THE ROLE OF AARDVARKS (*ORYCTEROPUS AFER*) AS ECOSYSTEM ENGINEERS IN ARID AND SEMI-ARID LANDSCAPES OF SOUTH AFRICA

A thesis submitted in fulfilment of the requirements for the degree of

MASTER OF SCIENCE

of

RHODES UNIVERSITY

By

Gareth Morgan Whittington-Jones
December 2006

ABSTRACT

Arid and semi arid environments are characterised by extreme fluctuations in temperature and low rainfall which present significant challenges to the animals inhabiting these areas. Mammals, such as aardvarks (*Orycteropus afer*, Pallas 1766), excavate burrows in order to avoid predators and climatic extremes and are termed “ecosystem engineers” as they physically modify their environment and in doing so create new habitats and alter the availability of resources to other species. In this study I assessed the microhabitat conditions (maximum and minimum temperature, relative humidity and seed abundance) of aardvark burrows in relation to paired control sites. In addition, I evaluated the use of aardvark burrows by other vertebrate and invertebrate species and investigated the impact of aardvark burrow mounds on landscape scale floristic diversity.

Maximum temperatures were significantly lower ($p < 0.05$) and minimum temperatures and midday humidity were significantly higher ($p < 0.05$) inside the burrows at the three study sites, Kwandwe Private Game Reserve (Kwandwe), Mountain Zebra National Park (MZNP) and Tswalu Kalahari Reserve (Tswalu). There were no significant differences between the concentration of seeds, the average numbers of unique individual small mammals, trap success or small mammal species richness recorded inside the burrows compared to outside ($p > 0.05$). At all three sites, small mammal species diversity was higher in the burrows but this result was also not significant ($p > 0.05$ for all). Trap success and the number of individuals captured was higher at Tswalu than the other two sites ($p < 0.05$ for both). The different methods used in this study revealed a total of 25 mammal, seven bird, one amphibian and six reptile species utilising aardvark burrows.

There were significant differences in insect community assemblages between the burrows and open control areas at Kwandwe and Tswalu ($p < 0.05$ for both) but not at MZNP ($p > 0.05$). The parasitic guild was more prominent inside the burrows than outside but their abundance was not as high as anticipated, possibly due to the placement of traps closer to the burrow entrances than the sleeping chambers. The complex structure of the burrows prevented the placement of traps in close proximity to the sleeping chambers.

As expected, the amount of bare earth was significantly higher on active and recently abandoned burrow mounds compared to the old burrow mounds and reference plots at all three sites ($p < 0.05$ for all), with the exception of the active burrows at Tswalu. Overall, the different plot types were characterised by significantly different plant communities during all the seasons at MZNP, during three of the seasons at Kwandwe and only during winter at Tswalu. The total species richness recorded on the reference plots was higher than on the burrow mounds at all three sites. However, species diversity on the reference plots was not significantly higher than the burrows at any of the sites ($p > 0.05$ for all sites). Although the results were not significant, the overall species diversity at a site level was greater than the reference patches at Kwandwe and Tswalu ($p > 0.05$ for both).

Aardvarks fulfil the criteria of a significant ecosystem engineer and their presence in arid and semi-arid environments is likely to be critical to the survival of other individual organisms and species, particularly when alternative burrowing animals are either absent or restricted in their activities. Thus, aardvark populations should be considered a conservation priority in arid and semi-arid ecosystems.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

The following individuals and organisations are thanked for their invaluable contributions to this study:

- My supervisor, Ric Bernard, for his wonderful enthusiasm and continued support throughout the project. His approach to this research has made working as his student a splendid experience.
- Ernest Oppenheimer & Sons, Ian MacKenzie scholarship for environmental studies, Ernst and Ethel Eriksen Trust bursary; K Abbot Putterill scholarship and Rhodes University for financial support.
- Prof. Martin Hill for his constant willingness to provide advice and constructive criticism and for providing a marvellous educational experience extending far beyond the bounds of academia!
- Duncan MacFadyen (Ernest Oppenheimer & Sons) for his assistance in developing the project and for his logistical support, advice and enthusiasm.
- The management and staff of Kwandwe Private Game Reserve, Mountain Zebra National Park and Tswalu Kalahari Reserve for their willingness to allow me to work on their reserves and for their logistical support and hospitality. Special thanks to Angus Sholto-Douglas, Keith Craig, Johan De Klerk, Lyle Kelly, Andrew Stainethorpe and Gus van Dyk. Thanks also to Ray, Elané and Lea at Kwandwe for driving me around and helping to collect data.
- Craig Whittington-Jones, Brendan Whittington-Jones, Farah Murrani, Gareth P. Moore and Derek Brown for accompanying me on the various fieldtrips. Your hard work and humour made the fieldtrips memorable occasions. Hopefully the beers and sunsets were worth it.
- Candy Roux for her assistance in the field and for making the GIS maps.
- The South African Weather Service for climatic data.
- Prof. William Froneman for his assistance with PRIMER.
- Prof. Martin Villet for his advice regarding project design, statistical quandaries and the identification of insect specimens.

- Kendall Crous and John Midgley for their patience in helping me identify some of the insect specimens.
- Ashley Kirk-Spriggs for verifying the identification of all the insect voucher specimens.
- Tony Dold of the Selmar Schonland Herbarium for his help identifying some of my plant species.
- All those who took the trouble to complete the questionnaire.
- Charlene Bissett for providing me with logistical support, accommodation and entertainment during field trips to Kwandwe.
- Dan Parker for his motivation and continuous support regarding all aspects of the project ranging from project design and statistics through to the large volumes of sweat that were shed whilst helping out with the highly enjoyable summer fieldwork at Tswalu. Your input has been enormous squire.
- And last but by no means least, to my family and friends for their tremendous support, encouragement and entertainment during this adventure.

CHAPTER 1

GENERAL INTRODUCTION

1.1 THE BIOLOGY OF THE AARDVARK

1.1.1 Taxonomy and phylogeny

The aardvark (Orycteropodidae: *Orycteropus afer* Pallas, 1766) is the sole surviving species of the order Tubulidentata, a group of primitive ungulates (Rahm, 1990; Taylor & Skinner, 2004). Recent evidence suggests that the aardvark should also be added to the Superorder Afrotheria, an ancient African lineage that includes the elephants (Elephantidae), hyraxes (Procaviidae) and elephant shrews (Macroscelididae) (Springer *et al.*, 1997; Springer *et al.*, 2004). No significant phylogenetic relationship exists between the aardvark and either the pangolins (Manidae) or the South American anteaters (Myrmecophagidae). The similarities in appearance and behaviour of these species have been ascribed to convergent evolution (van Aarde, 2004).

1.1.2 Physical Characteristics

The aardvark bears little physical similarity to any single extant mammal. Its appearance is occasionally compared to that of a pig and this combined with its digging behaviour has given rise to its colloquial name, the aardvark, which means “earth-pig” in Afrikaans (Kingdon, 1971). The head is elongated and tapers into a long, rounded, pig-like snout that ends in a blunt muzzle (Melton, 1976). The ears are tube-like and resemble those of a donkey. Adult aardvarks possess simplified dentition with no enamel or roots and only four to five grinding teeth are held on each half of the jaw (Skinner & Smithers, 1990). The mouth also contains an elongated worm-like tongue and well developed salivary glands (Melton, 1976; Skinner & Smithers, 1990). The back is hunched and slopes dramatically towards the strong, muscular tail which resembles that of kangaroo (Skinner & Smithers, 1990). The body is a pale colour and is sparsely haired, whilst the tail and legs are usually covered in darker hair. The legs are squat and powerful with the hind legs being longer than the fore legs (van Aarde, 2004). The aardvark is digitigrade and the forefeet have four digits with sharp claws adapted for digging. The hind feet have five digits that are shorter and weaker compared to the forefeet. Total adult length can vary between 1.5 m and 2.0 m (Kingdon, 1971; Taylor, 2002) and adult weight can range from 40 kg to 80 kg (Kingdon, 1971; Taylor, 2002; van Aarde, 2004). Aardvarks do not exhibit sexual dimorphism (Skinner & Smithers, 1990).

1.1.3 Distribution and habitat

During the Pliocene period numerous aardvark species occurred throughout Africa as well as in southern Europe and western Asia. Their range extended to include Madagascar during the Pleistocene (Melton, 1976; van Aarde, 2004). The present distribution of the aardvark is restricted to an extensive area of sub-Saharan Africa (Skinner & Smithers, 1990) (Figure 1.1). Aardvarks have been documented living in a diverse range of habitats including all varieties of savanna, open woodland, scrub, grassland and records even exist for the rainforests of the Congo Basin (Smithers, 1971; Skinner & Smithers, 1990; Taylor & Skinner, 2004; van Aarde, 2004). It is, however, suggested that they favour areas with sandy soils and that they generally tend to avoid true forests and very arid areas. They may also be locally absent in mountainous and rocky areas and regions where the soil is either too shallow or too hard to excavate or where their prey is scarce (Skinner & Smithers, 1990; van Aarde, 2004).

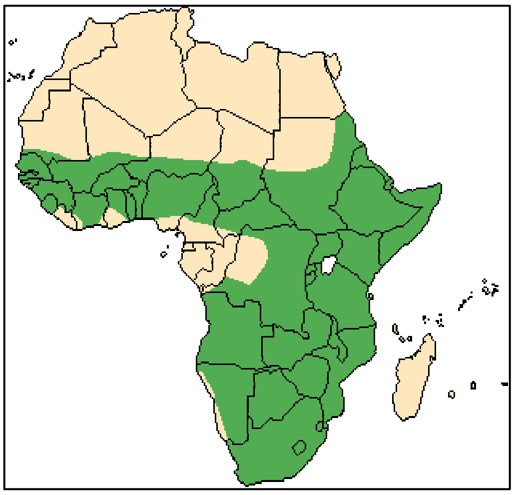

Figure 1.1: The present distribution of aardvarks in Africa (www.ultimateungulate.com/Tubulidentata/Orycteropus_afer.html).

1.1.4 Diet

The diet of aardvarks is dominated by termites and ants, with termites being favoured in the wet season and ants in the dry season when many termite species are quiescent (Kingdon, 1971; Melton, 1976; Taylor *et al*., 2002). Kingdon (1971) claims that they may also consume large numbers of scarab beetle larvae. In addition, aardvarks have also been recorded eating the fruit of the wild cucumber (*Cucumis humifructus*), possibly to increase moisture intake (Melton, 1976; van Aarde, 2004).

1.1.5 Behaviour and habits

Aardvarks are primarily nocturnal, although during the cold winter months they may emerge from their burrows to forage in the late afternoon. (A full description of their burrowing behaviour will follow in chapter 4). Aardvarks tend to be solitary and rarely interact with other individuals except during the mating season which occurs in early summer in southern Africa (Taylor, 2002; Taylor & Skinner, 2003). It is unknown whether these animals are territorial but distinct core areas exist within the overlapping home ranges of individuals (Taylor & Skinner, 2003; van Aarde, 2004). Home ranges in South Africa varied between 2.0 km^2 and 4.6 km^2 with no significant difference for male or female home ranges (van Aarde *et al*., 1992; Taylor & Skinner, 2003).

1.1.6 Reproduction

Information regarding the reproductive biology of aardvarks is scarce. The gestation period is approximately seven months and usually only a single young is born (Melton, 1976). The altricial young will stay in the burrow for two weeks before joining their mother on foraging outings (Melton, 1976). Young first start to excavate their own burrows, in close proximity to their mother's, at six months of age and will continue to accompany their mother until the following mating season. At this point male offspring leave the area whilst females may continue to associate with their mothers. The roaming nature of males suggests that aardvarks may be polygynous (Melton, 1976). Aardvarks are thought to reach sexual maturity after two years (Rahm, 1990).

1.2 CONSERVATION STATUS

The aardvark is currently listed as an animal of least concern (Friedman & Daly, 2004) despite a lack of data regarding population sizes and trends. It has been implied that previous classifications of the aardvark as ''vulnerable'' could be attributed to their nocturnal and elusive behaviour which may have resulted in them being viewed as uncommon (Taylor, 2002; Friedman & Daly). The low densities at which they occur has probably enhanced the perception of these animals being uncommon and it was estimated that eight animals occupied 10 km^2 during a study in the Karoo (Taylor & Skinner, 2003).

Aardvarks are preyed on by all the large terrestrial predators including lions (*Panthera leo*). However, it is the spotted hyaena (*Crocuta crocuta*), which regularly kills young, and man which pose the biggest threat (Kingdon, 1971). Aardvarks are hunted for bushmeat and recreation in numerous countries in Africa. Various body parts are also sought after items in traditional medicine and may be used for a variety of purposes including preventing illness, as good luck charms and poison (Kingdon, 1971; Melton, 1976). Loss of habitat as a result of land development and crop farming may also a pose a threat to aardvarks. Contrary to this, intensive cattle farming may result in increased trampling of grass pastures which creates favourable conditions for termites thereby increasing prey availability and potentially expanding the distribution of aardvarks, as occurred in Mt. Elgon, Kenya (Kingdon, 1971). In some cases aardvarks may be persecuted by farmers as they can be a nuisance when digging into roads and dam walls or under fences (Cilliers, 2002).

1.3 ECOSYSTEM ENGINEERING

Arid and semi arid environments are characterised by extreme fluctuations in temperature and generally experience much greater evapo-transpiration than precipitation over the course of a year (Brown *et al*., 1979; Kinlaw, 1999). Such factors present significant challenges to the animals inhabiting these areas, a situation which may be exacerbated by limited or complete lack of vegetative cover. Certain burrowing mammals such as aardvarks, warthogs (*Phacochoerus aethiopicus*) and Cape porcupines (*Hystrix africaeaustralis*) create three-dimensional underground structures which are utilised by other species seeking refuge from predators and harsh environmental conditions (Reichman & Smith, 1990; Kinlaw, 1999). Soil has insulating properties which results in the moderate below-ground environment of burrows providing suitable shelter in both hot summers and cold winters for a variety of species (Reichman & Smith, 1990; Finlayson *et al*., 2005).

The animals which create these structures can be viewed as “ecosystem engineers” in accordance with the definition of Jones *et al*. (1994, p374) who proposed that “ecosystem engineers are organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic materials. In doing so they modify, maintain and/or create habitats”. Unlike the keystone species concept, ecosystem engineering does not encompass trophic or competitive interactions (Mills *et al*., 1993; Power *et al*., 1996; Jones *et al*., 1997). However, Jones *et al*. (1994) hypothesize further that many ecosystem engineers may in fact be keystone species despite their limited involvement in community food webs.

Ecosystem engineers can be separated into two further categories, autogenic engineers and allogenic engineers (Jones *et al*., 1994). Autogenic engineers alter their environment via their own physical structures and at the same time remain as a component of the engineered environment (Berkenbusch & Rowden, 2003). Trees and plants provide numerous examples of autogenic engineering. For instance they grow roots that bind the soil and consequently reduce erosion. They also shed dead branches which can alter stream flow dynamics and their leaf canopies may limit the light available to plants in the understorey (Jones *et al.*, 1994). Allogenic engineers, however, modify the environment by changing living or non-living matter from one physical state to another as a result of their behaviour, usually via mechanical processes (Jones *et al.*, 1994; Berkenbusch & Rowden, 2003). Examples of this include beavers (*Castor Canadensis)* creating dams in rivers and aardvarks digging burrows. Such examples of engineering, which directly influence the fitness of the engineer, have also been termed “extended phenotype engineering” because the modified environment directly benefits the fitness of the engineer (Dawkins, 1982; Jones *et al.*, 1997).

The concept of ecosystem engineering is applicable to both marine and terrestrial environments (Jones *et al.*, 1994) and it is suggested that physical engineering has a profound impact on the structure and functioning of most ecosystems and may even play a role in extreme environments such as the Negev desert and the Antarctic (Buynitskiy; 1968; Jones *et al.*, 1997; Alkon, 1999; Wilby *et al.*, 2001). It is further claimed that ecosystem engineering may be an important means of creating habitat heterogeneity and consequently may increase species richness on a landscape level (Dean & Milton, 1991a; Jones *et al.*, 1997; Wright *et al.*, 2002).

A large number of organisms inhabiting a variety of ecosystems exhibit behaviour which can be defined as ecosystem engineering however, their ecological impact may vary from significant through to relatively inconsequential (Jones *et al.,* 1997). For example, the damming of a river by beavers in order to create a pond is likely to have large landscape level effects (Wright *et al.*, 2002) whereas the hoof print of an ungulate which collects rain water is unlikely to have major ramifications for an ecosystem (Jones *et al*., 1994). Therefore, Jones *et al*. (1994) recommended that a scaling system be employed to facilitate the formal assessment of the impact (positive or negative) of any given engineering activity. This scaling system comprises six spatial and temporal factors and these criteria will be described later.

1.4 BROAD MOTIVATION

There is a paucity of literature on the ecology of aardvarks. Of the few studies conducted on this animal the majority have dealt with home range and burrow utilisation as well as their feeding ecology and phylogenetic history (Melton, 1976; Willis *et al*., 1992; Van Aarde *et al*., 1992; Springer *et al*., 1997; Lindsey, 1999; Taylor & Skinner, 2000; Taylor & Skinner, 2001; Taylor *et al*., 2002; Taylor & Skinner, 2003; Lehmann, 2004; Taylor & Skinner, 2004). Very few studies have investigated the role of their burrows in ecosystem functioning (Kingdon, 1971; Smithers, 1971; Melton, 1976; Skinner & Smithers, 1990). As a result of their burrowing behaviour aardvarks could be considered to be ecosystem engineers. In this study I use the six criteria of Jones *et al*. (1994) to evaluate the significance of aardvarks as ecosystem engineers in arid and semi-arid environments. These environments were selected because it was thought that the extreme environmental conditions which characterise these areas may result in the burrows being critical to the survival of other species. Given our limited knowledge of aardvarks and the potential threats they face, research of this nature is probably overdue.

CHAPTER 2

GENERAL DESCRIPTION OF THE STUDY SITES

2.1 LOCATION

The study was conducted at three sites in South Africa (Figure 2.1) which were selected on the basis of their aridity, different habitat types and the presence of extant populations of aardvarks. Kwandwe Private Game Reserve (hereon referred to as Kwandwe) is situated approximately 35 km north of Grahamstown in the Great Fish River Valley, in the Eastern Cape Province (33 º09’S, 26º62’E). The Mountain Zebra National Park (MZNP) lies approximately 12 km west of Cradock (32º06’S, 25º24’E) in the Eastern Cape Province, and Tswalu Kalahari Reserve (Tswalu) is located 100 km north-west of Kuruman in the Northern Cape Province (27°04’S, 22°10’E).

2.2. KWANDWE PRIVATE GAME RESERVE

2.2.1 Site description and history

Kwandwe was established as a private game reserve in 1999 and occupies an area of approximately 200 km^2 (Figure 2.2). The land was previously utilized for ostrich and small stock farming. At present the reserve is bordered by the R67 regional road in the east and by privately owned farmland and state-owned land in the north, west and south. The entire perimeter of the reserve is surrounded by an electrified game fence. The perennial Great Fish River and the non-perennial Botha’s River run through Kwandwe.

2.2.2 Climate

Due to the lack of long-term climatic data for Kwandwe, data from Grahamstown were used as a surrogate to facilitate comparison with the data obtained from Kwandwe for the study period (2005-2006).

The mean monthly maximum and minimum temperatures recorded on Kwandwe during 2005 and 2006 are indicative of a warm temperate climate (Figure 2.3). Kwandwe experienced hot summer months (December - March) with mean maximum monthly temperatures of approximately 30 ºC. The winter months (June - August), were cold with night-time temperatures dropping below 5 ºC. The mean monthly minimum temperature for these months ranged between 5 and 7.5 ºC. These trends are similar to those recorded in Grahamstown for the ten-year period 1997-2006 (Figure 2.4).

Rainfall events are highly variable at Kwandwe and may occur throughout the year with bimodal peaks usually during April and November. However, 2006 was an exception as the reserve experienced uncharacteristically high rainfall in February (111 mm) and August (141 mm) (Figure 2.5). The total annual precipitation at Kwandwe during the study period was 357 mm in 2005 and 410 mm (January to August) in 2006. This was lower than average annual rainfall measured at the Grahamstown weather station (511 ± 87 mm) for the ten-year period 1997-2006 (Figure 2.6). Kwandwe’s location on the leeward side of the *Kaprivierberge* may explain its decreased rainfall compared to Grahamstown (Parker, 2003). However, it must also be noted that the rainfall data presented in this chapter did not extend further than August 2006 and thus it is likely that the total annual rainfall for 2006 would have exceeded that of the ten-year mean. Rainfall and temperature patterns may also differ within Kwandwe due to the topographical complexity of the reserve and as a result the lower-lying areas experience higher temperatures and receive less rainfall than the areas of higher elevation.

2.2.3 Vegetation

The vegetation on Kwandwe can be divided into 10 major units: Bushclump Karroid Thicket, Medium *Portulacaria* Thicket, Euphorbia *Portulacaria* Mosaic, Short *Euphorbia* Thicket, Tall *Euphorbia* Thicket, Bushclump Savannah Thicket, Old Cultivated Areas (Old Lands), Karroid Shrubland, Drainage Line Thicket and Riverine Thicket. Bushclump Karroid Thicket and Riverine Thicket dominate Brandeston peninsula, the area where this study was conducted (figure 2.2). Bushclump Karroid Thicket is typically found on sandy/clay colluvial slopes adjacent to the alluvial plains of the Great Fish and Botha's Rivers. This vegetation type is characterised by scattered clumps of trees surrounded by grass and shrubs. Typical species of this vegetation type include *Rhus refracta*, *Rhus longispina*, *Euclea undulata*, *Gymnosporia polyacantha* (trees), *Setaria neglecta*, *Digitaria eriantha* (grasses) and *Pentzia incana* (shrub).

Riverine Thicket can be divided into two distinct zones, the alluvial *Acacia* zone consisting of *Acacia karroo* which border the watercourses of the Great Fish and Botha's Rivers, and secondly the vegetation zone which occurs on the steep banks of the Great Fish River. The dominant species in this zone include *Rhus lancea*, *Acacia karroo* and *Combretum caffrum*. *Panicum maximum* is the dominant grass species.

2.2.4 Topography and geology

The altitude of Kwandwe ranges from 170m above sea level (a.s.l.) in the Great Fish River Valley to approximately 600m a.s.l. on the north-east ridges. Steep valleys and gorges are prominent in the south and north-east regions of the reserve whilst the central portion is characterised by open plains and undulating hills (Bissett, 2004). Low & Rebelo (1996) describe the dominant geology and soils of the Eastern Cape Province as ranging from deep solonetic soils originating from dolerites of the Beaufort group through to the sandy clays and lithosols of the Cape Supergroup, Dwyka and Ecca formations. The underlying geology of Kwandwe is dominated by grey/red mudstone and sandstone of the Middleton formation (Johnson & Keyser, 1976). Brandeston peninsula is dominated by sandy-clay soils with sandy soils occurring on the banks adjacent to the Great Fish River. The topography of the study area ranged from steep north-facing slopes in the southern section through to a relatively flat middle section before sloping steeply down to the Great Fish River (Figure 2.2).

2.3 MOUNTAIN ZEBRA NATIONAL PARK

2.3.1 Site description and history

The Mountain Zebra National Park was initially established as a nature reserve in 1937 with the aim of protecting the remaining population of 11 Cape mountain zebra (*Equus zebra zebra*) (Brown & Bezuidenhout, 2005). The original protected area was only 17 km^2 and this was deemed insufficient to maintain a viable population of these animals. Consequently, in the 1960s adjacent farmland was purchased and incorporated into the park which increased its size to approximately 65 km^2 (Pond *et al*., 2002; De Klerk *et al*., 2003; Brown & Bezuidenthout, 2005). Since 1996 additional farms (and ecosystems) have been procured and the park now occupies an estimated 210 km^2 (Brown & Bezuidenhout, 2005). The recent acquisitions include the 18 km^2 Ebenhaezer section in 1999/2000 (De Klerk *et al*., 2003), of which a portion was used as the study area for this research (Figure 2.7). The Wilgerboom River flows seasonally through the central valley of the southern section of the park and exits in the north (Pond *et al*., 2002) (Figure 2.7).

2.3.2 Climate

Climate data recorded at a weather station at MZNP were used to describe the climate during the study period and data from the nearby Cradock weather station were used to analyse the long-term weather patterns at MZNP.

February 2005 and 2006 were the hottest months during the study period with mean maximum temperatures of approximately 29 ºC and temperatures often exceeding 30 ºC (Figure 2.8). During the study period the winter months of June and July experienced the lowest mean minimum temperatures of 0.8 ºC and 1.6 ºC (2005) and 1.0 ºC and 1.4 ºC (2006). In both 2005 and 2006 winter night-time temperatures regularly dropped below 0 ºC resulting in severe frost. These results are analogous to those recorded over the 10-year period 1997-2006 with December, January and February experiencing the hottest mean maximum temperatures and June and July experiencing the lowest mean minimum temperatures (Figure 2.9). The Bankberg provides a barrier to cold fronts in the winter months resulting in a more moderate climate existing in the sheltered valleys but snow may fall on the higher lying ridges (Pond *et al*., 2002).

MZNP is considered to fall within the summer rainfall zone of South Africa (De Klerk *et al*., 2003; Brown & Bezuidenhout, 2005), however, during the study period

2005-2006 rainfall was greatest in late summer and early autumn (Figure 2.10) which agrees with the findings of Pond *et al*. (2002). During this study, peaks of rainfall occurred in February 2005 (71.5 mm), January 2006 (93.8 mm) and February 2006 (130.2 mm) with very little rain falling in the winter months. The total annual rainfall during the study period was 398 mm in 2005 and 440 mm in 2006 (January to August) which was substantially higher than the 10–year average of 362 ± 65 mm (Figure 2.11).

2.3.3 Vegetation

The MZNP is located in a transitional zone or ecotone between the Nama Karoo Biome in the west and the Grassland Biome in the east but it is considered to form part of the Nama Karoo (Pond *et al*., 2002; Brown & Bezuidenhout, 2005). The Nama Karoo Biome is the second largest biome of South Africa and is situated on the hotter, drier, central plateau of the western half of country. This vegetation is comprised primarily of grass and dwarf shrubland (Low & Rebelo, 1996).

The Ebenhaezer section of the reserve has been classified as Eastern Mixed Nama Karoo and consists primarily of shrub and grass dominated vegetation communities (Hoffman, 1996; De Klerk *et al*., 2003). It is suggested that annuals and geophytes contribute approximately 50 % of the species in this vegetation type (Hoffman, 1996). De Klerk *et al*. (2003) identified five major plant communities in the Ebenhaezer section: *Buddleja glomerata-Rhus lucida* Woodland, *Themeda triandra-Merxmuellera disticha* Grassland, *Acacia karroo-Pentzia globosa* Woodland, *Panicum maximum-Acacia karroo* Woodland and *Salsola kali-Medicago sativa* Old cultivated fields. The area used for this project was dominated by *Acacia karroo-Pentzia globosa* Woodland. The western boundary of the study area bordered old cultivated lands whilst the seasonal Wilgerboom River served as a boundary on the eastern side. The vegetation along this drainage line consists primarily of *Acacia karroo* veld (De Klerk *et al*., 2003).

2.3.4 Topography and geology

The altitude at MZNP ranges from approximately 1000 m a.s.l. in the eastern and central parts of the park through to Rooiplaat and the Bankberg in the south at 1360 m and 1927 m a.s.l. respectively. The southern section of the reserve is dominated by mountainous territory with steep-side valleys (Pond *et al*., 2002). This high-lying area subsides into a mid-slope plateau, footslopes and eventually becomes the undulating plains of the central and eastern sections of the park. The dominant feature in the north-west is the steep-sided Saltpeterkop at 1514 m a.s.l. (Pond *et al*., 2002). The site of this research was relatively flat with gentle undulations in places (Figure 2.7).

The geology of MZNP is dominated by mudstone, sandstone and shale of the Balfour formation, Beaufort Group of the Karoo Supergroup (Pond *et al*., 2002; Brown & Bezuidenhout, 2005). The chemical and mechanical weathering of these mudstones and shales results in the deposition of sediment which contains large concentrations of clay and salt. Weathering of the prominent dolerite outcrops in the southern section of the park also results in the formation of highly fertile clayey soils (Pond *et al*., 2002).

2.4 TSWALU KALAHARI RESERVE

2.4.1 Site description and history

In the mid 1990’s Tswalu was established as a hunting reserve and conservation area on land which had previously been utilized for stock farming purposes. In 1999 Tswalu was purchased by the Oppenheimer family and presently occupies an area of approximately 874 km^2 (Van Rooyen *et al.*, 1999) (Figure 2.12). It is now run as an eco-tourism venture and breeding facility for endangered species such as roan (*Hippotragus equinus*) and sable antelope (*Hippotragus niger*).

The reserve is divided into nine management units of varying size: the main estate (278 km^2), predator section (130 km^2), Stofberg section (59 km^2), Kalkpan and Tsamma sections (323 km^2), roan and sable camp (13 km^2), Sonstraal south (12 km^2), Sonstraal north (13 km^2), Gosberg horse camp (7 km^2) and the Klochopiets triangle (37 km^2) (Van Rooyen *et al.*, 1999). No major rivers flow through the reserve (Van Rooyen *et al.*, 1999).

2.4.2. Climate

Due to the lack of long-term climatic data for Tswalu, data from the Van Zylsrus weather station, situated 50 km north of the reserve, were used for comparison with the data obtained from the Tsamma section of the reserve for the period covering this study (2005-2006). Once again climate data for 2006 are from January to August.

In 2005 the mean maximum temperature exceeded 35 ºC in the summer months of January, February and December. Mean maximum temperatures in 2006 were slightly lower with the 33 ºC recorded in January being the highest (Figure 2.13). However, temperatures exceeded 40 ºC regularly in the summer months both in 2005 and 2006. The mean monthly maximum recorded at Van Zylsrus for the ten year period 1997-2006 during the months of December, January and February was 35 ºC (Figure 2.14). During the 2005-2006 period mean monthly minimum temperatures were lowest in the winter months of June, July and August with average temperatures lower than

5 ºC (Figure 2.13). This was only marginally higher than the 10-year means for these months (Figure 2.14). Night-time temperatures in winter during 2005-2006 often dropped below freezing.

Rainfall in Tswalu peaked in January (149 mm) and April (77 mm) in 2005 and in January (96 mm) and February (133 mm) in 2006. During the ten-year period at Van Zylsrus peaks in rainfall were experienced in January and March (Figure 2.15). Little or no rain falls in winter. The total annual precipitation at Tswalu was 352mm during 2005 and 306 mm during 2006 (January to August). The annual mean for Van Zylsrus during the ten-year period was, however, only 191 ± 66 mm (Figure 2.16).

2.4.3 Vegetation

The vegetation of Tswalu consists of Shrubby Kalahari Dune Bushveld on the plains, Kalahari Mountain Bushveld on the mountains and hills and Kalahari Plains Thorn Bushveld in the north and north-east (Van Rooyen *et al.*, 1999). These vegetation types form part of the Savanna Biome, the largest biome in South Africa (Low & Rebelo, 1996). The vegetation in the Tsamma area (Figure 2.12), where this study was conducted, has been identified as containing five vegetation communities: *Acacia haemotoxylon – Grewia flava – Aristida meridionalis* open shrubveld, *Acacia haemotoxylon – Grewia flava – Eragrostis lehmanniana* dune valleys and plains, *Acacia haemotoxylon – Centropodia glauca – Hermannia burchellii* shrubveld, *Acacia mellifera – Rhigozum trichotonum – Monechema incanum* shrubveld and *Acacia mellifera - Rhigozum trichotonum – Stipagrostis uniplumis* bushy plains and valleys (Van Rooyen *et al.*,1999). The *A. haemotoxylon* open shrubveld is the dominant community and covers approximately 40 % of the area. The other community types are roughly equal in size (Van Rooyen *et al.*, 1999). The study area for this research contained all five vegetation types but was dominated by the *Acacia haemotoxylon – Grewia flava – Aristida meridionalis* community.

2.4.4 Topography and geology

The landscape at Tswalu comprises sandy plains, dunes and pans in the south and west of the reserve and hills and the Korannaberg mountains in the north and east of the reserve. Sandy valleys occur between the hills (Van Rooyen *et al*., 1999). The altitude at Tswalu ranges from 1020 m a.s.l. near Rogela pan in the west to 1586 m a.s.l. on the Korannaberg in the east (Van Rooyen *et al*.,1999). During the rainy season streams may flow through the mountain valleys, however, these terminate in the plains below the mountain and do not form a major river (Van Rooyen *et al*., 1999). The terrain on the Tsamma section of the reserve consists mainly of open plains with lowlands occurring between scattered parallel sand dunes.

The geology of the reserve can be divided into two main types; the Matsap Formation of the Korannaberg mountain range and the Kalahari Group of the Gordonia Formation of the plains. The Matsap Formation consists of quartzite and conglomerate with lenses of hematite whilst the Kalahari Group comprises predominantly of aeolian surface sand and dunes with limited amounts of alluvium, gravel, limestone and silcrete (Van Rooyen *et al*., 1999). Van Rooyen & Bredenkamp (1996a; 1996b) suggest that Shrubby Kalahari Dune Bushveld and Kalahari Plains Thorn Bushveld are associated with deep sandy to loamy sands of aeolian origin and underlain by calcrete. Kalahari Mountain Bushveld is thought to be restricted to acid banded ironstone and lava substrate which occurs on the hills and mountains of the region (Van Rooyen & Bredenkamp, 1996c). The predominant soil type in the study area was fine-grained red soil interspersed with widely-scattered outcrops of calcrete.

2.5 SOIL HARDNESS

Sixty readings of relative soil hardness were taken randomly within the control areas at each of the study sites using a S-170B pocket penetrometer (Brainard-Kilman,Stone Mountain, GA, USA). Due to the data not being normally distributed a Kruskal-Wallis one-way ANOVA was used to test if the sites had an affect on soil hardness. The results suggest that this was indeed the case ($H_{2,180} = 96.9907$, $p<0.001$) with the soil at Kwandwe (mean = 4.7 ± 3.03 kg/cm^2) and MZNP (mean = 4.29 ± 2.84 kg/cm^2) being significantly harder than the soil at Tswalu (mean = 0.75 ± 1.11 kg/cm^2). The implications of this shall be discussed in a later chapter.

2.6 BURROW DENSITY

In order to calculate the density of intact aardvark burrows occurring at each site, 40m x 100m belt transects were thoroughly searched for burrows by two observers (McCoy *et al.*, 2006). The two observers walked along the midline of the transect at a constant speed with one observer locating burrows to the left of the midline and the other to the right to prevent sampling bias (McCoy *et al.*, 2006). In no instances did the belt transects overlap. The number of transects surveyed at each study site differed due to the different size of the study areas at each site. At Kwandwe a total of 33 burrows were located in 16 completed transects compared to the 35 burrows in 11 transects at MZNP and 39 burrows in 80 transects at Tswalu. Thus burrow densities were calculated as 516 $/km^2$, 795 $/km^2$ and 122 $/km^2$ for Kwandwe, MZNP and Tswalu respectively.

2.7 TABLES AND FIGURES

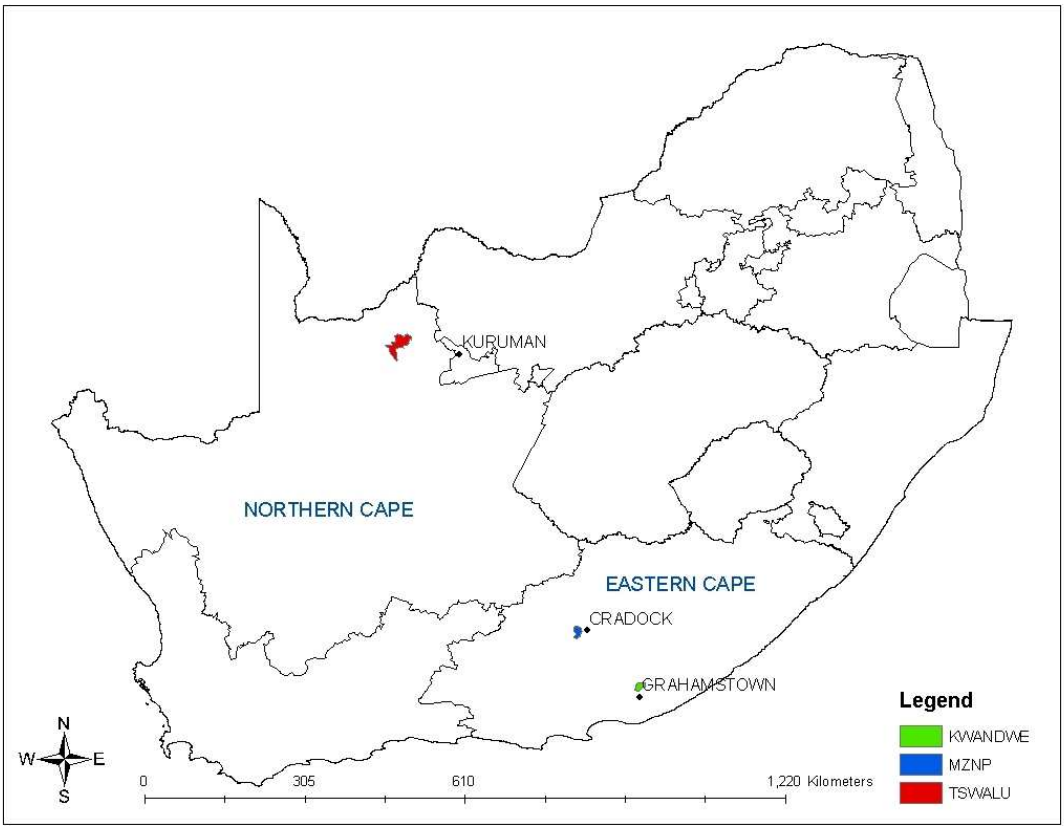

Figure 2.1: The location of the three study sites within South Africa (ArcGIS 9; map units: decimal degrees; not projected).

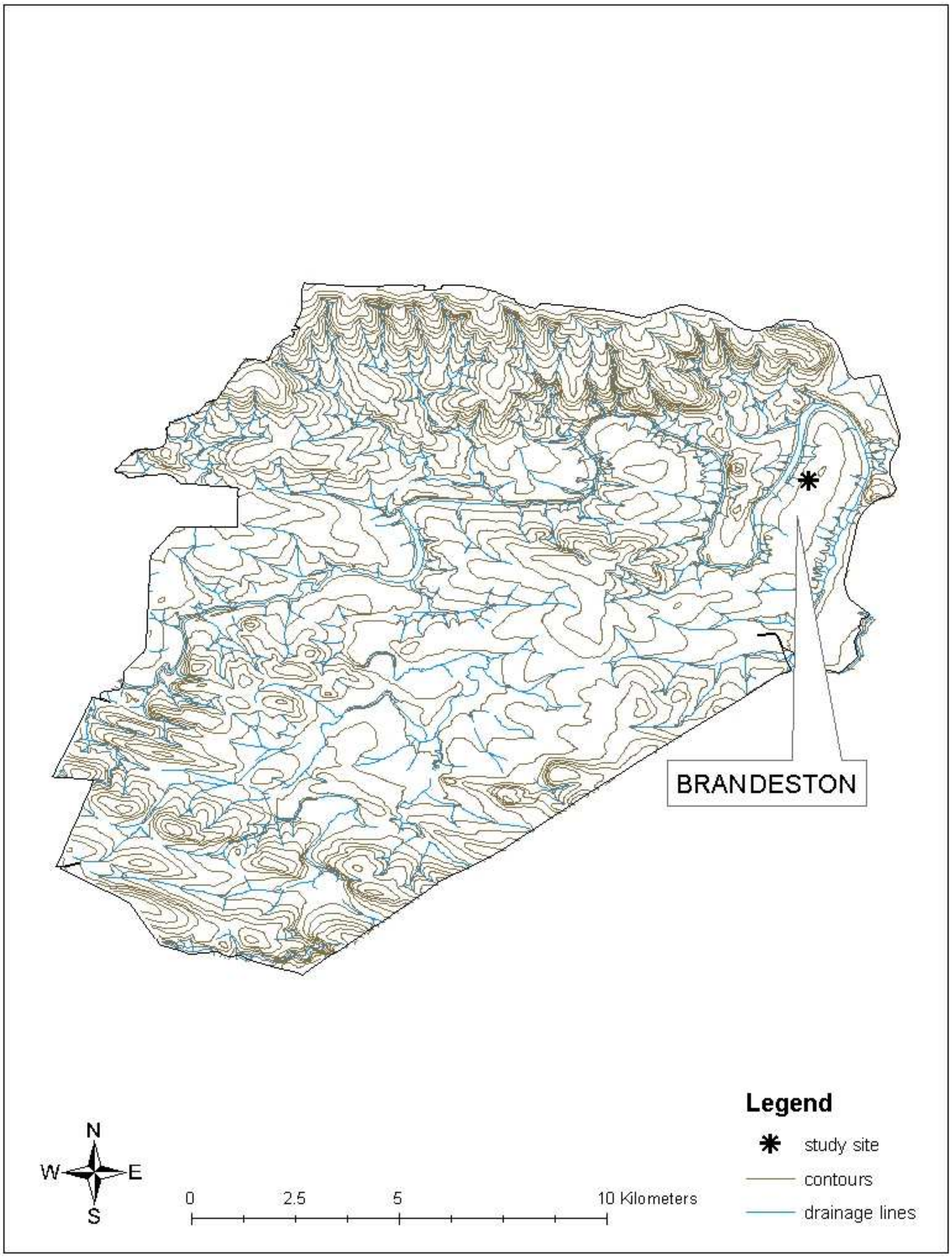

Figure 2.2: The topography and drainage patterns of Kwandwe Private Game Reserve (ArcGIS 9; map units: decimal degrees; not projected). The study site for this research was located on Brandeston peninsula section of the reserve.

