SMALL MAMMAL COMMUNITIES AT HIGH ALTITUDE WITHIN THE SNEEUBERG MOUNTAIN COMPLEX, EASTERN CAPE PROVINCE, SOUTH AFRICA

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by

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DEDICATION

This thesis is dedicated to my parents Jannet and Arend Kok. Thank you for the love, support and for all the opportunities you provided for me.

ABSTRACT

Due to their widespread and specious nature, small mammals are ideal for biogeographical studies. Small mammals also effectively connect various trophic levels by being both consumers and prey items for other animals. The Great Escarpment is the dominant mountain landscape in South Africa. Yet, very little small mammal research has been conducted on the Great Escarpment outside of the Main Drakensberg Mountains. This is surprising given the importance of mountains in shaping regional ecology.

In this study, I assessed the diversity and community composition of small mammals at three high altitude (>1700m) sites within the Sneeuberg Mountain Complex (SMC) from June 2009 to May 2010. I also tested the effectiveness of five different bait types for measuring small mammal diversity (i.e. number of individuals caught, species richness, Shannon diversity index and Simpson index of diversity).

Out of a total of 423 captures, 292 individuals of 12 small mammal species (one shrew, one elephant shrew and 10 rodents) were recorded over 5280 trap nights. The species richness and diversity of small mammals captured at the three sites were similar and this homogeneity was probably related to the regional processes (e.g. climate and latitude) that govern species richness and diversity.

The most effective bait type in terms of capture success, species richness and diversity measurements was peanut butter and oats. In addition, the use of richness estimators revealed that peanut butter and oats was the most effective bait for

sampling the species richness of small mammals. The effectiveness of peanut butter and oats was related to this bait having a more attractive scent, when compared to the other bait types.

Future studies should focus on researching the range of local and regional processes that drive small mammal diversity at high altitudes in South Africa. I also recommend the use of more than one bait type when planning to survey small mammal communities.

ACKNOWLEDGEMENTS

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TABLE OF CONTENTS

CHAPTER 1

GENERAL INTRODUCTION

1.1 IMPORTANCE OF HIGH ALTITUDE AREAS

Mountains are one of the most evident physical attributes of the global terrestrial landscape (Körner 2004). However, due to the diverse array of landscape features (e.g. altitude, volume, relief and steepness) present in mountainous areas, it has been almost impossible to provide a concise and scientifically accurate definition of a mountain (Gerrard 1990; Kapos *et al.* 2000; Körner 2004). Consequently, calculations of the extent to which the global land surface is covered by mountains vary greatly. Kapos *et al.* (2000) derived one of the most satisfactory definitions and concluded that 24.3% of the global land surface is covered by mountains, 11.3% of which is higher than 1500m. Their definition included a global minimum elevational limit (> 300 m), and slope inclination (calculated using vector data in ArcGIS), which excluded extensive highland plateaus such as the North American short-grass prairie (Kapos *et al.* 2000, Körner 2004).

Mountains and high altitude areas are of major importance to the modern world, mainly because they provide water to 50% of the world's population and play essential roles in numerous cultural and recreational practices (Parish 2003). Biologically, mountains are important because they are hotspots for biodiversity at the global and regional scale (Parish 2003; Körner 2004). Currently, almost a third of the world's protected areas (473 declared parks) are located in mountainous areas (Chakraborty 2002; Körner 2004). The rich diversity of mountain areas can be

accounted for by two biogeographical factors, environmental gradients and mountain isolation (Lomolino 2001; Körner 2004). The rapid changes in altitude cause various environmental gradients that facilitate the creation of multiple microhabitats and climates that are associated with specific sets of organisms (Körner 2004). The most common gradients include rainfall, temperature, habitat complexity, habitat diversity, resource abundance, area and competition (Brown 1971; Rickart *et al.* 1991; Heaney 2001; Lomolino 2001; Körner 2004; McCain 2005; Balete *et al.* 2009). These gradients vary in a non-random fashion with an increase in altitude (Lomolino 2001). With an increase in altitude, rainfall tends to increase, and temperatures tends to decrease, which affects habitat complexity, habitat diversity and resource abundance (Rowe 2009).

The isolation and fragmentation of mountain areas are important driving factors for mountain diversity (Lomolino 2001; Körner 2004). With an increase in altitude, habitats become smaller and more isolated from other mountains and zonal communities (Rickart *et al.* 2001; Lomolino 2001). This isolation of mountain summits could cause immigration rates to decline and extinction rates to increase (since the smaller populations at high altitude are less likely to be sustained by migration of individuals from other zones; Lomolino 2001 and the references therein). However, if isolated populations are large enough to persist and diverge over evolutionary time they may facilitate speciation (Heaney 2001; Lomolino 2001 and the references therein). Consequently, a high number of endemic species occur in mountain environments. Mountain ecosystems are thus ideal for investigating important aspects of evolutionary biology (e.g. speciation and gene flow) and biogeography (e.g. species assemblages along environmental gradients; Heaney 2001; Lomolino 2001; Bateman *et al.* 2010).

1.2 SMALL MAMMALS AT HIGH ALTITUDES

For the purpose of this study, small mammals are defined as the non-volant terrestrial mammal species that are not strictly fossorial, and weigh less than 300g. According to Skinner & Chimimba (2005), this group generally consists of three mammalian orders within southern Africa, Eulipotypha (shrews), Macroscelidea (elephant shrews or segni's) and Rodentia (rodents).

Small mammals are vital components of terrestrial ecosystems (Avenant & Cavallini 2007). They function in nutrient cycling, habitat modification, dispersal of seeds and constitute an important link between primary and secondary consumers (Avenant & Cavallini 2007). In addition, small mammals are often used in ecological surveys as indicators of overall mammalian diversity (Sullivan *et al.* 2003). Small mammals are appropriate indicators of mammalian diversity because they occupy a diverse array of niches (Skinner & Chimimba 2005).

Small mammals have been extensively studied in high altitude regions across the world and some examples include the Rocky Mountains,USA (Brown 1971; Rickart 2001; Rowe 2009) mountain ranges of Oaxaca, Mexico (Sanchez-Cordero 2001) Mount Isarog, Philippines (Rickart *et al.* 1991; Heaney 2001) Mount Kinabalu, Malaysia (Nor 2001), Mount Qilian, China (Sheng Li *et al.* 2003) Mount Lewis, Australia (Bateman *et al.* 2010), Uluguru-Mulanje Mountains, Malawi (Happold & Happold 1989) the Albertine Rift, Uganda (Kasangaki *et al.* 2003), Eastern Arc Mountains, Tanzania and Kenya (Makundi *et al.* 2006; Burgess *et al.* 2007 and references therein), Mount Kilimanjaro, Tanzania (Mulungu *et al.* 2008), the Bale Mountains, Ethiopia (Yalden 1988) and the Chilalo-Galama Mountains, Ethiopia

(Kasso *et al.* 2010). Most of these studies have focussed on the effects of elevational gradients on small mammal diversity (Rickart *et al.* 1991; Heaney 2001; Lomolino 2001; Nor 2001 Rickart 2001; Sánchez-Cordero 2001; Kasangaki *et al* 2003; Sheng Li *et al.* 2003; Mulungu *et al.* 2008; Balete 2009; Rowe 2009; Bateman *et al.* 2010) and conclude that there is a mid-elevational (e.g. 1800-2700 m in the Unita Mountains) peak in small mammal diversity, especially in the tropical regions of the world (Heaney 2001; Nor 2001; Rickart 2001; McCain 2005). Although small mammal diversity tends to peak at the mid-altitudes, small mammal communities that occur on mountain summits can be diverse but very few studies have been conducted in these areas (Brown 1971; Happold & Happold 1989). Small mammal communities on mountain summits are diverse because long-term isolation facilitates the existence of unique communities that are not found in lowland areas (Brown 1971; Happold & Happold 1989; Bateman *et al.* 2010).

