and nomenclature

The nomenclature used above the family level follows Durette-Desset and Chabaud (1993). The synlophe was studied according to the method of Durette-Desset (1985). The nomenclature used for the study of the synlophe follows Durette-Desset and Digiani (2005) and that of the caudal bursa Durette-Desset and Chabaud (1981). The numbering of the cuticular ridges follows Beveridge and Durette-Desset (1992). The curve of the strut of the left ala is not included in the measurement of its length. The caudal bursae of 10 males from the type material (427 MQ) and 20 males from voucher material (10 males 428 MQ and 10 males 430 MQ) were examined in order to determine the relative disposition of rays 3 to 6 and the symmetrical/asymmetrical arising of rays 8 on the dorsal ray. The measurements are in micrometers except where otherwise stated. The material (types and voucher material) is deposited in the Collections of the Muséum National d'Histoire Naturelle (MNHN) of Paris (France). The nomenclature of the hosts follows Musser and Carleton, 2005.

Description

Heligmonina wakelini n.sp.

(Figs 20-34)

Type material: 52 males, 41 females MNHN 427 MQ.

Studied material: holotype male, allotype female MNHN 427 MQa, 15 male, 15 female paratypes MNHN 427MQb.

Host: *Mastomys natalensis* (Smith, 1834) (Muridae, Murinae).

Site: Small intestine.

Geographic origin: Middleveld, Luyengo, Swaziland.

Voucher material: from the small intestine of three *Mastomys natalensis*; 69 specimens MNHN 428 MQ, same locality than type material; 10 specimens MNHN 429 MQ, 81 specimens 430 MQ MNHN from Vuvulane in the Lowveld region of Swaziland.

General

Small nematodes with body sinistrally coiled along ventral side with 2 spires in male, 3 in female. Excretory pore situated within posterior third of oesophagus. Deirids generally situated at same level as excretory pore or just posterior to it (Fig. 2). Oesophagus length/ body length less 10 % on average in male and 9 % in female. Very short uterus less than 20% of body length.

Head: Cephalic vesicle present. In apical view, triangular oral opening surrounded by two amphids, four externo- labial papillae and four cephalic papillae (Fig. 20).

Synlophe (studied in one male and two female paratypes): In both sexes, body bearing uninterrupted cuticular ridges except on the right ventral side, which is free of ridges. All ridges arising just posterior to cephalic vesicle (Figs. 23, 27) and disappearing just anterior to the caudal bursa in males (Fig.10) and at the vulvar opening in females (Fig.26).

Presence of left hypertrophied ala, straight in females, strongly curved towards ventral side in the male. In the male, the size of the ala increasing progressively from the cephalic vesicle to posterior part of the body, reaching 60 anterior to caudal bursa (Fig. 29). In females, the size of the ala reaching maximum size (45) at mid-body (Fig. 24) and decreasing progressively down to 20 anterior to vulva (Fig. 26).

Number of ridges: 12 (ala, 6 dorsal, 5 ventral) in the male all along the body (Figs 27-29); 10 (ala, 5 dorsal, 4 ventral) in females at the oesophageal region (Fig. 23) and at the mid-body (Fig. 24). At about 1 mm anterior to the vulva 11 (ala, 6 dorsal, 4 ventral) with origin of ridge n° 1 (Fig. 25), then at the level of the *vagina vera* 8 (ala, 5 dorsal, 2 ventral) with disappearance of ridges n° 6, 2' and 3' (Fig. 26).

At mid-body, double gradient of size from left to right on ventral side and from right to left on dorsal side (with exception of ridge n° 1 in male very thin and longer than ridge n° 2 (Figs. 23-25, 27-29). In the posterior region in females, ridges of equivalent size, except ala (Fig. 7).

At mid-body, the axis of orientation directed from the right ventral quadrant to the left dorsal quadrant, inclined at 53 ° to sagittal axis in both sexes.

Holotype male: 2.4 mm long and 130 wide at mid-body, including left ala. Cephalic vesicle 51 long and 28 wide. Nerve-ring, excretory pore and deirids situated at 150, 210 and 210 from apex, respectively. Oesophagus 260 long.

Caudal bursa strongly asymmetrical with left lateral lobe most developed. Pattern of caudal bursa of type 1-3-1 for right lobe and 1-4 for left lobe (Fig. 30 a-d). Prebursal papillae not observed. In both lobes, rays 3 arising more distally than rays 6 on common trunk. In right lobe, rays 3 to 5 arising at the same level and extremities of rays 3 and 4 closer to each other than those of rays 4 and 5; in the left lobe ray 3 arising first from a common trunk of rays 3 to 5 and extremities of rays 3 and 4 more distant from each other than those of rays 4 and 5. Small rays 6. Rays 8 longer than dorsal ray arising asymmetrically at its base, first left ray 8 (Fig. 34a). Dorsal ray deeply divided, just posterior to the origin of rays 8, into two branches. Each branch divided into two small twigs, rays 9 (external branches) slightly thicker than rays 10 (internal branches) (Fig. 34a). Filiform spicules 390 long, with sharp tips (Fig. 33). Spicule length/body length: 16.2 %. Semi-circular genital cone 40 long and 20 wide at base with small rounded papilla 0 on ventral lip and papillae 7 on dorsal lip (Fig. 31). Gubernaculum not observed.