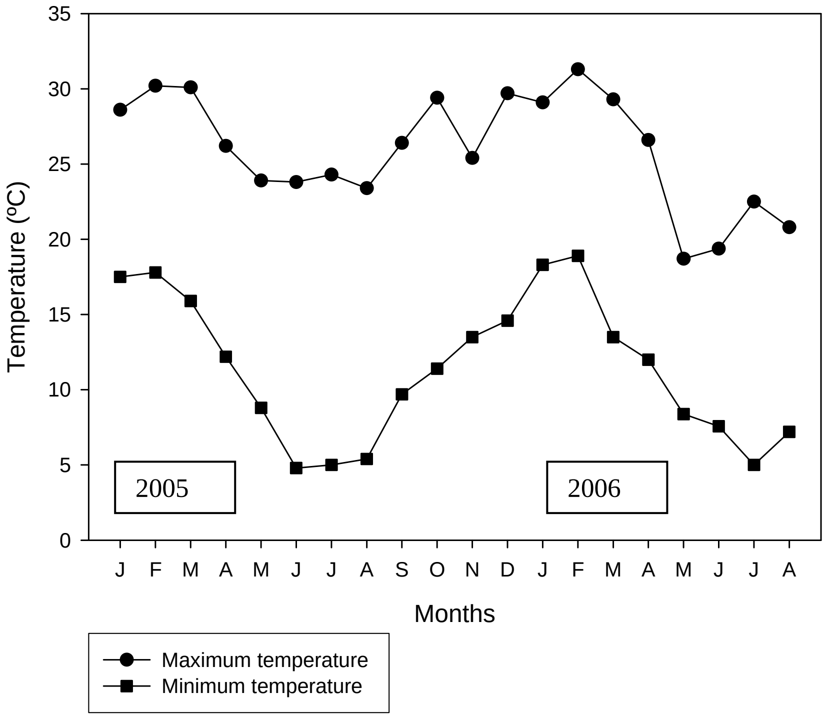

Figure 2.3: The mean monthly maximum and minimum temperatures for Kwandwe during the study period 2005-2006.

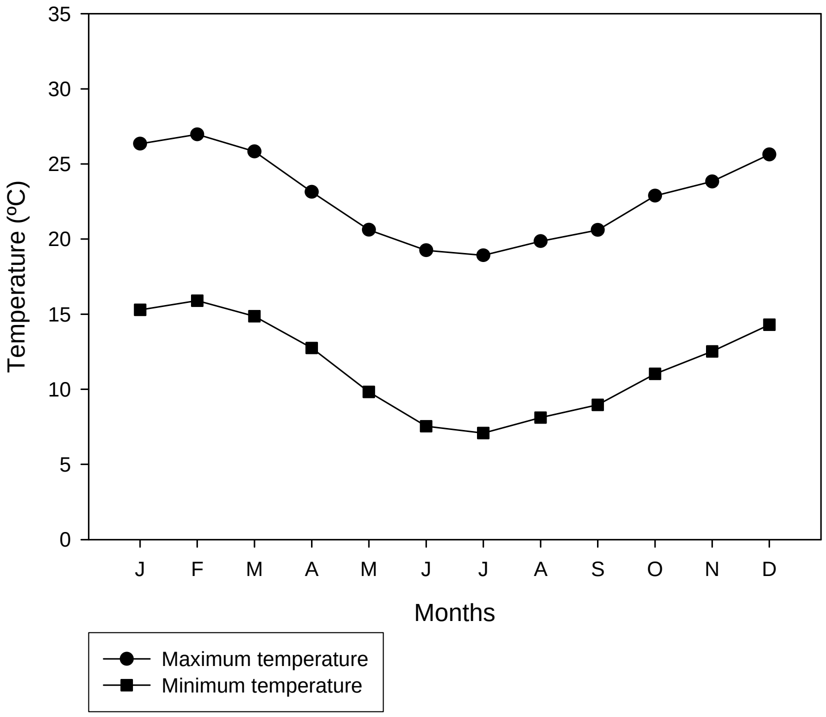

Figure 2.4: The mean monthly maximum and minimum temperatures for Grahamstown over the ten-year period 1997-2006.

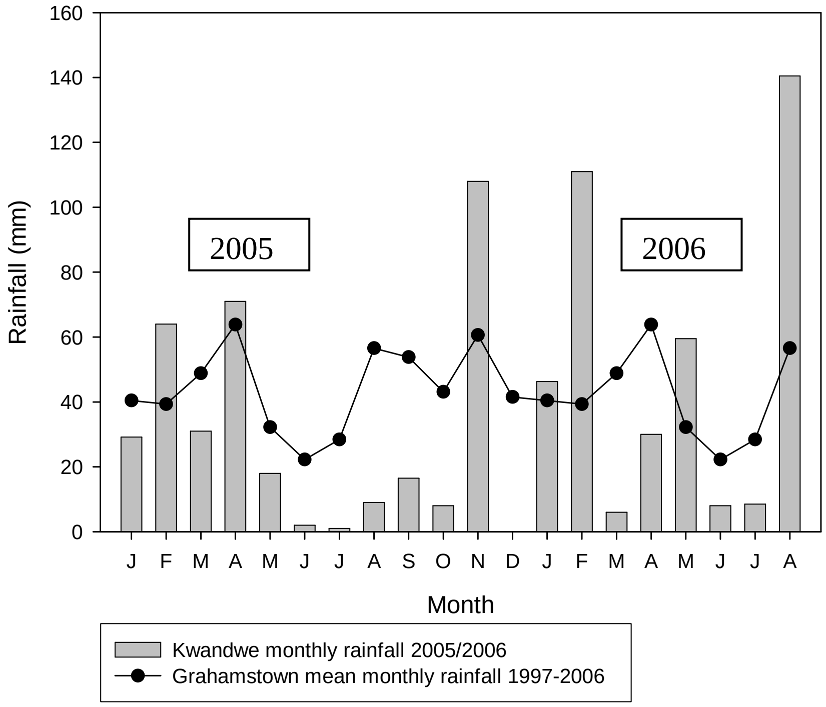

Figure 2.5: The total monthly rainfall for Kwandwe during the study period (2005-2006) in relation to the meanly monthly rainfall for Grahamstown over the ten-year period 1997-2006.

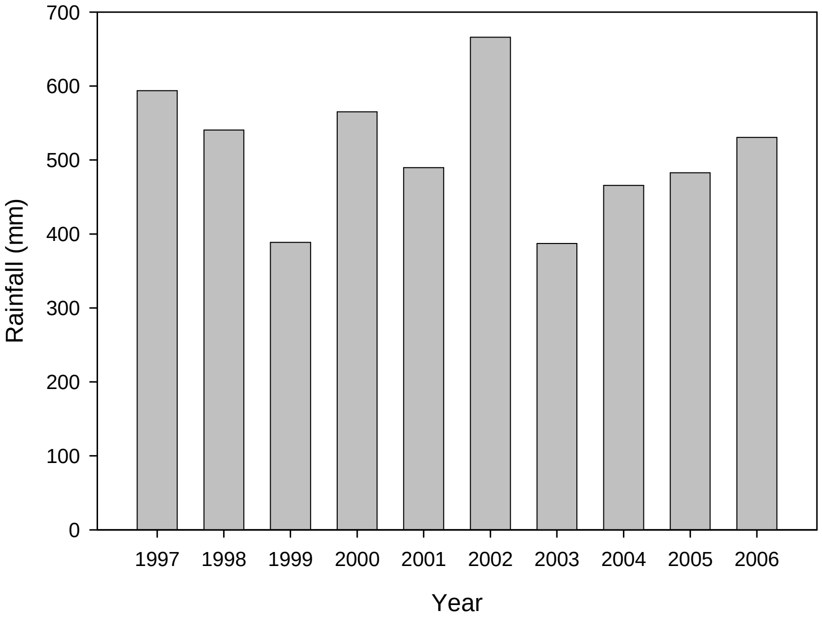

Figure 2.6: The total annual rainfall in Grahamstown over the ten-year period (1997-2006). Data for 2006 are January to August.

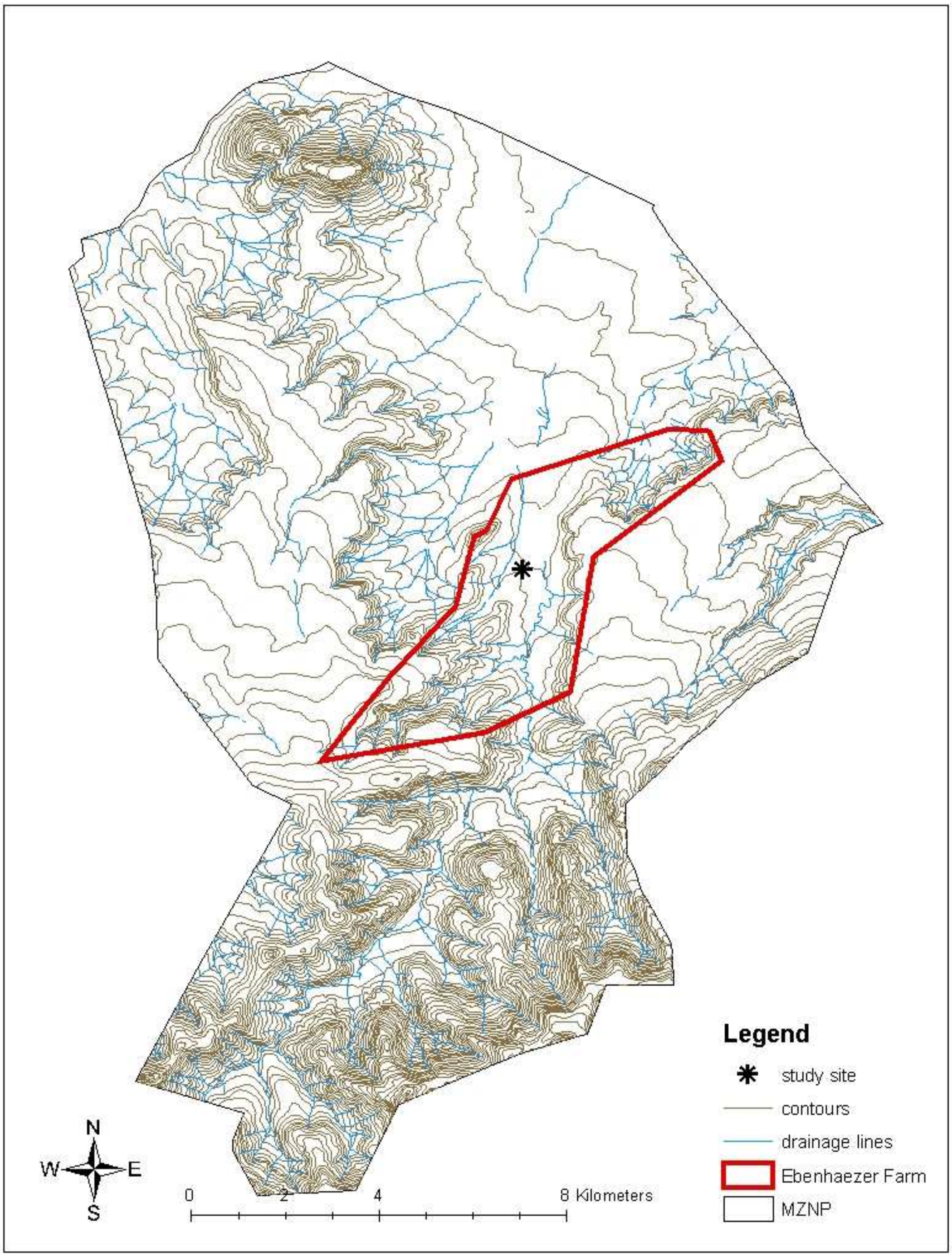

Figure 2.7: Topography and drainage patterns for Mountain Zebra National Park. (ArcGIS 9; map units: decimal degrees; not projected). The study site for this research was located on what was previously the Ebenhaezer farm.

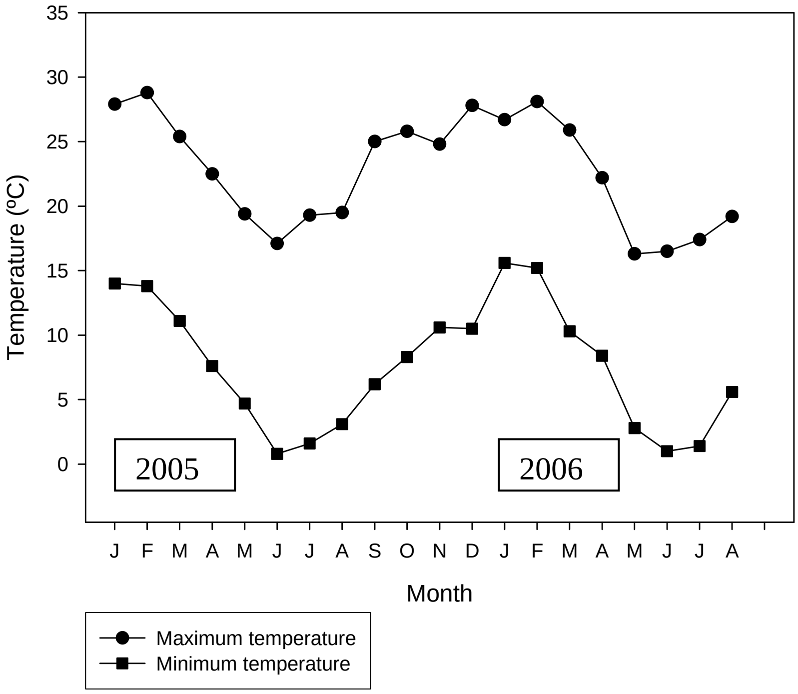

Figure 2.8: The mean monthly maximum and minimum temperatures for MZNP during the study period 2005-2006.

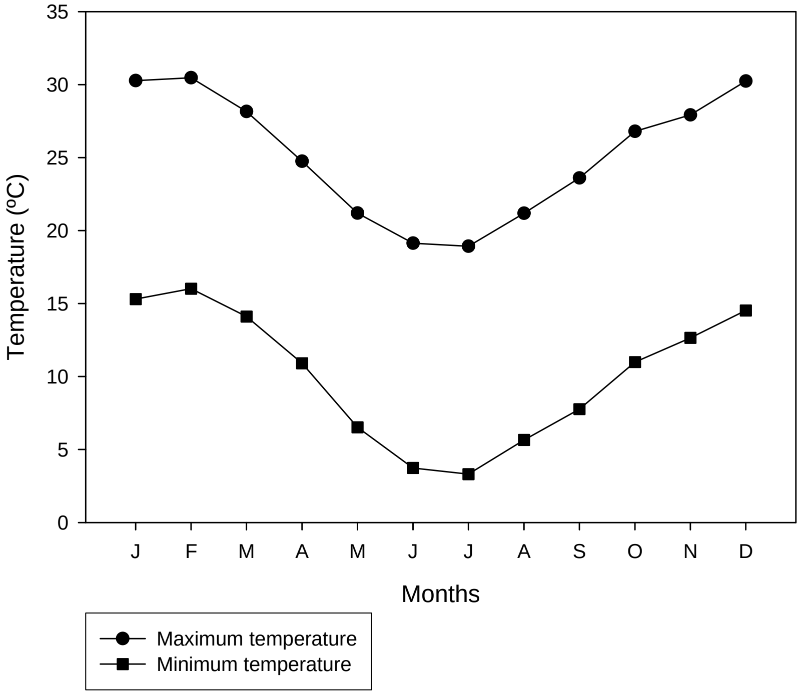

Figure 2.9: The mean monthly maximum and minimum temperatures for Cradock over the ten-year period 1997-2006.

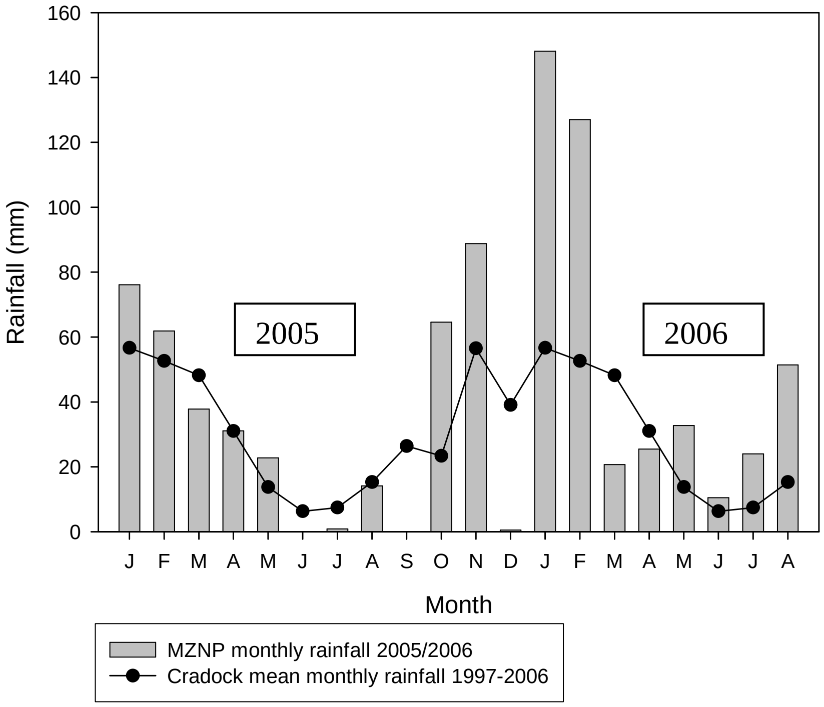

Figure 2.10: The total monthly rainfall for MZNP during the study period (2005-2006) in relation to the meanly monthly rainfall over the ten-year period 1997-2006.

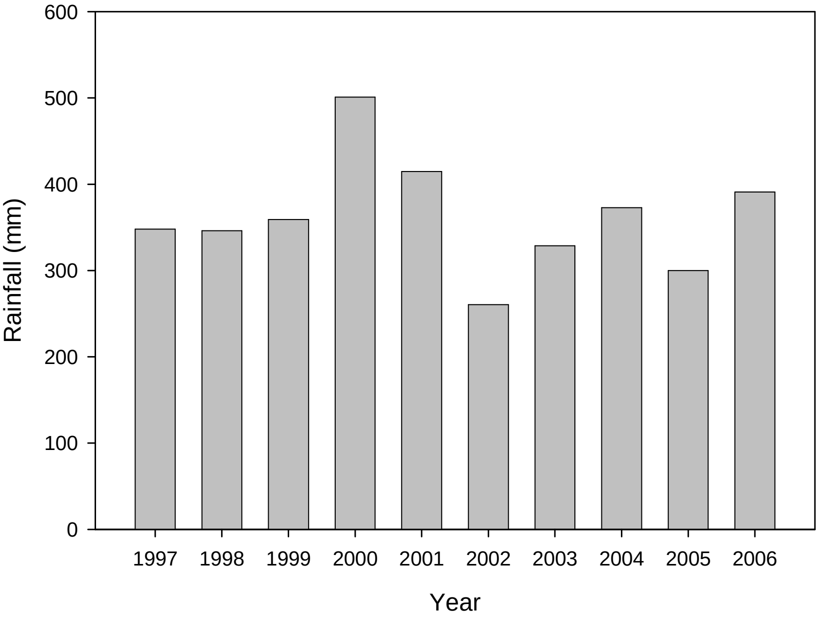

Figure 2.11: The annual rainfall for Cradock over the ten-year period (1997-2006). Data for 2006 are January to August.

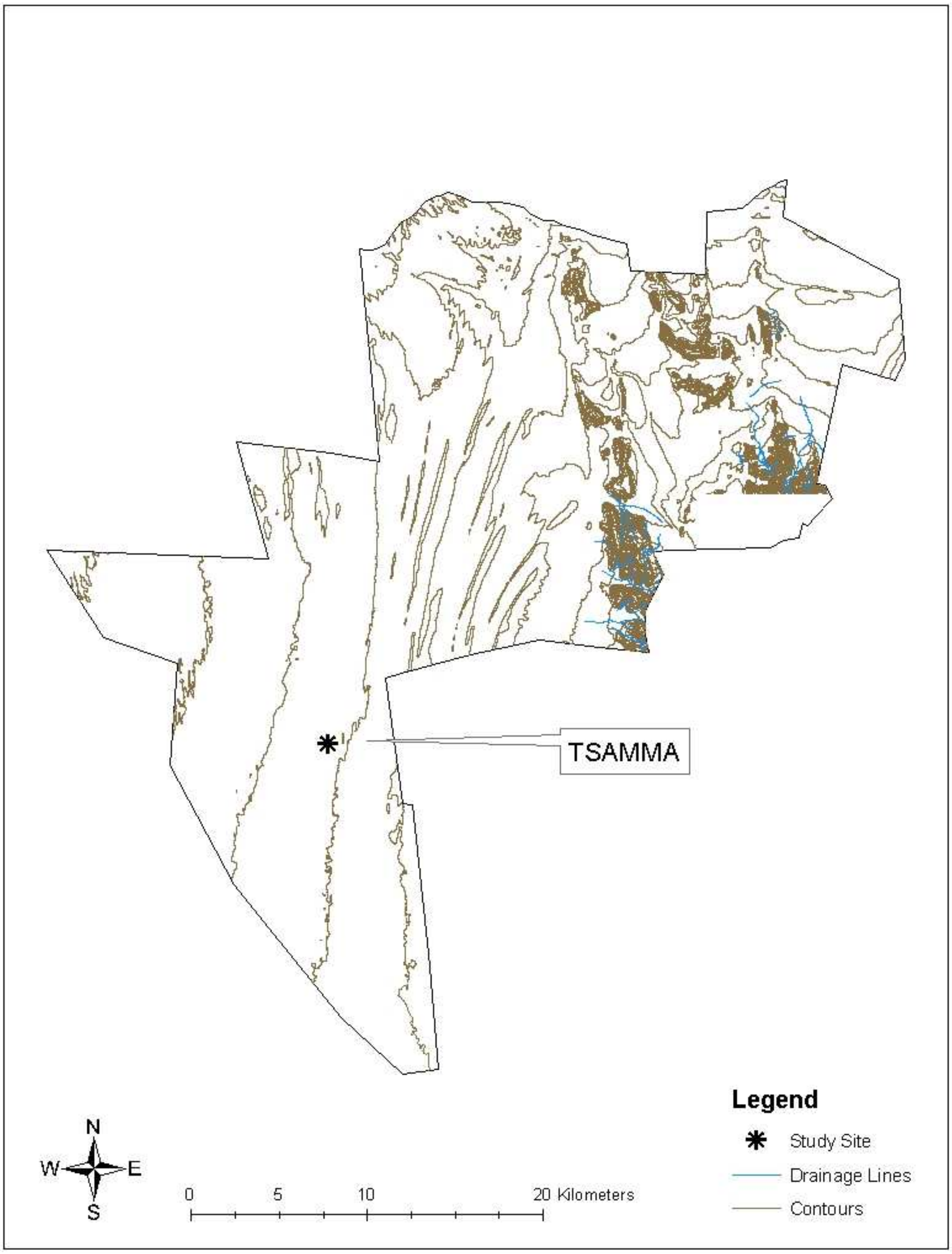

Figure 2.12: Topography and drainage patterns for Tswalu Kalahari Reserve. (ArcGIS 9; map units: decimal degrees; not projected). The study site for this research was located on the Tsamma section of the reserve.

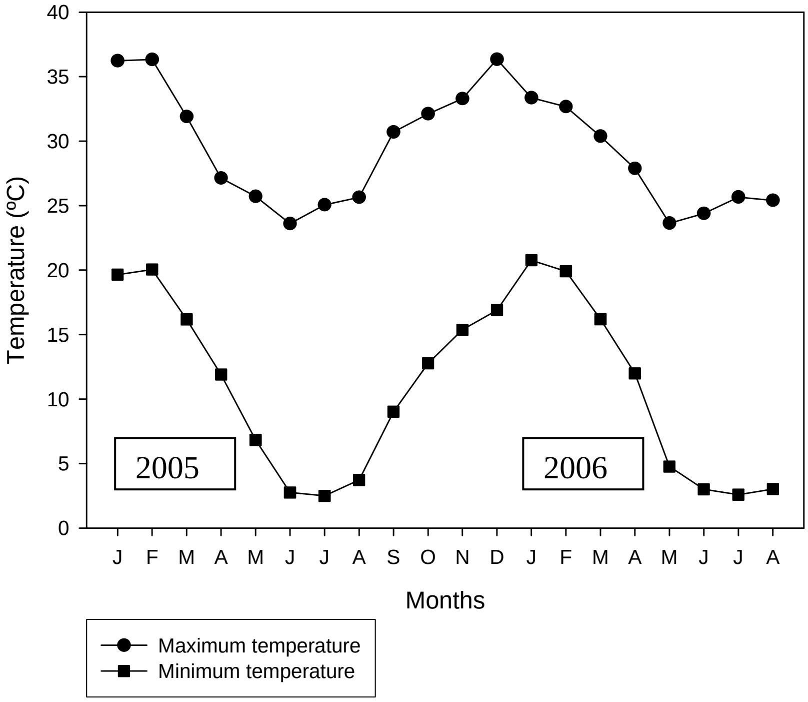

Figure 2.13: The mean monthly maximum and minimum temperatures for Tswalu during the study period 2005-2006.

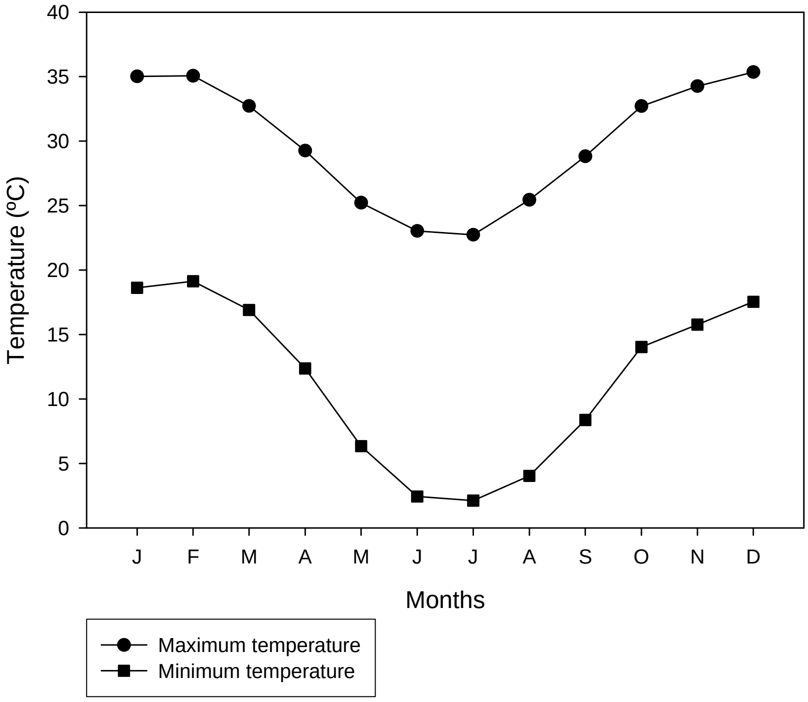

Figure 2.14: The mean monthly maximum and minimum temperatures for Van Zylsrus over the ten-year period 1997-2006.

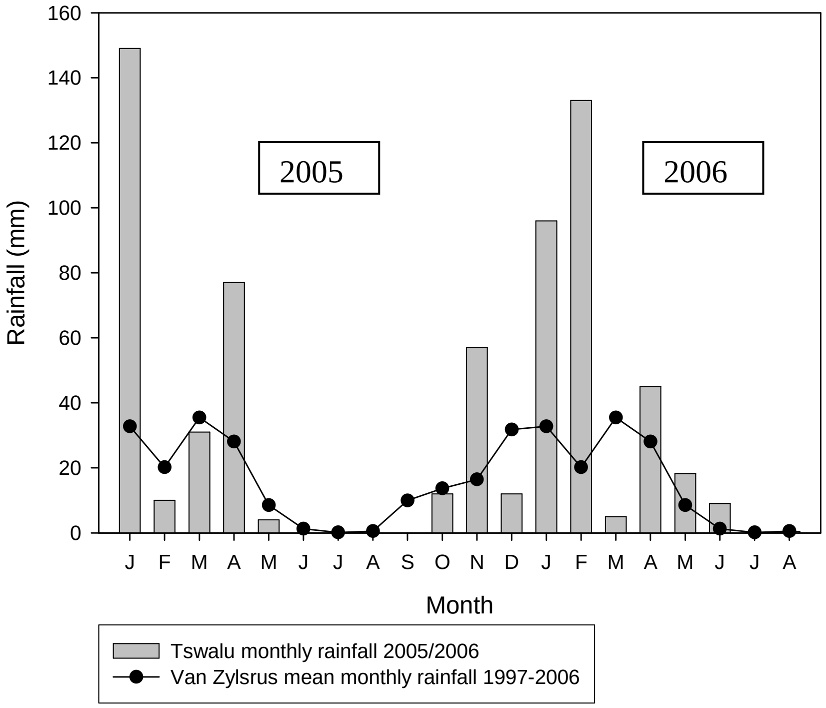

Figure 2.15: The total monthly rainfall for Van Zylsrus during the study period (2005-2006) in relation to the meanly monthly rainfall over the ten-year period 1997-2006.

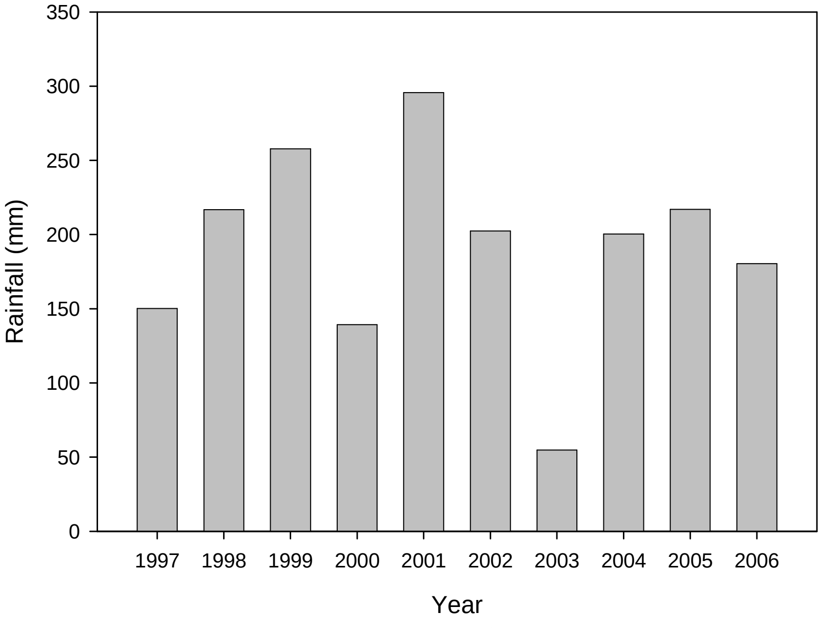

Figure 2.16: The annual precipitation for Van Zylsrus over the ten-year period (1997-2006). Data for 2006 are January to August.

CHAPTER 3

MICROHABITAT OF AARDVARK BURROWS

3.1 INTRODUCTION

Water, shelter and food are the three critical elements required for survival in all environments on earth (Krebs, 1985). This is especially true in arid and semi-arid ecosystems where temperatures may fluctuate on a diurnal and seasonal basis from very hot to very cold. Water may also be scarce and levels of evaporation are usually elevated (Taylor & Skinner, 2004). The use of burrows in these harsh environments may assist in the provision of water, shelter and food.

The main contributors to water loss for terrestrial vertebrates living in these environments are urine formation and evaporation from the lungs and skin. In response, animals have developed a range of mechanisms, both physiological and behavioural to facilitate their existence (Smith, 1990; Williams *et al*., 1999; Milton & Dean, 2004; Finlayson *et al*., 2005). One such strategy is to remain quiescent during times of environmental stress, a tactic which is employed by spadefoot toads (*Pelobates fuscus*) which remain underground for months until a major rainfall event when they emerge, mate and lay eggs before returning to their underground chambers (Smith, 1990). Reptiles are also known to aestivate, for example, the Horsfield's tortoise (*Testudo horsfieldi*) which lies dormant under the desert sands of Uzbekistan and only emerges for three months in spring, thus avoiding the very hot summers and very cold winters (Milton & Dean, 2004). However, many vertebrates which occur in arid and semi-arid areas do not aestivate and have developed alternative strategies for survival. For example, members of the Heteromyidae (kangaroo rats, kangaroo mice and rock pocket mice) in North America, and the Dipodidae and Muridae (jerboas and gerbils) of the Middle East and Africa only derive a small amount of moisture from their diet which consists predominantly of dry seeds and plant material (Schmidt-Nielsen & Schmidt-Nielsen, 1950; Smith, 1990). They do, however, acquire water generated by their own metabolism and supplement their diet with insects and green vegetation (Walsberg, 2000; Tracey & Walsberg, 2002). In addition to not having sweat glands, they limit water loss by producing dry faeces, excreting highly concentrated urine (twice the concentration of seawater), remaining in sealed burrows for most of the day and only foraging at night or during cooler periods of the day (Kirmitz, 1962; Smith, 1990). The sealed burrows remain humid throughout the day and this greatly reduces evaporation from the lungs (Schmidt-Nielsen & Schmidt-Nielsen, 1950; Reichman & Smith, 1990; Smith, 1990; Williams *et al.*, 1999).

Numerous studies across a range of vertebrates, have suggested that relative humidity in burrows is high and in many instances exceeds that on the surface (Schmidt-Nielsen & Schmidt-Nielsen, 1950; Coulombe, 1971; Kay & Whitford, 1978; Wood, 1997; Cortés *et al.*, 2000). For example, research conducted by Bulova (2002) revealed that relative humidity in the burrows of the desert tortoise (*Gopherus agassizii*) ranges from 6.1 – 44.5 %, whereas at the same time relative humidity on the surface ranges from 4.1 – 32.2 %. Importantly, throughout the study period the relative humidity inside the burrows was higher than on the surface and this, in conjunction with higher recorded surface temperatures, resulted in the conclusion that the potential for evaporative water loss is greater outside of the burrows (Bulova, 2002).

A wide variety of animals utilise microhabitats such as rocks, vegetation and burrows to avoid extreme temperatures. These include reptiles such as Egyptian spiny-tailed lizards (*Uromastyx aegypticus*) which avoid soil surface temperatures that can exceed 55 °C, by retiring to their burrows which may be 15 – 20 °C cooler during the heat of the day (Williams *et al*., 1999; Dean & Williams, 2004). The diurnal burrowing owl, *Speotyto cunicularia*, makes use of gular fluttering as well as employing its wings as a ‘’heat shield’’ (Coulombe, 1971). Mammals and birds also utilise burrows to escape high diurnal temperatures (Coulombe, 1971; Reichman & Smith, 1990; Beck & Lowe, 1991; Kinlaw, 1999; Williams *et al*., 1999). In the case of the fossorial rodent, *Ctenomys fulvus*, which is found in the Atacama desert, the temperature difference between the burrows and the surface is greater than 20 ºC during the warmest part of the day in both summer and winter. The opposite trend occurs at night with the burrow temperatures being higher than those on the surface (Cortés *et al.,* 2000).

Apart from providing a microhabitat where animals are buffered from thermal extremes and may experience reduced evaporative water loss compared to the external environment (Reichman & Smith, 1990; Kinlaw, 1999), burrows may act as seed traps which concentrate food resources for granivorous and omnivorous animals (Dean & Milton, 1991b; Alkon, 1999, Bragg *et al*., 2005). Research in the Negev desert highlands of southern Israel and the Bokkeveld region of South Africa support this hypothesis as it has been recorded that even relatively shallow depressions in the soil created by foraging Indian crested porcupines (*Hystrix indica*), Cape porcupines and aardvarks trap seeds (Dean & Milton, 1991b; Alkon, 1999, Bragg *et al*., 2005).

Aardvarks dig three types of burrows. The first is dug when the animal is excavating for food, usually in open ground or in termitaria. These burrows range from being relatively shallow to occasionally being large enough to cover the entire body. They are rarely, if ever, used for refuge (Smithers, 1971; Melton, 1976; Skinner & Smithers, 1990). The second type is used for temporary refuge and may be several metres in length and terminates in a simple sleeping chamber. These burrows are usually only occupied for a day or two but the animal may return to them periodically (Smithers, 1971; Melton, 1976; Skinner & Smithers, 1990). The third type of burrow is thought to be where aardvarks take up permanent residence when they are not on the move or are used to rear young. As a result of re-excavation during lengthy periods of occupation these burrows may increase to a substantial size with numerous chambers and entrance points. It has been suggested that these larger burrows are used more often by females as males tend to be more nomadic (Smithers, 1971; Melton, 1976; Skinner & Smithers, 1990).

Aardvarks are predominantly nocturnal and this is thought to reduce the chance of hyperthermia which can be induced when animals are active during the heat of the day (Taylor & Skinner, 2004). Digging requires a significant amount of muscle activity which results in increased heat production (McNab, 1979; Ivanov, 2006) and thus may exacerbate the risk of hyperthermia if performed during the day in an environment where the ambient temperature is high and shade is minimal (Taylor & Skinner, 2004). Conversely, aardvarks are prone to hypothermia if they do not seek shelter in burrows when night-time temperatures in winter reach sub-zero levels as they are sparsely haired and have a high thermal conductance, a physiological adaptation that is thought to prevent them overheating in their burrows (McNab, 1979; Taylor & Skinner, 2004). Thus, aardvarks tend to emerge in the late afternoon to forage during winter and retreat to their burrows when the outside temperature drops below approximately 2 ºC (Taylor, 1998; Taylor & Skinner, 2003).

The use of an existing slope for burrowing and the orientation of the burrow could potentially influence the thermal microclimate of a burrow if the entrance faces in the direction of the greatest thermal input (McCoy *et al*., 1993; Wood, 1997). However, the use of slopes for burrowing and the orientation of aardvark burrow entrances have not received much attention in the literature and therefore this facet of burrow ecology shall also be investigated

It is hypothesised that aardvark burrows which are abundant, persist for a long time and large, could provide important protection from climatic extremes for both the aardvark and other animals that use them. In addition, it is likely that seeds will accumulate in the burrows and the burrows could thus contribute to all three key elements of survival.

The specific aims of this chapter of the study were:

- ➢ To determine if aardvark burrows provide a more thermally stable microclimate than the external environment in semi-arid and arid ecosystems;
- ➢ To ascertain if burrows provide a humid microhabitat which could facilitate water conservation in aardvarks and other animals;
- ➢ To determine if burrows act as seed traps which concentrate food resources for granivorous and omnivorous animals.

3.2 METHODS AND MATERIALS

3.2.1 Burrow location

Each season (autumn [March-May], winter [June-August], spring [September-November] and summer [December-January]) 20 intact aardvark burrows were randomly selected at each study site. Intact burrows were those which did not exhibit obvious signs of collapse. In addition, a corresponding control area was identified between 15 m and 20 m away from each burrow in an area with similar aspect and slope to that of the burrow.

3.2.2 Temperature recordings

Twenty standard dry bulb maximum/minimum thermometers were available for this part of the research. Therefore, one thermometer was inserted 1 m inside 10 of the burrows which had been randomly selected from the original 20 burrows. A further 10 thermometers were placed in the shade at the corresponding control areas. The maximum and minimum temperatures for the previous 24 hours were recorded each morning for a period of four days.

3.2.3 Humidity

A digital hygro-thermometer pen (Extech instruments, Waltham, Massachusetts, U.S.A.), attached to a wooden dowel, was inserted 1m into each of the 20 burrows to measure the relative humidity inside the burrows. In many instances the structure of the burrows made it impractical to insert the hygro-thermometer pen any further than 1 m. The relative humidity outside the burrows was measured 1 m above the burrows (Platt *et al.*, 2004). Readings were taken early every morning, when humidity was likely to be highest and every afternoon when humidity was likely to be lowest (Cortés *et al.*, 2000). Readings were taken for four consecutive days.

3.2.4 Seed concentration

Every season a single soil sample (500 cm^3) was collected from each of the 20 burrows and its control area using a hand trowel and a cylindrical container. Soil was collected from the top 2 cm as previous research (Nelson & Chew, 1977; Reichman, 1984; Price & Reichman, 1987; Price & Joyner, 1997) suggests that most of the seeds in the seed bank are located in this upper layer. Soil samples were stored in ziplock bags before being transported to the laboratory and dried in an oven (60 ºC for 10 days). Four sub-samples weighing 50 g each were removed from each sample to make seed removal more efficient. Each of these sub-samples were passed through a set of five sieves with mesh apertures of 4750 µm, 2360 µm, 1000 µm, 500 µm and 250 µm, in order to separate soil particles and organic debris. The soil residue trapped in each sieve was transferred into a white sorting dish (29 cm diameter) and spread evenly across the base. The sorting dish was then placed under a binocular microscope (35 x magnification) and seeds were removed with a pair of fine forceps. All seeds that were collected from the four sub-samples were divided into two containers, one for monocotyledonous seeds and another for dicotyledonous seeds. Once all four sub-samples were sorted the monocotyledonous and dicotyledonous seeds were weighed and these values were converted to biomass of seeds per kilogram of soil.

3.2.5 Burrow orientation

The orientation of 60 burrow entrances (those burrows used in winter, spring and summer) were recorded at each site during the course of the study using a handheld GPS (Garmin, GPS 72, Olathe, Kansas, U.S.A). Burrow orientations were divided into eight directions for analysis: N (=337.5-22.4º), NE (=22.5-67.4º), E (=67.5-112.4º), SE (=112.5-157.4º), S (=157.5-202.4º), SW (=202.5-247.4º), W (=247.5-292.4º), NW (=292.5-337.4º) (McCoy *et al*., 1993).

A protractor was placed on the ground in front of the burrow and this used to determine whether the 60 burrows at each site were dug into substrate with a slope angle greater than 15º. This value was selected on the basis of the figure used by Taylor & Skinner (2003) to establish if aardvarks used steep slopes when foraging.

3.2.6 Burrow entrance size

The height and width (cm) of each burrow entrance was measured 10 cm inside the opening as the visible tunnel dimensions usually remained uniform after an initial widening at the entrance. Burrow measurements were taken from all 20 of the burrows located at each site each season.