1.3 SAMPLING OF SMALL MAMMAL COMMUNITY STRUCTURE

The accurate quantification of small mammal diversity is reliant on the thorough sampling of communities (Woodman *et al.* 1996). Failure to accurately sample communities may yield incorrect information, which can ultimately affect decisions regarding the general ecology and conservation of such communities. Sampling effort and the ability to detect species are two factors that greatly affect estimates of small mammal diversity (Magurran 2004). Greater sampling effort (e.g. more samples or longer-term studies) increases the chances of detecting all the species within a community (Magurran 2004). However, some species are less detectable than others are and this lowers estimates of observed species richness and

estimates of abundance (Southwood & Henderson 2002; Magurran 2004). For example, the abundance of trap shy *Otomys* spp. is believed to be under-represented in samples of small mammal studies throughout southern Africa (Bond *et al.* 1980; Rowe-Rowe & Meester 1982; Happold & Happold 1986; Willan 1986; Happold & Happold 1989). In addition, detection of some species can be limited by the methodological approach used (Slade *et al.* 1993; O'Farrell *et al.* 1994). No single sampling regime is sufficiently capable of estimating true diversity at a specific site (Magurran 2004; Jones *et al.* 1996). For example, Sherman traps are less effective at sampling shrews, when compared to pitfall trapping (Brown 1967; Slade *et al.* 1993).

1.4 MOTIVATION AND BROAD AIMS

Mountains currently cover 8.3% of South Africa's land surface (Browne *et al.* 2004). Most of these mountains form part of the Great Escarpment of South Africa, which is the most significant geomorphic feature south of the African Rift Valley (Maud 2008). It separates the high interior plains of southern Africa from the marginal lowland areas around the eastern, southern and western coastlines (Maud 2008). Many of the mountain ranges that form part of the Great Escarpment have altitudes of 1800m and higher (Figure 1.1). In South Africa, the escarpment starts in the Limpopo Province in the North with the Mpumalanga-Limpopo Drakensberg Mountains which extend south into the KwaZulu-Natal Drakensberg Mountains, and eventually the main Drakensberg Mountains in Lesotho (Figure 1.1). Extending to the west of the Main Drakensberg Mountains is a series of isolated mountain ranges (the southern Great Escarpment) that stretches from the Eastern Cape Province into the Western Cape and Northern Cape Provinces (Mountain ranges from East to West are: Stormberg, Winterberg-Amatolas, Sneeuberg Mountain Complex, Nuweveldberge

and the Roggeveldberge; Figure 1.1). Hereafter, the escarpment continues northward parallel to the West coast of South Africa but the elevation is mostly below 1800m (Figure 1.1).

Although being one of the most significant physical features of the southern African landscape, very little is known about the floral and faunal diversity of the Great Escarpment (Broadman *et al.* 2003; Clark *et al.* 2009). A recent floristic survey by Clark *et al.* (2009) in the Sneeuberg Mountain Complex (SMC) revealed that the area has exceptionally high floristic diversity, so much so that they declared the area a new centre of floristic diversity. The authors found 1195 plant species of which 2.8% are endemic to the SMC (Clark *et al.* 2009). Since there is a strong positive relationship between floristic diversity and mammalian diversity (Andrews & O'Brien 2000), I was interested in investigating the small mammal communities that occur at high altitudes in the SMC. The SMC is situated between the only two areas (Cape Fold Mountains and the main Drakensberg Mountains) in South Africa that have received any attention with respect to small mammal diversity at high altitudes (Figure 1.1).

The broad aims of my study were:

- To provide basic knowledge on the community composition and diversity of small mammals at high altitudes within the SMC; and
- To test the effectiveness of small mammal sampling trapping protocols to maximize captures and estimates of small mammal diversity at high altitudes, focussing specifically on use of different bait types.