Measurements (average and range) of 10 paratypes: 2.8 (2.1–3.3) mm long and 140 (110-160) wide at mid-body; cephalic vesicle, 51 (42-60) long and 26.5 (21-32) wide; nerve ring (n = 8), excretory pore and deirids (*n* = 8) situated at 152 (130-170), 220 (180-250) and 228 (205-260) from apex, respectively; oesophagus 270 (250-300) long; spicules 406 (310-445) long, spicules length/body length 14.5 % (13.3-17.1)%. Very thin gubernaculum observed only in some paratypes (Figs 30d, 33).

Examination of several male specimens in the material studied indicated some variation in the relative arrangement of rays 3-4-5 in both lobes of the caudal bursa. These variations are as follows:

In the right lobe, rays 3, 4 and 5 arising at the same level from their common trunk (Figs. 30a, 30b) or rays 3 and 4 arising more distally than ray 5 from the common trunk of rays 3 to 5 and diverging only at their extremities (Figs. 30c, 30d).

In the left lobe, rays 3, 4 and 5 arising at the same level from their common trunk (Figs, 30b, 30c) or rays 3 arising first from the common trunk of rays 3 to 5 and rays 4 and 5 diverging only at their extremities (Figs. 30a, 30d).

Similarly, the relative distances between the extremities of rays 3 to 5 showed some variation linked to the origin of the rays. When rays 3, 4 and 5 arise at the same level, their extremities are approximately equidistant (both left and right lobes). When rays 3 and 4 arise more distally than rays 5 on their common trunk, the extremities of rays 3 and 4 are closer to each other than those of rays 4 and 5 (right lobe). When rays 4 and 5 arise more distally than rays 3, the extremities of rays 4 and 5 are closer to each other than those of rays 3 and 4 (left lobe).

The combination of the relative origins of rays 3-5 and the relative distances between their extremities provides the four different patterns of caudal bursae (types A-D) observed in the material studied:

The type A (Fig. 30a) was observed in the holotype, 6 paratypes 427 MQ and 9 specimens from the voucher material (7 males 428 MQ and 3 males 430 MQ). In the right lobe, rays 3, 4 and 5 arising at the same level from their common trunk and extremities of rays 3 and 4 closer to each other than those of rays 4 and 5. In the left lobe, ray 3 arising first from the common trunk of rays 3 to 5, and extremities of rays 4 and 5 closer to each other than those of rays 3 to 4.

The type B (Fig. 30b) was observed in 4 specimens from the voucher material (3 males 428 MQ and one male 430 MQ). In the right lobe, rays 3, 4 and 5 arising at the same level from their common trunk, extremities of rays 3, 4 and 5 almost equidistant. In the left lobe: same pattern as in right lobe.

The type C (Fig. 30c) was observed in one paratype 427 MQ and 2 males from voucher material 430 MQ. In the right lobe, ray 5 arising first from the common trunk of rays 3 to 5, extremities of rays 3 and 4 closer to each other than those of rays 4 and 5. In the left lobe rays 3, 4 and 5 arising at same level from their common trunk, extremities of rays 3, 4 and 5 almost equidistant.

The type D (Fig. 30d) was observed in one paratype 427 MQ and 4 males from voucher material 430 MQ. In the right lobe, ray 5 arising first from the common trunk of rays 3 to 5, extremities of rays 3 and 4 closer to each other than those of rays 4 and 5. In the left lobe ray 3 arising first from the common trunk of rays 3 to 5, extremities of rays 4 and 5 closer to each other than those of rays 3 and 4.

Notably, the origin of rays 8 on the dorsal ray of the caudal bursa may be asymmetrical (AS) as in the holotype (15 cases) (Fig. 34a) or symmetrical (S) (14 cases) (Fig. 34b). This character was independent of the pattern of the lateral lobes (Table 10).

Allotype female: 3 mm long and 90 wide at mid-body including left ala. Cephalic vesicle 48 long and 30 wide. Nerve-ring, excretory pore and deirids situated at 150, 220 and 230 from apex, respectively. Oesophagus 270 long (Fig. 2).

Table 10: Patterns of rays 8 and 9 and 3 and 5 in *Heligmonina wakelini*.

Pattern of rays 8 & 9	**Material n°**	**Pattern of rays 3-5**			
		Type A	Type B	Type C	Type D
	427 MQ	6 paratypes			
Symmetrical	428 MQ	5 males			
	430 MQ	2 males			1 male
	427 MQ	Holotype, 1 paratype		1 male	1 male
Asymmetrical	428 MQ	2 males	3 males		
	430 MQ	1 male	1 male	2 males	3 males

Monodelphic (Fig. 22). Vulva situated at 150 from caudal extremity, *vagina vera* 40 long. Ovejector 229 long with vestibule 46 long, sphincter 23 long and 35 wide, infundibulum 160 long. Uterus 480 long with 6 eggs at morula stage, 65 long and 40 wide. Uterus length/body length 16.2% . Conical tail 36 long (Fig. 22).

Measurements (average and range) of 10 paratypes: 3.25 (2.9-3.5) mm long and 82 (60-100) wide at mid-body, left ala included, cephalic vesicle 48 (43-55) long and 22 (18-30) wide; nerve ring (n=7), excretory pore (n= 7) and deirids (n= 5) situated at 144 (110-180), 206 (158-235) and 219 (200-235) from apex, respectively; oesophagus (n=9) 258 (210-290) long; vulva situated at 146 (130-160) from caudal extremity; *vagina vera* 34 (30-40) long; vestibule 52

(40-65) long, sphincter 29 (23-31) long and 35.5 (30-45) wide, infundibulum (n=5) 125 (100-150) long; uterus 485 (350-600) long with 8 (2-14) eggs, 60.5 (52-70) long and 34 (30-46) wide; uterus length/body length 14.9 % (10-19)%; tail 49 (30-70) long.