3.2.7 Data analysis

Three-way ANOVAs (Statistica 7.0, Statsoft, Inc., Tulsa, Oklahoma, U.S.A., 2004) were used to test the effect of burrow, site and season on the following variables; maximum temperatures, minimum temperatures, average daily temperature range (maximum temperature minus minimum temperature), morning humidity, afternoon humidity, change in humidity (morning humidity minus afternoon humidity), monocotyledonous seed biomass and dicotyledonous seed biomass. The orientation of the burrows at each site was analysed using circular descriptive statistics. The Rayleigh test of uniformity (vectorial model) (Oriana version 1.0, Kovach Computing Services, Anglesey, Wales, 1994) was used to determine if the orientation of the burrows was random or if they demonstrated evidence of a preferred direction**.** The data from Tswalu were re-analysed using the axial model as a result of the bimodal distribution of the data from that site. One-way ANOVAs were used to test if the orientation of burrows influenced the maximum temperature of burrows and to test if site had an effect on the height and width of the burrow entrances. In all cases where ANOVAs were used normality was tested and data were transformed where necessary. Scheffé's post-hoc tests were used to analyse where differences in mean values occurred. Z-tests (Sigma Stat, Jandel Corporation, San Rafael, California, U.S.A., 1995) were used to test if there was a difference in the proportion of burrows on slopes and on flat ground at each of the sites. Yates correction was applied to all calculations. Data are presented as a mean ± 1 SD.

3.3 RESULTS

The mean maximum temperature outside the burrows was significantly higher than inside ($F_{1,916}$ =1125.28, $p < 0.001$) after controlling for the significant effects of site and season ($p < 0.001$ for both) (Figure 3.1). The exception was MZNP in autumn where the difference between inside and outside was not significant ($p > 0.05$). Kwandwe and Tswalu experienced significantly higher mean maximum temperatures compared to MZNP both inside and outside of the burrows. As expected the mean maximum temperature inside and outside the burrows was greatest in summer and lowest in winter, except for outside at Kwandwe where it was greatest in autumn (Figure 3.1).

Conversely, the minimum temperatures were significantly lower outside the burrows than inside ($F_{1,916}$ = 1137.85, $p < 0.001$) after accounting for the significant effects of site and season ($p < 0.001$ for both) (Figure 3.2). However, no significant differences

were detected at either Kwandwe or Tswalu during the summer ($p > 0.05$ for both). The mean minimum temperatures differed at each site with MZNP experiencing the lowest mean temperatures and Tswalu the highest. The mean minimum temperatures inside the burrows at Tswalu were higher compared to the other two sites and Kwandwe was higher than the MZNP. However, Tswalu and Kwandwe also experienced higher minimum temperatures outside of the burrows in comparison to MZNP. Unsurprisingly, the mean minimum temperature differed each season with winter experiencing the lowest temperatures and summer the highest. The only situation where the mean minimum temperature averaged below zero degrees Celsius was outside the burrows at MZNP during the winter (-2.6 ºC). The next lowest mean minimum temperature was recorded at Tswalu where the temperature was nearly 4 ºC warmer. All the reserves demonstrated the same trend with the highest minimum temperatures in the burrows occurring in summer and the lowest in winter
(Figure 3.2).

The average daily temperature fluctuation (maximum temperature minus minimum temperature) outside the burrows was significantly greater than inside ($F_{1,916}$ = 2083.52, $p < 0.001$) with the effect of site and season again being significant ($p < 0.05$ for both) (Figure 3.3). Post-hoc tests revealed that at a site level, MZNP experienced significantly greater fluctuations than Tswalu ($p < 0.05$) whilst in the burrows both MZNP and Kwandwe experienced greater fluctuations than Tswalu ($p < 0.01$ for both). No significant difference existed between the sites outside of the burrows. On a seasonal level winter experienced the greatest fluctuations and summer the lowest.

The morning relative humidity in the burrows was significantly higher than outside ($F_{1,1776}$ = 75.289, $p < 0.001$) after accounting for the significant effects of site and season ($p < 0.001$ for both) (Figure 3.4). However, only the internal burrow readings at MZNP in the spring and summer were significantly higher than those outside ($p < 0.05$). Moreover, the autumn readings at Kwandwe revealed higher humidity outside the burrows than inside although the difference was not significant ($p > 0.05$). Significantly higher values were recorded at both Kwandwe and MZNP compared to Tswalu on a site level inside and outside the burrows ($p < 0.001$ for all), with the humidity inside the burrows significantly higher at MZNP compared to Kwandwe ($p < 0.001$). A difference existed between all the seasons with summer experiencing the highest morning humidity and winter the lowest. At all three sites the humidity was highest in the burrows in summer.

The afternoon relative humidity was also significantly higher inside the burrows than outside ($F_{1,1336} = 775.33$, $p < 0.001$) after controlling for the significant effects of site and season ($p < 0.001$ for both) (Figure 3.5). Despite following the general trend the afternoon humidity readings taken in the burrows at Kwandwe during summer, MZNP during autumn and spring and at Tswalu during autumn were not significantly higher than those taken outside (all $p > 0.05$). The relative humidity recorded at MZNP was significantly higher than that at Kwandwe ($p < 0.01$) which was higher than Tswalu ($p < 0.\ 01$). Post-hoc tests revealed that this trend applied to humidity readings on a site level as well as inside the burrows and outside the burrows.

A significant difference existed between all the seasons ($p < 0.01$ for all) with summer having the highest humidity and winter the lowest. Within the burrows the same seasonal trend emerged as was noted with the morning relative humidity. That is, humidity was highest inside the burrows at all three sites in summer and lowest in winter with the exception of Kwandwe, where spring and autumn values were the lowest.

The average daily fluctuation in relative humidity (morning humidity minus afternoon humidity) was significantly less inside the burrows compared to outside ($F_{1,1336}$ = 7.9586, $p < 0.01$) after controlling for the significant effects of site and season ($p < 0.001$ for both) (Figure 3.6). Post-hoc tests showed that on site level fluctuations at Kwandwe were greater than at the other reserves ($p < 0.001$). The burrows at Kwandwe demonstrated greater fluctuations than the burrows at Tswalu ($p < 0.05$) with no difference existing between Kwandwe and MZNP or between MZNP and Tswalu ($p > 0.05$ for both). Outside the burrows Kwandwe exhibited greater fluctuations than either MZNP ($p < 0.001$) or Tswalu ($p < 0.01$). No difference existed between Tswalu and MZNP ($p > 0.05$). Summer experienced significantly greater fluctuations than the other seasons ($p < 0.001$). No difference was detected between the other seasons ($p > 0.05$ for all).

Neither the biomass of the monocotyledonous ($F_{1,216}$ = 3.11, $p > 0.05$) (Figure 3.7) nor the dicotyledonous ($F_{1,216}$ = 26.09, $p > 0.05$) (Figure 3.8) seeds were significantly higher inside the burrows compared to outside after controlling for the effect of site ($p < 0.001$ for both) and season (monocotyledonous $p < 0.001$, dicotyledonous $p > 0.05$). The biomass of monocotyledonous seeds in the burrows and outside was generally very low at all sites except at Tswalu in the winter where the biomass was significantly elevated compared to the other sites during the other seasons ($p < 0.001$ for all). No difference in monocotyledonous seed biomass was detected between the inside and outside of the burrows at Tswalu during the winter ($p > 0.05$). A higher biomass of dicotyledonous seeds was retrieved from the soil compared to the monocotyledonous seeds, however, the results were more variable. A higher biomass of seeds was recorded at Kwandwe compared to the other sites ($p < 0.001$ for both) particularly in spring compared to Tswalu ($p < 0.05$) and in summer compared to MZNP ($p < 0.05$).

The vectorial model suggests that the burrows at Kwandwe ($p < 0.001$, 0.94º ± 89.36°) (Figure 3.9) and MZNP ($p < 0.001$, 72.81º ± 73.68°) (Figure 3.10) show a strong directional effect. Burrows orientated in a northerly direction were most common at Kwandwe (modal class size = 15) whilst burrows at MZNP tended to face in an easterly direction (modal class size = 21). A non-significant result was recorded for Tswalu ($p > 0.05$, 289.23º ± 133.80°), however, this was attributed to the bimodal nature of the data recorded at that site (Figure 3.11). Following re-analysis in the axial model, the burrows at Tswalu were found to demonstrate a significant preference along the north/south axis ($p < 0.001$, 179.18º ± 59.47°) (Figure 3.12).

The effect of burrow orientation on the maximum temperature recorded in the burrows was significant ($F_{7,342} = 2.4392$, $p < 0.001$). However, the scheffé's post-hoc test did not reveal any significant difference in individual means. The burrows facing in a southerly direction experienced the highest maximum temperatures (mean = 23.60 °C ± 2.63 °C) whilst the west-facing burrows recorded the lowest maximum temperatures (mean = 19.25 °C ± 5.71 °C). Burrow orientation also influenced the minimum temperature ($F_{7,342} = 12.780$, $p < 0.001$). North-west orientated burrows experienced the lowest minimum temp (mean = 10.27 °C ± 4.57) and south-facing burrows the highest (mean = 18.46 °C ± 5.48).

The z-tests revealed that a significantly higher proportion of burrows were located on slopes compared to flat ground at Kwandwe ($p < 0.05$) (Figure 3.13). The opposite result was evident at MZNP ($p < 0.05$) where a higher proportion of burrows occurred on flat ground. No significant difference was evident at Tswalu ($p > 0.05$).

Site had a significant effect on the height of the burrow entrances ($F_{2,237} = 38.187$, $p < 0.001$). The height of the burrows at MZNP (mean = 41.89 cm ± 9.62 cm) were significantly greater than those at Kwandwe (mean = 35.06 cm ± 5.97 cm) which were greater than those at Tswalu (mean = 32.15 cm ± 5.38 cm). No significant difference in burrow width was detected between the sites ($F_{2,237} = 2.7316$, $p > 0.05$) although the burrows at MZNP (mean = 41.79 cm ± 9.97 cm) were wider than those at Kwandwe (mean = 38.60 cm, SD ± 5.50 cm) and Tswalu (mean = 37.05 cm, SD ± 5.38 cm).

3.4 DISCUSSION

It is apparent from the results of this study that aardvark burrows provide a favourable microclimate for aardvarks and other animals attempting to seek refuge from harsh environmental conditions. The burrows were cooler than the external environment during daily and seasonal periods of extreme heat and remained warmer when the surface temperatures were low. The aardvark burrows also maintained a higher relative humidity throughout the day, and thus animals sheltering in them would be less susceptible to the effects of evaporative water loss. Although high burrow humidity may reduce the potential for evaporative cooling, animals may still offload excess heat through the process of conductive cooling when their bodies come into contact with the cooler burrow soil (Peinke & Brown, 2003). In addition, the internal environment remained more stable with regards to relative humidity and temperature as fluctuations were less pronounced than those of the external environment. These results are consistent with those of Taylor & Skinner (2004) for aardvark burrows.

Numerous factors are thought to influence the microclimate of burrows, for example the size of the entrance hole, the presence of ground cover, soil characteristics (including soil structure and moisture content), complexity of the burrows and the length and the depth of the burrow. (Kirmitz, 1962; Kay & Whitford, 1978; Downs & Perrin, 1989; Degen, 1997; Wood, 1997; Bulova, 2002; Moore & Roper, 2003; Finlayson *et al.*, 2005). Temperature is strongly negatively correlated with vertical depth below the soil surface of the underground dwellings of two animals of contrasting size, the badger (*Meles meles*) and the banner-tailed kangaroo rat (*Dipodomys spectablis*) (Kay & Whitford, 1978; Moore & Roper, 2003). In addition, Schmidt–Nielsen & Schmidt–Nielsen (1950) recorded greater daily temperature fluctuations in the shallower burrows of *Dipodomys merriami* compared to the deeper burrows of *D. spectablis*. However, at 30 cm below the surface, their study revealed that the temperature variation was minimal. Those results concur with research conducted in the Namib desert where soil temperatures measured at 120 cm below the surface demonstrated only minor daily or seasonal fluctuations (Downs & Perrin, 1989). Degen (1997) suggests that diurnal temperature fluctuations vary as little as 3 ºC at a depth of 20 cm and that fluctuations are minimal at 80 – 100 cm below the surface. Indeed, at a depth of 20 cm the burrows of four *Gerbillurus* species exhibit little variation despite the large fluctuations of the external environment (Downs & Perrin, 1989). The temperature fluctuations inside the aardvark burrows at all the reserves, however, were greater than those recorded in similar habitat inside gerbil burrows, aardwolf (*Proteles cristatus*) dens and springhare (*Pedetes capensis*) burrows where temperatures remained relatively constant and the range did not exceed 5 ºC (Downs & Perrin, 1989; Peinke & Brown, 2003; Anderson & Richardson, 2005).

Although the depths of the aardvark burrows were not measured in this study they were deeper than those dug by springhares at the same sites (pers. obs.). Aardwolfs generally use springhare or aardvark burrows as den sites (Skinner & Smithers, 1990) and therefore it is unlikely that the depth of burrows occupied by springhares and aardwolfs is the sole factor in their burrows exhibiting reduced thermal fluctuation. The size and complexity of the burrows may partially account for the greater than expected temperature and humidity fluctuations in the aardvark burrows. Research conducted by Bulova (2002) proposes that burrows with smaller entrance holes and longer tunnels are cooler and more humid due to an increased buffering effect of the soil. As mentioned earlier in the chapter, aardvarks create burrows with very long tunnels, however, they also make use of temporary burrows which may only be a few metres long (Skinner & Smithers, 1990). Unfortunately, due to the sharp bends common in the tunnels of aardvark burrows it is often difficult to estimate their length without performing laborious and potentially invasive excavations. Therefore, it is assumed that on occasion aardvark burrows may be shorter than those used by springhares and aardwolfs which have a mean length of approximately 42 m and 5 m respectively (Buytynski & Mattingly, 1979; Anderson & Richardson, 2005). As one would expect, the size of the entrance holes of gerbil (3 – 5 cm in diameter) (Skinner & Smithers, 1990), springhare (13.2 cm x 16.8 cm) and aardwolf burrows (38 cm x 25.5 cm) (Anderson & Richardson, 2005) are smaller than those which were recorded for aardvark burrows during this study and this may explain the elevated temperature and greater fluctuations.

The size and complexity of a burrow is influenced by the size of the animal, the substrate into which the burrow is dug, the stabilising influence of the surrounding vegetation and the energetic cost of creating the burrow (Downs & Perrin, 1989, Reichman & Smith, 1990, Woolnough & Steele, 2001). If the purpose of digging a burrow is to create a refuge with a stable microclimate then ideally the burrow should be several times the length of the excavator and will have a small diameter which permits the excavator access (Woolnough & Steele, 2001). Whilst the dimensions of the aardvark burrows at all three sites in this study fit the allometric scaling equation for semi-fossorial animals (White, 2005), those measured at Tswalu were, on average, smaller than those at the other sites. This may be ascribed to smaller aardvark digging the burrows at Tswalu or to the softer soil at Tswalu not offering as much structural support, thereby limiting the size and complexity of burrows. Shimmin *et al*. (2002) noted that southern hairy nosed-wombat (*Lasiorhinus latifrons*) burrows dug into clay-dominated soil were generally more architecturally complex compared to those in sandy soils, and kangaroo rats (*Dipodomys ordii*) have been recorded digging deeper, more complex burrows in soils with a higher silt and clay content (Laundre & Reynolds, 1993).

In addition to providing less structural support, fine-grained sands which characterise Tswalu are thought to offer less insulation than hard soils topped with a surface crust (Degen, 1997; Cortés *et al*., 2000) such as those that occur at MZNP and Kwandwe. Soil affects burrow humidity as the moisture contained between soil particles is thought to be an important factor in maintaining high burrow humidity (Reichman &

Smith, 1990). Clay-dominated soils retain moisture better than sandy soils and thus one would expect that humidity would be greatest in burrows in these soils and fluctuations would be the least (Jain *et al.,* 2004). Humidity was typically higher at Kwandwe and MZNP than at Tswalu, but daily variation in humidity was greatest at Kwandwe thus contradicting the suggestion of Jain *et al*. (2004). It is possible that the reduced entrance sizes of the burrows at Tswalu may act to moderate internal humidity and temperature fluctuations.

Larger entrance holes and burrow architecture (e.g. numerous entrance holes and short tunnels) may reduce the risk of hypercapnia and hypoxia in burrow inhabitants (Wood, 1997; Woolnough & Steele, 2001**.** Gas composition in burrows is thought to be affected by a number mechanisms including the diffusion of oxygen and carbon dioxide through the soil pores (Maclean, 1981). When soil particles are tightly packed, for instance in clay dominated soils, this diffusion is unlikely to provide large mammals with sufficient oxygen. Therefore air flow through the entrance caused by temperature and pressure gradients increases in importance (Wood, 1997; Woolnough & Steele, 2001).

Increased ventilation may also be achieved through burrowing into slopes (which increases convection) (Wood, 1997) or by orientating burrow entrances in the direction of the prevailing winds. Increased airflow may, however, result in the desiccation of the burrow environment and greater fluctuation in temperature and humidity (Schmidt-Nielsen & Schmidt-Nielsen, 1950, Kay & Whitford, 1978). The aardvark burrows in this study did not show any clear pattern with regards to favouring flat ground or slope as all three reserves yielded different results. However, the availability of sloping land was not quantified in this study as contour maps do not provide enough clarity on a microscale and it was not possible to measure preference for slope. Despite the evidence to suggest that aardvarks at all three sites favour orientating their burrows in a particular direction these were not directed towards the prevalent winds at any of the reserves (Kwandwe: east (summer), west (winter), south-west (cold fronts); MZNP: north-west & Tswalu north-east). Research on other burrowing vertebrates has yielded conflicting results. The burrows of the nine-banded armadillo (*Dasypus novemcinctus*) and the bearded lizard (*Heleoderma horridum*) are randomly orientated (Beck & Lowe, 1991; Platt *et al*., 2004) whereas those of four other armadillo species (*Priodontes maximus*, *Euphractus sexcinctus*, *Cabassous unicinctus* and *Cabassous tatouay*) are orientated in such a way that the wind blows away from the entrance (Carter & Encarnaçao, 1983). It is proposed that armadillos use their sense of smell to locate prey and therefore they approach digging sites downwind, hence the trend of burrow entrances facing away from the wind (Carter & Encarnaçao, 1983). Although aardvarks also locate ants and termites by smell (Skinner & Smithers, 1990) it is unlikely that this is the correct explanation for burrows being orientated away from on-coming wind as feeding burrows are not often utilised as sleeping shelters. The armadillo, *Dasypus hybridus*, and the coyote (*Canis latrans*) orientate their burrows to increase exposure to sunlight in addition to avoiding the prevailing winds (Harrison & Gilbert, 1985; Platt *et al*., 2004). Despite predictions to the contrary, the results from my study revealed that aardvark burrows facing in a southerly direction (away from the sun) experienced significantly higher maximum and minimum temperatures. This also contradicted Coulombe (1971) who found no correlation between the orientation and temperatures within the burrows of the burrowing owl. However, these results may be somewhat biased as one site, Tswalu, contributed the majority of the south-facing burrows.

Season had an effect on presence of monocotyledonous and dicotyledonous seeds in the soil seedbank, possibly as a result of the rainfall patterns experienced at the three study sites. The pronounced peak in winter biomass of monocotyledonous seeds at Tswalu may be ascribed to the summer grasses, which flower in response to the favourable summer rains, shedding their seeds at the onset of the dry winter period (Haase *et al.*, 1995; Chesson *et al.*, 2004). The biomass of dicotyledonous seeds was greater than that of the monocotyledonous and this was probably because shrub seeds generally weigh more than monocotyledonous seeds (Nelson & Chew, 1977). Dicotyledonous seed biomass was also more variable than monocotyledonous seed biomass possibly as a result of the presence of a greater diversity of dicotyledonous plants occurring at the study sites (refer to chapter 5) which may react differently to temperature and the timing and volume of rainfall events (Nelson & Chew, 1977). Furthermore, the greatest biomass of dicotyledonous seeds was recorded at Kwandwe, the site with the greatest floral diversity (refer to chapter 5). The variability of dicotyledonous seed biomass in the soil may also be affected by seed harvesting rates as it is thought that large seeds of woody plant species are prone to predation when lying on the soil surface thus reducing the chance of them infiltrating the soil seed bank (Teketay & Granström, 1995). Although it was surprising that no significant difference existed in seed biomasses inside and outside of the burrows (Dean & Milton, 1991b) one might conclude that foraging in burrows may be safer than in the exposed open areas where animals are more vulnerable to predators (Brown *et al.*, 1988; Kotler *et al.*, 1991; Longland & Price, 1991). This topic and the effect of seed predation by rodents on the soil seedbank shall be discussed in greater detail in the following chapter.

In conclusion, aardvark burrows provide a thermally stable microclimate which promotes water conservation and which may contain a concentration of seeds equal to that of the exposed open areas.

3.5 TABLES AND FIGURES

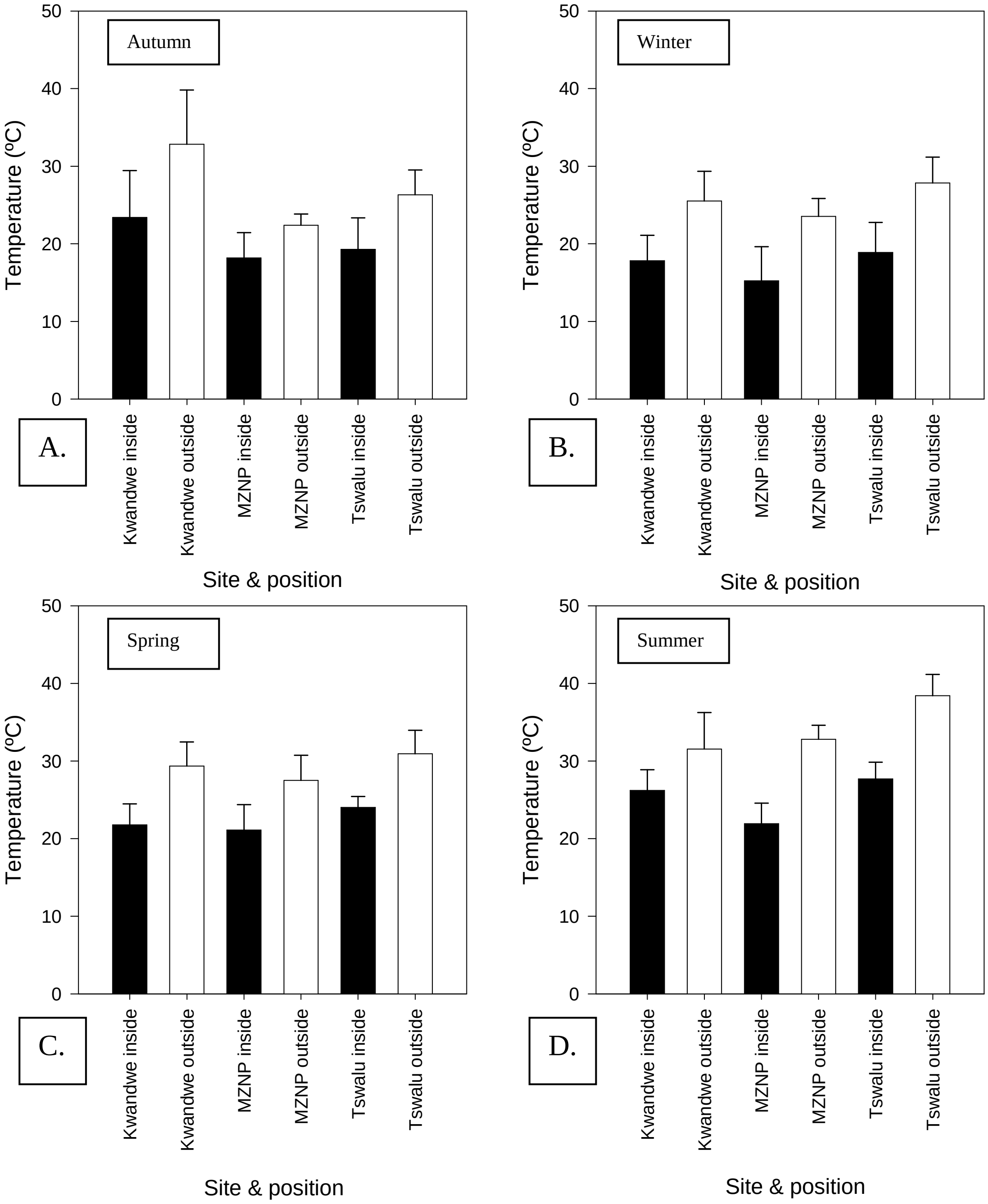

Figure 3.1: Mean maximum temperature (± 1 SD) inside (solid bars) and outside of the burrows (clear bars) at the three sites in (A) autumn, (B) winter, (C) spring and (D) summer.

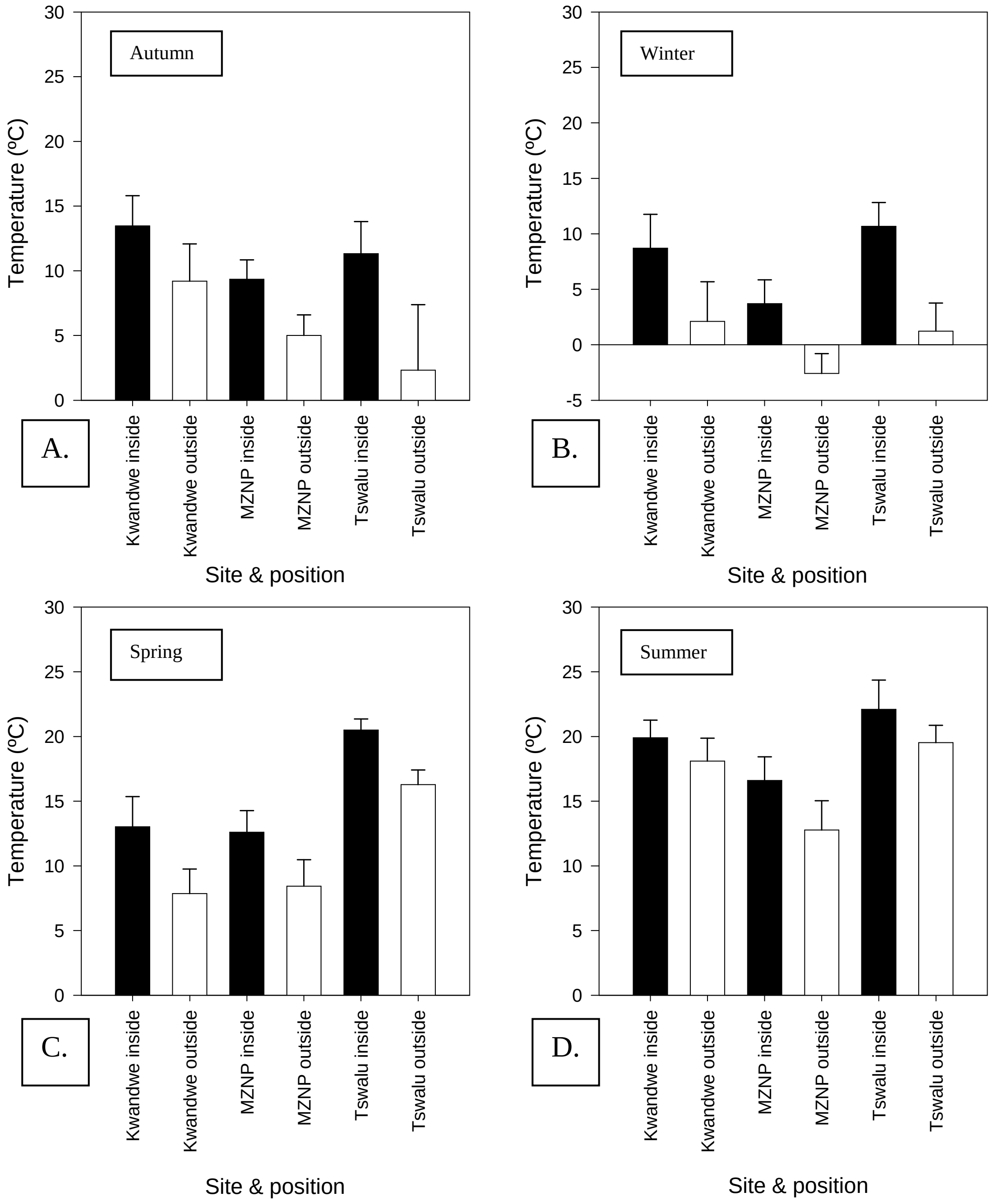

Figure 3.2: Mean minimum temperature (± 1 SD) inside (solid bars) and outside of the burrows (clear bars) at the three sites in (A) autumn, (B) winter, (C) spring and (D) summer.

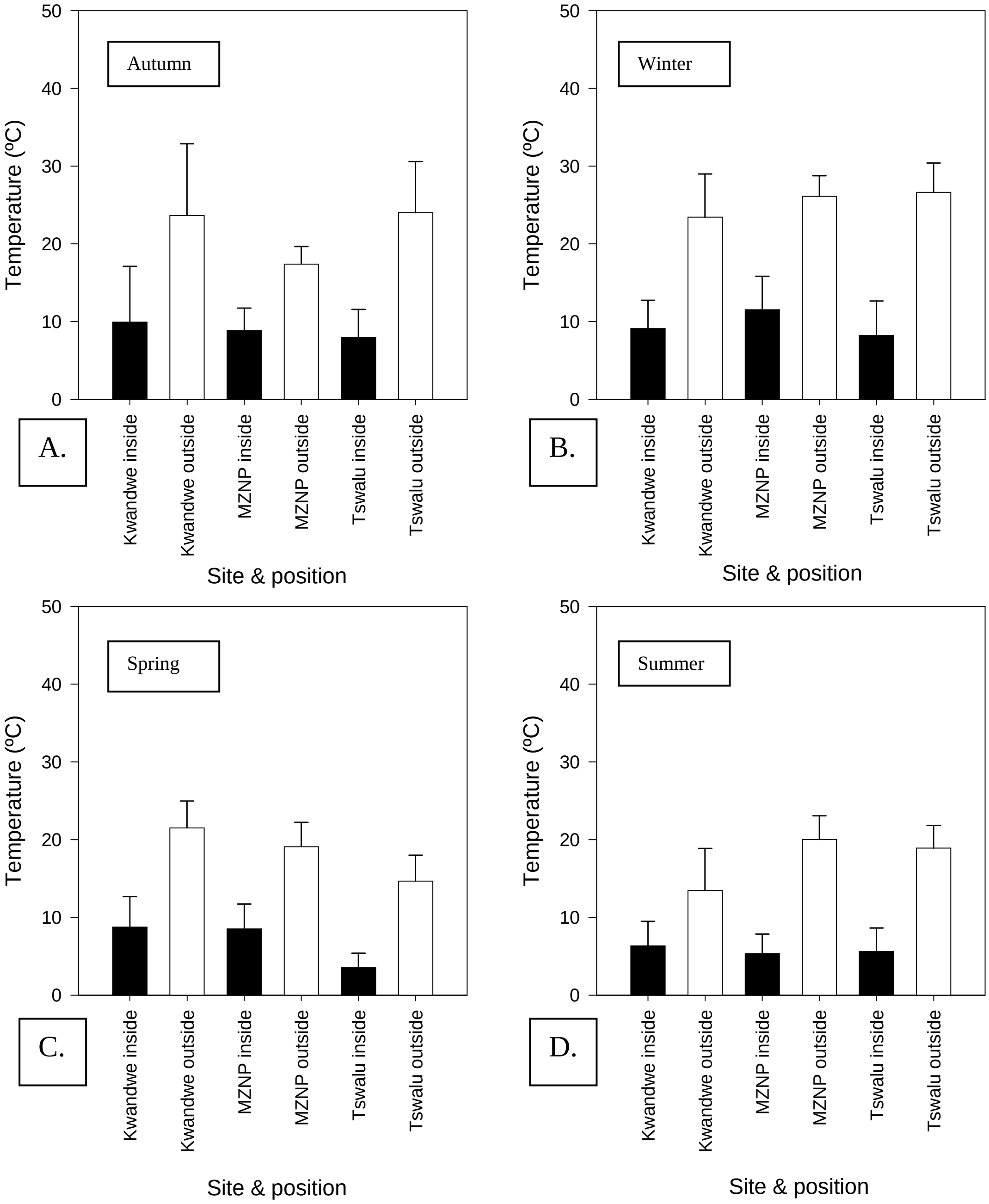

Figure 3.3: Mean daily temperature fluctuations (maximum temperature minus minimum temperature) (± 1 SD) inside (soild bars) and outside (clear bars) of the burrows at the three sites in (A) autumn, (B) winter, (C) spring and (D) summer.

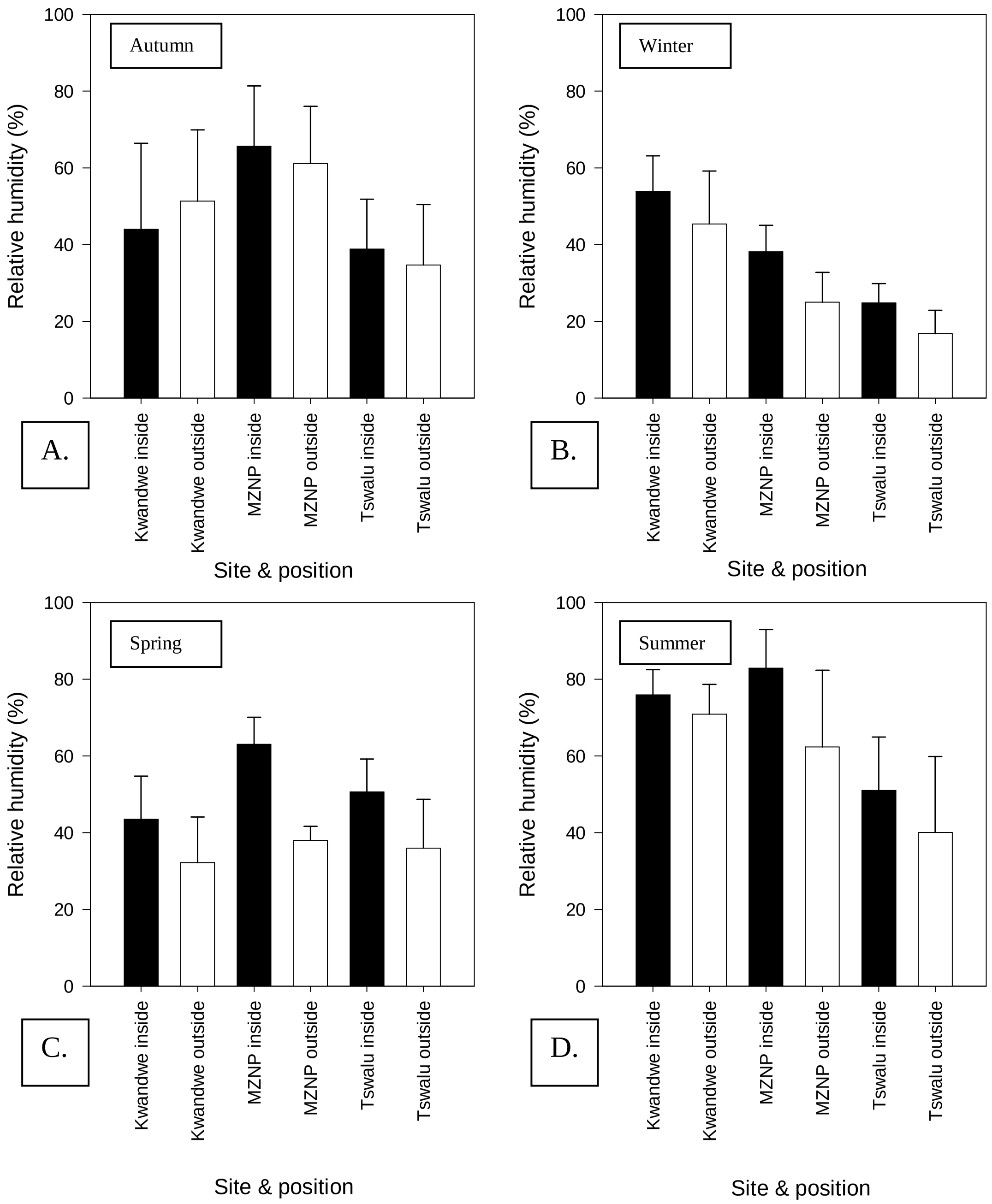

Figure 3.4: Mean morning relative humidity (± 1 SD) inside (solid bars) and outside of the burrows (clear bars) at the three sites in (A) autumn, (B) winter, (C) spring and (D) summer.

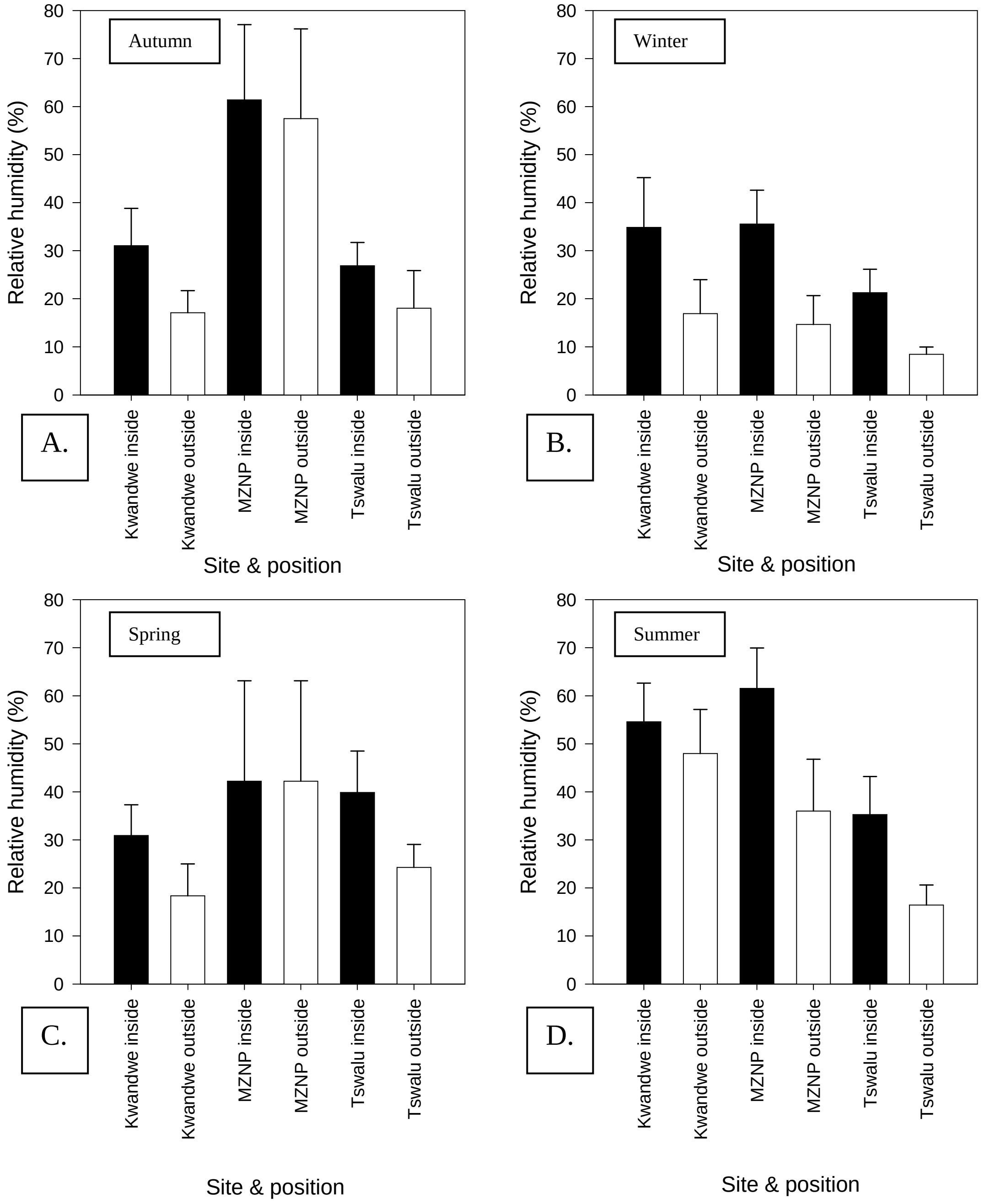

Figure 3.5: Mean afternoon relative humidity (± 1 SD) inside (solid bars) and outside of the burrows (clear bars) at the three sites in (A) autumn, (B) winter, (C) spring and (D) summer.