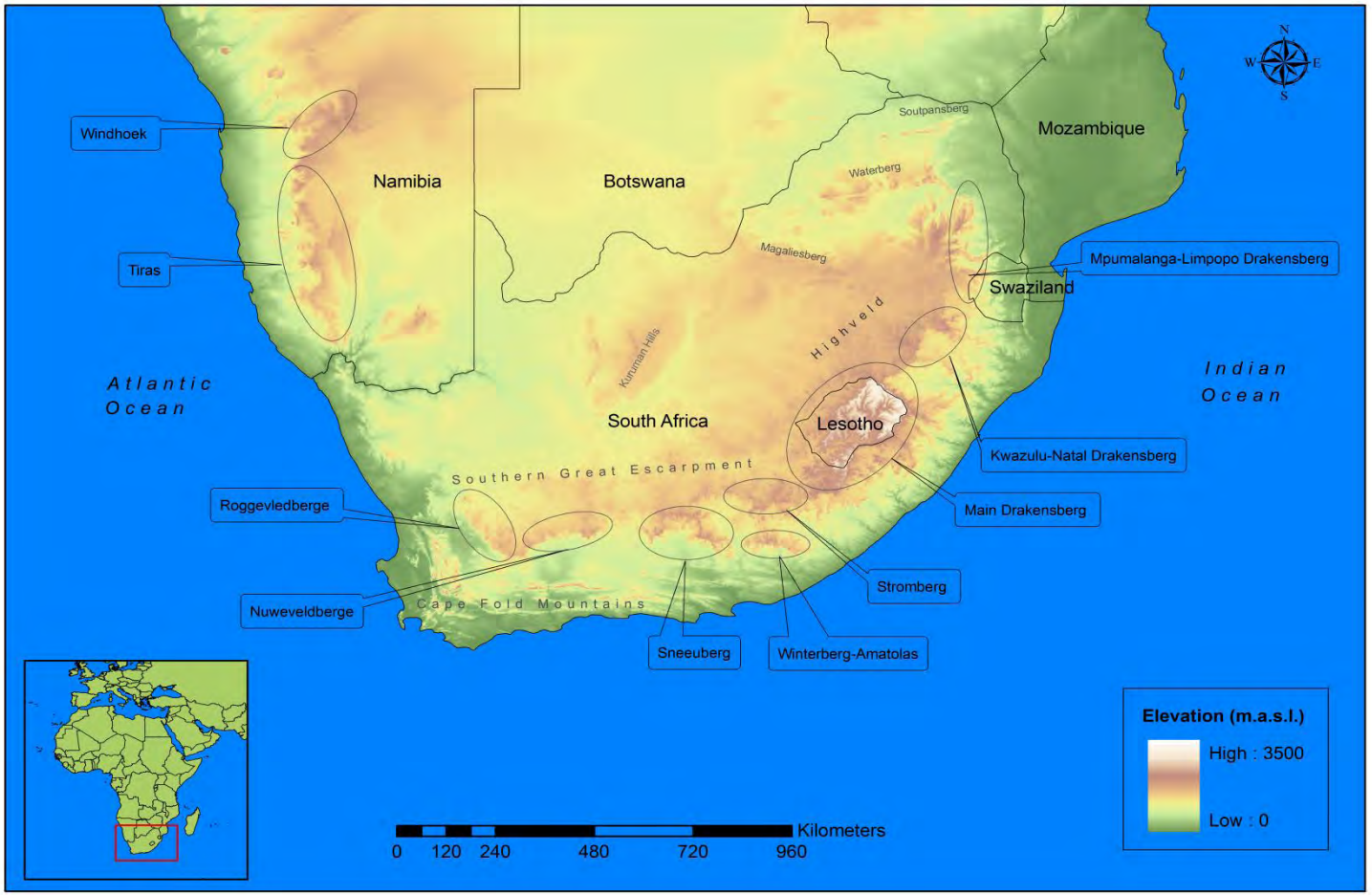

Figure 1.1: Topographical map of southern Africa indicating the mountain ranges that constitute the Great Escarpment of South Africa. Other major mountain ranges outside of the Great Escarpment are also shown. GIS data source: GeoNetwork (2000). (ArcGIS 9.3; map units: decimal degrees; not projected).

CHAPTER 2

GENERAL DESCRIPTION OF STUDY SITES AND METHODOLOGY

2.1 Sneeuberg mountain complex

Location

The Sneeuberg mountain complex (hereon referred to as SMC) consists of a collection of mountain ranges that form an arc roughly 200km in length (Figure 2.1; Clark *et al.* 2009). The SMC is located at the meeting point of the Eastern, Northern and Western Cape Provinces of South Africa. The larger part of the SMC is situated in the Eastern Cape Province. This complex was first defined by Clark *et al.* (2009), and will be used as a collective reference for the smaller mountain ranges that occur within the area. From West to East these mountain ranges include the Onder-Sneeuberg, Toorberg, Winterhoekberge, Sneeuberge, Renosterberg, Agter-Renosterberg, Joubertsberg, Wapadsberg, Coetzeesberg, Bankberg and Boschberg (Figure 2.1; Clark *et al.* 2009). The complex is separated from the western escarpment (Nuweveldberge) by the Nelspoort Interval (Nordenstam 1969; Clark *et al.* 2009) and the eastern escarpment by the Great Fish River Interval (Phillipson 1987; Clark *et al.* 2009).

Study sites were selected based upon their average altitude and land-use type. It was essential that each site had high altitudinal areas (> 1700 metres above sea level (m)), large enough to accommodate the transects required for small mammal trapping (see section 2.5 for further details on the trapping protocol). In addition,

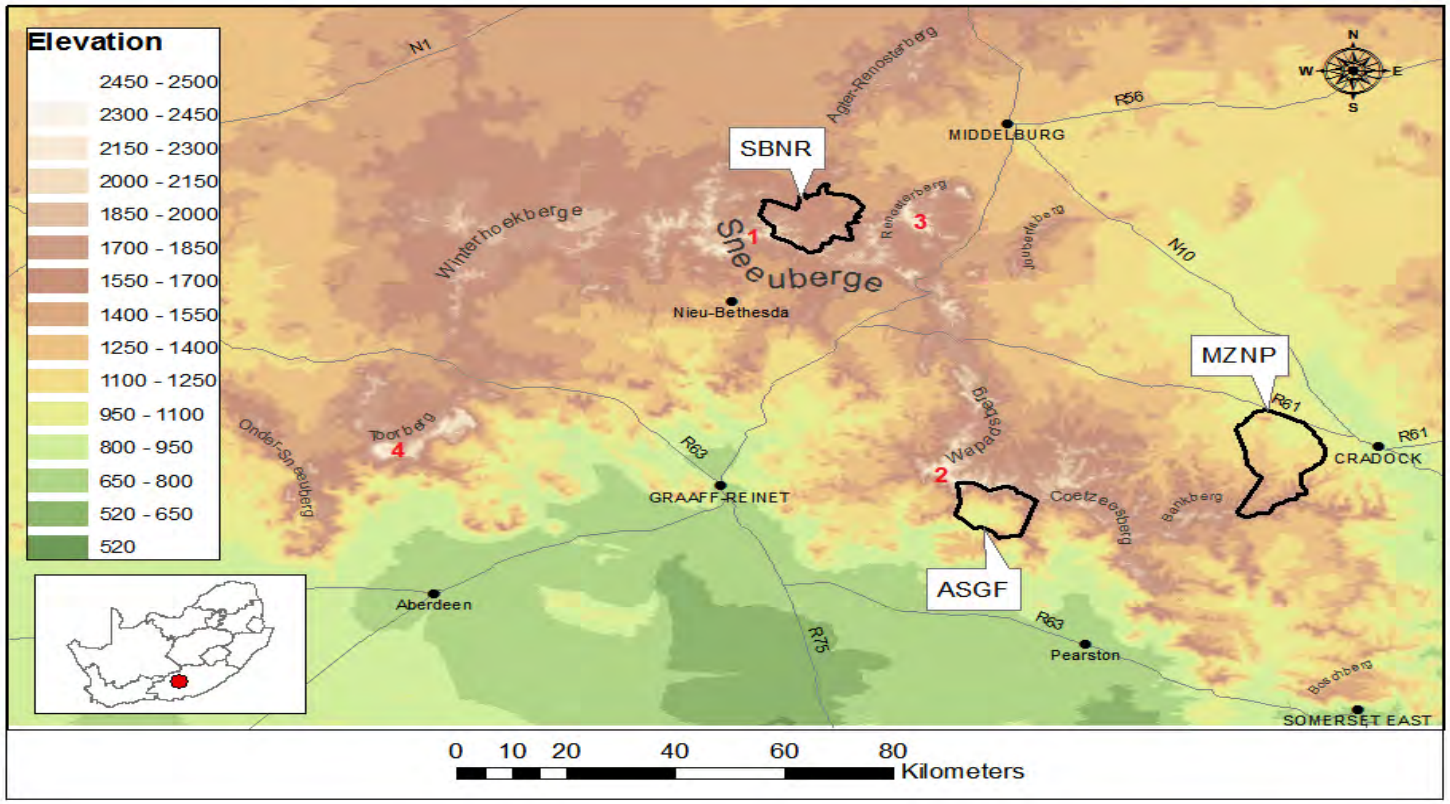

Figure 2.1: Topographical map of the Sneeuberg Mountain Complex, depicting the smaller mountain ranges and the location of three study sites (SBNR = Sneeuberg Nature Reserve; ASNR = Asante Sana Private Nature Reserve; MZNP = Mountain Zebra National Park) (ArcGIS 9.3; map units: decimal degrees; not projected). Numbers 1 to 4 indicate positions of the highest peaks in the SMC (1. Compassberg (2504 m), 2. Nardousberg (2490 m), 3. Renosterberg (2298 m) and 4. Toorberg (2278 m).

easy access to these high altitude areas, by means of a 4x4 vehicle, was important as this facilitated the transportation of important equipment (e.g. Sherman traps). Due to the decline of small mammal diversity at sites where grazing pressure by livestock is high (Eccard *et al.* 2000; Hoffmann & Zeller 2005; Yarnell *et al.* 2007), I chose study sites where grazing pressure was minimal (e.g. conservation areas). Based on the above criteria, three sites were selected for my study. These sites were located in the eastern section of the SMC (Figure 2.1) and were; Sneeuberg Nature Reserve (SBNR) 31º42'S, 24º38'E, situated 35km north-east of Nieu-Bethesda (Figure 2.1); Asante Sana Private Nature Reserve (ASNR) 32º14'S, 24º55'E, situated 50km east of Graaff-Reinet (Figure 2.1); and Mountain Zebra National Park (MZNP) 32º18'S, 25º24'E, situated 15km west of Cradock (Figure 2.1). To ensure that sites were statistically independent, they were separated by intervals that were greater than 40km (Figure 2.1).