Diagnosis

The specimens described above possess the main features of the genus *Heligmonina* (Baylis 1928) (Heligmonellidae, Nippostrongylinae) redefined by Durette-Desset (1971). This genus is mainly characterised by the pattern of the synlophe with a hypertrophied left ala and the absence of cuticular ridges totally or pro parte on the right ventral quadrant of the body. The pattern of the caudal bursa varies greatly among species and generally differs for each lobe.

To date, 23 species have been described in this genus, all parasites of Muridae, 18 in Africa and 5 in Madagascar.

Concerning the synlophe, the females in the material described in this paper are the only species amongst all the known species of *Heligmonina* having a synlophe with a left ala, 5 dorsal and 4 ventral ridges. Whereas the males share the synlophe, characterised by the left ala, 6 dorsal and 5 ventral ridges with 3 species: *Heligmonina albignaci* Quentin & Durette-Desset, 1974 and *Heligmonina tanala* Durette-Desset, Lehtonen & Haukisalmi, 2002, parasitic, respectively in *Brachyuromys betsileoensis* (Bartlett, 1880) and *Eliurus tanala* Major, 1896, both from Madagascar; and with *H. boomkeri* Durette-Desset & Digiani, 2005, parasitic in *Aethomys chrysophilus* (de Winton, 1897) from South Africa. *Heligmonina albignaci* is mainly distinguished from these specimens by the development of the dorsal ridge nº 1, which induces the presence of a carene. It is distinguished on the other hand by the pattern of the caudal bursa, with left ray 3 arising before ray 6 on the common trunk of rays 3 to 6. *H. tanala* resembles our material through the similar synlophe in males, but it differs by the pattern of the caudal bursa, with the left ray 3 arising at the same level as ray 6 on the common trunk of rays 3-6, and by the strong development of the dorsal lobe. The most similar species is *H. boomkeri*, which has the same pattern of caudal bursa, with the left ray 6 arising anteriorly to ray 3 from their common trunk. More exactly, the bursal pattern of *H. boomkeri* corresponds best to the type C observed in our material. However, some differences were found between both species in the female synlophe and in some body measurements. The female of *H. boomkeri* has a synlophe with 12 cuticular ridges: ala, 6 dorsal, 5 ventral and all ventral ridges disappear at vestibular level. In addition, the ovejector is shorter than that of the new species. In males, the length of the left ala at mid-body does not exceed the body diameter limited by the hypodermis.

We consider the specimens collected in *M. natalensis* as belonging to a new species that we have named *Heligmonina wakelini* n sp. in honour to Professor Derek Wakelin, who retired in 2002 from the University of Nottingham, after an eminent career in research on the genetics of the immune response to intestinal nematodes in rodents.

Heligmonina chabaudi (Desset, 1964) Durette-Desset, 1971

= *Longistriata chabaudi* Desset, 1964

(Figs. 20-34)

Studied material: 1 male, 1 female MNHN 230 CU.

Host: *Mastomys natalensis* (Smith, 1834) (Muridae, Murinae).

Site: small intestine.

Geographical origin: Boukoko, Central African Republic.

Head: Cephalic vesicle present. In apical view, circular oral opening surrounded by 2 amphids, 6 externo-labial papillae of which lateral ones joined to amphids and 4 submedian cephalic papillae (Fig. 25).

Synlophe (studied in one male, one female): In both sexes, body bearing uninterrupted cuticular ridges except on the right ventral side, all arising just posterior to the cephalic vesicle (Fig. 20) and disappearing anterior to the caudal bursa in males (Fig. 20) and at the vulvar opening in females (Fig. 24).

Presence of a left hypertrophied ala, at mid-body with a sinuous strut in males, but straight in females. In males, size increasing progressively from the cephalic vesicle to mid-body, reaching 100 at this level (Fig. 22). At about two-thirds of body length, ala still same width and strongly sinuous. At about 100 anterior to the caudal bursa, size decreasing down to 40 (Fig 24). In females, width of ala reaching 80 at mid-body (Fig. 26) and decreasing progressively down to 20 anterior to vulva (Fig. 28).

Number of ridges: in both sexes 11 (left ala, 6 dorsal, 4 ventral) except in the posterior region. In males, at 80 anterior to the caudal bursa, 9 (left ala, 4 dorsal, 4 ventral) with disappearance of ridges n° 1 and n° 2 (Fig. 23), then posteriorly, 7 ridges (left ala, 3 dorsal, 3 ventral) with disappearance of ridges n° 3 and 2' (Fig. 24). In females, at about 200 anterior to vulva, 10 (left ala, 6 dorsal, 3 ventral) with disappearance of ridge n° 5' (Fig. 27), then at about 100 anterior to vulva, 9 (left ala, 5 dorsal, 3 ventral) with disappearance of ridge n° 6 (Fig. 24). At mid-body, double gradient of size from left to right on the ventral side and from right to left on dorsal side (with exception of ridge n° 1 very thin and longer than ridge n° 2). Double gradient distinct at mid-body (Figs. 22, 26). In the posterior region, except ala, the ridges are of equivalent size (Figs. 23, 24, 27, 28). The axis of orientation is directed from right ventral quadrant to the left dorsal quadrant and at mid-body inclined at 45° to the sagittal axis in both sexes (Figs. 18, 22).