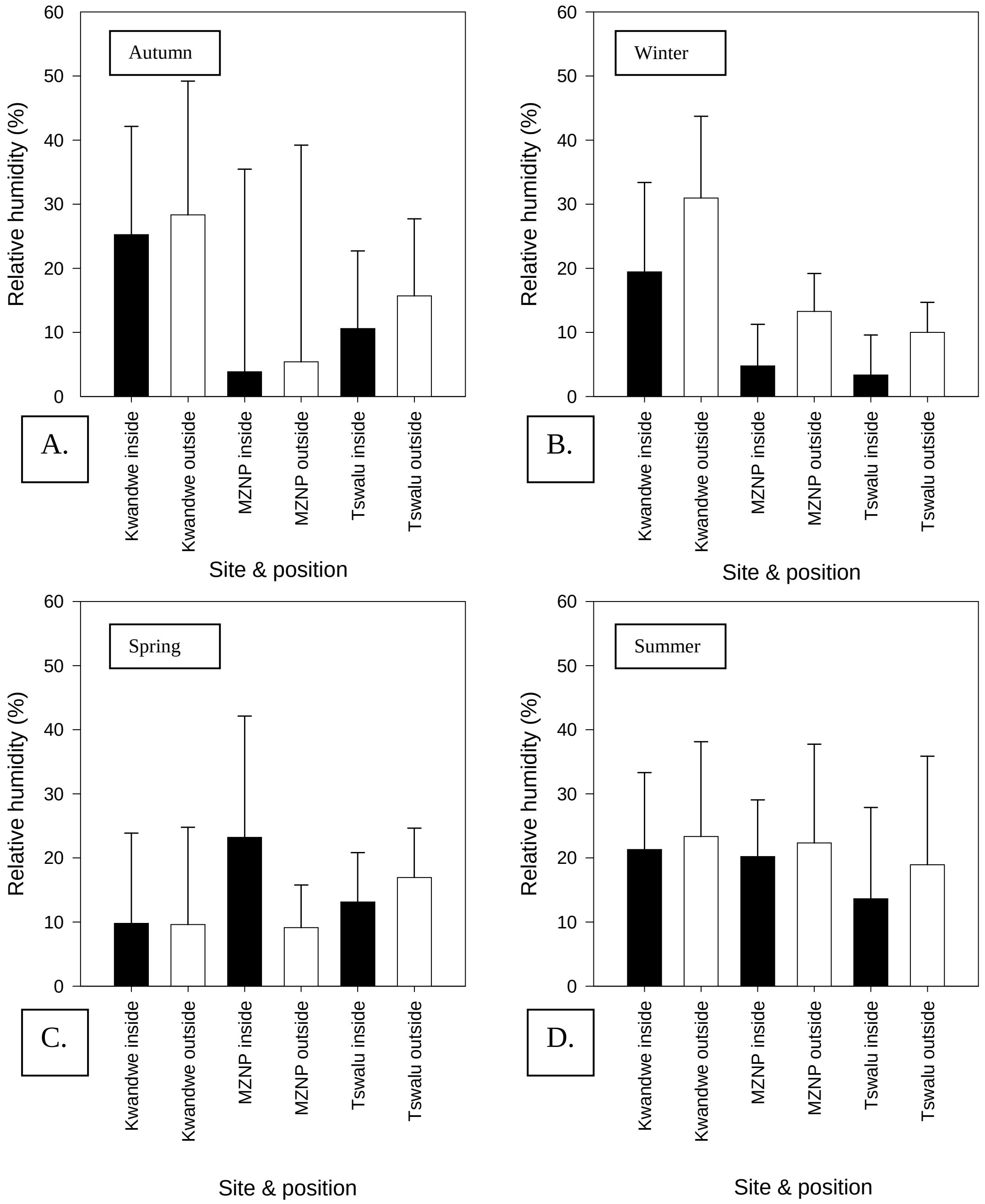

Figure 3.6: Mean daily relative humidity fluctuations (morning relative humidity minus afternoon relative humidity) (± 1 SD) inside (solid bars) and outside of the burrows (clear bars) at the three sites in (A) autumn, (B) winter, (C) spring and (D) summer.

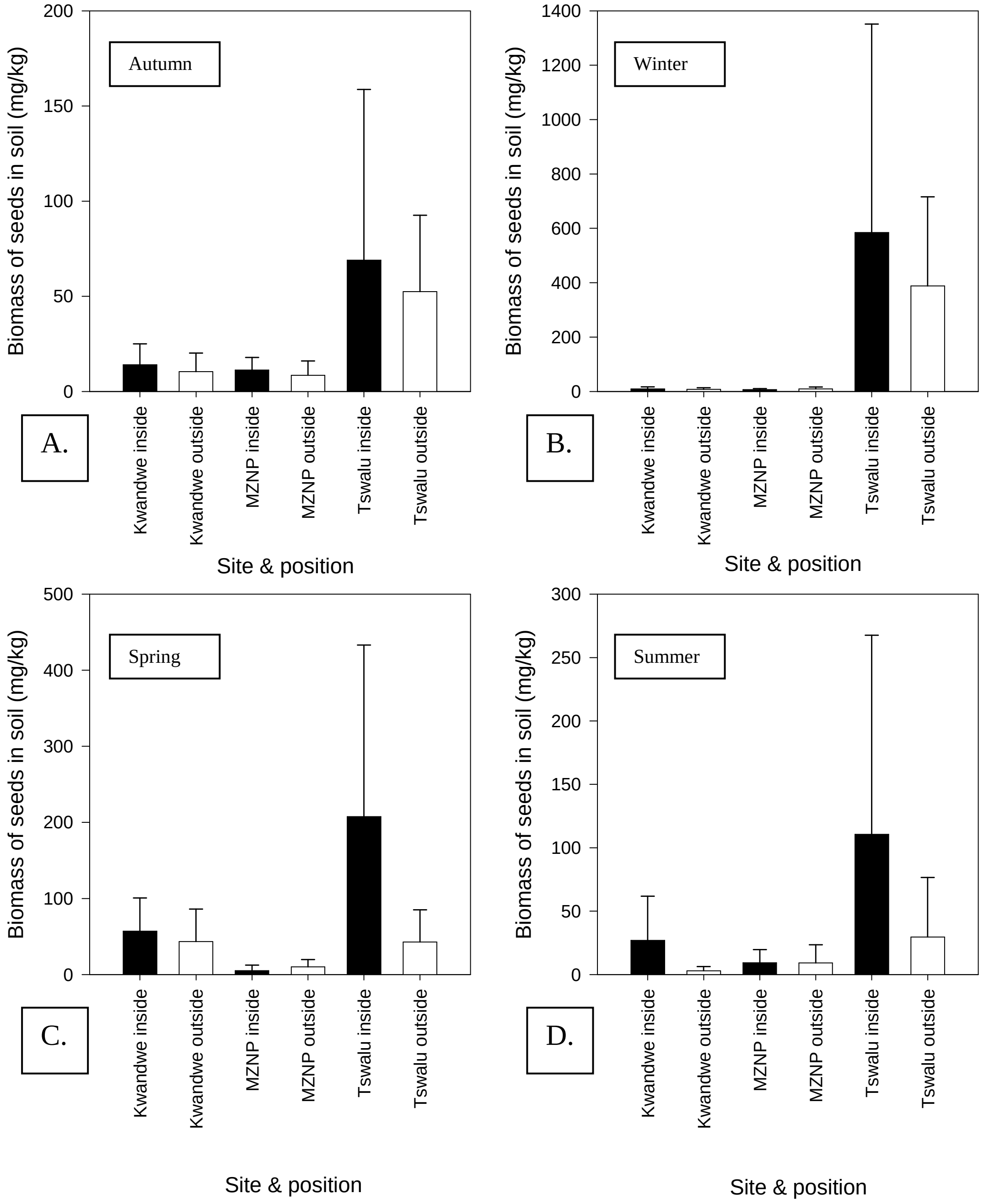

Figure 3.7: Biomass of monotyledonous seeds (± 1 SD) in the soil inside (solid bars) and outside of burrows (clear bars) at the three sites in (A) autumn, (B) winter, (C) spring and (D) summer. Note that the scale on the y-axis differs on all the graphs due to the large differences in seed biomass.

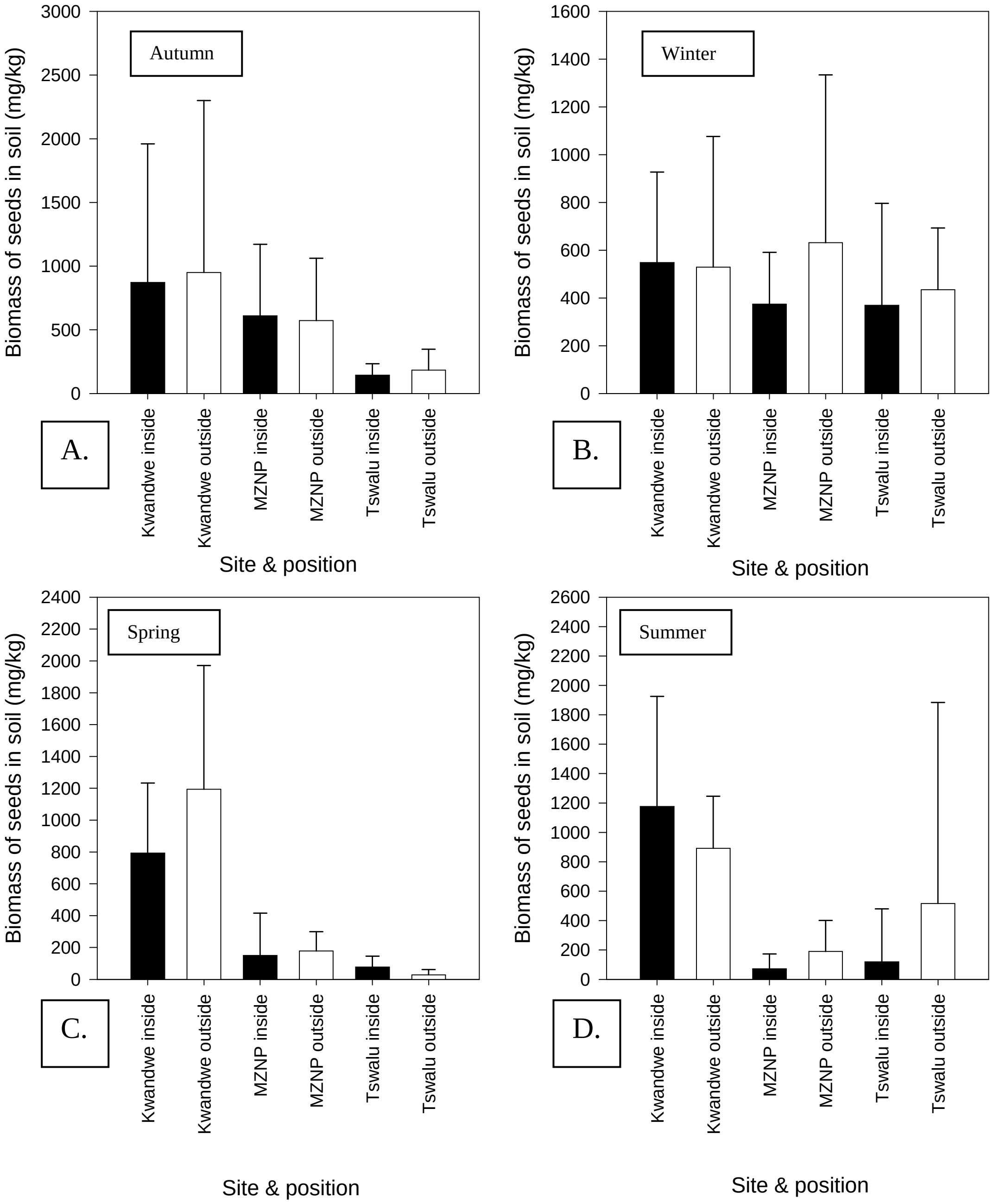

Figure 3.8: Biomass of dicotyledonous seeds in (± 1 SD) the soil inside (solid bars) and outside of burrows (clear bars) at the three sites in (A) autumn, (B) winter, (C) spring and (D) summer. Note that the scale on the y-axis differs on all the graphs due to the large differences in seed biomass.

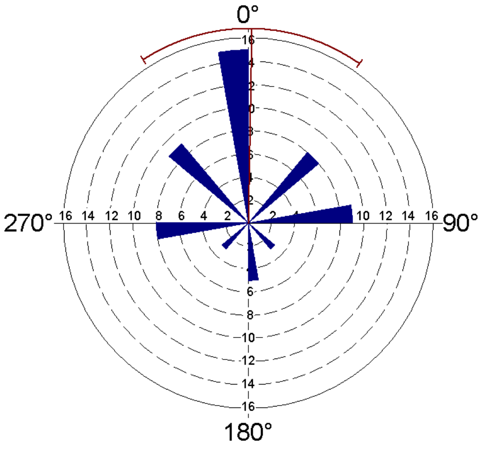

Figure 3.9: A rose diagram (vectorial model) illustrating the burrow entrance orientations of 60 aardvark burrows at Kwandwe. The frequency of observation in each directional class is represented by the radius of the blue wedge. The red line running from the centre of the diagram to the outer edge represents the mean direction, while the red outer arc represents the 95% confidence intervals of the mean.

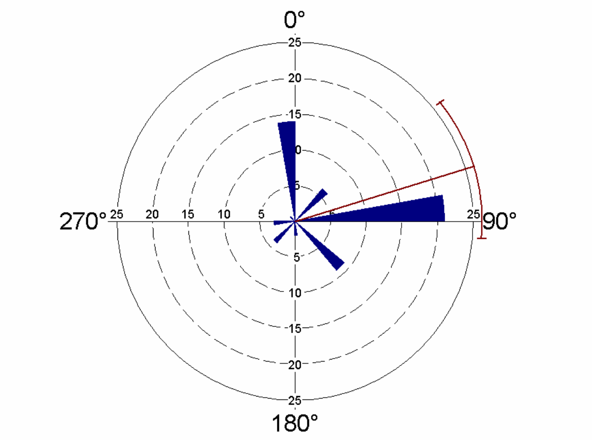

Figure 3.10: A rose diagram (vectorial model) illustrating the burrow entrance orientations of 60 aardvark burrows at MZNP. The frequency of observation in each directional class is represented by the radius of the blue wedge. The red line running from the centre of the diagram to the outer edge represents the mean direction, while the red outer arc represents the 95% confidence intervals of the mean.

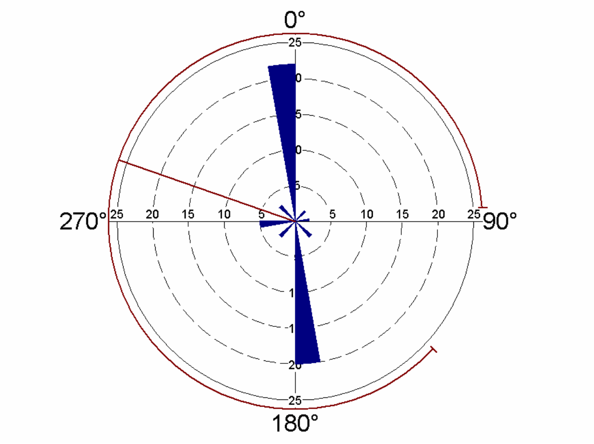

Figure 3.11: A rose diagram (vectorial model) illustrating the burrow entrance orientations of 60 aardvark burrows at Tswalu. The frequency of observation in each directional class is represented by the radius of the blue wedge. The red line running from the centre of the diagram to the outer edge represents the mean direction, while the red outer arc represents the 95% confidence intervals of the mean.

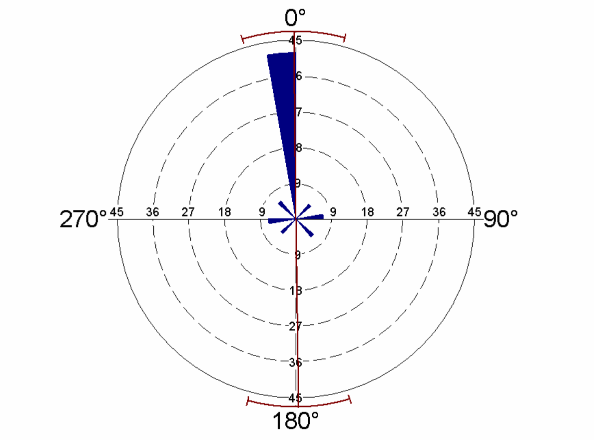

Figure 3.12: A rose diagram (axial model) illustrating the burrow entrance orientations of 60 aardvark burrows at Tswalu. The frequency of observation in each directional class is represented by the radius of the blue wedge. The red line running from the centre of the diagram to the outer edge represents the mean direction, while the red outer arc represents the 95% confidence intervals of the mean.

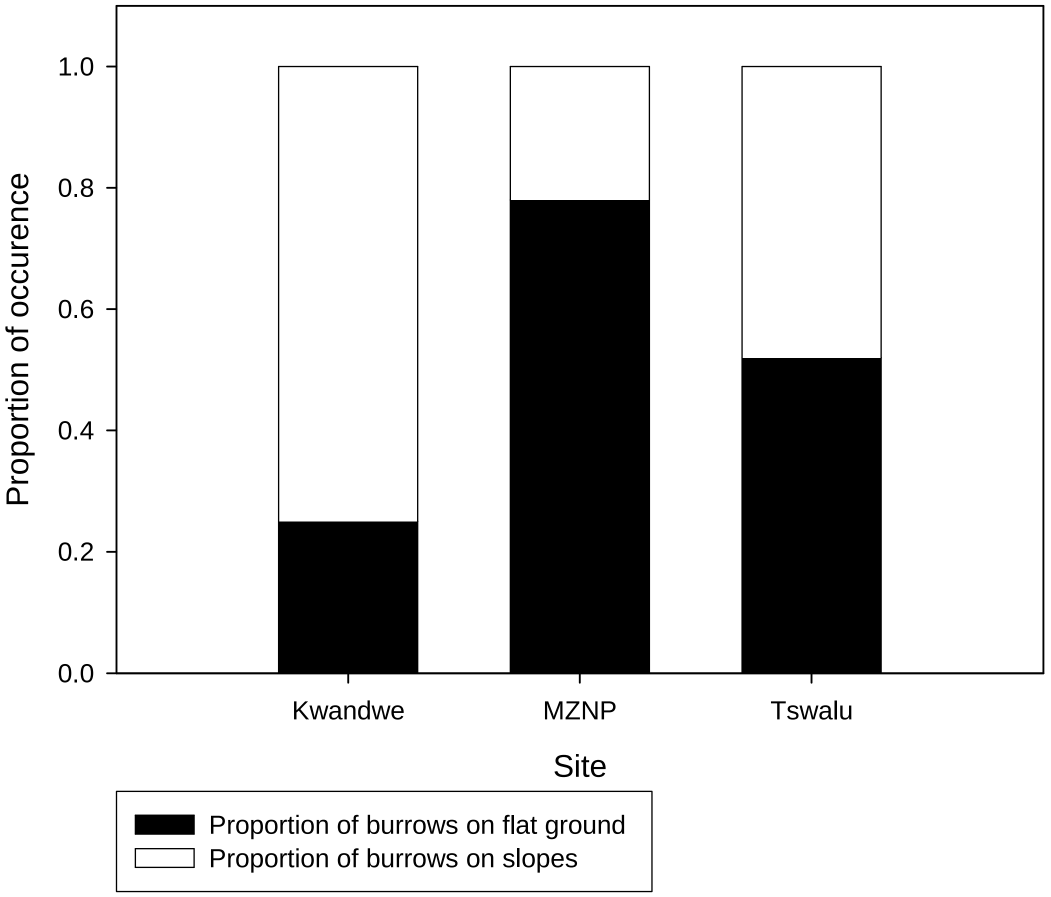

Figure 3.13: The proportion of burrows occurring on flat ground (angle < 15º) and on slopes (angle < 15º) at the three sites (n = 60 burrows for each site).

CHAPTER 4

COMMENSAL FAUNA OF AARDVARK BURROWS

4.1 INTRODUCTION

A large variety of terrestrial and aquatic organisms use burrows, with vertebrates having been associated with these structures since the carboniferous period (Meadows, 1991; Kinlaw, 1999). Burrows provide shelter and protection, facilitate communication and provide areas to forage as well as to cache food (Reichman & Smith, 1990; Meadows, 1991; Kinlaw, 1999; Finlayson *et al*., 2005).

As was demonstrated in the previous chapter, aardvark burrows provide a moderate and stable microclimate compared to the above-surface environment. Some animals such as short-tailed gerbils (*Desmodillus auricularis*) and jerboas (Muridae) plug the entrances of their burrows in order to increase burrow humidity and thus reduce evaporative water loss (Kirmitz, 1962; De Graaf, 1981). Plugging of burrow entrances may also hinder the access of predators to the burrows. Although sealing off burrows may be performed purely to deter predators such as snakes, it does on occasion have the opposite effect as some carnivores may be attracted to the burrow by the recently disturbed soil (Jarvis, 1991). Burrow plugs may also have little effect when animals are sought out by larger carnivores such as the honey badger (*Mellivora capensis*) because they are powerful diggers and soil barriers do not offer much protection (Skinner & Smithers, 1990).

Mammals attempting to protect their defenceless, altricial young from predators may construct dens or burrows which have large entrances but which narrow considerably as they progress further underground (Anderson & Richardson, 2005). These constrictions in the burrow are usually only just large enough to contain the young and thus preclude large predators from gaining access to the offspring. This phenomenon has been in noticed in the dens of brown hyaenas (*Hyaena brunea),* spotted hyaenas and aardwolfs, particularly in areas where large predators such as lions and leopards (*Panthera pardus*) are still present (Anderson & Richardson, 2005). Burrows with single entrances may limit predator access, however, the disadvantage of this strategy is that no alternative escape route is available and the prey animal may become trapped in the event that a predator does gain access to the burrow. Some burrows, including those excavated by aardvarks, may have many entrance points and consist of long and highly complex tunnels which may serve to confuse potential predators (Bronner, 1992; Kinlaw, 1999). Animals may also use burrows as a refuge to recover from disease or injury (Kinlaw, 1999) and deeper burrows may afford animals protection from fire (Lawrence, 1966; Kinlaw, 1999).

Burrows also influence the food gathering and storage capability of certain organisms (Reichman & Smith, 1990; Meadows, 1991; Kinlaw, 1999). For instance, the true moles (Talpidae) spend the majority of their lives underground in burrows which afford them protection from predators and aboveground climatic conditions as well as providing areas for them to forage and in some cases, store their food (Smith & Reichman, 1984; Reichman & Smith, 1990). Food hoarding has the benefit of allowing rodents a broader diet than would otherwise be possible if they foraged every day or night in the company of other competitors, as they are able to store high-value food items for consumption in the future (Reichman & Fay, 1983; Smith & Reichman, 1984). Food caches are of particular importance when resource availability is low as is generally the case in winter (Reichman & Fay, 1983). The kangaroo rats are amongst the best-known food hoarders and they have ability to select seeds that will generate the most metabolic water (MacMillen & Hinds, 1983; Kinlaw, 1999). In addition, rodents may also use seeds to soak up water vapour in their humid burrows before ingesting the seeds, thus conserving scarce water resources (Reichman & Smith, 1990). Numerous species of southern African rodents, including the pouched mouse (*Saccostomus campestris*) and the short-tailed gerbil, are also known to hoard food in their burrows (De Graaf, 1981). Given that aardvark burrows have been shown to contain concentrations of seeds approximately equal to that of the exposed open areas outside, it is possible that rodents may use these structures for foraging purposes.

The animals that utilize burrows can be grouped into three broad categories; primary excavators/tunnelers, secondary modifiers and burrow occupants (Kinlaw, 1999). Digging is an important aspect in the lives of primary excavators and they possess the ability to dig large, complex burrows that can have a significant ecological impact (Kinlaw, 1999). Although the energetic cost of creating a relatively simple burrow may not be particularly high, with certain animals such as armadillos digging new shelters sometimes on a nightly basis, the cost increases the larger and more complex the burrows become (Reichman & Smith, 1990; Woolnough & Steele, 2001). Even the most notable example of a primary excavator, the aardvark, may not dig a new burrow every night but will rather return to an old burrow or modify a burrow abandoned by another individual (Skinner & Smithers, 1990). Secondary modifiers are restricted to digging their own burrows in softer soils and may live in and alter burrows created by primary excavators. Cape porcupines, warthogs and bat-eared foxes (*Otocyon megalotis*) are a few examples of vertebrates recorded modifying and inhabiting aardvark burrows (Cumming, 1970; Peirce, 1974; Skinner & Smithers, 1990). The third category of animals, burrow occupants, save time and energy by living in or using the burrows of other animals without making any alterations to them (Kinlaw, 1999). Many invertebrates, birds, amphibians and reptiles such as the southern African python (*Python natalensis*) are members of this group (Branch, 1993; Kinlaw, 1999). Burrow occupants which regularly inhabit a burrow of a particular excavator or modifier are known as commensal organisms. These organisms may be further divided into obligate commensals, which are only found associated with that burrow type, and non-obligate commensals, which will use whatever refuge is available (Kinlaw, 1999). The literature contains many studies documenting the presence of vertebrate commensals in the burrows of primary excavators (e.g. Vaughn, 1961; Kiviat, 1978; Heidger, 1988; Neal & Roper, 1991; Witz *et al*., 1991; Swihart & Picone, 1995; Ceballos *et al*., 1999; Williams *et al*., 1999; Shimmin *et al*., 2002; Lomolino & Smith, 2003; Dean & Williams, 2004; Platt *et al*., 2004; Bragg *et al*., 2005). Information regarding vertebrate and invertebrate commensals inhabiting aardvark burrows does exist but is usually embedded in the literature pertaining to the individual commensal organism. At present only one comprehensive article exists on the commensal organisms inhabiting aardvark burrows and this does not contain any information on invertebrate fauna (Smithers, 1971).

Arthropods are known to be common in the burrows of many mammals and may include members of all the major feeding guilds including; herbivores, detritivores, predators and parasites (Peirce, 1974; Hancox, 1988; Reichman & Smith, 1990). Mammalian burrow dwellers generally remain in their burrows for a large portion of the day and in some instances, such as is the case for the badger, may occupy their underground shelters for months or even years (Reichman & Smith, 1990; Neal &

Roper, 1991). Therefore, given the combination of regular access to a host and a warm, humid environment burrows could contain high parasite loads. This may have management repercussions especially if the parasites are vectors of disease, an example of which are the phlebotomine sand flies which inhabit rodent burrows and carry the protozoa that cause leishmaniasis (Desjeux *et al*., 1983; Schlein *et al*., 1984; Reichman & Smith, 1990). Other parasites, such as ticks, may (if occurring in large enough numbers in burrows) either cause the death of warthog piglets through blood-loss anaemia, or weaken the animals to such an extent that they are vulnerable to other diseases or predation, thereby regulating warthog populations (Peirce, 1974).

Identifying what and understanding why other animals rely on aardvark burrows for survival may have important conservation implications, particularly in areas where aardvarks are routinely persecuted. Miller (1994) states that the extermination of prairie dogs (*Cynomys* spp.), which function as important ecosystem regulators in certain areas of the United States, has resulted in the near extinction of the black-footed ferret (*Mustela nigripes*). The worrying population declines of at least three other species; the mountain plover (*Charadrius montanus*), the ferruginous hawk (*Buteo regalis*) and the swift fox (*Vulpes velox*) have been directly attributed to the poisoning of prairie dogs (Miller, 1994). Miller (1994) further contends that protecting keystone species is more cost-effective than trying to protect each species which is dependent on it.

Given the limited availability of information regarding the commensal fauna of aardvark burrows the objectives for this chapter are:

- To determine what vertebrates species utilise aardvark burrows;
- To determine whether the burrows contain a unique insect community;
- To infer the importance of aardvark burrows for the survival of other species.

4.2 METHODS AND MATERIALS

The 20 burrows that were randomly selected each season for microhabitat analysis and their corresponding control areas were also used to study the commensal fauna of the aardvark burrows in comparison to the surrounding environment. Methods used to record the commensal fauna of aardvark burrows included small mammal trapping, burrow surveys and opportunistic sightings, questionnaires and invertebrate pitfall trapping.

4.2.1 Small mammal trapping

Two Sherman small mammal traps were baited with rolled oats and peanut butter (Perrin & Johnson, 1999) and placed 0.5 m inside the entrance of each aardvark burrow. The traps were placed along the side walls in an attempt to minimise the obstruction at the entrance. One trap was orientated facing out of the burrow and the other facing into the burrow. A further two traps were set up at each corresponding control area situated approximately 15 to 20 m from the burrows. The traps were left in place for a period of four nights and were checked every morning (Kutiel *et al.*, 2000). The traps were closed during the day to avoid trap mortalities as a result of high midday temperatures (Perrin & Johnson, 1999; Kutiel *et al.*, 2000). It was anticipated that this would be more of a problem in the open control areas where shade was minimal but for the purposes of consistency it was decided to close the traps in the burrows as well. Traps were reopened in the afternoon in order to maximise the opportunity of catching crepuscular species. Traps set during the winter months were insulated with a blanket to reduce the potentially lethal effects of the low night-time temperatures (Perrin & Johnson, 1999). Small mammals that were captured were emptied into a plastic ziplock packet, weighed, sexed, had flank hair clipped with scissors to facilitate the analysis of rodent movement patterns (mark and recapture), and were identified to species. In the event that an animal could not be identified in the field, body measurements were taken and a digital camera was used to take photographs for further examination. De Graaf (1981) and Stuart & Stuart (1990) were used to identify "specimens" from the photographic evidence and measurements. No animals were intentionally sacrificed during this study.

In order to assess trap success the data were adjusted to a standard 100 trap nights. A trap night was defined as a 24-hour trapping period (Rowe-Rowe & Meester, 1982; Swihart & Picone, 1995). Although traps were closed for a period each day this was not deemed sufficient to alter the evaluation of trap success. Traps that were disturbed (by other animals), or otherwise accidentally triggered were excluded from the calculation of trap success (Varty, 1990).

4.2.2 Burrow surveys and opportunistic sightings

Each of the burrows used for the small mammal trapping were divided into one of two groups, active or abandoned, based on the presence of aardvark footprints and flies around the entrance indicating current occupation of the burrow by an aardvark (Kingdon, 1971; Skinner & Smithers, 1990; Platt *et al.*, 2004). The visible portion of each of the 20 burrows were checked every morning and afternoon using a torch and the presence of any vertebrates were recorded. The sloping roofs of each of the burrows used for the small mammal trapping were also checked for the presence of tunnels or nests constructed by birds.

The presence of hair, quills and droppings in the burrows and animal tracks entering or exiting the burrows were also noted. These tracks and signs were identified using a field guide (Stuart & Stuart, 2000). Opportunistic observations of animals using burrows during the course of other data collection were also recorded.

4.2.3 Questionnaires

A questionnaire regarding sightings of animals using aardvark burrows was circulated amongst the staff of the reserves and other field researchers who were known to have conducted field work in similar ecosystems. A copy of the questionnaire is attached as Appendix A. A request for information was also published in popular literature.

4.2.4 Insect sampling

The heuristic value of using morphospecies/ relative taxonomic units (RTUs) is the subject of a contentious debate in the literature and the benefits and limitations of the method have been extensively debated (Cranston, 1988; Cranston & Hillman, 1992; Oliver & Beattie, 1993; Oliver & Beattie, 1996a; 1996b; Goldstein; 1997; Oliver & Beattie, 1997; Pik *et al*., 1999; Derraik *et al*., 2002; Krell, 2004). One of the major criticisms of using morphospecies is that accurate interpretation of faunal compositions is thought to be impossible in the absence of species-level information (Goldstein, 1997). Another drawback of using this method is the accuracy with which samples are allocated to morphospecies. If interspecific variations are small they may not be detected and specimens may be lumped together as a single morphospecies thus resulting in an underestimation of true species richness. The converse occurs if intraspecific variation is high as specimens may be split into separate morphospecies, resulting in an overestimation of true species richness (Derraik *et al*., 2002). Sexual dimorphism and large morphological differences between adults and non-adults are the main cause of the latter problem (Derraik *et al*., 2002). Despite the criticisms regarding the accuracy of the method there is general consensus that it may serve a purpose if morphospecies voucher specimens are checked by trained taxonomists following initial sorting by parataxonomists (Derraik *et al*., 2002). The recognition of this method as a valid and reliable (if managed correctly) tool has even led trained entomologists to use it when attempting to solve conservation issues (Derraik *et al*., 2002; Krell, 2004). Due to the decrease in taxonomic specialists (Krell, 2004), a lack of taxonomic information pertaining to some poorly studied groups (Oliver & Beattie, 1993) and the limited time and resources available for identification, it was decided that the benefits of using this method outweighed the potential problems associated with it. The insect survey was only conducted in summer as this is the season when insects are most abundant. Pitfall trapping was used to assess the insect fauna of burrows because it is a commonly used technique which is inexpensive, the traps are easy to collect and replace and the catches are often large with many species being caught (Topping & Sutherland, 1992; Thomas & Marshall, 1999; Ward *et al*., 2001). A pitfall trap (depth = 8 cm, diameter = 10 cm) was sunk into the soil until the rim was flush with the ground at the entrance of each of the burrows and at all the control areas. Each trap was then three-quarters filled with water. Commercial liquid soap was added to the water in order to break the surface tension so that the invertebrates could not escape (Thomas & Marshall, 1999). No alcohol preservative was added to the water in case vertebrates drank from the traps. Every morning the traps were emptied into separate sealed containers labelled with the date and their burrow/control number. Samples were transported to the laboratory at the completion of each fieldwork period. Once at the laboratory the large organic debris was removed by hand and the samples were transferred into sealed bottles containing 70 % alcohol and stored for later identification to family and then morphospecies level.

The contents of each sample bottle was emptied into a white sorting tray (diameter 29 cm) and the specimens identified to family level using keys and guidelines where necessary (Borror & White, 1970; Unwin, 1981; Scholtz & Holm, 1986; Picker *et al*., 2004). Non-adults were excluded from this study in an attempt to minimise misidentifications (Oliver & Beattie, 1993). Insect specimens were then divided into morphospecies on the basis of obvious differences in external morphological characteristics (Derraik *et al*., 2002). A reference collection was compiled as new morphospecies were encountered. The first specimen of each new morphospecies was kept as a voucher specimen (Cranston, 1990) and stored in a vial containing 70 % alcohol. All voucher specimens were catalogued and are housed in the Department of Zoology and Entomology, Rhodes University. The classification of insects to family level was subsequently checked by A. Kirk –Spriggs, the curator of entomology at the Albany Museum, Grahamstown.

Individual morphospecies were assigned to broad feeding guilds on the basis of their family-level natural history and the structure of their mouthparts, which were viewed under a binocular microscope (30 X) when necessary. In some cases morphospecies were allocated to more than one guild, for example where adults feed on nectar but also prey on other invertebrates to feed their offspring. Guilds are defined as “a group of species that exploits the same class of environmental resources in a similar way” (Adams, 1985). Although Simberloff and Dayan (1991) stress the importance of similarity in foraging behaviour when dividing organisms into guilds, they acknowledge that the assessment of similarity is subjective and that other studies have de-emphasised this aspect in favour of broader feeding guilds. The definition of guild categories is also inherently subjective (Root, 1967) and the designated feeding guilds used in this study were modified from those derived from Moran and Southwood (1982) and Gurgel-Gonçalves *et al*. (2006). As such, the following broad feeding guild groups were established: predatory/hematophagous, phytophagous, fungivorous, detritivorous/saprophagous, parasitic and ants. The guild concept is used widely in ecological studies as it is thought to be a useful means to compare communities (Adams, 1985; Simberloff & Dayan, 1991). In this case it was aimed at complementing the morphospecies approach as it divides complex communities into functional units which are not bound by taxonomic relationships (Adams, 1985).

4.2.5 Data analysis

A Kruskal-Wallis one-way ANOVA (Statistica 7.0) was used to determine whether site had an effect on the proportion of burrows containing tunnels or nests constructed by birds.

In order to determine if the status of the burrows (active or abandoned) affected small mammal trap success a student’s t-test was performed for each of the sites after the data had been normalised using an arcsine transformation.

The small mammal trapping data have been analysed as follows. Capture rates were too low to allow analyses on a daily basis and for each season, site and position. Thus, data were pooled and species diversity, richness (the number of species caught), number of individuals caught and trap success were calculated. In other words, at each site and for each season a single value for each parameter (species richness etc.) was calculated for both the burrows and for the control areas. These values were then used to calculate means for the burrows and control areas and a two-way ANOVA was used to examine the effects of site (i.e. reserve) and position (i.e. burrow or control) on the parameters. This analysis allowed the key question, which was the effect of burrows to be addressed, but there was no measure of variability within each season and thus the effect of season could not be tested statistically. Although the effect of season was not an important question in the study, seasonal changes in the parameters will be described in the results.

The Shannon-Wiener index (H’) was used to measure the species diversity of small mammals and insect morphospecies inside the burrows and in the control areas whilst Pielou’s index (J’) was used as a measure of evenness (PRIMER 5, PRIMER Ltd, Plymouth, UK). The Shannon-Wiener index takes into account both the number and evenness of (morpho)species whilst Pielou’s index provides a numerical representation of the evenness of a community.

The pitfall traps were emptied on a daily basis so that the Michaelis Menten (MM) species richness estimator (EstimateS 7.5.0, R.K. Colwell, Connecticut, U.S.A.) could be used to estimate total morphospecies richness inside and outside of the burrows by functional extrapolation. These estimations are based on species accumulation calculated by MaoTau (EstimateS 7.5.0) and were performed in order to assess the efficiency of the sampling technique.

The similarity of the insect morphospecies communities recorded inside the burrows and in the control areas were analysed in PRIMER using the Log (x + 1) transformation function. Log (x + 1) transforming data is a powerful method which focuses attention on the whole community because it mixes the contributions from both common and rare morphospecies. This was preferred to presence/absence transformations which completely down-weigh effects of common species. Following this the ANOSIM function was used to detect if any significant differences in community structure occurred between the burrows and control areas. SIMPER analysis was then used to determine which morphospecies contributed most to the Bray-Curtis dissimilarities between the burrow communities and those outside at each of the sites. SIMPER arranges species on the basis of their average contribution to the total average dissimilarity between samples (burrows and control areas).

4.3 RESULTS

4.3.1 Small mammal community

The average numbers of unique individual small mammals captured per season were not significantly greater outside the burrows compared to inside ($F_{1,18}$ = 2.86734, $p > 0.05$) (Table 4.1). However, site ($F_{2,18}$ =10.97585, $p < 0.05$) did have an effect as the number of trapped individuals was significantly higher at Tswalu compared to MZNP ($p < 0.001$) and Kwandwe ($p < 0.05$)(Figure 4.1).

The average small mammal trap success was not significantly higher outside the burrows compared to inside ($F_{1,18}$ = 1.30944, $p > 0.05$), however site did have a significant effect ($F_{2,18}$ = 7.41357) with Tswalu experiencing significantly higher trap success than MZNP ($p < 0.05$) (Table 4.1). Trap success inside the burrows was highest during summer at Tswalu (47.3 %) and Kwandwe (25.3 %) and in winter at MZNP (2.7 %) (Figure 4.2). This pattern differed outside of the burrows with Kwandwe (17.5 %) and MZNP (4.8 %) experiencing greater trap success in winter and Tswalu (84.6 %) in summer (Figure 4.2). Average trap success was higher in abandoned burrows than active burrows at all three sites but the differences were not significant (Kwandwe: $t = -0.2157$, $df = 6$, $p > 0.05$; MZNP $t = -0.1447$, $df = 6$, $p > 0.05$; Tswalu: $t = 0.3537$, $df = 6$, $p > 0.05$) (Figure 4.3).

The average small mammal species richness was not significantly greater inside than outside the burrows ($F_{1,18} = 0.0462$, $p > 0.05$) despite more species being caught inside the burrows than outside at Kwandwe and MZNP (Table 4.1). Tswalu showed the opposite pattern and average seasonal species richness was greater in the open control areas compared to inside the burrows. Again, site had a significant effect ($F_{2,18} = 16.8$, $p < 0.001$) with Tswalu having a significantly higher species richness than both Kwandwe and MZNP ($p < 0.05$ and $p < 0.001$ respectively). Species richness at Kwandwe was significantly higher than MZNP ($p < 0.05$). Species richness inside the burrows was greatest in winter and spring at Kwandwe (four), in autumn at MZNP (three) and in winter, spring and summer at Tswalu (four). This differed to the pattern observed outside as species richness was highest in the control areas in spring at Kwandwe (four), in summer at MZNP (two) and in winter at Tswalu (six) (Table 4.2).

Neither site ($F_{2,14} = 2.1189$, $p > 0.05$) nor position ($F_{1,14} = 3.4991$, $p > 0.05$) had a significant effect on average small mammal species diversity even though higher values were calculated for the burrows at all three sites (Table 4.1). Species diversity values were highest at Kwandwe in spring (inside and outside), in winter at Tswalu (inside and outside) and in autumn at MZNP inside the burrows and in summer outside the burrows. Pielou’s eveness values for all the sites and seasons were high (all values were greater than or equal to 0.73) except for the control areas at Tswalu in spring (0.55) and summer (0.29) (Table 4.2). The most abundant species in the small mammal community at Tswalu were the gerbils *Gerbillurus paeba* and *Tatera* *leucogaster* followed by *Saccostomus campestris* and *Mus indutus*. *Rhabdomys pumilio* and *Praomys natalensis* were the most abundant small mammals at Kwandwe whilst *R. pumilio* was the most common species at MZNP. The patterns of numerical dominance of these species was generally the same inside and outside the burrows even though absolute numbers were often not similar. The only insectivorous species caught during the study was a forest shrew (*Myosorex varius*) inside a burrow at MZNP (Table 4.3).

The regression analyses did not reveal any significant positive relationships between either trap success or the number of individual small mammals caught and the combined biomass of the monocotyledonous and dicotyledonous seeds recorded inside and outside the burrows at each of the three sites. In some instances a non-significant negative relationship was observed between the two variables and seed abundance. The R and p values are recorded in Table 4.4**.**

At all the sites where small mammals were recaptured, except for Kwandwe in autumn and MZNP in winter where the number of recaptures were limited to one and three respectively, in excess of 50 % of the recaptures occurred in the same trap station as the time before, that is, no movement between traps took place (Figure 4.4). When movement was recorded taking place it was usually between the traps in the control sites and the burrows or vice versa. Very little movement appeared to take place between different burrows or between different control sites.

4.3.2 Burrow surveys, opportunistic sightings and questionnaires

Site had a significant effect on the proportion of burrows containing tunnels in the roof excavated by birds ($F_{2,9}$ = 219.25, $p < 0.001$), with Tswalu (77.5 %) having a significantly higher proportion of nests than either MZNP (7.5 %) or Kwandwe (0 %) ($p < 0.001$). The proportion of burrows containing nests at MZNP was significantly higher than at Kwandwe ($p < 0.001$).

The burrow surveys and opportunistic sightings yielded five mammal species and one bird species at Kwandwe; five mammal species, two bird species, two reptile species and one amphibian at MZNP and six mammal species, one bird species and one reptile species at Tswalu using aardvark burrows (Table 4.5). Of these species only bat-eared foxes and ant-eating chats (*Myrmecocichla formicivora*) were observed at all three sites. The bat eared-foxes and warthogs were frequently observed using aardvark burrows at Kwandwe and adults were often seen accompanied by young. At MZNP the bat-eared foxes were the only animals regularly seen entering and exiting burrows and were also the only species seen emerging from burrows with young. At Tswalu no animals were seen using burrows whilst in the presence of young and only the highveld gerbil (*Tatera brantsii*) and the ant-eating chat were regularly observed entering the burrows.

Quills of the Cape porcupine were regularly found in the aardvark burrows at all three sites and footprints were often observed entering and exiting the burrows. Footprints of unidentified mongoose and rodent species were also recorded regularly at all the sites. The only ungulate to make use of the aardvark burrows was the steenbok (*Rhaphicerus campestris*) whose tracks were noticed entering burrows on two separate occasions at Tswalu during the summer (Table 4.6).