General Climate

The SMC is situated in a transitional rainfall zone, where rainfall is highest during either summer, autumn or both (Kopke 1988; Clark *et al.* 2009). Precipitation throughout the SMC is very localized, and heavily dependant on altitude (Van der Walt 1980; Kopke 1998; Clark *et al.* 2009). Higher altitude areas are known to have higher mean annual precipitation, compared to the surrounding lowlands (Van der Walt 1980; Pond *et al.* 2002; Mucina & Rutherford 2006; Clark *et al.* 2009). For example, the mean annual ten-year (2001-2010) precipitation for Graaff-Reinet (760 m) was 282 mm, while it was 517 mm at Compassberg farm (1700 m; Boardman *et al.* 2003). A west-east rainfall gradient is present in the higher altitude areas in the

SMC, where mountains in the east receive more annual precipitation (~600mm) than the mountains in the west (~ 500mm; Clark *et al.* 2009). Other forms of precipitation in the SMC include hail (Van der Walt 1980), mist (Pond *et al.* 2002) and regular snowfalls during the colder months of the year (Van der Walt 1980; Mucina & Rutherford 2006; Clark *et al.* 2009).

The SMC is situated within a temperate climate zone (Kopke 1988). Maximum temperatures in summer vary from 23-28°C and in winter from 16-23°C (De Klerk *et al.* 2001). Minimum temperatures vary between 6-14°C in summer, and 0-8°C in winter (De Klerk *et al.* 2001). However, due to the inverse relationship between altitude and temperature, the high mountainous areas tend to be cooler than the surrounding lowland areas (Van der Walt 1980; Kopke 1988). The higher peaks within the SMC are known to have unique microclimates that are characterised by colder temperatures (as low as -10°C) and stronger winds (Boardman *et al.* 2003; Clark *et al.* 2009).

Vegetation Units

Six of South Africa's eight biomes are represented within the SMC (Clark *et al.* 2009), because of climatic, geological and topographical transitions (Cowling 1983; Vlok *et al.* 2003). These biomes are the Grassland, Nama-Karoo, Thicket, Fynbos, Forest and Azonal vegetation. Due to the overlap of various vegetation units among the three study sites, selected vegetation units (Karoo Escarpment Grassland, Upper Karoo Hardeveld, Eastern Upper Karoo, Southern Karoo Riviere, Eastern Cape Escarpment Thicket and Camdeboo Escarpment Thicket) will be described in more detail below to avoid unnecessary repetition of vegetation descriptions for each site.

Karoo Escarpment Grassland is the most abundant grassland vegetation unit in the SMC (Mucina & Rutherford 2006; Clark *et al.* 2009). This vegetation type generally occurs in a broad altitudinal range (1100-2504 m; Mucina & Rutherford 2006). Common grass species include *Merxumuellera disticha, Eragrostis chloromelas, Aristida congesta, Targus koelerioides, Themeda triandra* and *Karroochloa purpurea* (Mucina & Rutherford 2006).

The Upper Karoo Hardeveld is one of the richer floras of the Nama-Karoo biome and consists of a mixture of dwarf Karoo shrubs and drought-tolerant grasses that occur on steep slopes (Mucina & Rutherford 2006; Clark *et al.* 2009). Characteristic species are *Lycium cinereum, Euryops lateriflorus, Chrysocoma ciliata, Aristida diffusa, Eragrostis curvula* and *Stipagrostis ciliata* (Mucina & Rutherford 2006).

The Eastern Upper Karoo vegetation unit occurs on plains and gently sloping hills in the northern sections of the SMC (Mucina & Rutherford 2006). Microphyllous shrubs, together with grasses from the genera *Aristida* and *Eragrostis* (Mucina & Rutherford 2006), dominate this vegetation type.

The Southern Karoo Riviere vegetation type is embedded within the southern parts of the Eastern Upper Karoo, where it occurs mainly in drainage lines between 250-1550 m (Mucina & Rutherford 2006). Common species include *Acacia karroo, Tamarix usneoides, Leucosidea sericea, Rhamus prunoides* and *Ehrharta erecta* (Van der Walt 1980; Mucina & Rutherford 2006).

Eastern Cape Escarpment Thicket is distributed along the steep northern and southern slopes of the Bankberg and Boschberg (Mucina & Rutherford 2006, Clark *et al.* 2009). Common species include *Olea europaea* subsp*. africana, Acacia natalitia, A. karroo, Euphorbia tetragona* and *Rhus lucida* (Mucina & Rutherford 2006).

Camdeboo Escarpment Thicket occurs on the south-sloping faces of the SMC at low elevations (700-1200 m) between Aberdeen and Pearston (Mucina & Rutherford 2006; Clark *et al.* 2009). Characteristic species are *Portulacaria afra, A. karroo, Euclea crispa* and *Aloe ferox* (Mucina & Rutherford 2006; Clark *et al*. 2009).

General Topography and Geology

The sedimentary rocks of the Beaufort Group dominate the geology of the SMC, which is part of the Karoo Supergroup (Van der Walt 1980; De Klerk *et al.* 2001; Johnson *et al.* 2006). These Beaufort sandstones, mudstones and shales belong to the Late Permian Adelaide Subgroup, which includes the Koonap, Middleton, Balfour, Abrahamskraal, and Tweekloof formations (Johnson *et al.* 2006). Igneous rocks have intruded into sediments of the older Beaufort Group at various localities in the SMC, during the Jurassic Period, in the form of dolerite sills (Van der Walt 1980; De Klerk *et al.* 2001; Duncan & Marsh 2006; Clark *et al.* 2009).

Stream erosion and scarp succession is the main geomorphological process responsible for the current topography of the Great Escarpment (Partridge & Maud 1987; Moore & Blenkinsop 2006; Clark *et al.* 2009). Large south flowing rivers (Sundays, Great Fish, Kei, Mbashe) have caused the headward erosion of the Great Escarpment, forcing the scarp to retreat inland by some 150km (Nicol 1988). In addition, the Sundays River and its tributaries have caused the scarp to retreat a further 60km in the SMC, giving rise to the current arc shaped outline of the complex (Clark *et al.* 2009). The present continental watershed runs from the Winterhoekberge West towards the Compassberg, northeast along the Agter-Renosterberg and East along the Suurberg before reaching the Central Drakensberg Mountains (Figure 2.1; Clark *et al.* 2009). Furthermore, this steam erosion process

is responsible for the dissection of the landscape into various smaller mountains (Clark *et al.* 2009).