Remarks

As stated above, the genus *Heligmonina* is characterised by the presence of a hypertrophied left ala supported by a sole cuticular ridge. However, in contrast to this relative uniformity among species, the pattern of the caudal bursa and especially the relative arrangement of rays 2 to 6 vary greatly among species and within each lobe.

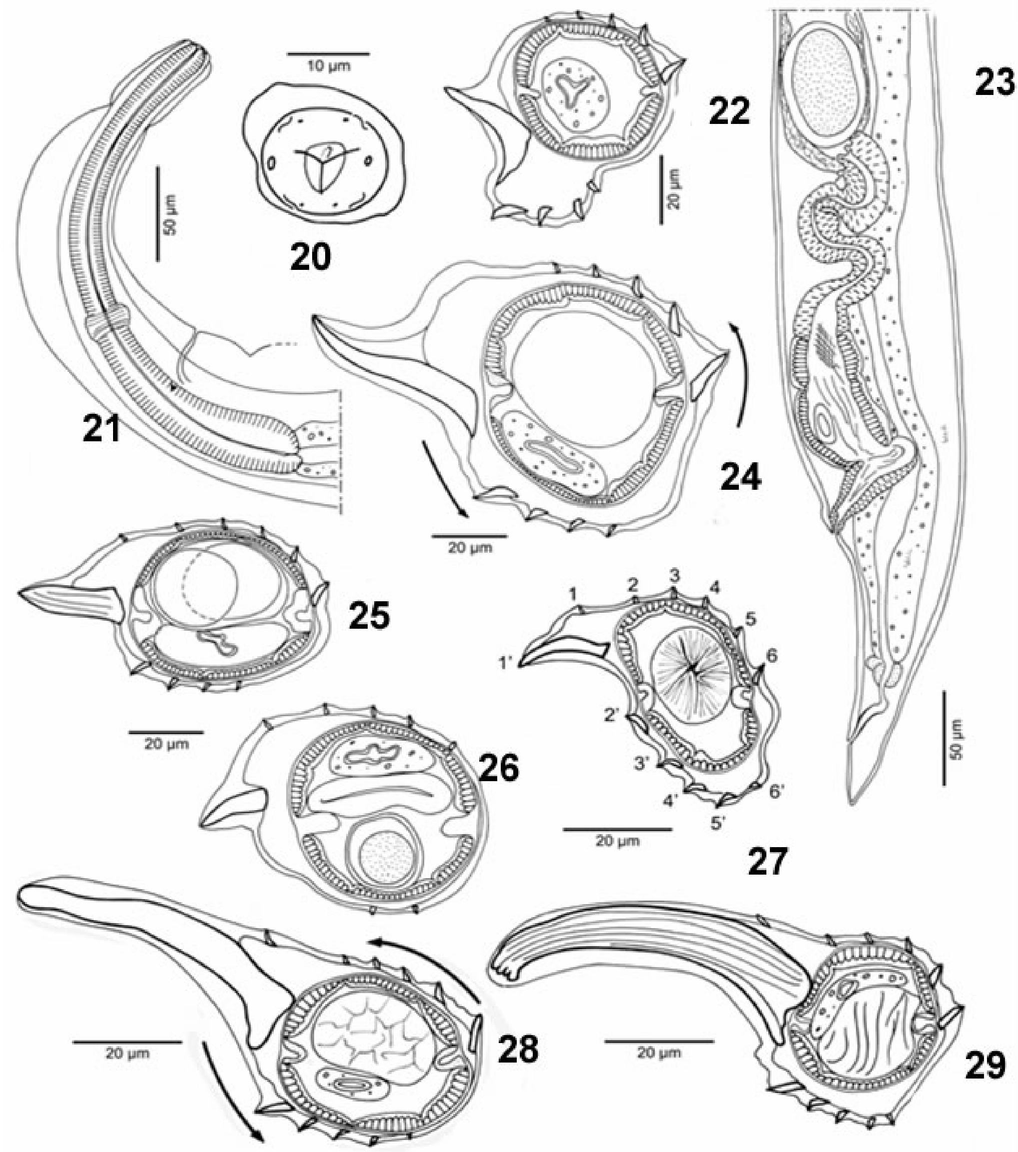
In *H. wakelini*, the pattern for the right lobe is of type 1-3-1 i.e., rays 2 and 6 arising at the same level from their common trunk. For the left lobe the pattern is of type 1-4 (ray 2 arising first from the common trunk of rays 2 to 6). In both lobes rays 3 always arise more distally to rays 6 on their common trunk, in all the specimens studied. This relative arrangement of rays 2, 3 and 6 may be considered as specific, whereas the variations concerning the relative origins of rays 3 to 5 on their common trunk, as well as the relative distances of their extremities may be considered as infra-specific, along with the symmetrical/asymmetrical origins of rays 8 on the dorsal ray.

Currently, three species of *Heligmonina* have been described from the genus *Mastomys: H. bignonensis* Diouf et al., 1997 in *M. erythroleucus* from Senegal, *H. chabaudi* (Desset, 1964) from the Democratic Republic of Congo and Central African Republic and *H. kotoensis* (Diouf et al., 2005) in *M. natalensis* from Benin. These three species are morphologically closely related to each other and parasitize closely related hosts (Lecompte et al., 2002).