The response to the questionnaires was very poor with few completed surveys being returned. Unfortunately, in some instances information pertaining to the sightings, for example frequency and location of observations, was also not available. There was a strong overlap between the species observed using aardvark burrows in this study and those documented in the questionnaires (Table 4.7). However, the questionnaires did include a few new species such as the Cape fox (*Vulpes chama*), honey badger, African pygmy kingfisher (*Ispidina picta*), little bee-eater (*Merops pusillus*), puff adder (*Bitis arietans*), southern African python (*Python natalensis*) and Cape cobra (*Naja nivea*). When the results from the different methods were combined, 25 mammal species, seven bird species, six reptile species and one amphibian species were recorded using aardvark burrows.

4.3.3 Insects

The insect trapping at Kwandwe yielded 946 individuals from nine orders, 22 families and 30 morphospecies inside the burrows and 968 individuals from seven orders, 18 families and 33 morphospecies outside the burrows. At MZNP 627 individuals from six orders, 26 families and 43 morphospecies were trapped in the burrows compared to 532 individuals from seven orders, 18 families and 30 morphospecies outside of the burrows. The traps inside the burrows at Tswalu caught 12023 individuals from seven orders, 32 families and 50 morphospecies, whereas the traps outside the burrows contained 49996 individuals from six orders, 30 families and 50 morphospecies (Table 4.8). The Formicidae (ants) were the most abundant family captured inside and outside of the burrows at all the sites. Following the Formicidae, the next most abundant groups inside the burrows differed at each site with the Pulicidae and the Calliphoridae at Kwandwe, the Hodotermitidae and Gryllidae at MZNP and the Tenebrionidae and Histeridae at Tswalu featuring prominently.

ANOSIM showed that there were significant differences in insect community assemblages between the burrows and open control areas at Kwandwe ($R = 0.865$, $p < 0.05$) and Tswalu ($R = 0.927$, $p < 0.05$) but not at MZNP ($R = 0.25$, $p > 0.05$). The global statistic (R) at MZNP was relatively low, indicating overlap in community composition. SIMPER analysis calculated the average similarity between each of the four days trapping inside the burrows to be 53.16 % at Kwandwe, 44.51 % at MZNP and 61.05 % at Tswalu. Average similarity between each of the four days trapping outside the burrows was 40.54 % at Kwandwe, 55.40 % at MZNP and 64.94 % at Tswalu. Average dissimilarity between the groups inside the burrows and those outside the burrows were 74.98 % at Kwandwe, 52.17 % at MZNP and 50.81 % at Tswalu. The 12 morphospecies which caused most of the Bray-Curtis dissimilarities between the burrows and control areas at each site are listed in Tables 4.9 – 4.11. At MZNP and Tswalu a minimum of 12 morphospecies were required to account for 50% of the dissimilarity which existed. Eleven morphospecies were required to do the same at Kwandwe. At all three sites the formicid morphospecies accounted for a substantial portion of the dissimilarity between the burrows and the control areas. Other morphospecies which were influential at all three sites included the tenebrionid beetle morphospecies and the Pulicidae (fleas) which only occurred in the burrows.

The average abundance of individual insects caught on a daily basis was not significantly affected by position as the traps in the control areas did not contain significantly more insects than the burrows ($F_{1,18} = 1.477769$, $p > 0.05$). The effect of site was significant ($F_{2,18} = 3.763181$, $p < 0.05$) although scheffé’s post-hoc test did not reveal any significant differences between individual sites. Position did not significantly affect the average daily morphospecies diversity of trapped insects ($F_{1,18} = 0.3642$, $p > 0.05$), however, site was very significant ($F_{2,18} = 45.7879$, $p < 0.001$). A scheffé's post-hoc test showed that morphospecies diversity at MZNP and Kwandwe was significantly higher than at Tswalu ($p < 0.001$ for both), whilst MZNP was higher than Kwandwe ($p < 0.001$) (Table 4.12). When the Formicidae were removed from the average daily morphospecies diversity analysis neither position ($F_{1,18} = 3.1292$, $p > 0.05$) nor site ($F_{2,18} = 1.3145$, $p > 0.05$) had a significant effect (Table 4.13). However, morphospecies diversity and evenness values did increase in all instances except outside the burrows at MZNP. The most notable increase in morphospecies diversity and evenness, after the removal of the Formicidae from the analyses, was observed inside and outside of the burrows at Tswalu (compare tables 4.12 and 4.13).

There was no significant effect of position on the average daily insect morphospecies richness ($F_{1,18} = 0.0058$, $p > 0.05$) despite the daily morphospecies richness outside the burrows at Kwandwe and Tswalu exceeding the morphospecies richness inside (Table 4.14). The effect of site was again significant ($F_{2,18} = 6.5834$, $p < 0.05$) with the morphospecies richness significantly higher at Tswalu compared to Kwandwe ($p < 0.01$). Total morphospecies richness inside and outside of the burrows was very similar at Kwandwe (inside: outside = 30:33) and Tswalu (50:50), while at MZNP (43:30) 13 more morphospecies were recorded in the burrows compared to the control areas (Table 4.14). The results of the Michaelis-Menten species richness estimator suggest that the insects were under-sampled in this study as in all cases less than 67 % of the estimated morphospecies available were trapped. At all three sites at least 33 % of the morphospecies were common to both the burrows and the controls (Table 4.14).

Analysis of the feeding guilds highlights the numerical dominance of the ants (Figure 4.5A). The ant guild contributed in excess of 70 % of the insects caught at all the sites and this value increased to 98 % inside the burrows and 99 % outside the burrows at

Tswalu where 11803 and 49647 individuals were trapped respectively. When the ants were removed from the analysis the results became less uniform. Members of the phytophagous guild were dominant inside and outside of the burrows at MZNP and outside the burrows at Kwandwe. At Kwandwe both the phytophagous and detritivorous/saprophagous guilds became numerically superior with the predatory/hematophagous and parasitic guilds only marginally less abundant. The predatory/hematophagous and detritivorous/saprophagous guilds were dominant inside the burrows at Tswalu whilst the detrivorous/saprophagous guild was clearly the most numerically abundant guild outside the burrows (Figure 4.5B).

4.4 DISCUSSION

The foraging behaviour of many animal species is thought to be influenced by the seemingly incompatible requirements of maximising food attainment whilst at the same time minimising exposure to predators (Longland & Price, 1991). In addition to predation and food availability, small mammal populations may also be sensitive to the presence of cover (Perrin & Johnson, 1999). Research on striped field mice (*Rhabdomys pumilio)* found that this species did not utilise open areas where ground cover was absent or sparse, due to the high risk of predation, even though large volumes of food were present (Perrin & Johnson, 1999). Kotler *et al*. (1991) recorded higher rates of predation amongst rodents per unit of seed acquired in open areas compared to patches with protective vegetation, whilst Brown *et al*. (1988) noted decreased seed harvesting rates amongst kangaroo rats, especially in open areas, when owls were present. It has also been demonstrated that desert rodents are more prone to attack and capture by owls in open areas as opposed to those in bush microhabitats (Longland & Price, 1991). In this respect the cover provided by aardvark burrows may be analogous to that of shrubby vegetation. It is highly improbable that an avian predator will successfully attack a small mammal foraging in a burrow and therefore it is surprising that, given the lack of notable differences in seed abundance inside and outside of the burrows (chapter 3), the results of this study did not reveal significantly greater trap success inside these microhabitat structures compared to the open areas. Indeed, Kwandwe was the only site where trap success was regularly higher inside the burrows than outside. Furthermore, the greatest disparity between the open areas and the burrows, with regards to the number of individuals captured and trap success, occurred at Tswalu, the site where vegetative cover was generally the most sparse and thus predation risk by avian predators and mammalian carnivores was probably the greatest.

An advantage of foraging in open areas may be the reduced risk of predation by ambush predators, for example puff adders, which strike from underneath bushes (Pough & Groves, 1983; Longland & Price, 1991; Young 2003). Although no snakes were encountered whilst carrying out this fieldwork, feedback from the questionnaires suggests that they regularly use burrows. It is, however, difficult to assess whether this is for the purpose of ambushing prey, sheltering from unfavourable environmental conditions or to avoid their own predators. The regularity with which snakes are seen in aardvark burrows suggests that they may be an important resource for these animals and in the case of the pythons they may be critical for their survival as they are important for thermoregulation and breeding purposes. (G. Alexander, University of the Witwatersrand, pers. comm.).

Despite the possible risk of being ambushed by predators, aardvark burrows potentially provide a stable microclimate in which to forage even when external conditions are unfavourable, such as in winter when the temperatures can drop below freezing (refer to chapter 3). However, the value of the soil seed bank as a food resource for granivorous rodents has been questioned (Price & Joyner, 1997). There is evidence to suggest that rodents may prefer harvesting newly produced seeds and that in some instances the resources contained in the soil seed bank may be unavailable to them (Johnson & Jorgensen, 1981; Price & Joyner, 1997). This would limit the value of foraging in the burrows to harvesting freshly produced seeds which had recently accumulated on the burrow floor after being blown in by the wind. The lack of any significant positive relationship between either trap success or the number of individuals and the biomass of seeds present in the soil, particularly inside the burrows, further supports this hypothesis.

The low capture rates in burrows at Tswalu compared to controls may simply reflect the frequency with which rodents come into contact with burrows. *Parotomys brantsii* has a large foraging range in open areas and creates an extensive burrow system with many entrances that can be used to escape from predators when needed (Jackson, 2000). By contrast, the lesser Egyptian gerbil (*Gerbillus gerbillus*) forages in a small, localized area centred around its burrow and thus virtually exhausts the food resource available in this area (Kinlaw, 1999). If the gerbil species present at Tswalu exhibit the same behaviour this would limit their foraging activity in aardvark burrows if these structures did not occur in close proximity to their own burrows. It may follow that the small mammals were trapped less frequently in the aardvark burrows because the traps in the control areas were situated closer to the safety of the rodents' own burrows. The high proportion of rodents which were recaptured in the same traps as the original trapping event took place supports the theory that the risk of predation may limit rodent foraging distance (Hay & Fuller, 1981). An alternative explanation is that they recognise that the traps offer a food reward and thus purposefully re-visit them (Magnusson *et al*., 1995).

The composition of the small mammal communities and the soil hardness at the three sites may also affect the use of aardvark burrows as a resource. The gerbils, in particular *G. paeba*, were the most common small mammals trapped at Tswalu and are known to be prodigious diggers (De Graaf, 1981). Thus for these species, digging their own burrows in the soft sand at the base of vegetation may be preferable to inhabiting aardvark burrows as their own smaller burrows are subject to increased thermal buffering (refer to chapter 3), limit the access of predators (other than snakes) and the roots of the shrubby vegetation provide structural support which is not necessarily available in aardvark burrows. The small mammal communities at the other two sites were dominated by rodents which, while capable of digging their own burrows, also use alternative shelter if it is available, particularly in areas where the ground is hard and therefore difficult to excavate (De Graaf, 1981; Reichman & Smith, 1990). Rodents may also dig their own burrows within a larger burrow and on three occasions pouched mice were witnessed entering small burrows located within abandoned aardvark burrows. The active or abandoned status of the aardvark burrows did not, however, appear to influence the trap success within the burrows. These findings are in accordance with those of Witz *et al*. (1991) who found no significant difference in the number of vertebrate commensals among active, inactive and abandoned gopher tortoise (*Gopherus polyphemus*) burrows. The simultaneous use of burrows by a primary excavator and other vertebrates appears to be widespread as badgers are known to co-exist with rabbits (*Oryctolagus cuniculus*) and foxes (*Vulpes vulpes*) (Neal & Roper, 1991) while Cape porcupines have been observed sharing burrows with vertebrates such as bat-eared foxes, striped polecats (*Ictonyx striatus*) and a variety of rodent species (C. Bragg, University of Cape Town, pers. comm.). The structural complexity of a burrow may influence the diversity of the vertebrate commensals contained within it, as several sleeping chambers and entrance holes may allow a range of vertebrates to utilise the burrow simultaneously and for different reasons, with minimal interaction between them (Kinlaw, 1999). Burrows may also be subject to successional invasion and thus the occurrence of species in a particular burrow may not overlap (Kinlaw, 1999).

The pouched mouse was the only rodent species trapped in this study which had previously been documented by Smithers (1971) and Skinner & Smithers (1990) as using aardvark burrows. Thus, 11 new small mammal species can be added to their lists. One must, however, be cautious when interpreting these results and commenting on the reliance of these species on aardvark burrows, as a number of the trap records and observations are for one or two individuals of a particular species, which suggests that these animals are probably non-obligate commensals of aardvark burrows (Kinlaw, 1999).

The low species richness and diversity of small mammals recorded at MZNP, together with very limited trap success (never exceeding 5 %), contrasted with the direct observations made of vertebrates using aardvark burrows as it was at MZNP where the highest number of species were seen entering or exiting burrows. Very few of the vertebrate species observed making use of the burrows were seen on a frequent basis at any of the sites and this can be attributed to the fact that most of them are nocturnal animals (Skinner & Smithers, 1990). Given that none of the observed species are considered rare, another explanation is that they are simply opportunistic burrow-users and thus unlikely to be encountered on a regular basis (Kinlaw, 1999). Certain species may also only be observed using burrows at particular times of the day as is the case with the larks using lizard burrows to escape the early afternoon heat in the Arabian desert (Williams *et al*., 1999). Both the sightings of pearl-breasted swallows (*Hirundo dimidiata*), for instance, occurred at midday on days where the temperature exceeded 35 °C and thus it is likely that they were simply seeking temporary refuge from the heat. Steenbok are also known to seek shade during the heat of the day (Stuart & Stuart, 1990) and their tracks were observed leading into burrows at Tswalu on days which were particularly hot. Steenbok are regularly seen lying in the entrance of burrows during aerial game counts at Tswalu (A. Stainethorpe, Tswalu Kalahari Reserve pers. comm.). Although the steenbok tracks were easy to discern in the sand due to the previous night's rain, the use of burrows by other vertebrate species may have been underestimated as dry soil often proved to be a poor tracking substrate, thus making accurate identification of footprints difficult (Platt *et al*., 2004). Initial attempts to use the track pad method followed by Bragg *et al*. (2005) were also unsuccessful as rain damaged the paper substrate and wind dispersed the powder paint designed to capture the footprint.

Bat-eared foxes and warthogs were the only two species which were regularly observed using aardvark burrows in addition to frequently having their tracks recorded entering and exiting burrows. These two species are known to be regular inhabitants of abandoned burrows (Sowls & Phelps, 1966; Cumming, 1970; Skinner & Smithers, 1990). Sowls & Phelps (1966) claim that young warthogs rely on shelter at night-time for survival and it has been proposed that their distribution and abundance could be affected by the presence or absence of burrow excavators such as aardvarks (Sowls & Phelps, 1966; Melton, 1976). Birds may also be reliant on aardvark burrows for shelter, especially in areas where suitable nesting sites and protective vegetation are limited (Cilliers, 2002), hence the much greater proportion of burrows containing nests at Tswalu in comparison with Kwandwe and MZNP. Although not an inhabitant of arid and semi-arid environments, the blue swallow (*Hirundo atrocaerulea*) is critically endangered in South Africa and is thought to be heavily reliant on the presence of aardvark burrows and sinkholes for nesting sites[1]. Of the 16 bird species documented in Hockey *et al*. (2005) (Appendix C) as using aardvark burrows for nesting purposes, only the ant-eating chat was regularly observed to do so during this study.

The number of vertebrate species recorded using aardvark burrows during this study compares favourably with the lists of Smithers (1971) and Skinner & Smithers (1990) (Appendix D) and the use of alternative track-pad methods, camera traps, more nocturnal burrow surveys and burrow excavations would in all likelihood have increased the number of species which were recorded (Lomolino & Smith, 2003). Despite this, the number of vertebrates documented using the burrows of aardvarks is greater than in similar studies conducted in the burrows of nine-banded armadillos (six species), woodchucks (*Marmota monax*) (four species) and pocket gophers (22 species) (Vaughan, 1961; Swihart & Picone, 1995; Platt *et al*., 2004), although it is considerably less than the 55 and 60 species recorded in the burrows of black-tailed prairie dogs and muskrats (*Ondatra zibethicus*) respectively (Kiviat, 1978; Lomolino & Smith, 2003).

Invertebrates are an integral component of ecosystems (Romoser & Stoffolano, 1998) and are regarded as common inhabitants of mammal burrows (Reichman & Smith, 1990). The results of this study reveal that aardvark burrows are no exception.

---

[1] http://www.ewt.org.za/workgroups_overview.aspx?group =swallow&page=activities&morePage=activities_more&activity=1

However, the morphospecies richness of insects recorded in aardvark burrows was substantially less than were found in the burrows of the gopher tortoise (302 invertebrate species) (Kinlaw, 1999), badger setts (81 insect species, eight tick species) (Hancox, 1988) and gerbil burrows (over 250 invertebrate species) (Reichman & Smith, 1990). However, the Michaelis-Menten analysis estimated that less than two-thirds of the total available morphospecies had been trapped. The first possible cause of this under-trapping may have been the use of pitfall traps to collect insect specimens. Despite the benefits of pitfall trapping, this method also has disadvantages such as variable trap efficiency caused by its reliance on insect activity and a bias towards surface dwelling insects (Topping & Sutherland, 1992; Thomas & Marshall, 1999). It is therefore possible that soil-dwelling and flying insects were under-represented in the samples. This is especially true of the calliphorid flies which lay eggs on the skin of aardvarks that later develop into bots (Kingdon, 1971). These flies were very common around the entrance of occupied burrows but this was not accurately reflected in their occurrence in the pitfall traps. Attempts were made to collect insect specimens using sticky traps attached to metal stakes but this method also had flaws as wind deposited sand on the traps and substantially reduced their stickiness and ultimately their effectiveness. There was also evidence to suggest that vertebrate species may have affected the trap results as some pitfall traps had clearly been disturbed whilst on other occasions the water level in certain traps was greatly diminished overnight, possibly as a result of animals drinking from the traps. This may have resulted in morphospecies being removed from the pitfall traps and others escaping due to the low water levels. Another possible explanation for the under-trapping of the pitfall traps suggested by the Michaelis-Menten analyis is that dividing insects into morphospecies may have resulted in an underestimation of true species richness as a consequence of "lumping" (Oliver & Beattie, 1996). However, this is unlikely, because as the number of sorted morphospecies increases so to does the chance that a previously recorded morphospecies will not be recognised, thus resulting in a “splitting” effect which ultimately causes an overestimation of morphospecies richness (Oliver & Beattie, 1993).

Although the parasitic guild (which was dominated by the Pulicidae) made up a greater proportion of the insect community in the burrows compared to the open areas outside, it was not as dominant as expected, even after the removal of the ants from the analyses. Cumming (1970) states that fleas, mites and hematophagous maggots (*Auchmeromyia* and *Pachychoeromyia* spp., Calliphoridae, Diptera) are common inhabitants of warthog burrows and may survive for months in abandoned burrows before requiring food (Cumming, 1970; Peirce, 1974). High densities of parasites (including ticks and mites) inhabiting burrows has even been proposed as a possible explanation as to why animals such as aardvarks and warthogs frequently move burrows (Cumming, 1970). It is possible that placement of pitfall traps in the sleeping chambers of burrows would have yielded a greater richness of invertebrates, in particular parasites such as fleas and ticks (Hancox, 1988). Unfortunately this is impractical without performing the highly laborious and invasive task of excavating burrows. Colonies of honeybees (*Apis mellifera*) have also been observed utilising porcupine burrows in the Nieuwoudtville region of South Africa (Bragg *et al*., 1995), but were never encountered inhabiting aardvark burrows during this study. Although the lack of parasites and honeybees was surprising, the numerical abundance of the ant guild was not. Brown *et al*. (1979) estimated that ant biomass in deserts is equivalent to that of the rodents and that they may be responsible for the consumption of the majority of seeds produced in those environments. The overwhelming numerical dominance of the Formicidae family can also be seen in the increase in morphospecies diversity and evenness values at all the sites when they were removed from the analyses. This increase happened in spite of the fact that the formicid family contributed a high number of morphospecies inside and outside of the burrows at all three sites. The dominance of the phytophagous and detritivorous/saprophagous guilds, after the removal of the ants from the analyses, is also unsurprising as it has been claimed that arthropods are the most abundant herbivores and detritivores in many terrestrial ecosystems (Seastedt & Crossley, 1984). Burrows may also experience successional invasion by insects with herbivores entering the burrows first, followed by detritivores and then predators (Kinlaw, 1999). This may also account for the numerical dominance of certain feeding guilds. Although successive days trapping did not exhibit high levels of similarity either inside the burrows or in the control areas outside, and despite the burrows and outside areas being dominated by the same guilds, the analysis revealed distinct insect communities within the burrows at Kwandwe and Tswalu which suggest that aardvark burrows may act as a valuable microhabitat for insects.

At times it is difficult to accurately determine the reason why an individual or species uses the burrow of another species and the extent to which it is reliant on that structure or the resources contained within it. However, aardvark burrows are utilised by a variety of vertebrates and invertebrates in arid and semi-arid environments, and it is reasonable to assume that at least some of these individuals and populations are reliant on the aardvark as an ecological engineer and that their burrows are essential for survival.

4.5 TABLES AND FIGURES

Table 4.1: SIMPER analysis breakdown of average dissimilarity between recently active burrow mounds and reference plots into contributions from the 10 most influential species at Tswalu during spring. Percentage cover was used as a surrogate for abundance.

Site	Position	Number of individuals	Total number of captures	Trap success (%)	Species richness	Species diversity
Kwandwe	Inside	19 ± 7.0	26.3 ± 11.0	18.4 ± 7.6	3.3 ± 1.0	1.0 ± 0.2
	Outside	13 ± 8.4	15.8 ± 9.8	10.3 ± 6.3	2.5 ± 1	0.7 ± 0.2
MZNP	Inside	2.8 ± 1.0	3.3 ± 1.0	2.2 ± 0.6	1.8 ± 1.0	0.8 ± 0.4
	Outside	2.8 ± 2.8	3 ± 3.2	2.1 ± 2.2	1 ± 0.8	0.4 ± 0.5
Tswalu	Inside	19.5 ± 18.9	28 ± 30.5	18.7 ± 20.4	3.5 ± 1	1.1 ± 0.3
	Outside	57.5 ± 30.8	72.5 ± 46.2	49.1 ± 32.4	5 ± 0.8	0.9 ± 0.4

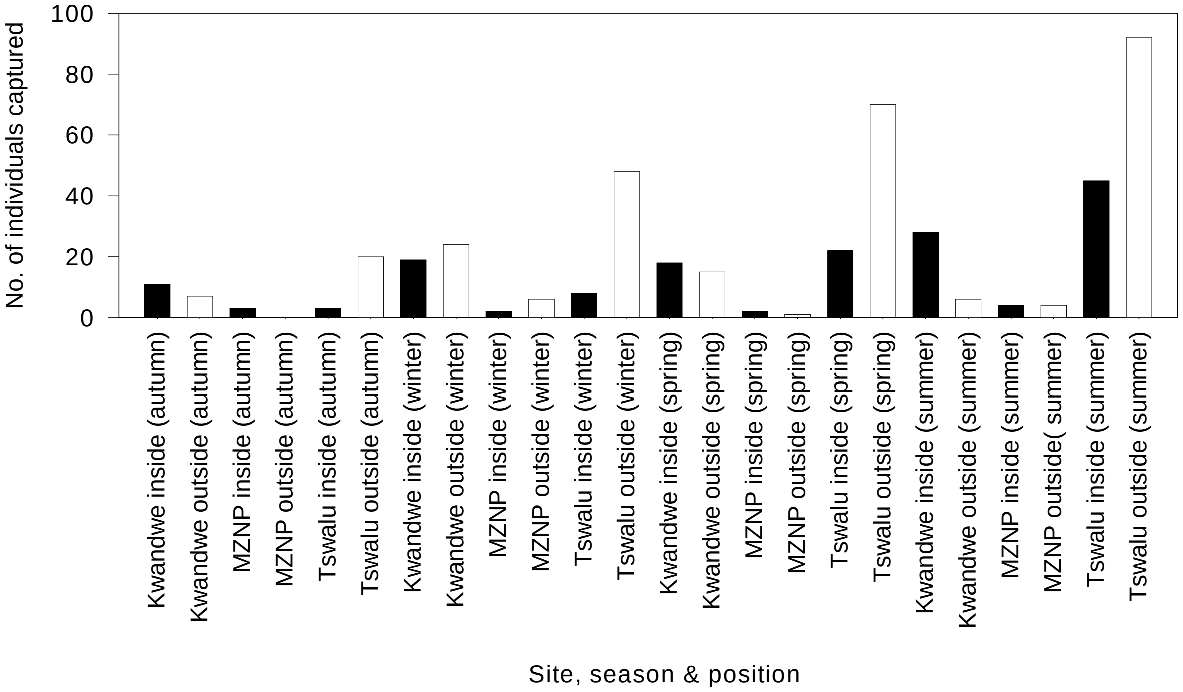

Figure 4.1: The number of unique individual small mammals caught inside (solid bars) and outside (clear bars) of the burrows at all sites during the four seasons.

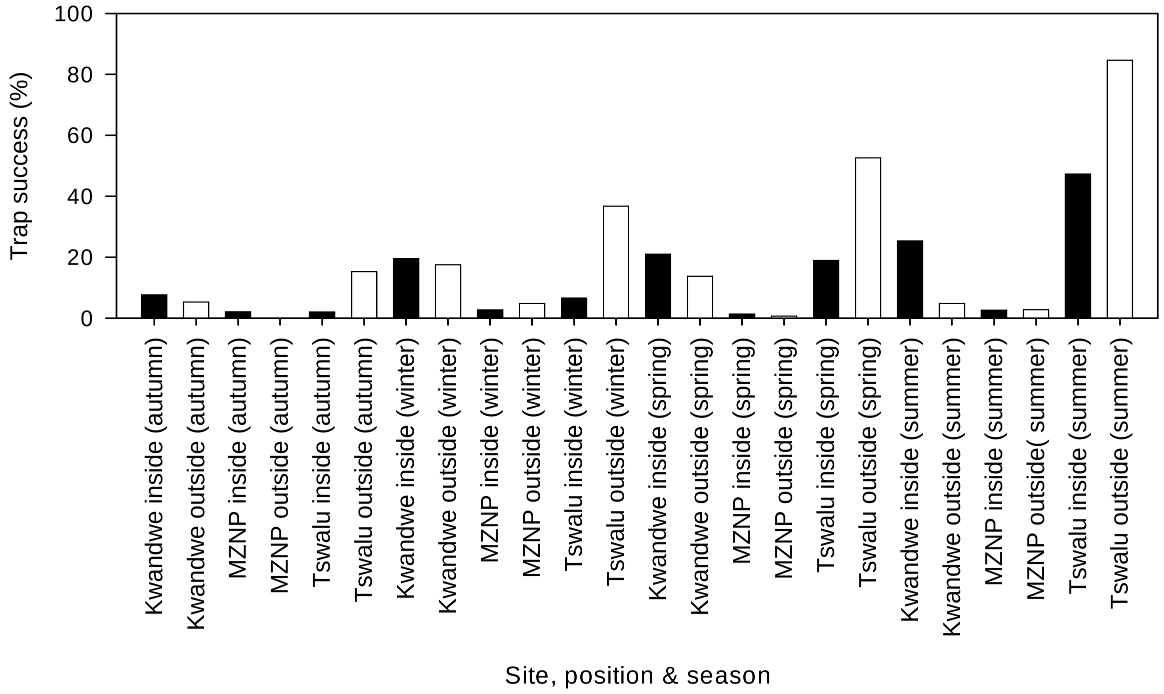

Figure 4.2: The small mammal trap success inside (solid bars) and outside of the burrows (clear bars) at all sites during the four seasons.

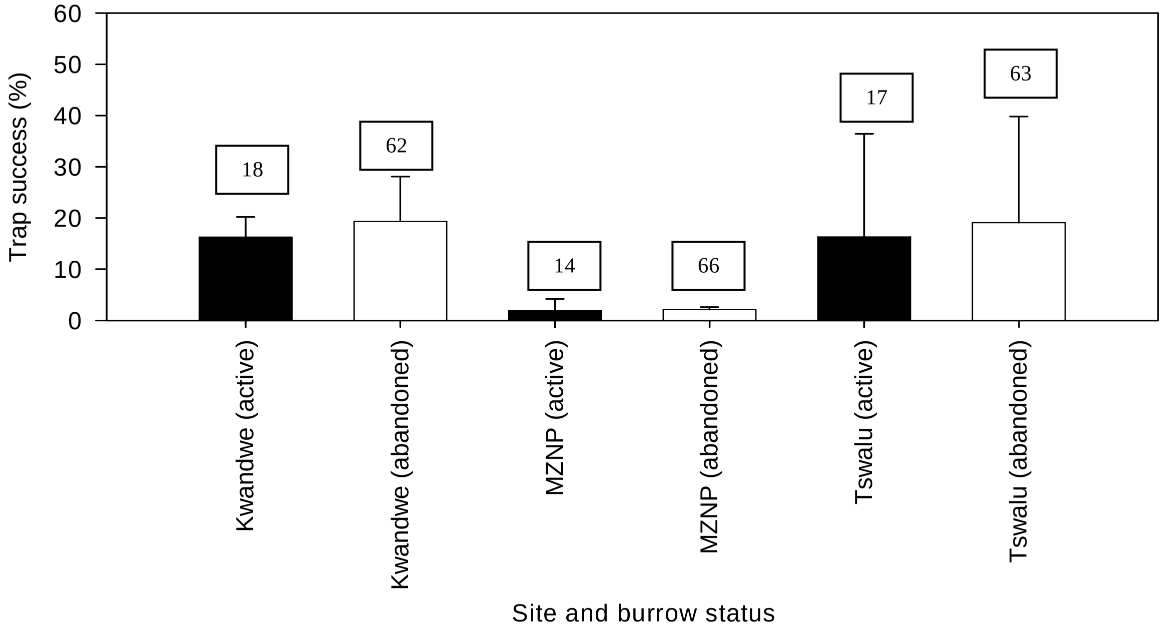

Figure 4.3: The average trap success in active (solid bars) and abandoned burrows (clear bars) at all the sites. Data are means per season ± 1 SD. Text boxes denote sample size.

Table 4.2: The species richness, diversity and evenness values inside and outside of the burrows at all the sites during the four seasons.

Season	Site	Position	Species Richness	Species Diversity (H')	Eveness (J')
Autumn	Kwandwe	Inside	2	0.68	0.99
		Outside	2	0.59	0.86
	MZNP	Inside	3	1.09	1
		Outside	0	0	0
	Tswalu	Inside	2	0.63	0.92
		Outside	4	1.09	0.78
Winter	Kwandwe	Inside	4	1.01	0.73
		Outside	2	0.63	0.91
	MZNP	Inside	1	N/A	N/A
		Outside	1	N/A	N/A
	Tswalu	Inside	4	1.32	0.95
		Outside	6	1.36	0.76
Spring	Kwandwe	Inside	4	1.22	0.88
		Outside	4	1.06	0.76
	MZNP	Inside	1	N/A	N/A
		Outside	1	N/A	N/A
	Tswalu	Inside	4	1.11	0.80
		Outside	4	0.75	0.54
Summer	Kwandwe	Inside	3	0.89	0.81
		Outside	2	0.63	0.91
	MZNP	Inside	2	0.56	0.81
		Outside	2	0.69	1.00
	Tswalu	Inside	4	1.12	0.81
		Outside	5	0.47	0.29

Table 4.3: The effect of site (the reserves) and position (burrows or open areas) on the numbers of unique individuals and species of small mammals trapped. Data are means of the four seasonal values ± 1 SD with total numbers in parentheses. Common names are listed in Appendix B.

	Kwandwe		MZNP		Tswalu	
Species	Burrows	Open areas	Burrows	Open areas	Burrows	Open areas
Praomys natalensis	8.3 ± 3.9 (33)	5 ± 2.45 (20)	0.3 ± 0.5 (1)	0	0	0
Rhabdomys pumilio	9.3 ± 3.9 (37)	7.5 ± 6.2 (30)	1.5 ± 1.3 (6)	2.3 ± 2.6 (9)	0	0
Saccostomus campestris	1.3 ± 1.5 (5)	0.3 ± 0.5 (1)	0	0	2.0 ± 2.3 (8)	4.5 ± 7.1 (18)
Mus minutoides	1.3 ± 1.9 (5)	0	0.8 ± 1.0 (3)	0.5 ± 1 (2)	0	0
Mus indutus	0	0	0	0	4.5 ± 6.1(18)	3.5 ± 3.3 (14)
Aethomys namaquensis	0.3 ± 0.5 (1)	0.3 ± 0.5 (1)	0	0	0	0
Myosorex varius	0	0	0.3 ± 0.5 (1)	0	0	0
Gerbillurus paeba	0	0	0	0	9.5 ± 11.0 (38)	39.0 ± 33.9 (156)
Tatera brantsii	0	0	0	0	1.3 ± 1.5 (5)	1.5 ± 1.7 (6)
Tatera leucogaster	0	0	0	0	1.5 ± 1.9 (6)	7.5 ± 8.9 (30)
Desmodillus auricularis	0	0	0	0	0.5 ± 1 (2)	0
Thallomys nigricauda	0	0	0	0	0	0.3 ± 0.5 (1)
Mystromys albicaudatus	0	0	0	0	0.3 ± 0.5 (1)	0.3 ± 0.5 (1)
Parotomys brantsii	0	0	0	0	0	0.8 ± 1.5 (3)

Table 4.4: The R and p values for the regression analyses between trap success and the number of unique individuals caught, and the combined biomass of the monocotyledonous and dicotyledonous seeds removed from the soil samples inside and outside of the burrows. * = p > 0.05

Variable	Site	Position	R	P value
Trap success	Kwandwe	Inside	0.2838	*
		Outside	-0.3198	*
	MZNP	Inside	0.1004	*
		Outside	0.2848	*
	Tswalu	Inside	-0.3884	*
		Outside	0.1530	*
No. of individuals caught	Kwandwe	Inside	0.5227	*
		Outside	-0.5039	*
	MZNP	Inside	-0.2074	*
		Outside	0.2025	*
	Tswalu	Inside	-0.3926	*
		Outside	0.0987	*

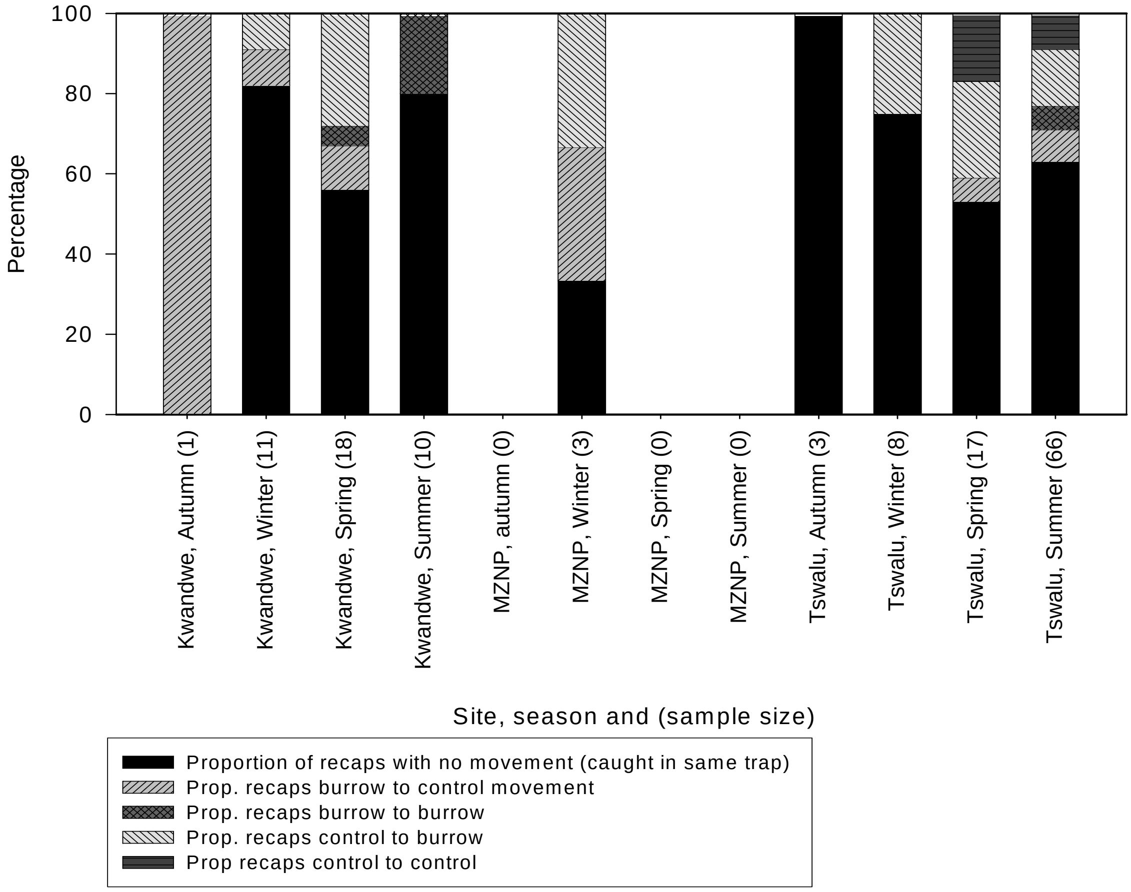

Figure 4.4: The percentage movement between traps of recaptured small mammals.

Table 4.5: Vertebrate species observed using burrows during the course of this study. Infrequent observations are considered to be less than ten sightings. The purpose of burrow use is denoted either by "+" or "-". "?" is used when the purpose of burrow use is unknown. Common names are listed in Appendix B.

Site	Species name	Frequency of observation	Young present	Purpose of use	
				Refuge	Breeding
Kwandwe	*Phacochoerus aethiopicus*	frequently	Yes	+	+
	Otocyon megalotis	frequently	Yes	+	+
	Rhabdomys pumilio	infrequently	No	+	-
	Canis mesomelas	infrequently	No	+	-
	Cynictis penicillata	infrequently	No	+	-
	Myrmecocichla formicivora	infrequently	No	+	+
MZNP	*Proteles cristatus*	infrequently	No	+	-
	Otocyon megalotis	frequently	Yes	+	+
	Hystrix africaeaustralis	infrequently	No	+	-
	Lepus saxatilis	infrequently	No	+	-
	Cynictis penicillata	infrequently	No	+	-
	Myrmecocichla formicivora	infrequently	No	+	+
	Hirundo dimidiata	infrequently	No	+	-
	Varanus albigularis	infrequently	No	+	-
	Mabuya capensis	infrequently	No	+	-
	Bufo gariepensis	infrequently	No	?	?
Tswalu	*Felis lybica*	infrequently	No	+	-
	Tatera brantsii	frequently	No	+	-
	Mus indutus	infrequently	No	+	-
	Hystrix africaeaustralis	infrequently	No	+	-
	Otocyon megalotis	infrequently	Yes	+	+
	Xerus inauris	infrequently	No	+	-
	Agama aculeata	infrequently	No	+	-
	Myrmecocichla formicivora	frequently	No	+	+

Table 4.6: Tracks and signs of vertebrate species using aardvark burrows. Infrequent observations are considered to be less than ten sightings. Common names are listed in Appendix B.

Site	Species name	Tracks/sign	Frequency of occurrence
Kwandwe	*Hystrix africaeaustralis*	quills and footprints	frequently
	?	footprints	frequently
	Canis mesomelas	scats and footprints	Infrequently
	Phacochoerus aethiopicus	footprints	frequently
	?	footprints	frequently
MZNP	*Canis mesomelas*	scats	infrequently
	Hystrix africaeaustralis	quills and footprints	frequently
	Otocyon megalotis	Latrine sites	frequently
	?	footprints	frequently
	?	droppings	frequently
Tswalu	*Hystrix africaeaustralis*	quills and footprints	frequently
	?	footprints	frequently
	?	footprints	frequently
	Rhapicerus campetris	footprints	infrequently
	Otocyon megalotis	footprints	infrequently

Table 4.7 List of vertebrates observed using aardvark burrows according to information derived from questionnaires. The purpose of burrow use is denoted either by “+” or “-“. “?” is used when the purpose of burrow use is unknown. Common names are listed in Appendix B.

Location	Species Name	Purpose of use	
		Refuge	Breeding
Kwandwe, Tussen die Riviere (Free State) & Tswalu	*Phacochoerus aethiopicus*	+	+
Kwandwe, MZNP & Unknown	*Otocyon megalotis*	+	+
Kwandwe, MZNP, Tussen die Riviere, Tswalu & unknown	*Hystrix africaeaustralis*	+	+
Kwandwe, MZNP & Tussen die Riviere	*Proteles cristatus*	+	+
Kwandwe, MZNP & Tussen die Riviere	*Canis mesomelas*	+	+
Tussen die Riviere	*Cynictis penicillata*	+	-
Gauteng	*Mellivora capensis*	?	?
Unknown	*Vulpes chama*	+	+
Tussen die Riviere	Rodent spp.	+	?
Nylsvley & Zimbabwe	*Ispidina picta*	+	+
Zimbabwe	*Halcyon leucocephala*	+	+
Nylsvley & Zimbabwe	*Merops pusillus*	+	+
Zimbabwe	*Hirundo semirufa*	+	+
MZNP, Kimberley, Tierberg, Prince Albert, Tussen die Riviere & Tswalu	*Myrmecocichla formicivora*	+	+
Kwandwe	*Thamnolaea cinnamomeiventris*	?	?
Tussen die Riviere	*Bitis arietans*	+	-
Unknown	*Python natalensis*	+	+
MZNP & Kwandwe	*Naja nivea*	+	-
Kwandwe	*Varanus albigularis*	+	-

Table 4.8: The richness, abundance and guild allocations of insect morphospecies inside and outside of burrows. Phyt = phytophagous, Pred/hem = predatory/hematophagous, Fungi = fungivorous, Det/sap = detritivorous/saprophagous and para = parasitic.