The SMC contains some of the highest mountain peaks west of the Eastern Cape Drakensberg Mountains (Clark *et al.* 2009). The four highest peaks within the area include the Compassberg, Nardousberg, Renosterberg and Toorberg (Figure 2.1; Clark *et al.* 2009).

2.2 SNEEUBERG NATURE RESERVE

Site description and history

The SBNR is a private reserve dedicated to the conservation of biodiversity. Initially the first land was for conservation was bought in 1999, while the last big cattle were removed from the reserve in 2006. The reserve is 14 500Ha in size, with a perimeter of roughly 70km. Prior to the establishment of the reserve it was used for cattle (*Bos* spp.) and sheep (*Ovis* spp.) farming. Various antelope black wildebeest (*Connochaetes gnou*), springbok (*Antidorcas marsupialis*), red hartebeest (*Alcelaphus buselaphus*), blesbok (*Damaliscus pygargus*) and Burchell's zebra (*Equus zebra*) have been re-introduced to the reserve. The upper carrying capacity of the reserve is 900 large stock units (as determined by the Grootfontein Agricultural Development Institute, Middleburg, South Africa). The Klein Seekoei River bisects the reserve and runs towards the North (Figure 2.2). Sample sites within the reserve were located in the southwestern highlands at altitudes between 1750-2120 m (Figure 2.2).

Climate

Although rainfall data were available for the SBNR, no temperature data existed. Thus, the temperature data for Graaff-Reinet (closest weather station to SBNR), provided by the South African Weather Service, was used to describe temperature trends.

The SBNR is situated in an area where rainfall mostly occurs in summer and autumn, with the highest rainfall occurring in March (Figure 2.3; Kopke 1988; Mucina & Rutherford 2006). A similar trend was observed during the study period (2009-2010), where rainfall was highest during February 2009 (144 mm), March 2009 (89

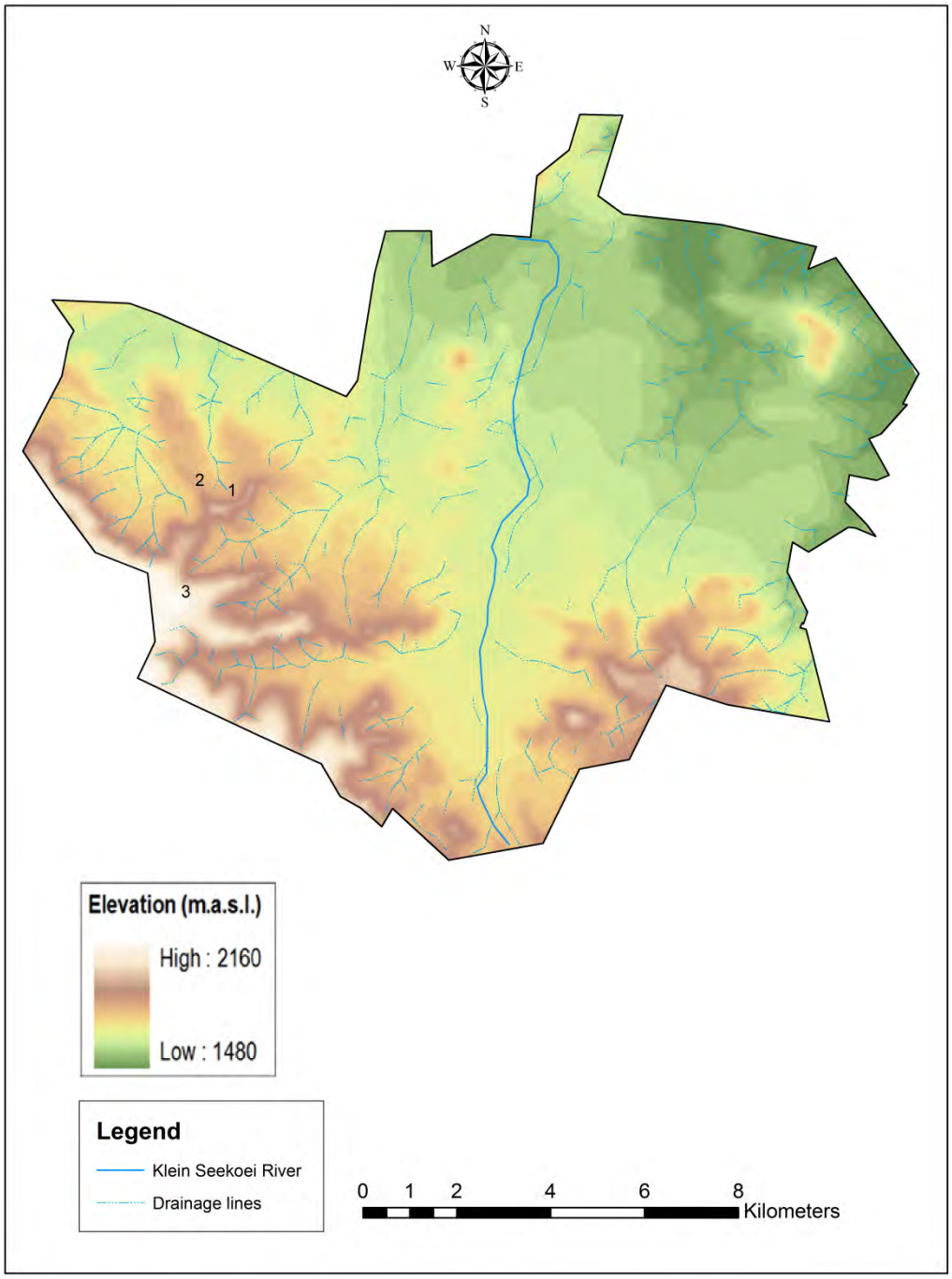

Figure 2.2: The topography and drainage patterns of the Sneeuberg Nature Reserve (SBNR) (ArcGIS 9.3; map units: decimal degrees; not projected). Numbers (1, 2, 3) depict the position of transects.

mm) and January 2010 (172 mm; Figure 2.3). However, rainfall also peaked in October 2009 (110 mm). Rainfall was lowest from April-August 2009 (Figure 2.3). The total rainfall during 2009 (563 mm) was higher than the ten-year mean rainfall (413 ± 118 mm) observed for SBNR (Figure 2.4). In contrast, during 2010 total rainfall (398mm) was slightly lower than the ten-year mean annual precipitation (Figure 2.4).

Coinciding with the temperate climate of the southern hemisphere, the mean, maximum ten-year (2001-2010) temperatures were highest during summer (December to February) and lowest during June and July (Figure 2.5). During the study period (2009-2010) extreme temperatures ranged from a maximum of 41.9°C (December 2009) to minimum of -5.3°C (July 2009). The hottest month during the study period was January 2009, while the coldest month was July 2009 (Figure 2.6). There were 31 frost days (days with temperatures below 0°C) during 2009 and three during 2010.