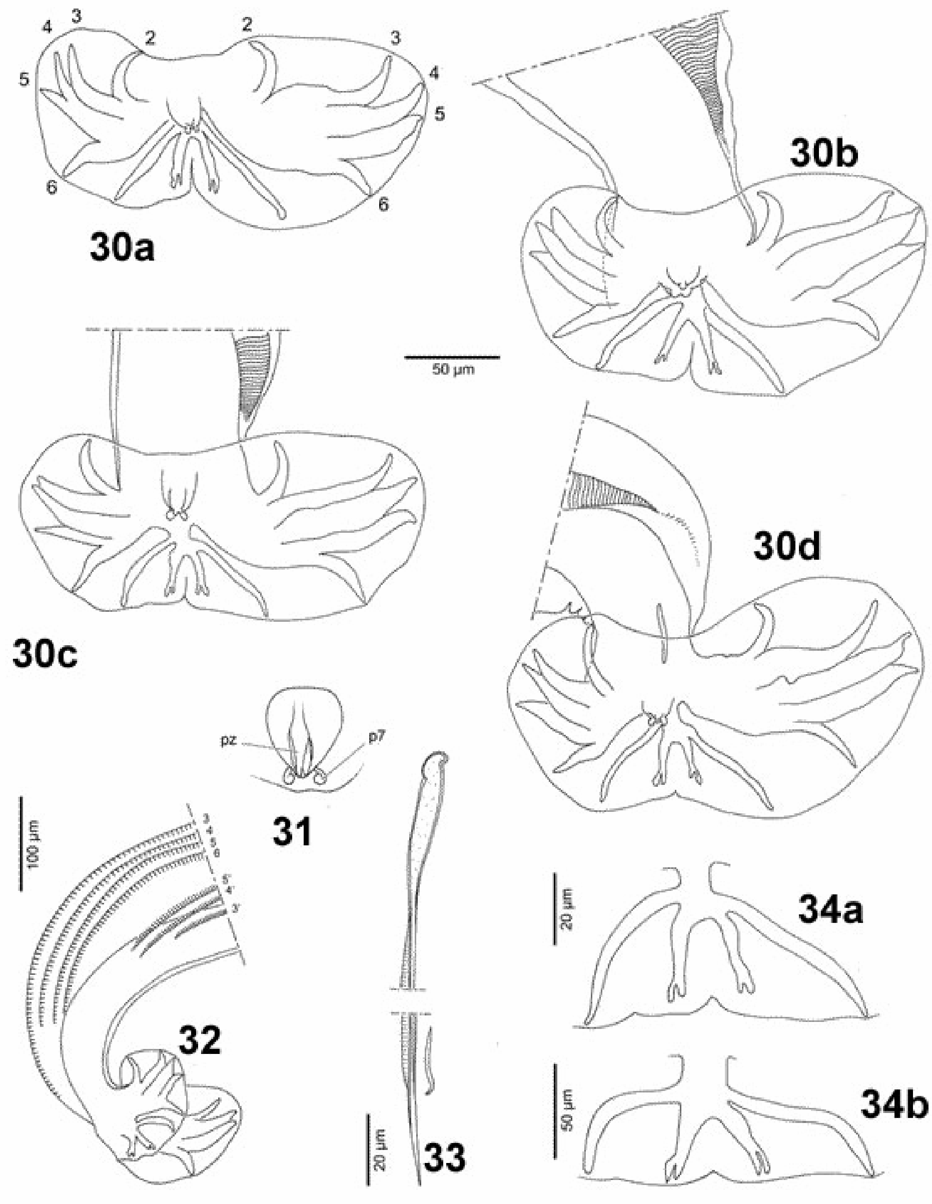
Although they have different patterns of caudal bursae, they are very similar in respect of their synlophes, with 11 cuticular ridges arranged as: left ala, 6 dorsal and 4 ventral. This type of synlophe is shared with two other species in the genus but only in the males: *H. possompesi* (Durette-Desset, 1966), parasitic in *Mus (Leggada) minutoides* Smith, 1834 from the Democratic Republic of Congo and *H. thamnomysi* (Durette-Desset, 1966), parasitic in *Grammomys rutilans* (Peters, 1876) (=*Thamnomys rutilans*) and *Cricetomys gambianus* Waterhouse, 1840 from the Central African Republic.

Heligmonina wakelini n. sp., which parasitizes a host belonging to this group but from South East Africa, is morphologically closer to a South African and two Malagasy species (*H. boomkeri*, *H. albignaci*, *H. tanala*), all 4 species having a synlophe with 12 cuticular ridges arranged as: left ala, 6 dorsal and 5 ventral at least in males.