Site	Position	Order	Family	No. of Morpho species	No. of individuals	Guild
Kwandwe	Inside	Thysanura	Lepismatidae	1	1	Det/sap
		Blattodea	Blaberidae	1	1	Det/sap
		Isoptera	Hodotermitidae	1	1	Phyt
		Orthoptera	Gryllidae	1	4	Phyt
			Acrididae	2	3	Phyt
		Hemiptera	Reduviidae	1	4	Pred/hem
		Coleoptera	Trogidae	1	1	Det/sap
			Tenebrionidae	3	8	Det/sap
			Histeridae	2	7	Pred/hem
			Curculionidae	2	4	Phyt
			Staphylinidae	1	1	Pred/hem
			Carabidae	2	3	Pred/hem
			Scarabaeidae	1	4	Det/sap
		Diptera	Muscidae	1	1	Det/sap
			Calliphoridae	1	17	Det/sap & phyt
			Culicidae	1	2	Pred/hem
		Siphonaptera	Pulicidae	2	19	Para
		Hymenoptera	Encyrtidae	1	1	Para
			Braconidae	1	1	Para
			Ceraphronidae	1	1	Para
			Formicidae	3	860	Ant
			Pompilidae	1	2	Pred/ hem & phyt
Kwandwe	Outside	Thysanura	Lepismatidae	1	1	Det/sap
		Isoptera	Hodotermitidae	1	122	Phyt
		Orthoptera	Acrididae	1	5	Phyt
		Hemiptera	Cicadellidae	2	6	Phyt
		Coleoptera	Carabidae	2	4	Pred/hem
			Scarabaeidae	1	5	Det/sap
			Coccinellidae	1	1	Pred/hem
			Tenebrionidae	2	23	Det/sap
			Histeridae	1	2	Pred/hem
			Curculionidae	5	17	Phyt
			Chrysomelidae	2	3	Phyt
		Diptera	Phoridae	1	1	Det/sap
			Sarcophagidae	1	3	Det/sap
		Hymenoptera	Formicidae	8	767	Ant
			Eumenidae	1	1	Pred/hem & phyt
			Pompilidae	2	4	Pred/hem & phyt
			Mutillidae	1	3	Para

		Isoptera	Hodotermitidae	1	51	Phyt
		Orthoptera	Acrididae	2	6	Phyt
			Gryllidae	1	34	Phyt
		Hemiptera	Cicadellidae	2	8	Phyt
			Reduviidae	1	2	Pred/hem
			Coreidae	1	1	Phyt
		Coleoptera	Carabidae	3	4	Pred/hem
			Scarabaeidae	3	16	Det/sap
			Coccinelidae	1	1	Pred/hem
			Tenebrionidae	2	5	Det/sap
			Histeridae	1	1	Pred/hem
			Curculionidae	3	7	Phyt
			Chrysomelidae	2	5	Phyt
		Diptera	Calliphoridae	1	8	Det/sap & phyt
			Sciaridae	1	4	Fungi
			Bibionidae	1	1	Phyt
			Ceratopogonidae	1	1	Pred/hem & para & phyt
			Sarcophagidae	1	1	Det/sap
			Pulicidae	2	12	Para
		Hymenoptera	Encyrtidae	1	1	Para
			Formicidae	7	453	Ant
			Eumenidae	1	1	Pred/hem & phyt
			Pompilidae	2	2	Pred/hem & phyt
			Megachilidae	1	1	Det/sap
			Apidae	1	1	Phyt
MZNP	Outside	Isoptera	Hodotermitidae	1	80	Phyt
		Orthoptera	Acrididae	1	4	Phyt
			Gryllidae	1	7	Phyt
		Hemiptera	Cicadellidae	3	14	Phyt
		Coleoptera	Carabidae	2	5	Pred/hem
			Scarabaeidae	1	1	Det/sap
			Tenebrionidae	2	8	Det/sap
			Histeridae	1	1	Pred/hem
			Curculionidae	5	10	Phyt
			Chrysomelidae	2	4	Phyt
		Diptera	Sciaridae	1	2	Fungi
			Empididae	1	1	Pred/hem
			Bombylidae	1	1	Phyt
			Phoridae	1	1	Det/sap
			Chloropidae	2	3	Phyt
		Siphonaptera	Pulicidae	1	1	Phyt
		Hymenoptera	Formicidae	7	389	Ant
Tswalu	Inside	Orthoptera	Gryllidae	1	1	Phyt
			Schizodactylidae	1	1	Phyt
			Acrididae	1	1	Phyt
			Pyrgomorphidae	1	1	Phyt
		Hemiptera	Cynidae	1	1	Phyt
			Scutteleridae	1	1	Phyt

			Cicadellidae	2	3	Phyt
		Coleoptera	Trogidae	1	1	Det/sap
			Tenebrionidae	8	59	Det/sap
			Histeridae	3	50	Pred/hem
			Curculionidae	2	5	Phyt
			Staphylinidae	1	5	Pred/hem
			Chrysomelidae	1	1	Phyt
			Scarabaeidae	1	1	Det/sap
			Anthicidae	1	4	Pred/hem
		Diptera	Sphaeroceridae	1	5	Det/sap & fungi
			Dolichopodidae	1	2	Pred/hem
			Phoridae	1	9	Det/sap
			Scatopsidae	1	4	Det/sap
			Chloropidae	1	3	Phyt
			Ceratopogonidae	1	1	Pred/hem & para & phyt
			Sarcophagidae	1	1	Det/sap
			Calliphoridae	2	2	Det/sap
			Sciaridae	1	11	Fungi
			Culicidae	1	1	Pred/hem
		Siphonaptera	Pulicidae	1	36	Para
		Hymenoptera	Formicidae	6	11803	Ant
			Eumenidae	2	2	Pred/hem & phyt
			Pompilidae	1	1	Pred/hem & phyt
			Mutillidae	1	4	Para
			Megachilidae	1	1	Det/sap
			Scelionidae	1	2	Para
Tswalu	Outside	Isoptera	Termitidae	1	2	Phyt
		Orthoptera	Acrididae	2	2	Phyt
			Pyrgomorphidae	1	3	Phyt
		Hemiptera	Cicadellidae	3	7	Phyt
			Reduviidae	1	1	Pred/hem
			Cynidae	1	1	Phyt
		Coleoptera	Carabidae	1	1	Pred/hem
			Scarabaeidae	3	21	Det/sap
			Anthicidae	1	11	Pred/hem
			Trogidae	1	1	Det/sap
			Tenebrionidae	9	232	Det/sap
			Curculionidae	2	3	Phyt
		Diptera	Calliphoridae	2	5	Det/sap & phyt
			Sciaridae	1	1	Fungi
			Empididae	1	3	Pred/hem
			Muscidae	1	1	Det/sap
			Sphaeroceridae	1	6	Det/sap & fungi
			Chloropidae	2	21	Phyt
			Sarcophagidae	1	1	Det/sap
			Agromyzidae	1	3	Phyt
			Formicidae	5	49647	Ant
			Mutillidae	1	1	Para

	Tiphiidae	1	1	Para
	Scoliidae	1	1	Para
	Megachilidae	1	16	Det/sap
	Sphecidae	1	1	Pred/hem & Phyt
	Scelionidae	1	1	Para
	Apidae	3	1	Phyt
	Tenthredinidae	1	1	Phyt

Table 4.9 SIMPER analysis breakdown of average dissimilarity between burrows and control areas into contributions from the most influential morphospecies at Kwandwe.

Morphospecies	Average abundance inside burrows	Average abundance in control areas	Average dissimilarity (%)	Contribution to dissimilarity (%)	Cumulative contribution
Formicidae sp 9	189.50	40.50	6.68	8.91	8.91
Formicidae sp 5	0	37	4.76	6.35	15.27
Hodotermitidae sp 1	0.25	30.50	4.10	5.47	20.74
Formicidae sp 1	24.0	65.50	3.82	5.10	25.84
Formicidae sp 12	0	9.75	3.62	4.82	30.66
Calliphoridae sp1	4.25	0	3.16	4.21	34.87
Pulicidae sp 1	4.5	0	3.07	4.1	38.96
Tenebrionidae sp 13	0	4	2.83	3.78	42.74
Formicidae sp 10	0	16.75	2.28	3.04	45.78
Formicidae sp 6	0	11.25	2.07	2.76	48.54
Formicidae sp 8	0	9.75	1.89	2.52	51.06
Tenebrionidae sp 3	1.5	0	1.85	2.47	53.53

Table 4.10 SIMPER analysis breakdown of average dissimilarity between burrows and control areas into contributions from the most influential morphospecies at MZNP.

Morphospecies	Average abundance inside burrows	Average abundance in control areas	Average dissimilarity (%)	Contribution to dissimilarity (%)	Cumulative % contribution
Hodotermitidae sp 1	12.75	20	3.92	7.51	7.51
Gryllidae sp 2	8.50	1.75	2.98	5.71	13.22
Formicidae sp 5	10.75	4.50	2.77	5.30	18.53
Formicidae sp 6	3.25	1.25	2.19	4.20	22.72
Formicidae sp 3	0.75	2.50	2.02	3.88	26.60
Formicidae sp1	69.75	53.75	1.99	3.82	30.43
Cicadellidae sp 5	1.75	3	1.94	3.73	34.15
Formicidae sp 2	3.25	3.25	1.92	3.67	37.83
Tenebrionidae sp 5	0	1.75	1.82	3.48	41.31
Scarabaeidae sp 5	2	0.25	1.76	3.38	44.69
Calliphoridae sp 2	2	0	1.68	3.21	47.90
Pulicidae sp 1	2	0.25	1.61	3.09	51.00

Table 4.11 SIMPER analysis breakdown of average dissimilarity between burrows and control areas into contributions from the most influential morphospecies at Tswalu.

Morphospecies	Average abundance inside burrows	Average abundance in control areas	Average dissimilarity (%)	Contribution to dissimilarity (%)	Cumulative contribution
Tenebrionidae sp 3	2.25	41	3.14	6.19	6.19
Histeridae sp 1	11.5	0	3.11	6.12	12.30
Pulicidae sp 2	9	0	2.66	5.23	17.53
Formicidae sp 1	2829	12239.75	2.48	4.87	22.40
Tenebrionidae sp 1	9.75	0.75	2.32	4.56	26.96
Formicidae sp 5	17	106	2.28	4.48	31.44
Tenebrionidae sp 5	1.25	11	2.23	4.39	35.83
Scarabaeidae sp 3	0	3.75	1.96	3.86	39.69
Formicidae sp 2	81.75	60.50	1.79	3.52	43.21
Formicidae sp 3	14.5	4	1.64	3.23	46.45
Megachilidae sp 1	0.25	4	1.32	2.61	49.05
Chloropidae sp 1	0.75	4.75	1.31	2.57	51.63

Table 4.12: Average daily (means ± 1 SD) and total morphospecies diversity and evenness with formicidae included at each site.

Site	Position	Average daily morphospecies diversity	Average daily evenness	Total morphospecies diversity	Total evenness
Kwandwe	Inside	0.62 ± 0.29	0.34 ± 0.17	0.90	0.26
	Outside	1.48 ± 0.24	0.54 ± 0.09	2.24	0.64
MZNP	Inside	1.86 ± 0.12	0.65 ± 0.11	2.14	0.57
	Outside	1.68 ± 0.16	0.62 ± 0.03	1.93	0.55
Tswalu	Inside	0.58 ± 0.27	0.19 ± 0.10	0.35	0.09
	Outside	0.29 ± 0.22	0.10 ± 0.08	0.14	0.04

Table 4.13: Average daily (means ± 1 SD) and total morphospecies diversity and evenness with formicidae excluded at each site.

Site	Position	Average daily morphospecies diversity	Average daily evenness	Total morphospecies diversity	Total evenness
Kwandwe	Inside	2.12 ± 0.08	0.88 ± 0.04	2.72	0.82
	Outside	1.89 ± 0.67	0.79 ± 0.26	1.76	0.54
MZNP	Inside	1.99 ± 0.11	0.79 ± 0.09	2.66	0.74
	Outside	1.55 ± 0.23	0.70 ± 0.09	1.94	0.59
Tswalu	Inside	2.30 ± 0.48	0.81 ± 0.05	2.79	0.74
	Outside	1.99 ± 0.67	0.66 ± 0.16	2.33	0.61

Table 4.14: Average daily (means ± 1 SD) and total morphospecies richness, Michaelis-Menten species richness estimate and the total number morphospecies common to the burrows and controls at each site.

Site	Position	Average daily morphospecies richness	Total morphospecies richness	MM richness estimate	Total number of morphospecies common to burrows and control areas
Kwandwe	Inside	13.3 ± 1.9	30	51.3	
	Outside	15.5 ± 2.1	33	52.8	10
MZNP	Inside	19.0 ± 6.8	43	73.0	
	Outside	14.8 ± 3.8	33	55.3	21
Tswalu	Inside	23.0 ± 7.8	50	79.7	
	Outside	24.5 ± 6.6	50	75.3	30

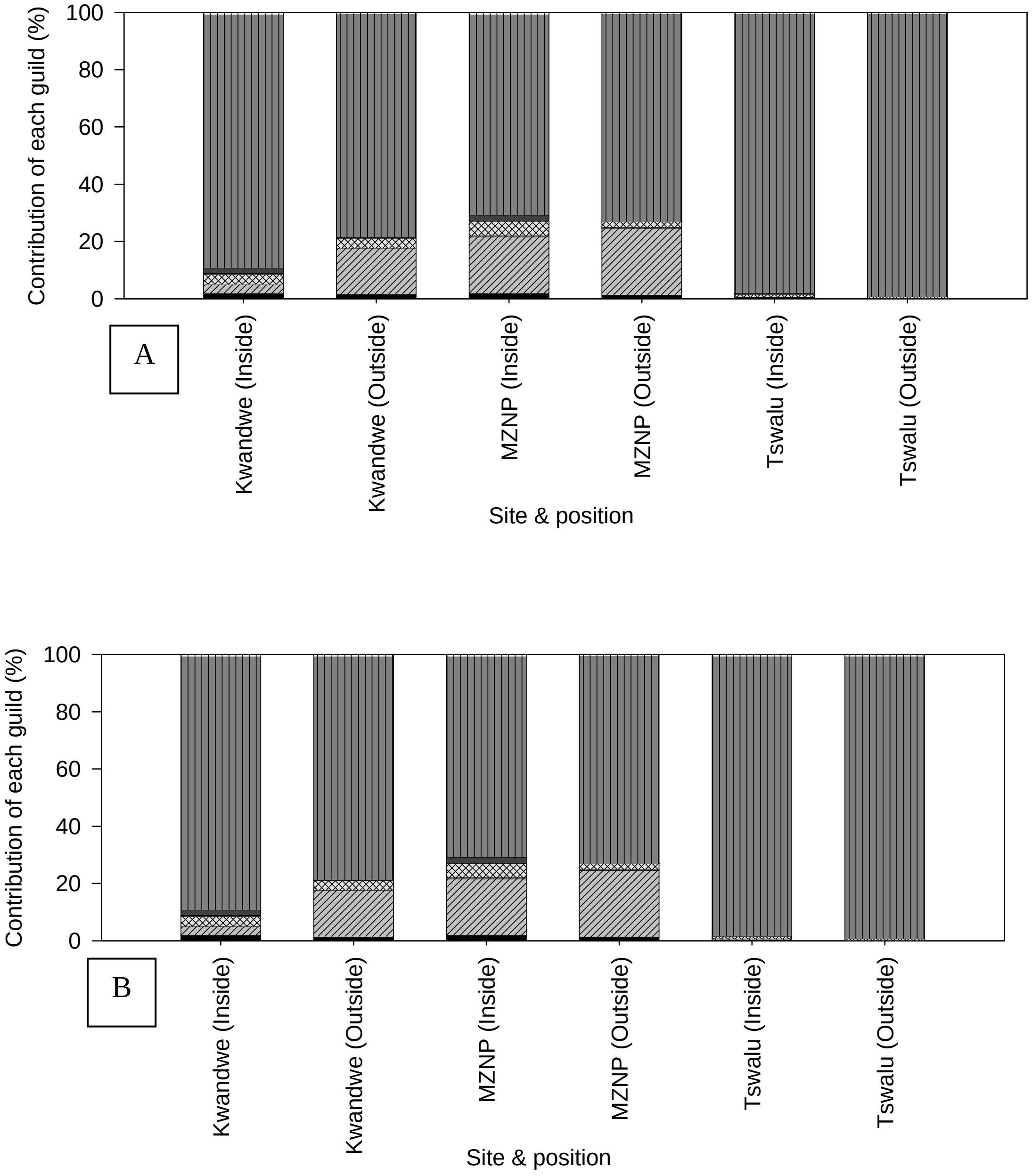

Figure 4.5 Percentage contribution of each guild to the total number of individual insects trapped at each site. Including ant the guild (A) and excluding the ant guild (B).

■ Predatory/hematophagous
▨ Phytophagous
▧ Fungivorous
⊠ Detritivorous/saprophagous
▤ Parasitic
▥ Ant

CHAPTER 5

THE IMPACT OF AARDVARK BURROWS ON FLORISTIC DIVERSITY

5.1 INTRODUCTION

A great deal of attention has been focused on the effect of direct consumption on the dynamics of vegetation communities, however, the influence of non-consumptive activities, such as burrowing, digging, trampling and the deposition of excreta, are now recognised as important drivers of vegetation structure and function within ecosystems (Kaczor & Hartnett, 1990; Dean & Milton, 1991a).

Burrowing mammals may significantly influence the faunal community of an ecosystem by creating structures which benefit themselves and other species (Reichman & Smith, 1990; Skinner & Smithers, 1990; Kinlaw, 1999). However, the impact of burrowing extends further than this and may have important consequences for the geomorphology, hydrology, soil and vegetation of an area (Kinlaw, 1999; Whitford & Kay, 1999). The creation of burrows facilitates water infiltration into the soil profile and generally this is enhanced as the density of burrows increases (Kinlaw, 1999; Whitford & Kay, 1999; Gabet *et al*., 2003). Burrowing animals also have the ability to shift enormous amounts of sediment, the evidence of which can, in some cases, be viewed from satellite images (Branch *et al*., 1996; Kinlaw, 1999; Eldridge & Myers, 2001). The soil that is deposited as mounds on the surface during burrow excavations may contain fragments of bedrock thus contributing to the weathering of the bedrock and consequently the promotion of soil formation (Gabet *et* *al*., 2003). The excavated soil is often different in texture and contains altered levels of nutrients, pH and moisture compared to the soil closer to the surface and when the mound patches erode the result is a mixing and redistribution of the soil and its properties (Reichman & Smith, 1990; Hansell, 1993; Kinlaw, 1999; Whitford & Kay, 1999; Schooley *et al*., 2000; Gabet *et al*., 2003; Eldridge, 2004).

Disturbances, such as burrowing and digging, which result in the development of local heterogeneity are important in arid and semi-arid ecosystems as the patches that are created promote biodiversity by facilitating the co-existence of vegetation species with different life history strategies, and different colonization and competitive capabilities (Kaczor & Hartnett, 1990; Dean & Milton, 1991b; Kinalw, 1999; Schooley *at al*., 2000; Eldridge, 2004). The impact of a particular disturbance at a landscape level will depend on a number of factors including its frequency, size, timing and intensity (Gibson, 1989). Low rates of disturbance are thought to favour competitive species (e.g. perennials), whereas high rates of disturbance may benefit colonizing species with high growth and dispersal rates (e.g. annuals) (Miller, 1982). The disturbance hypothesis predicts that at intermediate rates of disturbance, colonizing species may be out-competed and removed at a local scale through the establishment of competitively dominant species but will remain present at a landscape level (Miller, 1982).

The creation of small-scale disturbances or islands, generally less than 1 m^2 (Wiegand *et al*., 1997; Boeken & Shachak, 1998a; 1998b), is thought to have had profound impacts on the floral diversity of a number of ecosystems. This has been extensively documented in the literature in studies involving a variety of mammals, including American badgers (*Taxidea taxus*), European badgers, pocket gophers (*Geomys* *bursarius*), gopher tortoises, banner-tailed kangaroo rats (*Dipodomys spectabilis*) and alpine arctic foxes (*Alopex lagopus*) (Gibson, 1989; Kaczor & Hartnett, 1990; Neal & Roper, 1991; Andersen & Kay, 1999; Hermann *et al*., 2002; Eldridge, 2004; Bruun *et al*., 2005), which all create soil mounds at the entrance to their dens and burrows. Research has also documented the ecological role of southern African species such as the whistling rat and the Cape porcupine whose warrens and digging sites are recognised as important germination sites and are thus valuable in maintaining plant diversity (Dean & Milton, 1991a; 1991b; Bragg *et al*., 2005). The significant influence of aardvarks on the vegetation dynamics of arid and semi-arid areas has also been examined with the research focused primarily on the impact of their exploratory and feeding scratchings as sites for the accumulation of organic matter and germination (Dean & Milton, 1991b). Subsequent research has highlighted the inadvertent role of aardvarks as effective seed dispersal agents and the potential impact this has on the vegetation of semi-arid ecosystems (Milton & Dean, 2001). However, little attention has focused on the impact that their burrow mounds have on plant diversity and species richness. Although small-scale disturbances are considered beneficial in promoting biodiversity in many ecosystems, examples do exist when the opposite occurs. European rabbit (*Oryctolagus cuniculus*) warrens in Australian woodland cause patch formation that has negative effects on biodiversity and increases erosion (Eldridge & Myers, 2001).

The main objectives of this chapter are thus:

- To determine whether aardvark burrow mounds support a different community of plants compared to adjacent areas;
- To determine if aardvark burrow mounds promote floristic diversity and richness on a landscape level.

5.2 METHODS AND MATERIALS

5.2.1 Vegetation sampling

The 20 burrows that were randomly selected each season at the three sites for the small mammal trapping component were also used for the vegetation sampling. Paired reference plots were randomly located in areas approximately 5 m from the burrow mounds and were situated on the same slope, aspect and soil type as the burrow mounds (Gibson, 1989; Kaczor & Hartnett, 1990).

Burrow mounds were divided into three microtypes on the basis of successional age; active, recently abandoned and old (Kaczor & Hartnett, 1990). Mounds showing evidence of current disturbance and burrows with obvious signs of occupation (tracks, tail drag marks and flies at the entrance) were described as active (Kingdon, 1971; Skinner & Smithers, 1990; Platt *et al*., 2004). Burrows which were obviously not inhabited and did not show signs of fresh excavations but with mounds which had not been subjected to large amounts of erosion or crusting were classified as recently abandoned (Kaczor & Hartnett, 1990). Mounds displaying substantial amounts of erosion and containing a large covering of vegetation were categorized as old mounds (Kaczor & Hartnett, 1990).

A 1.5 m x 1.5 m quadrat was placed over each mound and each reference plot and each plant present was identified to species level where possible. The percentage cover of each species in the quadrat and the amount of bare earth was estimated visually (Gibson, 1989). A voucher specimen of each unidentifiable species was collected for later identification in the laboratory.

Species diversity for the mounds, reference plots and for the sites (mound and reference plot data combined at a reserve level) were calculated using the Shannon-Wiener index (H') function in PRIMER. Percentage cover of each plant species was used as a surrogate for the number of individuals when calculating the diversity scores. Pielou's index (J') was used as a measure of evenness (PRIMER 5.0).

5.2.2 Data Analysis

The data obtained from each season at each site (reserve) for the amount of bare earth in the quadrats were pooled for each mound type and control and analysed using a Kruskal-Wallis one-way ANOVA (Statistica 7.0), as the data were not normally distributed, even after transformation. A multiple comparison post hoc test was used to determine if any significant differences existed between the amount of bare earth on the different mound types and reference plots.

Kruskal-Wallis ANOVAs were also used analyse the data from each site in order to determine whether the average number of species contained on each plot differed between each of the burrow mound plot types and the references plots.

To test whether the burrow mounds (data for all of the three burrow mound types were pooled) increased the plant diversity at each site, non-parametric Wilcoxon matched paired t-tests were used. The species diversity of the burrow mounds was compared with the reference plots and the overall species diversity of the individual sites (burrows and reference plots combined) was compared with the values calculated for reference plots at each site. If the overall diversity of the site was greater than that calculated for the reference plots, the burrow mounds were deemed to have had a positive effect on plant diversity at that site. No seasonal analysis was conducted.

Plant species abundance data were Log (x + 1) transformed and the ANOSIM function in PRIMER 5.0 was used to detect differences in plant community composition data. Following this, SIMPER analysis was employed to determine which species were the most important in determining the dissimilarity between the communities, where a significant difference was detected.

5.3 RESULTS

Fourty-three plant species were recorded on the burrow mounds (all three burrow mound types combined) at Kwandwe compared to the 54 species recorded on the reference plots (Table 5.1). Six species which were recorded on the burrow mounds were not recorded on the reference plots. At MZNP 33 species were documented growing on the burrows, of which seven were found exclusively on the burrow mounds whilst 40 species were recorded on the reference plots (Table 5.2). Thirty-five species occurred on the burrow mounds at Tswalu in comparison with the 50 species on the reference plots. Five of the species recorded on the burrow mounds were not found on the reference plots (Table 5.3). The forb/herb growth form contributed the greatest number of species on the burrow mounds (all three burrow mound types combined) and on the reference plots at all three sites. The contribution of the other growth forms to species richness varied amongst the sites and between the burrow mounds and the reference plots. The geophytes were the only growth form absent from the burrow mound types at all the sites, whilst no succulent species were recorded either on the mounds or on the reference plots at Tswalu (Table 5.4).

Species diversity scores were higher for the reference plots than for the mounds at Kwandwe ($z = 0.78$, $N = 80$, $p > 0.05$), MZNP ($z = 0.16$, $N = 80$, $p > 0.05$) and Tswalu ($z = 1.72$, $N = 80$, $p > 0.05$) but none of the results were significant. Total species diversity values (data for burrow mounds and reference plots combined) were higher than the reference the sites at Kwandwe (z = 1.66, N = 80, p > 0.05) and Tswalu (z = 1.82, N = 80, p > 0.05) but not at MZNP (z = 0.21, N = 80, p > 0.05) (Table 5.5). Evenness values for the burrow mounds and reference plots were generally high with the exception of the reference plots during Spring at Kwandwe and during autumn and summer at MZNP where there was an overwhelming dominance of *Panicum maximum Pentzia globosa* and *Cynodon incompletus* respectively.

There was a significant effect of plot type on the average number of species recorded per quadrat at Kwandwe (H = 21.3109, N = 160, p < 0.001), MZNP (H = 22.9305, N = 160, p < 0.001) and Tswalu (H = 53.5034, N = 160, p < 0.001). Post-hoc pairwise comparisons revealed no differences between active burrow mounds and recently abandoned burrow mounds at any of the sites, however reference plots contained significantly more species per quadrat than recently abandoned burrow mounds at all three sites (Table 5.6). Active burrow mounds (3 species ± 0.9) were not significantly different from any of the other plot types at MZNP but active burrow mounds were significantly different from old burrow mounds at Kwandwe and Tswalu (Table 5.6).

Plant community similarity values within plot types were generally low at all the sites during all four seasons and zero similarity existed between the active burrow mound plots in both winter and spring at Tswalu. Contrary to this, the active burrow mound plots exhibited 100 % similarity at that site in autumn.

Despite the low R-values, overall, the different plot types were characterised by significantly different communities during all the seasons at MZNP (autumn R =

0.153, $p < 0.05$; winter R = 0.177, $p < 0.01$; spring R = 0.162, $p < 0.05$; summer R = 0.284, $p < 0.01$), during three of the seasons at Kwandwe (autumn R = 0.132, $p < 0.05$; winter R = 0.194, $p < 0.01$; spring R = 0.169, $p < 0.05$; summer R = 0.017, $p > 0.05$) and during winter only at Tswalu (autumn R = 0.033, $p > 0.05$; winter R = 0.199, $p < 0.05$; spring R = 0.065, $p > 0.05$; summer R = - 0.154, $p > 0.05$). Following the similarity calculations the pairwise comparison at Kwandwe revealed significant differences in community composition between the active burrow mounds and the old burrow mounds (R = 0.64, average dissimilarity = 94.72 %, $p < 0.05$) and between active and the reference plots (R = 0.539, average dissimilarity = 100 %, $p < 0.05$) during autumn. Significant differences were also recorded between recently abandoned burrow mounds and the old burrow mounds (R = 0.211, average dissimilarity = 82.84 %, $p < 0.05$) as well as between the recently abandoned burrow mounds and the reference plots (R = 0.164, average dissimilarity = 85.59 %, $p < 0.05$) in autumn. During winter at Kwandwe the only two differences occurred between the reference plots and the recently abandoned burrows (R = 0.222, average dissimilarity = 83.57 %, $p < 0.05$) as well as between the reference plots and the old burrow mounds (R = 0.323, average dissimilarity = 83.74 %, $p < 0.05$). In spring the only significant difference was detected between the active burrow mounds and the reference plots (R = 0.254, average dissimilarity = 83.82 %, $p < 0.05$). No significant differences were detected between the different mound types and references plots during summer at Kwandwe.

At MZNP during autumn, significant differences in community structure were calculated between the reference plots and the active burrow mounds (R = 0.501, average dissimilarity = 83.11%, $p < 0.05$) as well as the old burrow mounds (R = 0.121, average dissimilarity = 70.73 %, $p < 0.05$). During winter and spring differences occurred between the reference plots and active burrow mounds (winter R = 0.184, average dissimilarity = 81.58 %, $p < 0.05$; spring R = 0.367, average dissimilarity = 79.60 %, $p < 0.05$) as well as between the reference plots and recently abandoned burrow mounds (winter R = 0.27, average dissimilarity = 86.06 %, $p < 0.05$; spring R = 0.159, average dissimilarity = 75.03 %, $p < 0.05$). In summer differences occurred between the recently abandoned burrow mounds and the old mounds (R = 0.314, average dissimilarity = 85.72 %, $p < 0.05$) as well as the reference plots (R = 0.478, average dissimilarity = 79.23 %, $p < 0.05$). A significant difference also existed between the old burrow mounds and the reference plots (R = 0.334, average dissimilarity = 78.97 %, $p < 0.05$).

At Tswalu pairwise comparisons yielded significant differences between the reference plots and active burrow mounds (R = 0.476, average dissimilarity = 92.95 %, $p < 0.05$) as well as the recently abandoned burrow mounds in winter (R = 0.176, average dissimilarity = 85.19 %, $p < 0.05$) and between the active burrow mounds and reference plots in spring (R = 0.351, average dissimilarity = 93.20 %, $p < 0.05$).

In all instances where ANOSIM revealed significant differences between community compositions at Kwandwe, SIMPER analysis demonstrated the important contribution of four grass species, *Digitaria eriantha*, *Setaria neglecta*, *Eragrostis lehmanniana* and *Panicum maximum* (Tables 5.8 – 5.14). These species were particularly abundant on the old mounds and in the reference plots but were comparatively scarce on the active and recently abandoned burrow mounds and thus contributed substantially to the dissimilarity between the plot types during all the seasons. For instance, in autumn *Setaria neglecta* and *Digitaria eriantha* alone contributed to 60 % of the dissimilarity between the active burrow mounds and the old burrow mounds. Occasionally, for example autumn, the grass species *Cynodon dactylon* was more common on active and recently abandoned burrow mounds than on the old mounds or on the reference plots (Tables 5.10 and 5.11). The abundance of *Digitaria eriantha* and *Panicum maximum* on the reference plots and the greater presence of species such as *Syncolostemon densiflorus*, *Galenia* sp., *Alzoon* sp., *Malephora* sp. and *Cuspidia cernua* on the old burrow mounds were responsible for the differences which existed between those two plot types at Kwandwe during the winter. The greater abundance of *Argemone ochroleuca* on the active mounds together with the usual abundance of the four dominant grass species on the reference plots were the main contributors to the dissimilarity which occurred between those two plot types in Spring (Table 5.14).

The dominance of *Pentzia globosa* along with *Eragrostis obtusa*, *Cynodon incompletus* and *Drosanthemum hispidum* on the reference plots was the main cause of dissimilarity between the reference plots and the other plots at MZNP, particularly the active and recently abandoned burrow mounds (Tables 5.15-5.23). The exception was winter when *Pentzia globosa* was more abundant on the active burrow mounds than on the reference plots (Table 5.17). The only other species which were regularly more abundant on the active and recently abandoned burrow mounds compared to the reference plots were *Salsola kali* and the *Alzoon* sp (Tables 5.17-5.19 & 5.21). The abundance of *Eragrostis lehmanniana*, *Aristida meridionalis* and *Stipagrostis uniplumis* in the reference plots and the greater presence of *Ceropegia* sp., *Dicerocaryum ericocarpum* and *Hermannia burchellii* on the active mounds resulted in over 50 % of the dissimilarity between those two burrow types at Tswalu during winter (Table 5.24). The presence of dominant grass species in the reference plots together with the presence of *Senna italica*, *Schmidtia kalihariensis* and *Hermannia burchellii* on the recently abandoned mounds were the most significant contributors to the dissimilarity between those communities at Tswalu during winter (Table 5.25). The difference between the active burrow mounds and the reference plots at Tswalu during spring can be predominantly attributed to the greater amount of *Aristida meridionalis*, *Tribulus zeyheri*, *Senna italica* and *Harpagophytum procumbens* in the reference plots (Table 5.26).

The Kruskal-Wallis ANOVAs revealed significant differences at all three sites (Kwandwe $H = 73.8364$, $N = 160$, $p < 0.001$; MZNP $H = 72.3575$, $N = 160$, $p < 0.001$; Tswalu $H = 79.0726$, $N = 160$, $p < 0.001$) with regards to the amount of bare earth recorded on the different plot types. The amount of bare earth was significantly higher on active and recently abandoned burrow mounds compared to the old burrow mounds and reference plots at all three sites ($p < 0.05$ for all) with the exception of Tswalu where active mounds did not contain more bare ground than old burrow mounds ($p > 0.05$). No difference was recorded between the active mounds and recently abandoned burrow mounds at any of the sites ($p > 0.05$ for all). Old burrow burrow mounds contained significantly less vegetative cover than the reference areas at MZNP ($p < 0.05$) and Tswalu ($p < 0.001$) but not at Kwandwe ($p > 0.05$).

5.4 DISCUSSION

The colonization of open plots of vegetation as a result of disturbance has been equated with the colonization of islands as both involve similar phases of succession whereby species composition is altered as dominant species are recruited and begin to out-compete the pioneers species (Platt, 1975). Research conducted on the North American prairies suggests that the colonization of disturbed plots may take approximately two to three years with the plots usually remaining empty until the spring proceeding the disturbance (Platt, 1975). Eldridge & Myers (2001) recorded significantly more bare ground around the warrens of the European rabbit than in paired control sites, whilst Kaczor & Hartnett (1990) found significantly lower plant cover on recently abandoned gopher tortoise burrow mounds compared to undisturbed plots. Therefore, the significant difference between the amount of bare earth present on active and recently abandoned aardvark burrow mounds compared with the reference plots during this study was not unexpected. More surprising, however, was the significantly higher amount of bare earth on old burrow mounds compared to the reference sites at MZNP and Tswalu. This contradicted the findings of Kaczor & Hartnett (1990) who recorded an intermediate covering of vegetation on old burrow mounds which did not differ significantly from either the recently abandoned burrows or reference plots. The initial creation of aardvark burrows is likely to result in all but the largest and most durable plant species being covered by the excavated soil, and it is unlikely that the plant cover will increase rapidly following the soil deposition, particularly if the disturbance did not take place in a growing season (Platt, 1975), unless partially covered plants emerge from the soil. Bruun *et al*. (2005) did not find evidence to suggest that the length of time since the burrow was last inhabited affected the vegetation on artic fox burrows. It is possible that the regular use of abandoned aardvark burrows by other vertebrate species may result in increased trampling of the burrow mound thus inhibiting initial plant colonization and consequently affecting the establishment of plant cover even on old burrow mounds. However, the plant communities which are commonly present at the entrance of European badger setts are thought to be able to withstand regular disturbance (Neal & Roper, 1991).

A further point of congruence between this research and that conducted by Kaczor & Hartnett (1990) was the greater total species richness of the reference plots compared to the burrow mounds although they did emphasize that their results may have been exaggerated as a result of the sampled area in the reference sites being substantially larger than that sampled for the burrow mounds. Higher species richness on reference plots was also observed in comparisons with den sites belonging to arctic foxes (Bruun *et al.*, 2005). However, Kaczor & Hartnett (1990) encountered a higher number of species per 1 m^2 on the old mounds than on either the recently abandoned burrow mounds or indeed the reference plots. This was attributed to the intermediate successional stage of the old mounds which resulted from equilibrium being attained between annual colonizers and later successional herbs or perennial plants. This trend was only observed at Kwandwe during this research and even though the average species richness of the burrow mound types increased with successional age (i.e. species richness was lowest on active burrow mounds, and highest on old burrow mounds) at Tswalu, the reference plots contained the most species. Surprisingly, the active burrow mounds at MZNP contained a higher average number of species per mound than the recently abandoned burrows but this may have been an artefact of some of the larger plant species on the active mounds (e.g. *Pentzia globosa* and *Schotia afra*) not being completely covered by the initial soil deposition during burrow excavation (pers. obs.).

At all three sites, as was the case in other studies (Kaczor & Hartnett, 1990; Bruun *et al.*, 2005), certain species were recorded growing exclusively on aardvark burrow mounds and were absent from the reference plots. These results, however, must be interpreted with care as tree species such as *Azima tetracantha* and *Acacia karroo* were found on the burrow mounds at Kwandwe but were absent from the reference plots at that site. These two species are not restricted to growing on burrow mounds (pers. obs.) and it is very likely that the results were merely an anomaly of the sampling. Other species such as *Argemone ochroleuca*, a category one invasive weed, (Henderson, 2001) were recorded exclusively on burrow mounds at MZNP, yet occurred on the mounds and on the reference plots at Kwandwe. Further examples of this phenomenon include *Acanthosicyos naudinianus* and *Cucumis zeyheri* which were encountered on the burrow mounds at MZNP but were observed on both the burrow mounds and reference plots at Tswalu. *Atriplex semibaccata* was only found on the burrow mounds at Kwandwe but was observed on both the mounds and reference plots at MZNP.

Disturbance is thought to play and important role in facilitating the invasion of exotic weeds (Hobbs & Huenneke, 1992) and thus it was not unexpected that species such as *Argemone ochroleuca*, *Atriplex lindleyi* and *Salsola kali* were documented colonising the denuded soil at the burrow entrances. However, the reference sites were not devoid of alien weeds either. In fact, *Atriplex lindleyi* was a prominent component of the plant community on the reference plots at Kwandwe in winter whilst large tracts of *Salsola kali* and *Solanum sysimbrifolium* were observed in areas adjacent to the study sites at Tswalu and MZNP (pers. obs.). The large presence of weedy invaders on the reference sites at all the reserves suggests that these areas have been subjected to substantial disturbance. This may have contributed to the unexpected differences in community structure observed between the old burrow mound plot types, which are not as prone to weed invasion as the earlier successional stages, and the reference plots. In addition, the lack of difference between active or recently abandoned burrow mounds and the reference plots in some instances may also have been influenced by the abundance of these invasive weeds on the reference plots. The relatively high abundance of *Drosanthemum hispidum* and *Malephora* sp. on the reference plots at both Kwandwe and MZNP together with the substantial presence of *Eragrostis obtusa* and *Cynodon incompletus* (pioneer/sub-climax grass species) on the reference plots at MZNP is indicative of disturbance as these species are common components of early successional communities on old lands and road verges (Dean & Milton, 1995; van Oudtshoorn, 2002; O'Farrell & Milton, 2006). The disturbed nature of some of the reference plots may be attributed to a combination of the recent land-use practices of the study sites as well as current trampling and grazing by ungulate species and the creation of foraging pits by mammals such as Cape porcupines and aardvarks (Dean & Milton, 1991a; 1991b; 1995). Despite the presence of disturbance species, there was also a greater abundance of climax and sub-climax grass species for example *Eragrostis lehmanniana*, *Aristida meridionalis* and *Stipagrostis uniplumis* on the reference plots at Tswalu and *Digitaria eriantha*, *Setaria neglecta*, *Eragrostis lehmanniana* and *Panicum maximum* on the reference plots at Kwandwe compared to even the old burrow mounds, suggesting that the reference plots are generally in a later successional phase and closer to a climax community than any of the burrow mound plot types including the old mounds. However, the very small similarity values calculated for most of the burrow and reference plot types during all the seasons at all three sites suggests that there is considerable variation within communities occurring on the burrow mounds and on the adjacent "undisturbed" sites. In most instances the global statistic (R) was also low and thus the likelihood exists that there is a certain amount of overlap between the burrow plot communities and those on the reference plots. Further evidence to support this is that the majority of species found on burrow mounds were also encountered off the mounds, probably on areas subjected to disturbance as was observed during the study on the arctic fox dens (Bruun *et al*., 1995). Furthermore, the superior contribution of one growth form, the forbs/herbs, to the species richness of both the burrow mounds and the reference plots at all sites may also hint at possible community overlap. Eldridge and Myers

(2001) also noted large similarities in the plant community at the entrance of rabbit warrens compared to adjacent control sites.

In conclusion, despite the lack of significant numbers of species unique to burrow mounds and the lower species richness and diversity on the burrow mounds compared to the reference plots at all the sites, on a landscape level the presence of burrow mounds may increase floristic diversity as was evident at Kwandwe and Tswalu where combined species diversity of the burrow mounds and "undisturbed" reference plots was higher than that for the reference sites on their own. It is therefore concluded that aardvark burrows promote heterogeneity in the landscape and ultimately have the potential to promote floristic diversity in arid and semi-arid environments, although in some cases these benefits may be diminished by their facilitation of weed invasion.

5.5 TABLES AND FIGURES

Table 5.1: Species, family and growth form of plants present on burrow mounds and on reference plots at Kwandwe (Table continue overleaf).