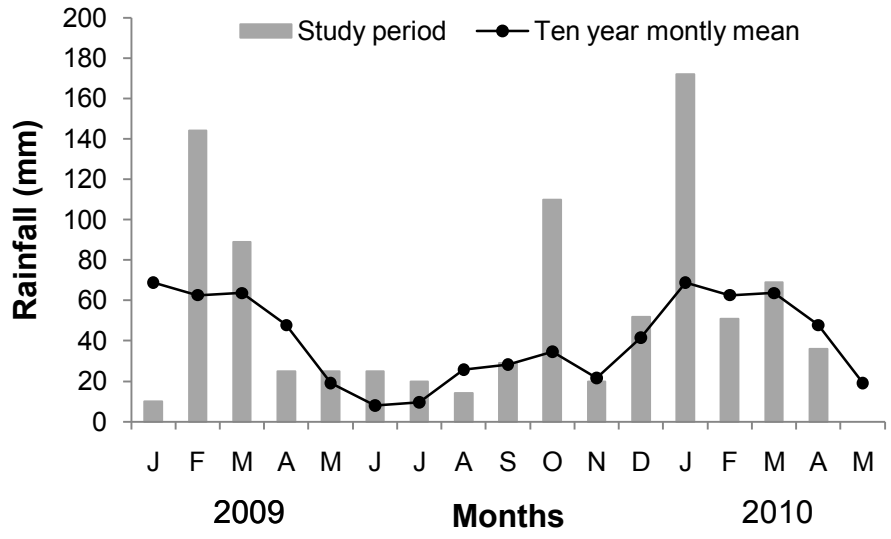

Figure 2.3: Total monthly precipitation during the study period (2009-2010) at Sneeuberg Nature Reserve (SBNR) in relation to the ten-year monthly mean.

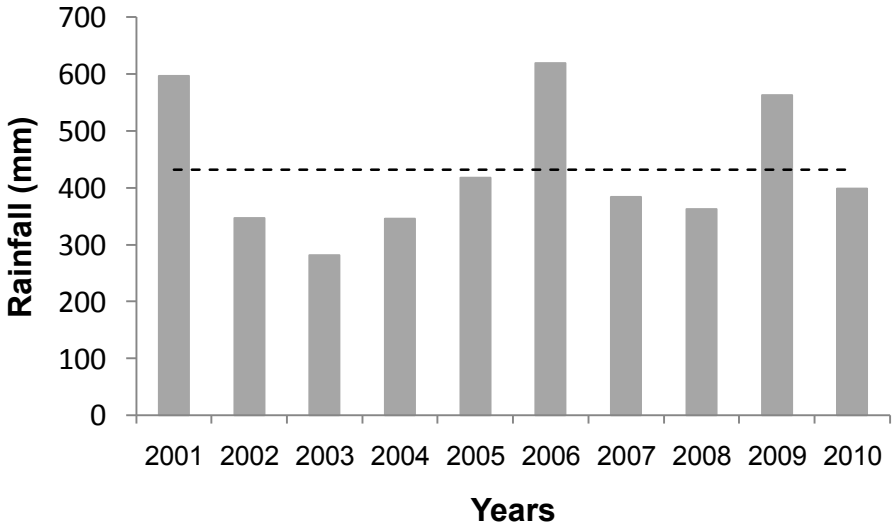

Figure 2.4: The annual precipitation for Sneeuberg Nature Reserve (SBNR) over a ten-year period (2001-2010). The dashed line indicates mean annual precipitation for the ten-year period.

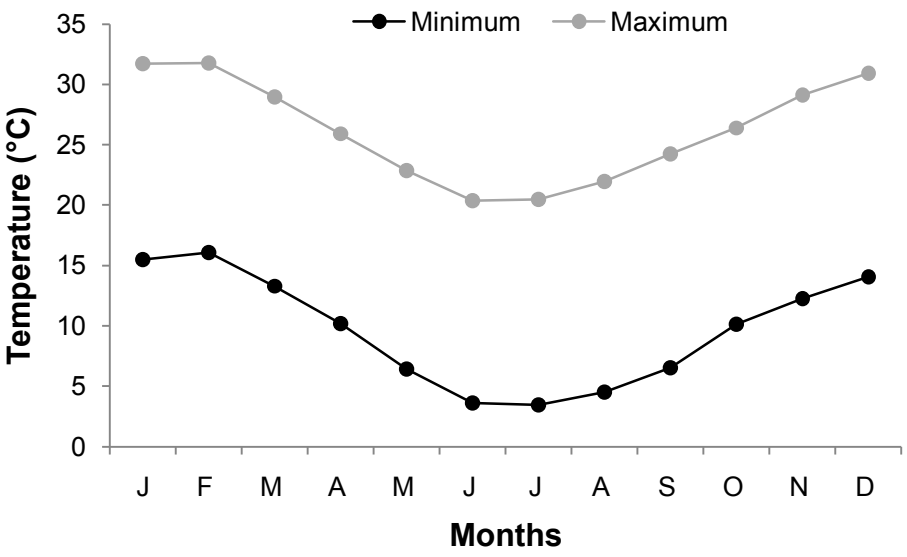

Figure 2.5: The mean monthly minimum and maximum temperatures for Graaff-Reinet during a ten-year period (2001-2010).

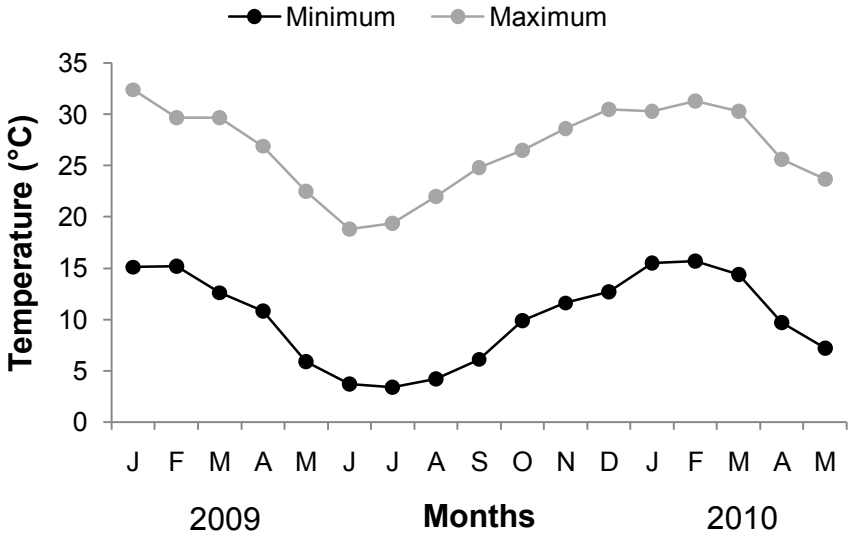

Figure 2.6: The mean monthly minimum and maximum temperatures from Graaff-Reinet during the study period (2009-2010).

Vegetation

Four major vegetation units are represented within the SBNR; Southern Karoo Riviere, Karoo Escarpment Grassland, Upper Karoo Hardeveld and Eastern Upper Karoo (Figure 2.7; Mucina & Rutherford 2006). The Eastern Upper Karoo dominates the lower lying areas within the reserve, while the Upper Karoo Hardeveld (Figure 2.7) dominates the higher altitude (> 1700 m) areas. Examples of the vegetation and general habitat for each transect at SBNR are provided in Figure 2.8.