As in W. Africa, besides *M. natalensis*, there are other closely related species of *Mastomys* endemic to S. Africa (e.g., *M. coucha* (Smith, 1836) and *M. shortridgei* (St. Leger, 1933); Granjon *et al.,* 1997), but their parasites have not yet been reported, and it is quite conceivable that new species of *Heligmonina* will be discovered when these hosts are examined. These may eventually help to explain better the evolution of the genus *Heligmonina*. However, from the available evidence it appears that the geographical location of the *Heligmonina* spp. parasitic in *Mastomys* spp. may be of greater significance than the host spectrum because the hosts of the *Heligmonina* spp. most closely related to *H. wakelini* in South-eastern Africa are not even in the same host genus (*Mastomys*) as the species from Western Africa. Thus host capture may have been an important element in the evolution of this genus with species transferring between sympatric rodents, rather than following a strict co-evolutionary route. *Heligmonina wakelini* may represent a linage of *Heligmonina* in *Mastomys* which diversified from those species in West Africa and spread to and diversified in the other genera of rodents in South Africa and Madagascar, or alternatively invaded *M. natalensis* in S. Africa from one of the other rodents. The eventual resolution of the evolutionary history of both rodent hosts and the genus *Heligmonina* will require examination of more specimens from east and south Africa, most likely also the recognition and description of new species, and the application of molecular tools to construct a robust molecular phylogeny in support of the relationships that have been suggested based on morphology.

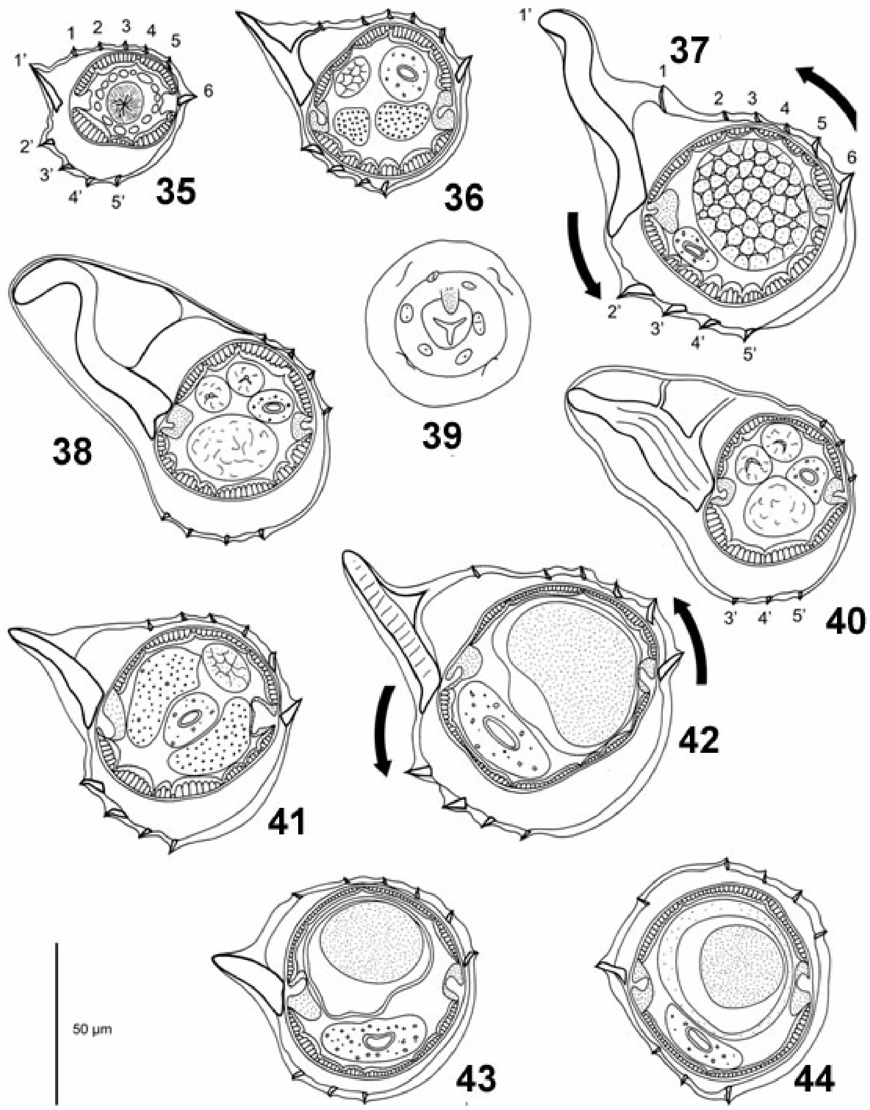


Figures 20-29. *Heligmonina wakelini* n.sp. 20-22. Female. 20- anterior extremity, right lateral view. 21- head, apical view. 22- posterior extremity, left lateral view. 23-29. Transversal sections of the body. 23-26. Female paratype 3.1 mm long. 22- at 220 µm posterior to cephalic vesicle. 24- at mid-body (1.9 mm from apex). 25- At 900 µm anterior to vulva 26- at level of *vagina vera*. 27-29. Male paratype 3.3 mm long. 27- just anterior to oesophageal intestinal junction. 28- at mid- body (1.8 mm from apex). 29- within posterior part of body. All sections are orientated as 20. Abbreviations: v: ventral side, r: right side.



Figures 30-34. *Heligmonina wakelini* n. sp. Male. 30a-d. Different patterns of the caudal bursa. 30a- Type A. 30b- Type B. 30c- Type C. 30d- Type D. 31- Genital cone, ventral view. 32. Caudal bursa, disappearance of cuticular ridges, right lateral view. 33- Gubernaculum, ventral view and spicules (proximal part and tips). 34a-b. Arising of rays 8 on dorsal ray, dorsal view. 34a- asymmetrical. 34b-symmetrical.

Abbreviations: pz: papilla zero; p7: papilla 7.