Species	Family	Growth form	Present on burrow mound	Present on reference plots
Acacia karroo	Fabaceae	Tree	Yes	No
Alzoon sp.	Cupressaceae	Forb/herb	Yes	Yes
Aregemone ochroleuca	Papaveraceae	Forb/herb	Yes	Yes
Asparagus africanus	Asparagaceae	Forb/herb	Yes	Yes
Atriplex lindleyi	Chenopodiaceae	Forb/herb	Yes	Yes
Atriplex semibaccata	Chenopodiaceae	Forb/herb	Yes	No
Azima tetracantha	Salvadoraceae	Tree	Yes	No
Cadaba aphylla	Brassicaceae	Forb/herb	No	Yes
Cenchrus ciliaris	Poaceae	Grass	Yes	Yes
Ceropegia africana	Asclepiadaceae	Forb/herb	Yes	Yes
Cuspidia cernua	Asteraceae	Forb/herb	Yes	Yes
Cymbogon plurinodis	Poaceae	Grass	No	Yes
Cynodon dactylon	Poaceae	Grass	Yes	Yes
Digitaria eriantha	Poaceae	Grass	Yes	Yes
Drosanthemum hispidum	Mesembryanthemaceae	Succulent	Yes	Yes
Enneapogon scoparius	Poaceae	Grass	No	Yes
Eragrostis chloromelas	Poaceae	Grass	Yes	No
Eragrostis lehmanniana	Poaceae	Grass	Yes	Yes
Eragrostis obtusa	Poaceae	Grass	Yes	Yes
Ehrharta calycina	Poaceae	Grass	No	Yes
Euphorbia bothae	Euphorbiaceae	Shrub	No	Yes
Euryops chrysanthemoides	Poaceae	Grass	Yes	No
Eustachys paspaloides	Poaceae	Grass	Yes	Yes
Falkia repens	Convolvulaceae	Forb/herb	No	Yes
Galenia sp.	Aizoaceae	Forb/herb	Yes	Yes
Gnidia capitata	Thymelaeaceae	Forb/herb	Yes	Yes
Grewia occidentalis	Malvaceae	Shrub	No	Yes
Grewia robusta	Malvaceae	Shrub	No	Yes
Helichrysum cymosum	Asteraceae	Forb/herb	Yes	Yes
Hermannia incana	Malvaceae	Forb/herb	Yes	Yes
Hypoestes forskaoli	Acanthaceae	Shrub	No	Yes
Indigofera alternans	Fabaceae	Forb/herb	Yes	Yes
Lepidium africanum	Brassicaceae	Forb/herb	Yes	Yes
Lobelia tomentosa	Campanulaceae	Forb/herb	Yes	Yes
Lycium ferocissimum	Solanaceae	Shrub	Yes	Yes
Lycium oxycarpum	Solanaceae	Shrub	Yes	Yes
Malephora crocea	Mesembryanthemaceae	Succulent	Yes	Yes
Maytenus capitata	Celastraceae	Tree	No	Yes
Mesembryanthemum crustalinum	Mesembryanthemaceae	Succulent	Yes	Yes
Moraea polystachya	Iridaceae	Forb/herb	No	Yes

Opuntia aurantiaca	Cactaceae	Shrub	Yes	Yes
Pachypodium bispinosum	Apocynaceae	Shrub	No	Yes
Panicum maximum	Poaceae	Grass	Yes	Yes
Pelargonium aridum	Geraniaceae	Shrub	Yes	Yes
Pentzia incana	Asteraceae	Shrub	Yes	Yes
Plumbago auriculata	Plumbaginaceae	Shrub	Yes	Yes
Psilocaulon sp.	Mesembryanthemaceae	Succulent	Yes	Yes
Rhus lancea	Anacardiaceae	Tree	No	Yes
Ruschia sp.	Mesembryanthemaceae	Succulent	No	Yes
Salsola aphylla	Chenopodiaceae	Shrub	Yes	Yes
Salsola kali	Chenopodiaceae	Forb/herb	No	Yes
Senecio radicans	Asteraceae	Shrub	Yes	Yes
Setaria neglecta	Poaceae	Grass	Yes	Yes
Spilanthes sp.	Asteraceae	Shrub	Yes	No
Syncolostemon densiflorus	Lamiaceae	Shrub	Yes	Yes
Teucrium trifidum	Lamiaceae	Forb/herb	Yes	Yes
Thunbergia capensis	Acanthaceae	Shrub	No	Yes
Tragus berteronianus	Poaceae	Grass	Yes	Yes
Tribulus terrestris	Zygophyllaceae	Forb/herb	Yes	Yes

Table 5.2: Species, family and growth form of plants present on burrow mounds and on reference plots at MZNP (Table continues overleaf).

Species	Family	Growth form	Present on burrow mound	Present on reference plots
Acanthosicyos naudinianus	Cucurbitaceae	Forb/herb	Yes	No
Acacia karroo	Fabaceae	Tree	No	Yes
Alzoon sp.	Cupressaceae	Forb/herb	Yes	Yes
Ammocharis coranica	Amaryllidaceae	Geophyte	No	Yes
Argemone ochroleuca	Papaveraceae	Forb/herb	Yes	No
Aristida congesta	Poaceae	Grass	Yes	Yes
Asparagus sp.	Asparagaceae	Forb/herb	Yes	Yes
Atriplex lindleyi	Chenopodiaceae	Forb/herb	Yes	Yes
Atriplex semibaccata	Chenopodiaceae	Forb/herb	Yes	Yes
Berkheya decurrens	Asteraceae	Shrub	Yes	No
Chrysocoma ciliata	Asteraceae	Shrub	Yes	Yes
Crassula sp.	Crassulaceae	Succulent	No	Yes
Cucumis zeyheri	Cucurbitaceae	Forb/herb	Yes	No
Cuspidia cernua	Asteraceae	Forb/herb	Yes	Yes
Cynodon incompletus	Poaceae	Grass	Yes	Yes
Drosanthemum hispidum	Mesembryanthemaceae	Suculent	Yes	Yes
Elionurus muticus	Poaceae	Grass	No	Yes
Eragrostis lehmanniana	Poaceae	Grass	No	Yes
Eragrostis obtusa	Poaceae	Grass	Yes	Yes
Eragrostis rigidor	Poaceae	Grass	No	Yes
Ericocephalus ericoides	Asteraceae	Shrub	Yes	Yes
Galenia sarcophylla	Aizoaceae	Forb/herb	Yes	Yes
Helichrysum agyrophyllum.	Asteraceae	Forb/herb	Yes	Yes
Helichrysum umbraculigerum	Asteraceae	Forb/herb	Yes	Yes
Hermannia sp.	Malvaceae	Forb/herb	No	Yes
Imperata cylindrica	Poaceae	Grass	No	Yes
Lepidium africanum	Brassicaceae	Forb/herb	Yes	Yes
Lobelia neglecta	Campanulaceae	Forb/herb	Yes	Yes
Lycium cinerium	Solanaceae	Shrub	Yes	Yes
Malephora crocea	Mesembryanthemaceae	Succulent	Yes	Yes
Mesembryanthemum aitonis	Mesembryanthemaceae	Succulent	Yes	Yes
Mesembryanthemum crustalinum	Mesembryanthemaceae	Succulent	No	Yes
Opuntia aurantiaca	Cactaceae	Shrub	Yes	Yes
Passerina obtusifolia	Thymelaeaceae	Shrub	No	Yes
Pentzia globosa	Asteraceae	Shrub	Yes	Yes
Psilocaulon junceum	Mesembryanthemaceae	Succulent	Yes	Yes
Ruschia crodockensis	Mesembryanthemaceae	Succulent	No	Yes
Salsola aphylla	Chenopodiaceae	Shrub	Yes	Yes
Salsola kali	Chenopodiaceae	Forb/herb	Yes	Yes
Schotia afra	Fabaceae	Tree	Yes	No
Setaria sphacelata	Poaceae	Grass	Yes	No
Setaria verticillata	Poaceae	Grass	Yes	No

Solanum sysimbrifolium	Solanaceae	Shrub	No	Yes
Talinum caffrum	Portulacaceae	Shrub	Yes	Yes
Thesium lineatum	Santalaceae	Forb/herb	No	Yes
Tragus koelerioides	Poaceae	Grass	Yes	Yes
Tribulus zeyheri	Zygophyllaceae	Forb/herb	No	Yes

Table 5.3: Species, family and growth form of plants present on burrow mounds and on reference plots at Tswalu. (Table continues overleaf)

Species	Family	Growth form	Present on burrow mound	Present on reference plots
Acacia mellifera	Fabaceae	Tree	No	Yes
Acanthosicyos naudinianus	Cucurbitaceae	Forb/herb	Yes	Yes
Aerva leucura	Amaranthaceae	Forb/herb	No	Yes
Ammocharis coranica	Amaryllidaceae	Geophyte	No	Yes
Anthephora pubescens	Poaceae	Grass	Yes	Yes
Aptosimun marlothii	Scrophulariaceae	Forb/herb	Yes	No
Aristida congesta	Poaceae	Grass	Yes	No
Aristida meridionalis	Poaceae	Grass	Yes	Yes
Aristida stipitata	Poaceae	Grass	Yes	Yes
Asparagus africanus	Asparagaceae	Forb/herb	Yes	Yes
Asparagus sauveolens	Asparagaceae	Forb/herb	Yes	Yes
Cenchrus ciliaris	Poaceae	Grass	Yes	Yes
Centropodia glauca	Poaceae	Grass	Yes	Yes
Ceropegia sp.	Asclepiadaceae	Forb/herb	Yes	Yes
Citrullus lanatus	Cucurbitaceae	Forb/herb	No	Yes
Crotalaria orientalis	Fabaceae	Shrub	No	Yes
Cucumis zeyheri	Cucurbitaceae	Forb/herb	Yes	Yes
Dicerocaryum eriocarpum	Pedaliaceae	Forb/herb	Yes	Yes
Ehrharta sp.	Poaceae	Grass	No	Yes
Elephantorrhiza elephantina	Fabaceae	Shrub	No	Yes
Eragrostis lehmanniana	Poaceae	Grass	Yes	Yes
Eragrostis pallens	Poaceae	Grass	No	Yes
Eragrostis rigidor	Poaceae	Grass	Yes	Yes
Ericocephalus ericoides	Asteraceae	Shrub	Yes	Yes
Gnidia polycephala	Thymelaeaceae	Forb/herb	No	Yes
Grewia flava	Fabaceae	Shrub	Yes	No
Harpagophytum procumbens	Pedaliaceae	Forb/herb	Yes	Yes
Hermannia burchelli	Malvaceae	Forb/herb	Yes	Yes
Hermannia tomentosa	Malvaceae	Forb/herb	Yes	Yes
Ipomoea bolusiana	Convolvulaceae	Forb/herb	No	Yes
Indigofera alternans	Fabaceae	Forb/herb	Yes	Yes
Indigofera flavicans	Fabaceae	Shrub	No	Yes
Leonotis leonurus	Lamiaceae	Forb/herb	No	Yes
Limeum fenestratum	Molluginaceae	Forb/herb	Yes	Yes
Lycium boscifolium	Solanaceae	Shrub	No	Yes

Lycium viscosum	Solanaceae	Shrub	Yes	No
Melinis repens	Poaceae	Grass	Yes	Yes
Monechma incanum	Acanthaceae	Forb/herb	No	Yes
Panicum maximum	Poaceae	Grass	Yes	Yes
Pentzia globosa	Asteraceae	Shrub	Yes	Yes
Plinthus sericeus	Aizoaceae	Shrub	No	Yes
Pteronia sp.	Asteraceae	Shrub	No	Yes
Rhigozum trichotonum	Bignoniaceae	Shrub	Yes	Yes
Rhynchosia venulosa	Fabaceae	Forb/herb	Yes	Yes
Salsola kali	Chenopodiaceae	Forb/herb	No	Yes
Schmidtia kalihariensis	Poaceae	Grass	Yes	Yes
Schmidtia pappophoroides	Poaceae	Grass	Yes	Yes
Schotia afra	Fabaceae	Tree	No	Yes
Senna italica	Fabaceae	Forb/herb	Yes	Yes
Sesamum indicum	Pedaliaceae	Forb/herb	No	Yes
Solanum linnaeanum	Solanaceae	Shrub	Yes	No
Solanum sysimbrifolium	Solanaceae	Shrub	No	Yes
Stipagrostis uniplumis	Poaceae	Grass	Yes	Yes
Tribulus zeyheri	Zygophyllaceae	Forb/herb	Yes	Yes
Xenostegia tridentata	Dennstaedtiaceae	Forb/herb	Yes	Yes

Table 5.4: Percentage contribution of each plant growth form to the total number of species present on the burrow mounds (data for all three mound types combined) and on the reference plots. All seasonal data was pooled.

Growth form	Kwandwe		MZNP		Tswalu	
	Burrow mounds	Reference plots	Burrow mounds	Reference plots	Burrow mounds	Reference plots
Trees	2.3 %	3.7 %	3.0 %	2.5 %	0 %	4.0 %
Shrubs	23.3 %	27.8 %	24.3 %	22.5 %	17.1 %	20.0 %
Forb/herbs	39.5 %	35.2 %	42.4 %	35.0 %	45.7 %	46.0 %
Succulents	25.6 %	9.25 %	12.1 %	17.5 %	0 %	0 %
Grasses	9.3 %	22.2 %	18.2 %	20.0 %	37.2 %	28.0 %
Geophytes	0 %	1.8 %	0 %	2.5 %	0 %	2.0 %

Table 5.5: Species richness, diversity and evenness scores for vegetation recorded each season on the burrow mounds, reference plots and the total for the site as a whole (vegetation on all mound types and reference plots combined).

Site	Season	Position	Species richness	Species diversity H’	Evenness J’
Kwandwe	Autumn	Total	24	2.06	0.64
		Burrow	8	1.50	0.72
		Reference	23	2.13	0.68
	Winter	Total	24	2.61	0.82
		Burrow	20	2.73	0.91
		Reference	21	2.29	0.75
	Spring	Total	24	1.91	0.60
		Burrow	21	2.23	0.73
		Reference	17	1.50	0.53
	Summer	Total	22	2.21	0.71
		Burrow	18	2.28	0.78
		Reference	21	1.96	0.64
MZNP	Autumn	Total	33	1.67	0.47
		Burrow	8	1.50	0.72
		Reference	31	2.40	0.70
	Winter	Total	21	2.61	0.85
		Burrow	15	2.46	0.91
		Reference	19	2.50	0.84
	Spring	Total	24	2.46	0.77
		Burrow	17	2.54	0.89
		Reference	22	2.29	0.74
	Summer	Total	26	2.31	0.71
		Burrow	15	2.48	0.91
		Reference	23	1.99	0.63
Tswalu	Autumn	Total	34	2.76	0.78
		Burrow	18	2.40	0.83
		Reference	27	2.70	0.81
	Winter	Total	29	2.63	0.78
		Burrow	12	2.32	0.93
		Reference	26	2.53	0.77
	Spring	Total	23	2.62	0.83
		Burrow	13	2.25	0.87
		Reference	18	2.46	0.85
	Summer	Total	22	2.73	0.88
		Burrow	14	2.44	0.92
		Reference	22	2.63	0.85

Table 5.6: Significant differences between plot types with regards to the average number of species recorded in each quadrat (n = 80). Active = Active burrow mound plot, Recent = Recently abandoned burrow mound plot, Old = Old burrow mound plot and Ref = Reference plot. * = p < 0.05, ** = p < 0.01, *** = p < 0.001.

Site	Plot type	Number of species ± 1 SD in each plot type	P-value
Kwandwe	Active and old	2.4 ± 1.2 and 3.9 ± 1.5	*
	Recent and old	2.2 ± 1.4 and 3.9 ± 1.5	**
	Recent and ref.	2.2 ± 1.4 and 3.4 ± 1.8	**
MZNP	Ref and recent	4.1 ± 1.8 and 2.8 ± 1.3	**
	Ref and old	4.1 ± 1.8 and 3.1 ± 2.2	***
Tswalu	Active and old	1.1 ± 1.1 and 2.9 ± 1.2	**
	Active and ref	1.1 ± 1.1 and 3.9 ± 1.8	**
	Recent and ref	1.9 ± 0.7 and 3.9 ± 1.8	***

Table 5.7: SIMPER analysis breakdown of similarity between plant communities within the different plot types each season at Kwandwe (A), MZNP (B) and Tswalu (C). N/A = not applicable as the plot type contained less than two quadrats with vegetation.

A

Season	Plot type	Similarity
Autumn	Active	5.03
	Recent	14.47
	Old	36.97
	Reference	18.34
Winter	Active	15.85
	Recent	9.29
	Old	30.89
	Reference	27.69
Spring	Active	13.39
	Recent	27.02
	Old	24.40
	Reference	32.83
Summer	Active	18.11
	Recent	32.08
	Old	23.24
	Reference	19.76

B

Season	Plot type	Similarity
Autumn	Active	46.10
	Recent	36.73
	Old	30.95
	Reference	37.09
Winter	Active	50.00
	Recent	8.57
	Old	15.63
	Reference	25.82
Spring	Active	25.64
	Recent	18.83
	Old	29.14
	Reference	32.60
Summer	Active	31.14
	Recent	36.04
	Old	23.70
	Reference	35.28

C

Season	Plot type	Similarity
Autumn	Active	100.00
	Recent	29.29
	Old	17.59
	Reference	22.64
Winter	Active	0.00
	Recent	N/A
	Old	20.76
	Reference	24.23
Spring	Active	0.00
	Recent	23.33
	Old	17.74
	Reference	15.74
Summer	Active	5.56
	Recent	24.76
	Old	18.03
	Reference	16.01

Table 5.8: SIMPER analysis breakdown of average dissimilarity between active burrow mounds and old burrow mounds into contributions from the seven most influential species at Kwandwe during autumn. Percentage cover was used as a surrogate for abundance.

Species	Average abundance on active burrow mounds	Average abundance on old burrow mounds	Average dissimilarity	Contribution %	Cumulative contribution
Setaria neglecta	0.00	12.22	29.93	31.60	31.60
Digitaria eriantha	0.00	23.33	27.64	29.18	60.78
Euryops chrysanthemoides	2.50	1.67	14.11	14.90	75.68
Eragrostis lehmanniana	0.00	5.00	11.24	11.87	87.55
Atriplex lindleyi	0.00	1.11	4.05	4.27	91.82
Teucreum trifidum	0.00	1.11	4.05	4.27	96.10
Lepidium africanum	0.00	1.11	3.70	3.90	100.00

Table 5.9: SIMPER analysis breakdown of average dissimilarity between active burrow mounds and reference plots into contributions from the 10 most influential species at Kwandwe during autumn. Percentage cover was used as a surrogate for abundance.

Species	Average abundance on active burrow mounds	Average abundance on reference plots	Average dissimilarity	Contribution %	Cumulative contribution
Digitaria eriantha	0.00	28.33	18.18	18.18	18.18
Setaria neglecta	0.00	5.00	10.33	10.33	28.51
Euryops chrysanthemoides	2.50	0.00	9.75	9.75	38.26
Eragrostis lehmanniana	0.00	6.11	9.69	9.69	47.95
Pentzia incana	0.00	1.39	8.54	8.54	56.48
Malephora sp.	0.00	1.94	5.42	5.42	61.91
Eragrostis obtusa	0.00	1.39	3.52	3.52	65.42
Lepidium africanum	0.00	0.83	3.40	3.40	68.82
Maytenus capitata	0.00	0.56	2.55	2.55	71.37
Ehrharta calycina	0.00	2.78	2.36	2.36	73.73

Table 5.10: SIMPER analysis breakdown of average dissimilarity between recently abandoned burrow mounds and old burrow mounds into contributions from the eight most influential species at Kwandwe during autumn. Percentage cover was used as a surrogate for abundance.

Species	Average abundance on recently abandoned burrow mounds	Average abundance on old burrow mounds	Average dissimilarity	Contribution %	Cumulative contribution
Setaria neglecta	0.00	12.22	23.20	28.01	28.01
Digitaria eriantha	2.14	23.33	21.41	25.85	53.86
Eragrostis lehmanniana	3.57	5.00	13.95	16.84	70.69
Euryops chrysanthemoides	0.71	1.67	7.78	9.39	80.08
Lepidium africanum	0.71	1.11	4.94	5.97	86.05
Cynodon dactylon	2.14	0.00	4.59	5.54	91.58
Atriplex lindleyi	0.00	1.11	3.49	4.21	95.79
Teucreum trifidum	0.00	1.11	3.49	4.21	100.00

Table 5.11: SIMPER analysis breakdown of average dissimilarity between recently abandoned burrow mounds and reference plots into contributions from the 10 most influential species at Kwandwe during autumn. Percentage cover was used as a surrogate for abundance.

Species	Average abundance on recently abandoned burrow mounds	Average abundance on reference plots	Average dissimilarity	Contribution %	Cumulative contribution
Digitatia eriantha	2.14	28.33	17.13	19.33	19.33
Eragrostis lehmanniana	3.57	6.11	11.90	13.43	32.76
Setaria neglecta	0.00	5.00	8.74	9.86	42.62
Pentzia incana	0.00	1.39	6.13	6.91	49.54
Cynodon dactylon	2.14	1.67	5.26	5.94	55.48
Malephora sp.	0.00	1.94	4.61	5.20	60.68
Lepidium africanum	0.71	0.83	4.18	4.72	65.40
Eragrostis obtusa	0.00	1.39	3.03	3.42	68.82
Euryops chrysanthemoides	0.71	0.00	2.78	3.14	71.96
Ehrharta calycina	0.00	2.78	2.11	2.38	74.34

Table 5.12: SIMPER analysis breakdown of average dissimilarity between recently abandoned burrow mounds and reference plots into contributions from the 10 most influential species at Kwandwe during winter. Percentage cover was used as a surrogate for abundance.

Species	Average abundance on recently abandoned burrow mounds	Average abundance on reference plots	Average dissimilarity	Contribution %	Cumulative contribution
Digitaria eriantha	1.88	12.50	17.91	21.44	21.44
Panicum maximum	0.00	4.50	9.24	11.06	32.49
Setaria neglecta	1.25	3.75	9.06	10.84	43.33
Pentzia incana	1.25	1.50	6.18	7.39	50.72
Lycium ferrisisimum	0.63	1.25	4.88	5.84	56.56
Drosanthemum hispidum	1.25	0.25	4.70	5.62	62.18
Malephora sp.	0.63	1.25	4.21	5.03	67.22
Atriplex lindleyi	0.63	0.75	3.76	4.50	71.72
Falkia repens	0.00	1.25	2.81	3.36	75.08
Acacia karroo	0.63	0.25	2.69	3.22	78.30

Table 5.13: SIMPER analysis breakdown of average dissimilarity between old burrow mounds and reference plots into contributions from the 10 most influential species at Kwandwe during winter. Percentage cover was used as a surrogate for abundance.

Species	Average abundance on old burrow mounds	Average abundance on reference plots	Average dissimilarity	Contribution %	Cumulative contribution
Digitaria eriantha	1.43	12.50	11.59	13.84	13.84
Drosanthemum hispidum	3.57	0.25	8.11	9.68	23.52
Setaria neglecta	2.86	3.75	6.62	7.91	31.42
Panicum maximum	1.43	4.50	6.47	7.72	39.15
Syncolostemon densiflorus	2.86	0.25	6.32	7.54	46.69
Alzoon sp.	2.14	0.75	4.96	5.92	52.61
Galenia sp.	1.43	0.25	3.84	4.58	57.19
Malephora sp.	1.43	1.25	3.79	4.53	61.72
Cuspidia cernua	1.43	0.50	3.46	4.13	65.85
Pentzia incana	0.71	1.50	3.36	4.01	69.86

Table 5.14: SIMPER analysis breakdown of average dissimilarity between active burrow mounds and reference plots into contributions from the 10 most influential species at Kwandwe during spring. Percentage cover was used as a surrogate for abundance.

Species	Average abundance On active burrow mounds	Average abundance on reference plots	Average dissimilarity	Contribution %	Cumulative contribution
Panicum maximum	1.92	29.25	20.80	24.81	24.81
Argemone ochroleuca	3.85	2.00	8.70	10.38	35.19
Digitaria eriantha	0.77	4.50	7.39	8.81	44.01
Cynodon dactylon	1.15	4.50	7.03	8.38	52.39
Pentzia incana	0.38	1.50	4.67	5.57	57.96
Eragrostis lehmanniana	1.92	0.00	4.57	5.45	63.41
Drosanthemum hispidum	1.15	0.50	3.84	4.58	67.99
Asparagus africanum	0.38	1.00	3.20	3.82	71.81
Lycium oxycarpum	0.77	0.75	3.04	3.63	75.44
Setaria neglecta	0.38	0.75	2.76	3.30	78.73

Table 5.15: SIMPER analysis breakdown of average dissimilarity between active burrow mounds and reference plots into contributions from the 10 most influential species at MZNP during autumn. Percentage cover was used as a surrogate for abundance.

Species	Average abundance On active burrow mounds	Average abundance on reference plots	Average dissimilarity	Contribution %	Cumulative contribution
Pentzia globosa	2.50	37.00	19.51	23.47	23.47
Drosanthemum hispidum	5.00	6.25	12.58	15.13	38.60
Eragrostis obtusa	0.00	12.25	12.38	14.89	53.50
Chryscoma ciliata	5.00	0.00	7.83	9.43	62.92
Malephora sp.	0.00	5.25	4.93	5.93	68.85
Tragus koelerioides	0.00	2.25	4.68	5.63	74.48
Lycium cinerium	0.00	5.75	3.56	4.29	78.77
Solanum sysimbrifolium	0.00	1.25	3.40	4.09	82.86
Atriplex lindleyi	0.00	0.75	2.30	2.77	85.63
Galenium sarcophylla	0.00	0.75	1.93	2.32	87.95

Table 5.16: SIMPER analysis breakdown of average dissimilarity between old burrow mounds and reference plots into contributions from the 10 most influential species at MZNP during autumn. Percentage cover was used as a surrogate for abundance.

Species	Average abundance on old burrow mounds	Average abundance on reference plots	Average dissimilarity	Contribution %	Cumulative contribution
Pentzia globosa	4.33	37.00	14.51	20.51	20.51
Eragrostis obtusa	16.33	12.25	11.01	15.57	36.08
Drosanthemum hispidum	6.33	6.25	7.05	9.97	46.05
Malephora sp.	5.67	5.25	6.74	9.53	55.58
Tragus koelerioides	3.00	2.25	5.40	7.63	63.21
Aristida congesta	2.00	0.50	3.20	4.52	67.74
Galenium sarcophylla	2.00	0.75	3.09	4.38	72.11
Lycium cinerium	0.00	5.75	2.76	3.90	76.01
Solanum sysimbrifolium	0.00	1.25	2.72	3.85	79.85
Atriplex lindleyi	0.33	0.75	2.27	3.21	83.06

Table 5.17: SIMPER analysis breakdown of average dissimilarity between active burrow mounds and reference plots into contributions from the 10 most influential species at MZNP during winter. Percentage cover was used as a surrogate for abundance.

Species	Average abundance on active burrow mounds	Average abundance on reference plots	Average dissimilarity	Contribution %	Cumulative contribution
Pentzia globosa	3.75	3.50	12.21	14.97	14.97
Cynodon incompletus	1.25	3.50	10.81	13.26	28.23
Drosanthemum hispidum	0.00	7.50	9.66	11.84	40.07
Malephora sp.	1.25	3.00	7.16	8.78	48.85
Psilocaulon sp.	1.25	1.75	6.57	8.06	56.91
Eragrostis obtusa	1.25	3.00	6.52	7.99	64.90
Lycium cinerium	0.00	2.25	5.24	6.42	71.32
Salsola kali	1.25	0.25	3.56	4.37	75.69
Opuntia aurantiaca	1.25	0.50	3.27	4.01	79.70
Eriocephalus ericoides	0.00	1.00	3.25	3.99	83.69

Table 5.18: SIMPER analysis breakdown of average dissimilarity between recently abandoned burrow mounds and reference plots into contributions from the 10 most influential species at MZNP during winter. Percentage cover was used as a surrogate for abundance.

Species	Average abundance on recently abandoned burrow mounds	Average abundance on reference plots	Average dissimilarity	Contribution %	Cumulative contribution
Drosanthemum hispidum	1.43	7.50	10.25	11.91	11.91
Cynodon incompletus	1.43	3.50	9.90	11.51	23.41
Pentzia globosa	0.00	3.50	6.92	8.04	31.45
Eragrostis obtusa	0.71	3.00	6.42	7.46	38.91
Psilocaulon sp.	0.71	1.75	6.16	7.16	46.07
Malephora sp.	0.00	3.00	5.92	6.87	52.94
Salsola kali	1.43	0.25	5.77	6.70	59.64
Lycium cinerium	0.00	2.25	5.07	5.89	65.53
Eriocephalus ericoides	0.71	1.00	5.01	5.82	71.35
Helichrysum umbraculigerum	1.43	0.00	4.06	4.72	76.07

Table 5.19: SIMPER analysis breakdown of average dissimilarity between active burrow mounds and reference plots into contributions from the 10 most influential species at MZNP during spring. Percentage cover was used as a surrogate for abundance.

Species	Average abundance on active burrow mounds	Average abundance on reference plots	Average dissimilarity	Contribution %	Cumulative contribution
Eragrostis obtusa	0.00	18.25	13.85	17.40	17.40
Pentzia globosa	7.50	9.25	8.14	10.23	27.63
Ericocephalus ericoides	6.25	1.25	6.96	8.75	36.37
Drosanthemum hispidum	0.00	7.50	6.58	8.27	44.64
Psicaulon sp.	2.50	1.00	5.79	7.27	51.91
Alzoon sp.	2.50	2.00	5.46	6.86	58.77
Malephora sp.	1.25	4.00	5.01	6.29	65.06
Cynodon incompletus	1.25	4.00	4.14	5.21	70.27
Talinum caffrum	1.25	1.00	3.90	4.90	75.17
Lycium cinerium	1.25	0.75	3.21	4.03	79.20

Table 5.20: SIMPER analysis breakdown of average dissimilarity between recently abandoned burrow mounds and reference plots into contributions from the 10 most influential species at MZNP during spring. Percentage cover was used as a surrogate for abundance.

Species	Average abundance on recently abandoned burrow mounds	Average abundance on reference plots	Average dissimilarity	Contribution %	Cumulative contribution
Eragrostis obtusa	3.13	18.25	11.03	14.70	14.70
Pentzia globosa	1.88	9.25	9.41	12.54	27.24
Drosanthemum hispidum	0.63	7.50	7.83	10.43	37.68
Alzoon sp.	1.25	2.00	5.40	7.19	44.87
Malephora sp.	0.63	4.00	5.12	6.83	51.70
Psicaulon sp.	1.88	1.00	5.05	6.72	58.42
Helichrysum umbraculigerum	1.25	1.50	4.61	6.14	64.56
Galenia sarcophylla	0.63	0.75	3.22	4.29	68.85
Talinum caffrum	0.63	1.00	3.12	4.15	73.00
Cuspidia cernua	0.63	0.50	2.79	3.71	76.72

Table 5.21: SIMPER analysis breakdown of average dissimilarity between recently abandoned burrow mounds and reference plots into contributions from the 10 most influential species at MZNP during summer. Percentage cover was used as a surrogate for abundance.

Species	Average abundance on recently abandoned burrow mounds	Average abundance on reference plots	Average dissimilarity	Contribution %	Cumulative contribution
Cynodon incompletus	3.75	37.50	12.65	15.97	15.97
Eragrostis obtusa	0.00	8.61	8.01	10.11	26.08
Schotia afra	3.75	0.83	7.89	9.96	36.04
Setaria verticillata	2.50	0.00	6.97	8.80	44.84
Salsola kali	6.25	1.94	5.79	7.31	52.15
Pentzia globosa	0.00	2.78	5.37	6.78	58.93
Drosanthemum hispidum	0.00	5.28	4.82	6.08	65.01
Alzoon sp.	2.50	0.56	3.71	4.68	69.69
Tragus koelerioides	1.25	0.83	3.56	4.49	74.19
Atriplex semibaccata	0.00	5.28	3.34	4.22	78.41

Table 5.22: SIMPER analysis breakdown of average dissimilarity between recently abandoned burrow mounds and old burrow mounds into contributions from the 10 most influential species at MZNP during summer. Percentage cover was used as a surrogate for abundance.

Species	Average abundance on recently abandoned burrow mounds	Average abundance on old burrow mounds	Average dissimilarity	Contribution %	Cumulative contribution
Atriplex semibaccata	0.00	5.50	9.69	11.31	11.31
Eragrostis obtusa	0.00	5.50	9.64	11.25	22.56
Salsola kali	6.25	4.50	9.55	11.14	33.70
Schotia afra	3.75	1.00	9.02	10.52	44.22
Setaria verticillata	2.50	0.00	8.38	9.77	53.99
Cynodon incompletus	3.75	1.50	8.36	9.76	63.75
Alzoon sp.	2.50	2.00	6.65	7.76	71.51
Malephora sp.	0.00	2.50	4.69	5.47	76.98
Tragus koelerioides	1.25	0.50	3.80	4.43	81.41
Drosanthemum hispidum	0.00	2.50	3.75	4.38	85.79

Table 5.23: SIMPER analysis breakdown of average dissimilarity between old burrow mounds and reference plots into contributions from the 10 most influential species at MZNP during summer. Percentage cover was used as a surrogate for abundance.

Species	Average abundance on old burrow mounds	Average abundance on reference plots	Average dissimilarity	Contribution %	Cumulative contribution
Cynodon imcompletus	1.50	37.50	15.28	19.34	19.34
Eragrostis obtusa	5.50	8.61	8.37	10.60	29.94
Atriplex semibaccata	5.50	5.28	8.06	10.21	40.15
Salsola kali	4.50	1.94	6.28	7.96	48.11
Drosanthemum hispidum	2.50	5.28	5.80	7.35	55.46
Pentzia globosa	1.00	2.78	5.18	6.56	62.02
Malephora sp.	2.50	0.56	4.14	5.24	67.26
Alzoon sp.	2.00	0.56	3.99	5.06	72.31
Lycium cinerium	2.00	0.56	3.04	3.85	76.17
Schotia afra	1.00	0.83	2.76	3.50	79.66

Table 5.24: SIMPER analysis breakdown of average dissimilarity between active burrow mounds and reference plots into contributions from the 10 most influential species at Tswalu during winter. Percentage cover was used as a surrogate for abundance.

Species	Average abundance on active burrow mounds	Average abundance on reference plots	Average dissimilarity	Contribution %	Cumulative contribution
Eragrostis lehmanniana	1.25	11.00	16.79	18.07	18.07
Aristida meridionalis	0.00	4.00	11.26	12.11	30.18
Stipagrostis uniplumis	0.00	3.25	6.41	6.90	37.08
Ceropegia sp.	1.25	0.25	5.19	5.58	42.66
Dicerocaryum eriocarpum	1.25	0.00	4.75	5.11	47.77
Hermannia burchellii	1.25	0.00	4.75	5.11	52.89
Senna italica	0.00	1.00	4.01	4.32	57.20
Aristida stipitata	0.00	1.50	3.54	3.81	61.01
Acacia mellifera	0.00	1.00	3.37	3.62	64.63
Schmidtia pappophoroides	0.00	2.00	3.28	3.53	68.17

Table 5.25: SIMPER analysis breakdown of average dissimilarity between recently abandoned burrow mounds and reference plots into contributions from the 10 most influential species at Tswalu during winter. Percentage cover was used as a surrogate for abundance.

Species	Average abundance on recently abandoned burrow mounds	Average abundance on reference plots	Average dissimilarity	Contribution %	Cumulative contribution
Eragrostis lehmanniana	1.43	11.00	15.12	17.75	17.75
Aristida meridionalis	0.71	4.00	10.19	11.96	29.71
Stipagrostis uniplumis	1.43	3.25	7.93	9.31	39.02
Senna italica	1.43	1.00	6.24	7.32	46.34
Schmidtia kalihariensis	0.71	0.50	3.43	4.02	50.37
Hermannia burchellii	1.43	0.00	3.41	4.00	54.37
Aristida stipitata	0.00	1.50	3.28	3.85	58.22
Limeum fenestratum	0.71	0.50	3.21	3.76	61.99
Acacia mellifera	0.00	1.00	3.11	3.65	65.63
Schmiditia pappophoroides	0.00	2.00	3.03	3.56	69.19

Table 5.26: SIMPER analysis breakdown of average dissimilarity between recently active burrow mounds and reference plots into contributions from the 10 most influential species at Tswalu during spring. Percentage cover was used as a surrogate for abundance.

Species	Average abundance on active burrow mounds	Average abundance on reference plots	Average dissimilarity	Contribution %	Cumulative contribution
Aristida meridionalis	0.00	5.83	16.41	17.61	17.61
Tribulus zeyheri	0.00	4.72	9.76	10.47	28.08
Senna italica	1.67	2.50	8.90	9.55	37.63
Eragrostis lehmanniana	0.00	3.61	8.75	9.39	47.02
Harpagophytum procumbens	0.00	5.00	7.12	7.64	54.66
Aristida stipitata	1.67	1.39	6.60	7.09	61.75
Cenchrus ciliaris	1.67	0.28	5.78	6.20	67.95
Indigofera alternans	1.67	0.00	5.51	5.91	73.86
Stipagrostis uniplumis	0.00	2.78	4.91	5.27	79.13
Melinis repens	0.00	1.39	4.13	4.43	83.56

CHAPTER 6

GENERAL DISCUSSION

Evidence has been presented in the preceding chapters which supports the hypothesis that aardvarks are important allogenic ecosystem engineers in arid and semi-arid environments as a result of their burrowing activities. However, in this general discussion, six criteria, as proposed by Jones *et al*. (1994), shall be used to formally evaluate the significance of their burrow construction. These criteria are: 1) Lifetime *per capita* activity of the organism; 2) population density of the engineering organism; 3) the spatial distribution, on a local and regional scale, of the population; 4) the length of time the population has occurred at the site; 5) the durability of the constructs in the absence of the original engineer; and 6) the number and types of resources that are influenced by the constructs and the number of other species dependent on these resources.

Accurately calculating the lifetime *per capita* output of aardvarks is problematic as little information exists on their lifespan in the wild or on their burrow production rate. Aardvarks have been documented living for up to 23 years in captivity (Rahm, 1990) but this figure is likely to be reduced in the wild, particularly in areas where they are subject to predation by large mammalian carnivores. Research conducted on game reserves in the Eastern Cape Province, where lions have been re-introduced, has shown that aardvarks form part of the diet of lions in particular (C. Bissett, pers. comm.). Furthermore, unlike some other species such as the nine-banded armadillo (Taber, 1945; Clark, 1951) which dig new burrows almost every night, the wandering lifestyle of aardvarks (especially males) results in the length of time they occupy a burrow varying from a single day in some instances through to 38 days in the case of a radio-collared female in the Karoo (Taylor & Skinner, 2003). The average length of burrow use for three aardvarks was recorded at 4.9, 6.9 and 8.6 days respectively (Taylor & Skinner, 2003). In addition, aardvarks may not always dig a new burrow when they abandon one but will rather renovate an old existing burrow (Skinner & Smithers, 1990; Taylor & Skinner, 2003). Therefore, if aardvarks live for approximately 10 years in the wild and they are conservatively estimated to excavate a new burrow every 30 days this results in approximately 120 burrows being created over the course a lifetime. In addition, they will make many more much smaller feeding excavations which, while not creating shelter for other organisms, are thought to be important in shaping the plant communities of semi-arid shrublands as they function as favourable germination sites for many plant species (Dean & Milton, 1991b).

As mentioned in chapter one, the density at which aardvark populations occur is usually low (Taylor and Skinner, 2003) although they do have a broad distribution range in sub-Saharan Africa (Skinner & Smithers, 1990). Evidence of aardvark activity was extensive at all three study sites (pers. obs.) and thus it is assumed that the species has a large distribution range at a local scale.

Determining the length of time aardvarks have existed at each site is also difficult, however, they have been present all three study sites at least since their proclamation as protected areas. It is, however, more likely they have occurred naturally in these areas for many thousands of years.

The high density of burrows (516 /km^2 at Kwandwe, 795 /km^2 at MZNP and 122 /km^2 at Tswalu) combined with the much lower density of aardvarks suggests a long life span for the burrows. However, the durability of aardvark burrows are likely to be heavily dependent on the type and depth of the substrate into which they are dug (Gordon *et al*., 1985; Reichman & Smith, 1990; Whitford & Kay, 1999; Woolnough & Steele, 2001; Shimmin *et al*., 2002). Sandy soils for instance are easier to excavate but are less likely to provide structural support than clay-dominated soils (Woolnough & Steele, 2001; Shimmin *et al*., 2002). At Tswalu the roofs of a number of burrows collapsed within two months after being excavated in fine-grained sandy soils whereas little evidence of structural collapse was noticed in some burrows dug in the clayey soil at MZNP, nearly a year after their initial excavation (pers. obs.). Burrows dug in the sandy banks adjacent to the Great Fish River at Kwandwe were also more prone to collapse than those constructed in the clayey soil at that site. The location of burrows in close proximity to trees or other vegetation with substantial root systems may also contribute to strengthening the constructs and thus adding to their durability (Gordon *et al*., 1985). Since aardvark burrows have a shorter lifespan in sandy soils, they may be of greater importance in hard soils where other animals are less capable of excavating their own burrows.

Finally, the creation of these burrows has been demonstrated to provide other species with a range of resources, which would otherwise be scarce in the absence of aardvarks. These resources include the provision of a thermally buffered and stable microhabitat which can be used when foraging, raising young, recovering from injuries or attempting to escape from predators. In addition, there is evidence to suggest that burrows may provide vital nesting sites for birds in areas where such resources are limited. The data collected during this study as well as previous studies, for example Smithers (1971), demonstrates that a large and diverse group of animals use aardvark burrows and the resources they provide either on a regular or opportunistic basis. In addition to their effect on animal communities, the creation of burrows has been shown to open up patches for plant colonisation resulting in an increase in plant species diversity on a landscape level.