Topography

The SBNR forms part of the central Sneeuberg Mountains of the SMC (Figure 2.1). Altitude ranges from 1480 m to 2160 m on the reserve (Figure 2.2). About 2500Ha of the reserve is located above 1800 m. These high altitude areas are mostly located in the southern section of the reserve (Figure 2.2). The Compassberg lies roughly 10km south-west of the highest point in the reserve.

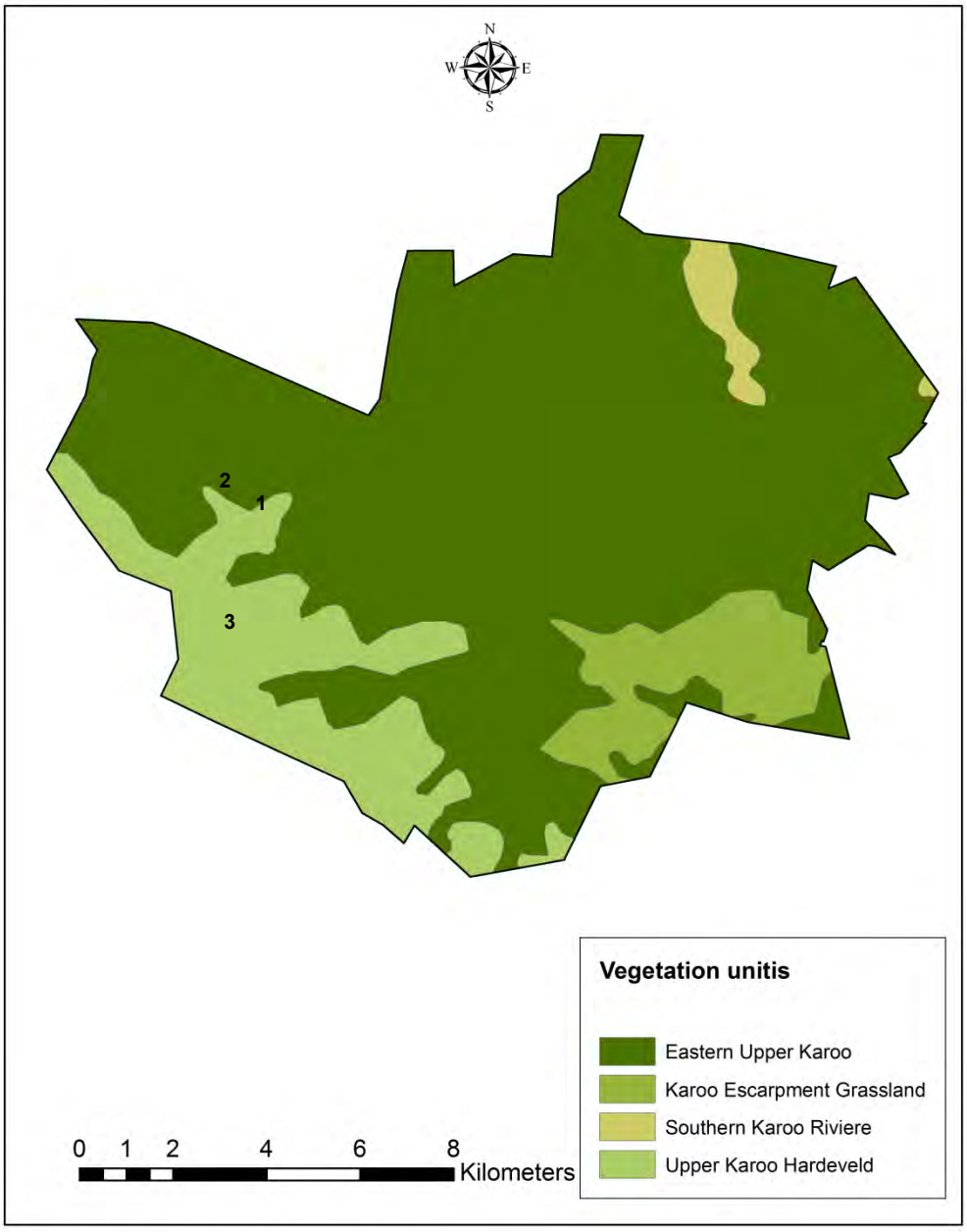

Figure 2.7: Vegetation map of the Sneeuberg Nature Reserve (SBNR), depicting the four vegetation units present on the reserve (ArcGIS 9.3; map units: decimal degrees; not projected; Mucina & Rutherford 2006). Numbers (1, 2, 3) depict the position of transects.