Figures 35-44. *Heligmonina chabaudi* (Desset, 1964). 35-34. Transversal sections of the body. 35-39. Male 2.2 mm long. 35- at level of the nerve ring.36- at level of the oesophago-intestinal junction. 37- at mid-body (1.3 mm from apex). 38- at about 150 µm anterior to caudal bursa. 39- All sections are orientated as 20. 40-44. Female 2.5 mm long. 40- at level of oesophago-intestinal junction. 41- at mid-body (1.3 mm from apex). 42- at proximal level of the uterus. 43- just anterior to vulva. 44- Female, head, apical view.

All sections are orientated as 41. Abbreviations: v: ventral side, r: right side.

References

BAYLIS H.A. 1928. On a collection of Nematodes from Nigerian mammals (chiefly rodents). *Parasitology* **20**: 287 – 295.

BEVERIDGE I. & DURETTE-DESSET M-C. 1992. The morphology of *Nippostrongylus magnus*, a parasite of native Australian rodents. *Transactions of the Royal Society of South Australia* **116**: 109-115.

BROUAT C., KANE M., DIOUF M., BÂ K., SALL-DRAMÉ R. & DUPLANTIER J.M. 2007. Host ecology and variation in helminth community structure in *Mastomys* rodents from Senegal. *Parasitology* in press.

DESSET M.C. 1964. Les systèmes d'arêtes cuticulaires chez les Nématodes Heligmosomes. Etude de cinq espèces parasites de Rongeurs de la Maboké. *Cahiers de la Maboké* **2**: 40-78.

DIOUF M., BÂ C.T. & DURETTE-DESSET M. C. 1997. Deux nouveaux Nippostrongylinae (Nematoda, Trichostrongylina) parasites de Muridae du Senegal. *Zoosystema* **19**: 223-231.

DIOUF M., BÂ CT & DURETTE-DESSET M.C. 1998. Deux nouveaux *Neoheligmonella* (Nematoda,Trichostrongylinae) parasites de *Mastomys erythroleucus* (Muridae) au Senegal. *Zoosystema* **20**: 23-30.

DIOUF M., DAOUDA I. & DURETTE-DESSET M.C. 2005. Two new species of Nippostrongylinae (Nematoda, Trichostrongylina, Heligmonellidae), coparasites of *Mastomys natalensis* (Rodentia, Muridae) from Benin. *Zoosystema* **27** (1): 27-35

DIOUF M., TIDIANE C.B.A. & DURETTE-DESSET M-C. 1998. Deux nouveaux *Neoheligmonella* (Nematoda, Trichstrongylina, Nippostrongylinae) parasites de *Mastomys erythroleucus* (Muridae) au Senegal. *Zoosystema* **20**: 23-30.

DUPLANTIER J.-M. & GRANJON L. 1988. Occupation et utilisation de l'espace par des populations du genre *Mastomys* au Sénégal: étude à trios niveaux de perception. *Sciences et Techniques de l'Animal de Laboratoire* **13**: 129-133.

DURETTE-DESSET M. C. 1966. Les systèmes d'arêtes cuticulaires chez les Nématodes Héligmosomes. II. Etude de cinq *Longistriata* parasites de Rongeurs africains. *Cahiers de La Maboké* **4**: 120-140.

DURETTE-DESSET M. C. 1970. Les systèmes d'arêtes cuticulaires chez les nématodes Héligmosomes. IV- Cinq nouvelles espèces parasites de Rongeurs africains. *Cahiers de La Maboké* **8**: 125-137.

DURETTE-DESSET M. C. 1971. Essai de classification des Nématodes Héligmosomes. Corrélations avec la paléobiogéographie des hôtes. *Mémoires du muséum National d'Histoire naturelle*, nouvelle série, série A, Zoologie **49**: 1-126.

DURETTE-DESSET M. C. 1985. Trichostrongyloid nematodes and their Vertebrate Host : Reconstruction of the phylogeny of a parasitic group. *Advances in Parasitology* **24**: 239-306.

DURETTE-DESSET M. C. & CHABAUD A. G. 1981. Nouvel essai de classification des Nématodes Trichostrongyloïdea. *Annales de Parasitologie Humaine et comparée* **56**: 297-312.

DURETTE-DESSET M. C. & CHABAUD A.G. 1993. Note sur la Nomenclature supra-familiale des Strongylida. *Annales de Parasitologie Humaine et Comparée* **68**: 111-112.

DURETTE-DESSET M. C. & DIGIANI M. C. 2005. The axis of orientation of the synlophe in the Heligmosomoidea (Nematoda, Trichostrongylina): a new approach. *Parasite* **12** (3): 195-202.

DURETTE-DESSET M. C. & GIBSON D. I. 1990, *Neoheligmonella acomysi* n. sp. (Trichostrongyloidea, Nippostrongylinae), parasite d'*Acomys dimidiatus* Muridae de Somalie. Systematic Parasitology **17**: 109-113.

GRANJON L., DUPLANTIER J.-M., CATALAN J. & BRITTON-DAVIDIAN J. 1997. Systematics of the genus *Mastomys* (Thomas, 1915) (Rodentia: Muridae). *Belgian Journal of Zoology* **127**: S7-S18.

LECOMTE E., GRANJON L., KERBIS PETERHANS J. & DENYS C. 2002. Cytochrome b-based phylogeny of the *Praomys* group (Rodentia: Murinae): a new African radiation.