Lawton (1994) and Lawton & Jones (1995) state that a vital component of ecosystem engineering is that the process should alter the availability of resources exploited by other organisms with regards to quality, quantity and distribution. It is clear from the evidence presented, that the excavation of burrows by aardvarks fulfils all three of these requirements. Lawton & Jones (1995) further contend that the most notable engineering feats are performed by species occurring at high densities, over a large area for a prolonged period of time, which create structures that last for decades, centuries or millennia and which mediate the availability of a large number of resources. However, it has also been acknowledged that not all six of the scaling factors necessarily have to be completely satisfied in order for an engineer to have a significant effect on an ecosystem (Lawton & Jones, 1995; Berkenbusch & Rowden, 2003). An ecosystem engineer may therefore make an important contribution to ecosystem functioning provided various combinations of the abovementioned criteria are fulfilled. Aardvarks occur at low densities, however, they are widespread (both regionally and locally), have a long lifespan, have been present at the three study sites for a considerable period of time and create burrows that may remain intact for many years in their absence and which increase the availability of numerous resources for a large number of plant and animal species. Thus, it is proposed that aardvarks should be considered important ecosystem engineers in arid and semi-arid environments. In addition, the high density of aardvark burrows at all three sites and the number of resources which they influence also complies with the criteria of a keystone species as the impact this species has is disproportionately high relative to its abundance (Power *et al*., 1996).

Humans have the ability to alter the abundance and distribution of ecosystem engineers (Machiote *et al*., 2004) yet, due to the lack of manipulative field studies, we possess very little information regarding the ecological consequences of such actions, for instance, the number of species which will be lost in their absence (Lawton, 1994; Wright *et al*., 2006). Beavers have been shown to increase species richness at a landscape level as a result of their dam-building behaviour (Wright *et al*., 2002) and their eradication is thought to have a deleterious effect on numerous other species. The reason for this is that no other species perform the same ecological engineering on a similar scale as do the beavers. Similarly, Casas-Crivillé & Valera (2005) argue that the importance of a bioturbator in an arid ecosystem increases in the absence of other species which can perform such a role. Therefore, the potentially significant impact of aardvarks as ecosystem engineers in arid and semi-arid environments may be important to the survival of other organisms and species, particularly when alternative burrowing animals are either absent or restricted in their activities. Thus given their role in ecosystem functioning it is recommended that aardvark populations are considered to be a conservation priority in arid and semi-arid ecosystems.

REFERENCES

Adams, J. (1985). The definition and interpretation of guild structure in ecological communities. *Journal of Animal Ecology* **54**: 43-59.

Alkon, P.U. (1999). Microhabitat to landscape impacts: crested porcupine digs in the Negev desert highlands. *Journal of Arid Environments* **41**: 183-202.

Andersen, M.C. & Kay, F.R. (1999). Banner-tailed kangaroo rat burrow mounds and desert grassland habitats. *Journal of Arid Environments* **41**: 147-160.

Anderson, M.D. & Richardson, P.R.K. (2005). The physical and thermal characteristics of aardwolf dens. *South African Journal of Wildlife Research* **35**: 147-153.

Beck, D.D. & Lowe, C.H. (1991). Ecology of the bearded lizard, *Heloderma horridum*, in a tropical dry forest in Jalisco, Mexico. *Journal of Herpetology* **25**: 395-406.

Berkenbusch, K. & Rowden, A.A. (2003). Ecosystem engineering – moving away from ‘just-so’ stories. *New Zealand Journal of Ecology* **27**: 67-73.

Bissett, C. (2004). The feeding ecology, habitat selection and hunting behaviour of re-introduced cheetah on Kwandwe Private Game Reserve, Eastern Cape Province. Unpublished MSc thesis. Rhodes University, Grahamstown.

Boeken, B. & Shachak, M. (1998a). Colonization by annual plants of an experimentally altered desert landscape: source-sink relationship. *Journal of Ecology* **86**: 804-814.

Boeken, B. & Shachak, M. (1998b). The dynamics of abundance and incidence of annual plant species during colonization in a desert. *Ecography* **21**: 63-73.

Borror, D.J. & White, R.E. (1970). *The Peterson field guide series: A field guide to insects, America north of Mexico*. Houghton Mifflin, Boston.

Bragg, C.J., Donaldson, J.D. & Ryan, P.G. (2005). Density of Cape porcupines in a semi-arid environment and their impact on soil turnover and related ecosystem processes. *Journal of Arid Environments* **61**: 261-275.

Branch, B. (1993). *Southern African snakes and other reptiles: A photographic guide*. Struik, Cape Town.

Branch, L.C., Villarreal, D., Hierro, J.L. & Portier, K.M. (1996). Effects of local extinction of the plains vizcacha (*Lagostomus maximus*) on vegetation patterns in semi-arid scrub. *Oecologia* **106**: 389-399.

Bronner, G.N. (1992). Burrow system characteristics of seven small mammal species (Mammalia: Insectivora; Rodentia; Carnivora). *Koedoe* **35**: 125-128.

Brown, L.R. & Bezuidenhout, H. (2005). The vegetation of the farms Ingleside and Welgedaht of the Mountain Zebra national Park, Eastern Cape. *Koedoe* **48**: 23-42.

Brown, J.H., Reichman, O.J. & Davidson, D.W. (1979). Granivory in desert ecosystems. *Annual Review of Ecology and Systematics* **10**: 201-227.

Brown, J.S., Kotler, B.P., Smith, R.J. and Wirtz II, W.O. (1988). The effects of owl predation on the foraging behaviour of heteromyid rodents. *Oecologia* **76**: 408-415.

Bruun, H.H., Österdahl, S., Moen, J. & Angerbjörn, A. (2005). Distinct patterns in alpine vegetation around dens of the arctic fox. *Ecography* **28**: 81-87.

Bulova, S.J. (2002). How temperature, humidity, and burrow selection affect evaporative water loss in desert tortoises. *Journal of Thermal Biology* **27**: 175-189.

Buynitskiy, V.K. (1968). The influence of microalgae on the structure and strength of Antarctic sea ice. *Oceanology* **8**: 771-776.

Buytynski, T.M. & Mattingly, R. (1979). Burrow structure and fossorial ecology of the springhare *Pedetes capensis* in Botswana. *African Journal of Ecology* **17**: 205-215.

Carter, T.S. & Encarnaçao, C.D. (1983). Characteristics and use of burrows by four species of armadillos in Brazil. *Journal of Mammalogy* **64**: 103-108.

Casas-Crivillé, A. & Valera, F. (2005). The European bee-eater (*Merops apiaster*) as an ecosystem engineer in arid environments. *Journal of Arid Environments* **60**: 227-238.

Ceballos, G., Pacheco, J. & List, R. (1999). Influence of prairie dogs (*Cynomys ludovicianus*) on habitat heterogeneity and mammalian diversity in Mexico. *Journal of Arid Environments* **41**: 161-172.

Chesson, P., Gebauer, R.L.E., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M.S.K., Sher, A., Novoplansky, A. & Weltzin, J.K. (2004). Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments. *Oecologia* **141**: 236-253.

Cilliers, S. (2002). The ecological importance of the aardvark. *Afrotherian Conservation: Newsletter of the IUCN/SSC Afrotheria Specialist Group*. no. 1.

Clark, W. (1951). Ecological life history of the armadillo in the eastern plateau region. *American Midland Naturalist* **46**: 337-358.

Cortés, A., Miranda, E., Rosenmann, M. & Rau, J.R. (2000). Thermal biology of the fossorial rodent *Ctenomys fulvus* from the Atacama desert, northern Chile. *Journal of Thermal Biology* **25**: 425-430.

Coulombe, H.N. (1971). Behavior and population ecology of the burrowing owl, *Speotyto cunicularia*, in the Imperial Valley of California. *The Condor* **73**: 162-176.

Cranston, P.S. (1988). Biomonitoring and invertebrate taxonomy. *Environmental Monitoring and Assessment* **14**: 265-273.

Cranston, P.S. (1990). Biomonitoring and invertebrate taxonomy. *Environmental Monitoring and Assessment* **14**: 265-273.

Cranston, P. & Hillman, T. (1992). Rapid assessment of biodiversity using 'biological diversity technicians'. *Australian Biologist* **5**: 144-154.

Cumming, D.H.M. (1970). A contribution to the biology of warthog (*Phacochoerus africanus*, Gmelin) in the Sengwa region of Rhodesia. Unpublished PhD thesis. Rhodes University, Grahamstown.

Dawkins, R. (1982). *The extended phenotype*. Oxford University Press, Oxford.

Dean, W.R.J & Milton, S.J. (1991a). Patch disturbances in arid grassy dunes: antelope, rodents and annual plants. *Journal of Arid Environments* **20**: 231-237.

Dean, W.R.J. & Milton, S.J. (1991b). Disturbances in semi-arid shrubland and arid grassland in the Karoo, South Africa: mammal diggings as germination sites. *African Journal of Ecology* **29**: 11-16.

Dean, W.R.J. & Milton, S.J. (1995). Plant and invertebrate assemblages on old fields in the arid southern Karoo, South Africa. *African Journal of Ecology* **33**: 1-13.

Dean, W.R.J. & Williams, J.B. (2004). Adaptations of birds for life in deserts with particular reference to Larks (Alaudidae). *Transactions of the Royal Society of South Africa: Proceedings of a colloquium on adaptations in desert fauna and flora: Special issue* **59**: 79-91.

Degen, A.A. (1997). *Ecophysiology of small desert mammals*. Springer, New York.

De Graaf, G. (1981). *The rodents of southern Africa*. Butterworths, Pretoria.

De Klerk, J., Brown, L.R. & Bezuidenhout, H. (2003). Plant communities of the Ebenhaezer section of the Mountain Zebra National Park. *Koedoe* **46**: 9-20.

Derraik, J.G.B., Closs, G.P., Dickinson, K.J.M., Sirvid, P., Barratt, B.I.P. & Patrick, B.H. (2002). Arthropod morphospecies versus taxonomic species: a case study with araneae, coleopteran, and lepidoptera. *Conservation Biology* **16**: 1015-1025.

Desjeux, P., Bryan, J.H. & Martin-Saxton, P. (1983). Leishmaniasis in The Gambia - A study of possible vectors and animal reservoirs, with the first report of a case of canine leishmaniasis in The Gambia. *Transactions of the Royal Society of Tropical Medicine and Hygiene* **77**: 143-148.

Downs, C.T. & Perrin, M.R. (1989). An investigation of the macro-and micro-environments of four *Gerbillurus* species. *Cimbebasia* **11**: 41-54.

Eldridge, D.J. (2004). Mounds of the American badger (*Taxidea taxus*): significant features of north American shrub-steppe ecosystems. *Journal of Mammalogy* **85**: 1060-1067.

Eldridge, D.J. & Myers, C.A. (2001). The impact of warrens of the European rabbit (*Oryctolagus cuniculus* L.) on soil and ecological processes in a semi-arid Australian woodland. *Journal of Arid Environments* **47**: 325-337.

Finlayson, G.R., Shimmin, G.A., Temple-Smith, P.D., Handasyde, K.A. & Taggart, D.A. (2005). Burrow use and ranging behaviour of the southern hairy-nosed wombat (*Lasiorhinus latifrons*) in the Murraylands, South Australia. *Journal of Zoology, London* **265**: 189-200.

Friedman, Y & Daly, B. (2004). *Red data book of the mammals of South Africa: A conservation assessment*. CBSG Southern Africa, CBSG (SSG/IUCN), EWT, South Africa

Gabet, E.J., Reichmann, O.J. & Seabloom, E.W. (2003). The effects of bioturbation on soil processes and sediment transport. *Annual Review of Earth and Planetary Science* **31**: 249-273.

Gibson, D.J. (1989). Effects of animal disturbance on tallgrass prairie vegetation. *American Midland Naturalist* **121**: 144-154.

Goldstein, P.Z. (1997). How many things are there? A reply to Oliver and Beattie, Beattie and Oliver, Oliver and Beattie, and Oliver and Beattie. *Conservation Biology* **11**: 571-574.

Gordon, G., Riney, T., Toop, J., Lawrie, B.C. & Godwin, M.D. (1985). Observations on the Queensland Hairy-nosed Wombat *Lasiorhinus krefftii* (Owen). *Biological Conservation* **33**: 165-195.

Gurgel-Gonçalves, R., Palma, A.R.T., Motta, P.C., Bar, M.E. & Cuba, C.A.C. (2006). Arthropods associated with the crown of *Mauritia flexuosa* (Arecaceae) palm trees in three different environments from Brazilian Cerrado. *Neotropical Entomology* **35**: 302-312.

Haase, P., Pugnaire, F.I. & Incoll, L.D. (1995). Seed production and dispersal in the semi-arid tussock grass *Stipa tenacissima* L. during masting. *Journal of Arid Environments* **31**: 55-65.

Hancox, M. (1988). The nidiculous fauna of badger setts. *Entomologist's monthly magazine* **124**: 93-95.

Hansell, M.H. (1993). The ecological impact of animal nests and burrows. *Functional Ecology* **7**: 5-12.

Harrison, D.J. & Gilbert, J.R. (1985). Denning ecology and movements of coyotes in Maine during pup rearing. *Journal of Mammalogy* **66**: 712-719.

Hay, M.E. & Fuller, P.J. (1981). Seed escape from heteromyid rodents: the importance of microhabitat and seed preferences. *Ecology* **62**: 1395-1399.

Heidger, C. (1988). Ecology of spiders inhabiting abandoned mammal burrows in South African savanna. *Oecologia* **76**: 303-306.

Henderson, L. (2001). *Alien weeds and invasive plants: A complete guide to declared weeds and invaders in South Africa, PPRI Handbook no.12*. Plant Protection Research Institute & Agricultural Research Council, Paarl.

Hermann, S.M., Guyer, C., Waddle, J.H. & Nelms, M.G. (2002). Sampling on private property to evaluate population status and effects of land use practices on the gopher tortoise, *Gopherus polyphemus*. *Biological Conservation* **108**: 289-298.

Hobbs, R.J. & Huenneke, L.F. (1992). Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology* **6**: 324:337.

Hockey PAR, Dean WRJ, Ryan P (Eds) (2005). *Roberts Birds of Southern Africa VII*. John Voelcker Bird Book Fund, Black Eagle Publishing, Cape Town.

Hoffman, T. (1996). Eastern Nama Karoo In: Low, A.B. & Rebelo A.G. (Eds), *Vegetation of South Africa, Lesotho and Swaziland: A companion to the vegetation map of South Africa, Lesotho and Swaziland*. p55, Department of Environmental Affairs and Tourism, Pretoria.

Ivanov, K.P. (2006). The development of the concepts of homeothermy and thermoregulation. *Journal of Thermal Biology* **31**: 24-29.

Jackson, T.P. (2000). Adaptation to living in an open arid environment: lessons from the burrow structure of the two southern African whistling rats, *Parotomys brantsii* and *P.littledalei*. *Journal of Arid Environments* **46**: 345-355.

Jain, S.K., Singh, V.P., van Genuchten, M.T. (2004). Analysis of soil water retention data using artificial neural networks. *Journal of Hydrologic Engineering* **9**: 415-420.

Jarvis, J.U.M. (1991). Introducing the African mole-rats, In: Sherman, P., Jarvis, J.U.M. & Alexander, R (Eds). *The biology of the naked mole-rat.* Princeton University Press, Princeton.

Johnson, M.R. & Keyser, A.W. (1976). Explanatory notes: 1:250 000 Geological Series 3226 King Williams Town. Government Printers, Pretoria.

Johnson, T.K. & Jorgensen, C.D. (1981). Ability of desert rodents to find buried seeds. *Journal of Range Management* **34**: 312-314.

Jones, C.G., Lawton, J.H. & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos* **69**: 373-386.

Jones, C.G. Lawton, J.H. & Shachak, M. (1997). Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* **78**: 1946-1957.

Kaczor, S.A. & Hartnett, D.C. (1990). Gopher tortoise (*Gopherus polyphemus*) effects on soils and vegetation in a Florida sandhill community. *American Midland Naturalist* **123**: 100-111.

Kay, F.R. & Whitford, W.G. (1978). The burrow environment of the banner-tailed kangaroo rat, *Dipodomys spectabilis*, in south-central New Mexico. *American Midland Naturalist* **99**: 270-279.

Kingdon, J. (1971). *East African Mammals, An atlas of evolution in Africa*. Vol. 1. Academic Press, London.

Kinlaw, A. (1999). A review of burrowing by semi-fossorial vertebrates in arid environments. *Journal of Arid Environments* **41**: 127-145.

Kirmitz, J.P. (1962). *Adaptation to desert environment: a study on the jerboa, rat and man*. Butterworths, London.

Kiviat, E. (1978). Vertebrate use of muskrat lodges and burrows. *Estuaries* **1**: 196-200.

Kotler, B.P., Brown, J.S., & Hasson, O. (1991). Factors affecting gerbil foraging behaviour and rates of owl predation. *Ecology* **72**: 2249-2260.

Krebs, C.J. (1985). *Ecology: The experimental analysis of distribution and abundance.* 3rd edition. Harper & Row, New York

Krell, F.T. (2004). Parataxonomy vs. taxonomy in biodiversity studies – pitfalls and applicability of 'morphospecies' sorting. *Biodiversity and Conservation* **13**: 795-812.

Kutiel, P., Peled, Y. & Geffen, E. (2000). The effect of removing shrub cover on annual plants and small mammals in a coastal sand dune ecosystem. *Biological conservation* **94**: 235-242.

Laundre, J.W. & Reynolds, T.D. (1993). Effects of soil structure on burrow characteristics of five small mammal species. *Great Basin Naturalist* **53**: 358-366.

Lawrence, G.E. (1966). Ecology of vertebrate animals in relation to Chaparral fire in the Sierra Nevada foothills. *Ecology* **47**: 278-291.

Lawton, J.H. (1994). What do species do in ecosystems? *Oikos* **71**: 367-374.

Lawton, J.H. & Jones, C.G. (1995). Linking species and ecosystems: organisms as ecosystem engineers. In: Jones, C.G. & Lawton, J.H. (Eds), *Linking species and ecoysytems*, pp. 141-150. Chapman and Hall, New York

Lehmann, T. (2004). Fossil aardvark (*Oycteropus*) from Swartkrans Cave, South Africa. *South African Journal of Science* **100**: 311-314.

Lindsey, A.P. (1999). The feeding ecology and habitat use of the aardvark *Orycteropus afer*. Unpublished MSc thesis. University of Pretoria, Pretoria.

Lomolino, M.V. & Smith, G.A. (2003). Terrestrial communities at black-tailed prairie dog (*Cynomys ludovicianus*) towns. *Biological Conservation* **115**: 89-100.

Longland, W.S. & Price, M.V. (1991). Direct observations of owls and heteromyid rodents: can predation risk explain microhabitat use ? *Ecology* **72**: 2261-2273.

Low, A.B., Rebelo, A.G. (1996). *Vegetation of South Africa, Lesotho and Swaziland: A companion to the vegetation map of South Africa, Lesotho and Swaziland.* Department of Environmental Affairs and Tourism, Pretoria.

Machiote, M., Branch, L.C. & Villarreal, D. (2004). Burrowing owls and burrowing mammals: are ecosystem engineers interchangeable as facilitators? *Oikos* **106**: 527-535.

Maclean, G.S. (1981). Factors influencing the composition of respiratory gasses in mammal burrows. *Comparative Biochemistry and Physiology* **69**: 373-380.

MacMillen, R.E. & Hinds, D.S. (1983). Water regulatory efficiency in heteromyid rodents: a model and its application. *Ecology* **64**: 152-164.

Magnusson, W.E., Francisco, A.D. & Sanaiotti,T.M. (1995). Home range size and territoriality in *Bolomys lasiurus* (Rodentia: Muridae) in an amazonian savanna. *Journal of Tropical Ecology* **11**: 179-188.

McCoy, E.D., Mushinsky, H.R. & Lindzey, J. (2006). Declines of the gopher tortoise on protected lands. *Biological Conservation* **128**: 120-127.

McCoy, E.D., Mushinsky, H.R. & Wilson, D.S. (1993). Pattern in the compass orientation of gopher tortoise burrows at different spatial scales. *Global Ecology and Biogeography* **3**: 33-40.

McNab, B.K. (1979). The influence of body size on the energetics and distribution of fossorial and burrowing mammals. *Ecology* **60**: 1010-1021.

Meadows, A. (1991). Burrows and burrowing animals: an overview. In: Meadows, P.S. & Meadows, A. (Eds). The environmental impact of burrowing animals and animal burrows. *Symposium of the Zoological Society of London* **63**: 1-13, Clarendon Press, Oxford.

Melton, D.A. (1976). The biology of aardvark (Tubulidentata: Orycteropidae). *Mammal Review* **6**: 75-88.

Miller, B., Ceballos, G. & Reading, R. (1994). The prairie dog and biotic diversity. *Conservation Biology* **8**: 677-681.

Miller, T.E. (1982). Community diversity and interactions between the size and frequency of disturbance. *The American Naturalist* **120**: 533-536.

Mills, L.S., Soulé, M.E. & Doak, D.F. (1993). The keystone-species concept in ecology and conservation. *BioScience* **43**: 219-224.

Milton, S.J. & Dean, W.R.J. (2001). Seeds dispersed in dung of insectivores and herbivores in semi-arid southern Africa. *Journal of Arid environments* **47**: 465-483.

Milton, S.J. & Dean, W.R.J. (2004). Adaptations in desert organisms: even the bad times may be good. *South African Journal of Science* **100**: 405-407.

Moore, J.A.H. & Roper, T.J. (2003). Temperature and humidity in badger *Meles meles* setts. *Mammal Review* **33**: 308-313.

Moran, V.C. & Southwood, Southwood, T.R.E. (1982). The guild composition of arthropod communities in trees. *The Journal of Animal Ecology* **51**: 289-306.

Neal, E.G. & Roper, T.J. (1991). The environmental impact of badgers (*Meles meles*) and their setts. In: Meadows, P.S. & Meadows, A. (Eds), The environmental impact of burrowing animals and animal burrows. *Symposium of the Zoological Society of London* **63**: 89-106.

Nelson, J.F. & Chew, R.M. (1977). Factors affecting the seed reserves in the soil of a Mojave desert ecosystem, Rock Valley, Nye County, Nevada. *American Midland Naturalist* **97**: 300-320.

O'Farrell, P.J. & Milton, S.J. (2006). Road verge and rangeland plant communities in the southern Karoo: exploring what influences diversity, dominance and cover. *Biodiversity and Conservation* **15**: 921-938.

Oliver, I. & Beattie, A.J. (1993). A possible method for the rapid assessment of biodiversity. *Conservation Biology* **7**: 562-568.

Oliver, I. & Beattie, A.J. (1996a). Designing a cost-effective invertebrate survey: a test of methods for rapid assessment of biodiversity. *Ecological Applications* **6**: 594-607.

Oliver, I. & Beattie, A.J. (1996b). Invertebrate morphospecies as surrogates for species: a case study. *Conservation Biology* **10**: 99-109.

Oliver, I. & Beattie, A.J. (1997). Future taxonomic partnerships: reply to Goldstein. *Conservation Biology* **11**: 575-576.

Parker, D.M. (2003). The feeding biology and potential impact of introduced giraffe (*Giraffa camelopardalis*) in the Eastern Cape Province, South Africa. Unpublished MSc thesis. Rhodes University, Grahamstown.

Peinke, D.M. & Brown, C.R. (2003). Metabolism and thermoregulation in the springhare (*Pedetes capensis*). *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* **173**: 347-353.

Peirce, M.A. (1974). Distribution and ecology of *Ornithodoros moubata porcinus* Walton (Acarina) in animal burrows in East Africa. *Bulletin of Entomological Research* **64**: 605-61.

Perrin, M.R. & Johnson, S.J. (1999). The effect of supplemental food and cover availability on a population of the striped mouse. *South African Journal of Wildlife Research* **29**:

Picker, M., Griffiths, C. & Weaving, A. (2004). *Field guide to insects of South Africa*. Struik, Cape Town.

Pik, A.J., Oliver, I. & Beattie, A.J. (1999). Taxonomic sufficiency in ecological studies of terrestrial invertebrates. *Australian Journal of Ecology* **24**: 555-562.

Platt, S.G., Rainwater, T.R. & Brewer, S.W. (2004). Aspects of the burrowing ecology of nine-banded armadillos in northern Belize. *Mammalian Biology* **69**: 217-224.

Platt, W.J. (1975). The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. *Ecological Monographs* **45**: 285-305.

Pond, U., Beesley, B.B. Brown, L.R. & Bezuidenhout, H. (2002). Floristic analysis of the Mountain Zebra National Park, Eastern Cape. *Koedoe* **45**: 35-57.

Pough, F.H. & Groves, J.D. (1983). Specializations of the body forms and food habits of snakes. *American Zoology* **23**: 443-454.

Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, L.S., Daily, G., Castilla, J.C., Lubchenco, J. & Paine, R. (1996). Challenges in the quest for keystones. *BioScience* 46: 609-620.

Price, M.V. & Joyner, J.W. (1997). What resources are available to desert granivores: seed rain or soil seed bank? *Ecology* **78**: 764-773.

Price, M.V. & Reichman, O.J. (1987). Distribution of seeds in Sonoran desert soils: implications for heteromyid rodent foraging. *Ecology* **68**: 1797-1811.

Rahm, U. (1990). Tubulidentates. In: *Grzimek's encyclopedia of mammals*. Volume 4. Parker, S. (Ed.), McGraw-Hill, New York.

Reichman, O.J. (1984). Spatial and temporal variation of seed distributions in Sonoran desert soils. *Journal of Biogeography* **11**: 1-11.

Reichman, O.J. & Fay, P. (1983). Comparison of the diets of a caching and non-caching rodent. *American Naturalist* **122**: 576-581.

Reichman, O.J. & Smith, S.C. (1990). Burrows and burrowing behaviour by mammals. In: Genoways, H.H. (Ed.), *Current Mammalogy*, **2**: 197-244.

Romoser, W.S. & Stoffolano, J.G. (1998). *The science of entomology*. 4th edition. McGraw-Hill, Boston.

Root, R.B. (1967). The niche exploitation pattern of the blue-gray gnatcatcher. *Ecological Monographs* **37**: 317-350.

Rowe-Rowe, D.T. & Meester, J. (1982). Habitat preferences and abundance relations of small mammals in the Natal Drakensberg. *South African Journal of Wildlife Research* **12**: 130-139.

Schlein, Y., Warburg, A., Schnur, L.F., LeBlancq, S.M., & Gunders, A.E. (1984). Leishmaniasis in Israel: reservoir hosts, sandfly vectors and leishmanial strains in the Negev, Central Arava and along the Dead Sea. *Transactions of the Royal Society of Tropical Medicine and Hygiene* **78**: 480-484.

Schmidt-Nielsen, B. & Schmidt-Nielsen, K. (1950). Evaporative water loss in desert rodents in their natural habitat. *Ecology* **31**: 75-85.

Scholtz, C. & Holm, E. (1986). *Insects of southern Africa*. Butterworths, Durban.

Schooley, R.L., Bestelmeyer, B.T. & Kelly, J.F. (2000). Influence of small-scale disturbances by kangaroo rats on Chihuahan desert ants. *Oecologia* **125**: 142-149.

Seastedt, T.R. & Crossley, D.A. (1984). The influence of arthropods on ecosystems. *BioScience* **34**: 157-161.

Shimmin, G, Skinner, J, B. & Baudinette, R. (2002). Life in a wombat burrow. *Nature Australia* **27**. Published electronically at http://web.ebscohost.com/ehost/detail?vid=6&hid=121&sid=30d9d3d4-9924-4276-b7a7-6145f91b84b9%40sessionmgr107.

Simberloff, D. & Dayan. (1991). The guild concept and the structure of ecological communities. *Annual Review of Ecology and Systematics* **22**: 115-143.

Skinner, J.D. & Smithers, R.H.N. (1990). *The mammals of the southern African subregion* 2nd edition. Pretoria, University of Pretoria Press.

Smith, C.C. & Reichman, O.J. (1984). The evolution of food caching by birds and mammals. *Annual Review of Ecology and Systematics* **15**: 329-351.

Smith, R.L. (1990). *Ecology and Field Biology*. 4th edition. Harper & Row, New York.

Smithers, R.H.N. (1971). The Mammals of Botswana. *Memoirs of the National Museum of Rhodesia* no. 4.

Sowls, L.K. & Phelps, R.J. (1966). Body temperatures of juvenile warthogs and bushpigs. *Journal of Mammalogy* **47**: 134-137.

Springer, M.S., Cleven, G.C., Madsen, O., de Jong, W.W., Waddell, V.G., Amrine, H.M. & Stanhope, M.J. (1997). Endemic African mammals shake the phylogenetic tree. *Nature* **388**: 61-64.

Springer, M.S., Stanhope, M.J., Madsen, O. & de Jong, W.W. (2004). Molecules consolidate the placental mammal tree. *Trends in Ecology and Evolution* **19**: 433-438.

Stuart, C. & Stuart, T. (1990). *Field guide to the mammals of southern Africa*. 2nd edition. Struik, Cape Town.

Stuart, C. & Stuart, T. (2000). *A field guide to the tracks & signs of southern & east African wildlife*. 2nd edition. Struik, Cape Town.

Swihart, R.K. & Picone, P.M. (1995). Use of woodchuck burrows by small mammals in agricultural habitats. *American Midland Naturalist* **133**: 360-363.

Taber, F.W. (1945). Contributions on the life history and ecology of the nine-banded armadillo. *Journal of Mammalogy* **26**: 211-226.

Taylor, W.A. (1998). The ecology of the aardvark, *Orycteropus afer* (Tubulidentata: Orycteropidae). Unpublished M.S.c. thesis, University of Pretoria, Pretoria.

Taylor, W.A. (2002). Biological synopsis of aardvark. Published electronically by IUCN/SSC Afrotheria Specialist Group at

www. Calacademy.org/research/bmammals/Afrotheria/Tubulidentata.html.

Taylor, W.A., Lindsey, P.A. & Skinner, J.D. (2002). The feeding ecology of the aardvark *Orycteropus afer*. *Journal of arid environments* **50**: 135-152.

Taylor, W.A. & Skinner, J.D. (2000). Associative feeding between Aardwolves (*Proteles cristatus*) and Aardvarks (*Orycteropus afer*). *Mammal Review* **30**: 141

Taylor, W.A. & Skinner, J.D. (2001). Associative feeding between anteating chats, *Myrmecocichla formicivora*, and aardvarks, *Orycteropus afer*. *Ostrich* **72**: 199-200.

Taylor, W.A., Skinner, J.D. (2003). Activity patterns, home ranges and burrow use of aardvark. *Journal of Zoology* **261**: 291-297.

Taylor, W.A. & Skinner, J.D. (2004). Adaptations of the aardvark for survival in the Karoo: a review. *Transactions of the Royal Society of South Africa: Proceedings of a colloquium on adaptations in desert fauna and flora: Special issue* **59**: 105-108.

Teketay, D. & Granström, A. (1995). Soil seed banks in dry Afromontane forests of Ethiopia. *Journal of Vegetation Science* **6**: 777-786.

Thomas, C.F.G. & Marhall, E.J.P. (1999). Arthropod abundance and diversity in differently vegetated margins of arable fields. *Agriculture, Ecosystems and Environment* **72**: 13-144.

Topping, C.J. & Sutherland, K.D. (1992). Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. *Journal of Applied Ecology* **29**: 485-491.

Tracy, R.L. & Walsberg, G.E. (2002). Kangaroo rats revisited: re-evaluating a classic case of desert survival. *Oecologia* **133**: 449-457.

Unwin, D.M. (1981). A key to the families of British diptera. *Field Studies* **5**: 513-553.

Van Aarde, R.J. (2004). Tubulidentata In: Hutchins, M., Kleiman, D.G., Geist, V. & McDade, M.C. (Eds), *Grzimek's Animal Life Encyclopedia*. 2nd edition. Volume 15. MI: Gale Group, Farmington Hills.

Van Aarde, R.J., Willis, C.K., Skinner, J.D. & Haupt, M.A. (1992). Range utilization by the aardvark *Orycteropus afer* Pallas 1766 in the Karoo, South Africa. *Journal of Arid Environments* **22**: 387-394.

Van Oudtshoorn, F. (2002). *Guide to grasses of southern Africa*. 2nd Edition. Briza, Pretoria.

Van Rooyen, N. & Bredenkamp, G. (1996a). Shrubby Kalahari Dune Bushveld. In: Low, A.B. & Rebelo A.G. (Eds.), *Vegetation of South Africa, Lesotho and Swaziland: A companion to the vegetation map of South Africa, Lesotho and Swaziland*. p33. Department of Environmental Affairs and Tourism, Pretoria.

Van Rooyen, N. & Bredenkamp, G. (1996b). Kalahari Plains Thorn Bushveld. In: Low, A.B. & Rebelo A.G. (Eds.), *Vegetation of South Africa, Lesotho and Swaziland: A companion to the vegetation map of South Africa, Lesotho and Swaziland*. p35. Department of Environmental Affairs and Tourism, Pretoria.

Van Rooyen, N. & Bredenkamp, G. (1996c). Kalahari Mountain Bushveld. In: Low, A.B. & Rebelo A.G. (Eds.), *Vegetation of South Africa, Lesotho and Swaziland: A companion to the vegetation map of South Africa, Lesotho and Swaziland*. Low p35. Department of Environmental Affairs and Tourism, Pretoria.

Van Rooyen N., van Rooyen M.W., Bredenkamp G.J. (1999). The vegetation types and veld condition of Tswalu Private Desert Reserve. Published electronically at http://ecoport.org/ep?SearchType=earticleView&earticleId=696&page=-2

Varty, N. (1990) Ecology of the small mammals in the riverine forests of the Jubba valley, Southern Somalia. *Journal of Tropical Ecology* **6**: 179-189.

Vaughn, T.A. (1961). Vertebrates inhabiting pocket gopher burrows in Colorado. *Journal of Mammalogy* **42**: 171-174.

Walsberg, G.E. (2000). Small mammals in hot deserts: some generalisations revisited. *BioScience* **50**: 109-120.

Ward, D.F., New, T.R. & Yen, A.L. (2001). Effects of pitfall trap spacing on the abundance, richness and composition of invertebrate catches. *Journal of Insect Conservation* **47**: 47-53.

White, C.R. (2005). The allometry of burrow geometry. *Journal of Zoology, London* **265**: 395-403.

Whitford, W.G. & Kay, F.R. (1999). Biopedturbation by mammals in deserts: a review. *Journal of Arid Environments* **41**: 203-230.

Wiegand, T., Dean, W.R.J. & Milton, S.J. (1997). Simulated plant population responses to small-scale disturbances in semi-arid shrublands. *Journal of Vegetation Science* **8**: 163 –176.

Wilby, A., Shachak, M. & Boeken, B. (2001). Integration of ecosystem engineering and trophic effects of herbivores. *Oikos* **92**: 436-444.

Williams, J.B., Tieleman,B.I. & Shobrak, M. (1999). Lizard burrows provide thermal refugia for larks in the Arabian desert. *The Condor* **101**: 714-717.

Willis, C.K., Skinner, J.D. & Robertson., H.G. (1992). Abundance of ants and termites in the False Karoo and their importance in the diet of the aardvark *Orycteropus afer*. *African Journal of Ecology* **30**: 322-334.

Witz, B.W., Wilson, D.S. & Palmer, M.D. (1991). Distribution of *Gopherus polyphemus* and its vertebrate symbionts in three burrow categories. *American Midland Naturalist* **126**: 152-158.

Wood, G. (1997). Ventilation of the burrow of the Southern Hairy-Nosed Wombat, *Lasiorhinus latifrons*, in bushland near the Murray River at Morgan in South Australia. Published electronically at http://www.adam.com.au/delta/arhives/wombat/wombat.htm

Woolnough, A.P. & Steele, V.R. (2001). The palaeoecology of the vombatidae: did giant wombats burrow? *Mammal Review* **31**: 33-45.

Wright, J.P., Jones, C.G., Boeken, B. & Shachak, M. (2006). Predictability of ecosystem engineering effects on species richness across environmental variability and spatial scales. *Journal of Ecology* **94**: 815-824.

Wright, J.P., Jones, C.G., & Flecker, A.S. (2002). An ecosystem engineer, the beaver, increases species richness at a landscape level. *Oecologia* **132**: 96-101.

Young, B.A. (2003). Snake bioacoustics: towards a richer understanding of the behavioural ecology of snakes. *The Quarterly Review of Biology* **78**: 303-325.

APPENDIX A

Appendix A: The covering letter and first page of the questionnaire requesting information regarding the utilisation of aardvark burrows by other vertebrate species.

Aardvark Burrow Questionnaire
MSc project introduction

Aardvarks create burrows that are reportedly used by a wide variety of other animals including mammals, birds, reptiles, amphibians and invertebrates as refuge from harsh climatic conditions as well for raising their young and to avoid predators. Although lists of species that utilise these burrows have been compiled for Botswana and East Africa, these lists are unlikely to be comprehensive and do not incorporate the semi-arid areas of South Africa. Burrows potentially play a vital role in the maintenance of biodiversity in semi-arid ecosystems and thus it is paramount that we understand the influence they exert over the plant and animal communities in these areas. Any information that you could provide in this regard would be greatly appreciated. I thank you in advance for your participation in this research. Should you wish to know more about this research or provide more updated information please do not hesitate to contact me.

Regards
Gareth Whittington-Jones

Contact details
Gareth Whittington-Jones
Wildlife and Reserve Management Research Group
Department of Zoology and Entomology
Rhodes University
PO Box 94
Grahamstown
6140
Phone: 046 603 8525
Fax: 046 622 8959
Email: gwjesquire@hotmail.com
http://www.ru.ac.za/WRMRG

Name…………………………………………………………………………………
Occupation………………………………………...
Reserve Name……………………………………………………………………..
Length of time you have been working at the reserve …………………………………
Have you seen any animals (including mammals, reptiles, birds, amphibians & invertebrates) other than aardvarks using aardvark burrows? ………………………....
If yes, please complete the relevant sections below.

Observation #1
Type of animal seen using the burrow………………………………………………….
How many animals did you observe (i.e. group size) ?...
Were there juveniles present, if yes how many?..
Was the animal(s) exiting or entering the burrow or stationary ?..................................
What was the purpose (if known) of using the burrow, e.g. hunting, refuge or breeding?....…………………………………………………………………………
What time of year did this observation take place?..
Approximately what time of day (e.g. dusk, dawn, midday, night etc) did this observation take place?..
Any additional information that may be relevant to the study………………………….
……………………………………………………………………………………..
……………………………………………………………………………………..

APPENDIX B

Appendix B: Common and species names of vertebrates recorded using burrows during this study. Data were obtained from personal sightings, records of tracks and signs and from the questionnaires.

Common name	Species name
Multimammate mouse	*Praomys natalensis*
Striped field mouse	*Rhabdomys pumilio*
Pouched mouse	*Saccostomus campestris*
Pygmy mouse	*Mus minutoides*
Desert pygmy mouse	*Mus indutus*
Namaqua rock mouse	*Aethomys namaquensis*
Forest shrew	*Myosorex varius*
Hairy-footed gerbil	*Gerbillurus paeba*
Highveld gerbil	*Tatera brantsii*
Bushveld gerbil	*Tatera leucogaster*
Short-tailed gerbil	*Desmodillus auricularis*
White-tailed mouse	*Mystromys albicaudatus*
Brants’s whistling rat	*Parotomys brantsii*
Cape porcupine	*Hystrix africaeaustralis*
Scrub hare	*Lepus saxatilis*
Ground squirrel	*Xerus inauris*
Black-backed jackal	*Canis mesomelas*
Bat-eared fox	*Otocyon megalotis*
Cape fox	*Vulpes chama*
Honey Badger	*Mellivora capensis*
Yellow mongoose	*Cynictis penicillata*
Aardwolf	*Proteles cristatus*
African wild cat	*Felis lybica*
Warthog	*Phacochoerus aethiopicus*
Steenbok	*Rhapicerus campetris*
Ant-eating chat	*Myrmecocichla formicivora*
Mocking chat	*Thamnolaea cinnamomeiventris*
Pearl-breasted swallow	*Hirundo dimidiata*
Red-breasted swallow	*Hirundo semirufa*
African pygmy-kingfisher	*Ispidina picta*
Grey-hooded kingfisher	*Halcyon leucocephala*
Little bee-eater	*Merops pusillus*
Karoo toad	*Bufo gariepensis*
Cape skink	*Mabuya capensis*
Ground agama	*Agama aculeata*
Puff adder	*Bitis arietans*
Southern African python	*Python natalensis*
Cape Cobra	*Naja nivea*
Monitor lizard	*Varanus albigularis*

APPENDIX C

Appendix C: List of birds recorded using aardvark burrows (Hockey *et al*., 2005).

Common name	Species name
Egyptian goose	*Alopochen aegyptiacus*
South African shelduck	*Tadorna cana*
Spur-winged goose	*Plectropterus gambensis*
Malachite kingfisher	*Alcedo cristata*
African pygmy kingfisher	*Ispidina picta*
Grey-hooded kingfisher	*Halcyon leucocephala*
Brown-hooded kingfisher	*Halcyon albiventris*
Little bee-eater	*Merops pusillus*
Swallow-tailed bee-eater	*Merops hirundineus*
Bohm’s bee-eater	*Merops boehmi*
Banded martin	*Riparia cincta*
Blue swallow	*Hirundo atrocaerulea*
Pearl breasted swallow	*Hirundo dimidiata*
Red-breasted swallow	*Hirundo semirufa*
Black saw-wing swallow	*Psalidoprocne holomelas*
Ant-eating chat	*Myrmecocichla formicivora*

APPENDIX D

Appendix D: List of mammals recorded using aardvark burrows (Skinner & Smithers, 1990).

Common name	Species name
Hairy slit-faced bat	*Nycteris hispida*
Hildebrandt’s horseshoe bat	*Rhinolophus hildebrandtii*
Pangolin	*Manis temminckii*
Cape hare	*Lepus capensis*
Cape porcupine	*Hystrix africaeaustralis*
Pouched mouse	*Saccostomus campestris*
Aardwolf	*Proteles cristatus*
Brown hyaena	*Hyaena brunnea*
Spotted hyaena	*Crocuta crocuta*
Leopard	*Panthera pardus*
Caracal	*Felis caracal*
African wild cat	*Felis lybica*
Small spotted cat	*Felis nigripes*
Bat-eared fox	*Otocyon megalotis*
Wild dog	*Lycaon pictus*
Side-striped jackal	*Canis adustus*
Black-backed jackal	*Canis mesomelas*
Small spotted genet	*Genetta genetta*
Slender mongoose	*Galerella sanguinea*
Banded mongoose	*Mungos mungo*
Warthog	*Phacochoerus aethiopicus*