Comptes Rendus de l'Académie des Sciences, Paris, Serie III, Sciences de la vie **325**: 827-840.

LEIRS H. 1994. Population Ecology of *Mastomys natalensis* (Smith, 1834). Implications for rodent control in Africa. Agricultural Edition – Nr 35. A report from the Tanzania-Belgium Joint Research project (1986-1989) Belgium Administration for Development Cooperation, Brussels.

LIMA M., STENSETH N.C., LEIRS H. & JAKSIC F.M. 2003. Population dynamics of small mammals in semi-arid regions: a comparative study of demographic variability in two rodent species. *Proceedings of the Royal Society London* B **270**: 1997-2007.

MONADJEM A. 1998. Reproductive biology, age structure, and diet of *Mastomys natalensis* (Muridae: Rodentia) in a Swaziland grassland. *Zeitschrift fur Saugetierkunde* **63**: 347-356.

MONADJEM A. 1999. Geographical distribution patterns of small mammals in Swaziland in relation to abiotic factors and human land-use activity. *Biodiversity and Conservation* **8**: 223-237.

MONADJEM A. & PERRIN M. 2003. Population fluctuations and community structure of small mammals in a Swaziland grassland over a three-year period. *African Zoology* **38**: 127-137.

MUSSER G. G. & CARLETON M. D. 2005. Family Muridae. In: “Mammal species of the World” Wilson D. E. & Reeder D. M. Eds. Smithsonian Institution Press, Washington 501-753.

STENSETH N.C., LEIRS H., SKONHOFT A., DAVIS S.A., PECH R.P., ANDREASSEN H.P., SINGLETON G.R., LIMA M., MACHANG’U R.S., MAKUNDI R.H., ZHANG Z., BROWN P.R., SHI D. & WAN X. 2003. Mice, rats, and people: the bio-economics of agricultural rodent pests. *Frontiers in Ecology and the Environment* **1**: 367-375.

UGBOMOIKO U.S. & OBIAMIWE B.A. 1991. Helminths of small mammals in a forest zone of Southern Nigeria. *Helminthologia* **28**: 19-22.

CHAPTER 7

CONCLUSION

The factors that determine small mammal community and population structures are numerous and complex with complicated relationships linking them. The role of food and cover has in this and other studies been demonstrated while that of predation and migration requires further investigation. The interactions between and within small mammal species and between small mammal species and their habitat and between small mammal species and abiotic factors such as rainfall are of great importance. The role of gastro-intestinal parasites and arthropod ectoparasites in the physiology and population structure of small mammals needs further exploration. There is a possibility of novel small mammal parasite species being found especially gastrointestinal parasites. Small mammals, as exemplified by *Mastomys natalensis,* are short-lived and in this study only a small percentage in both summer and winter populations were older than 3 months. This means anthropogenic and natural events will directly affect small mammal densities and community structure.

The paucity of information on *Mus minutoides* and its ecology has been highlighted in this and other studies. The habitat demands of this species, its community and population structures and its relationship with other small mammal species in its habitat need further exploration. The diet of this species at Mlawula Nature Reserve and the factors that determine variations in its density need to be investigated.

The role of small mammals as indicators of veld condition is a crucial one. The change in the densities, species richness and species diversity at Mlawula Nature Reserve in this study was concurrent with a change in the veld condition. The low densities of small mammals are concomitant with high grazing levels by ungulates and an invasion by the alien invasive plant species, *Parthenium hysterophorus*.

In summary, this study has attempted to explain the factors behind the low small mammal populations at Mlawula Nature Reserve (MNR). Although it was not always possible to use animals from MNR, with unknown factors that always confound field studies some observations and possibly conclusions can be made. The occupancy of the area by small mammals appeared to be determined by habitat factors such mainly food, and to a lesser extent cover availability. These were found to be interwoven with rainfall, both timing and quantity, alien weed infestation and the presence of large herbivores. The role of predators could not be explored in this study. Although, animals caught in MNR and in the other sites, were infested with parasites it could not be ascertained if this had a role in the low small mammal densities at MNR. The impact of the above and other unknown factors on small mammal populations is related to their short lifespan. *Mastomys natalensis* populations had no individuals surviving to a year.

Mlawula Nature Reserve, specifically the Siphiso Valley, is beset by a number of problems of both anthropogenic and natural origin. Recent and current veld management practices have resulted in the degradation of the area. The local extinctions of some species and low densities of small mammals in the study site may be a consequence of the poor condition of the habitat i.e., it does not provide sufficient shelter and food to support the high densities of small mammals it formerly supported. The lage numbers of ungulates that graze in the area further make the site unsuitable for small mammals. This is shown by the reduction in density, species richness and Shannon's diversity index. Culling practices (large herbivores) in this reserve have proved inadequate at controlling the ever increasing numbers of some of the ungulate species. Although the reserve is large in area, the majority of the ungulates are found in the Siphiso Valley. The invasion of the area by the alien invasive plant species, *Parthenium hysterophorus*, has played a big part in the reduction of cover and food available to small mammals. Decreasing rainfall has also contributed to the poor veld condition of the Siphiso Valley. The low irregular rainfall has negatively impacted on the productivity of the area such that there was no ground cover by the end of the study. A revision of the current culling and veld management policies and practices needs to be carried out at Mlawula Nature Reserve. However, nothing can be done about the diminishing rainfall.