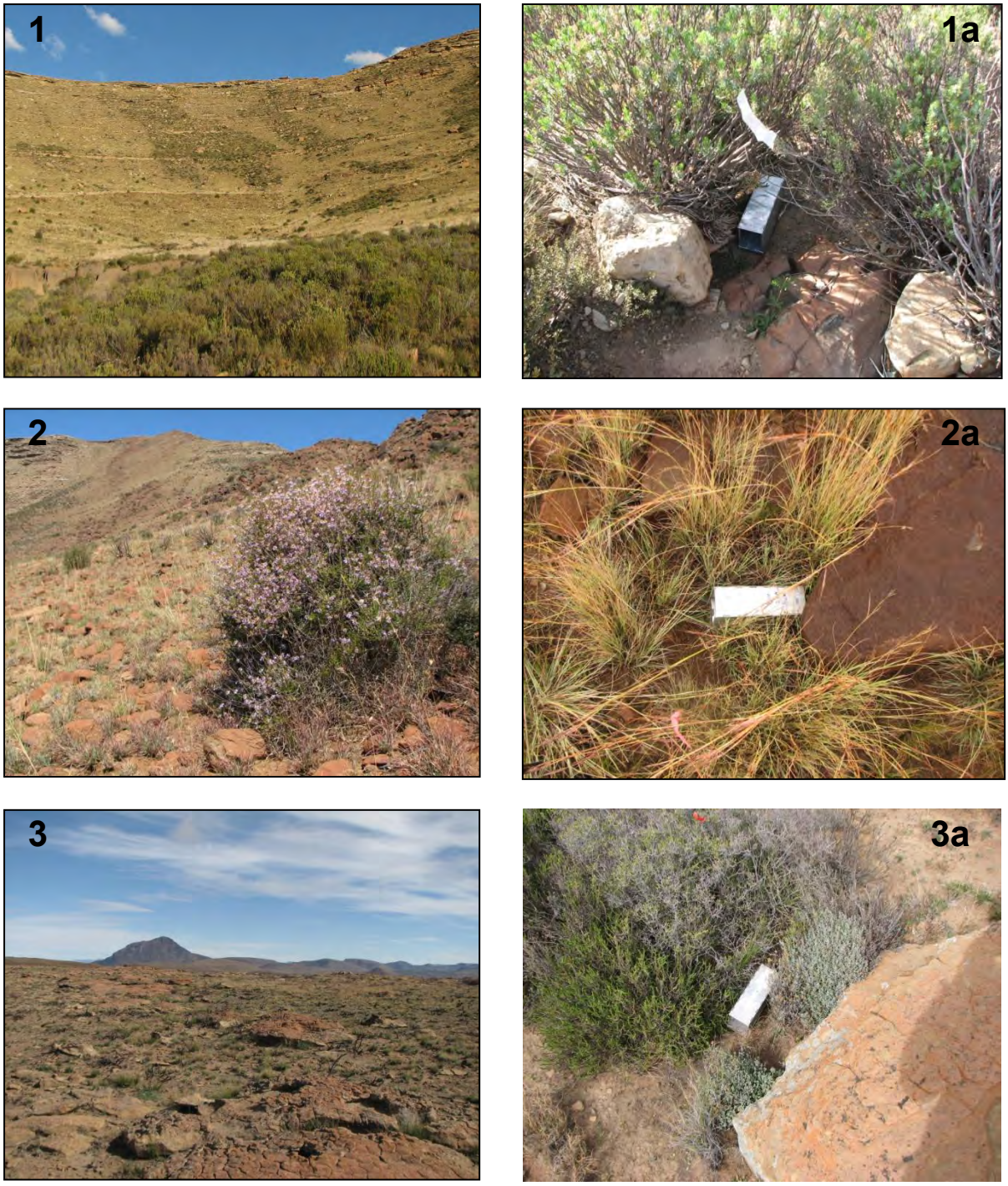

Figure 2.8: Photographs of the three habitats sampled (1, 2, 3) from Sneeuberg Nature Reserve (SBNR); together with close up photographs of selected trap stations (1a, 2a, 3a). Transect numbers coincide with numbers found on figures 2.2 and 2.7. (1 = Transect 1 (1750-1850masl); 2 = Transect 2 (1800-1850masl); 3 = Transect 3 (2150masl).

2.3 ASANTE SANA PRIVATE NATURE RESERVE

Site description and history

The ASNR is a privately owned hunting and game reserve ~10 700Ha in size. Prior to the establishment of the reserve, it was utilized as a series of small livestock farms. However, in 1995, these smaller farms were de-stocked, their internal fences removed and a 66km electric game fence erected. Thereafter, various antelope (kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), lechwe (*Kobus luche* a species that's not native in South Africa) and springbok) and other big game species (elephant (*Loxodonta africana*), white rhinoceros (*Ceratotherium simum*), African buffalo (*Syncerus caffer*), and giraffe (*Giraffa camelopardalis*)) were introduced onto the reserve. There are two perennial streams on the reserve, the Waterkloof and the Suurkloof. In addition, this site is also the source of the intermittent Milk River that flows West where it eventually joins the Sundays River (Figure 2.9). Sample sites were located in the northwestern highlands at altitudes of between 2050-2220 m (Figure 2.9).

Climate

Only five years of rainfall data for ASNR could be obtained to describe the precipitation of the site. Therefore, long-term rainfall and temperature data from the South African Weather Service for Graaff-Reinet (closest weather station to ASNR) were again used describe the overall the climate. Because the rainfall and temperature trends are the same as those described in section 2.2.2, they will not be repeated here.

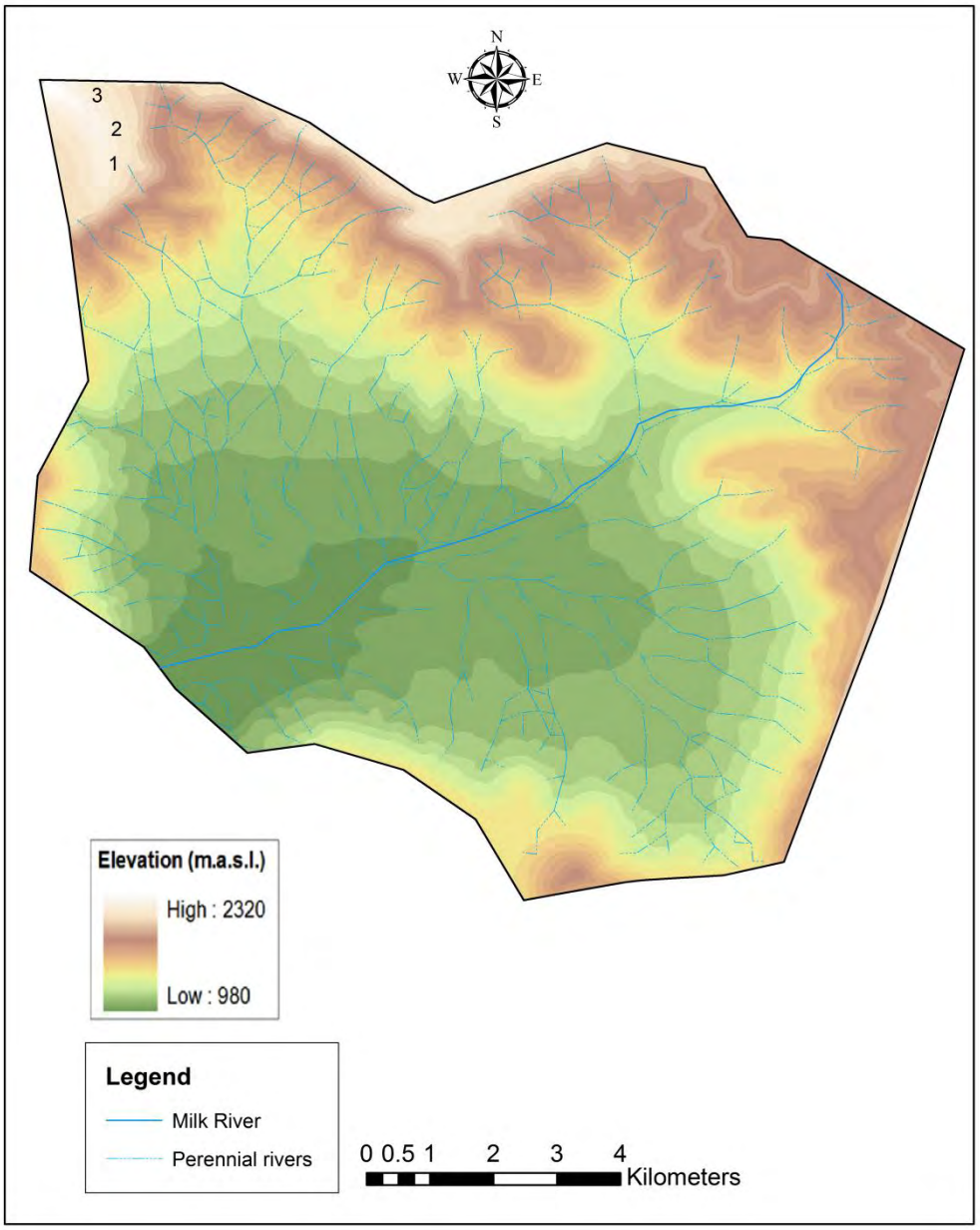

Figure 2.9: The topography and drainage patterns of the Asante Sana Private Nature Reserve (ASNR) (ArcGIS 9.3; map units: decimal degrees; not projected). Numbers (1, 2, 3) depict the position of transects.

The mean annual precipitation for the ten-year period (2001-2010) was 287 mm, the lowest for all three-study sites (Figure 2.10). Annual precipitation for Graaf-Reinet in 2009 (288 mm), and 2010 (244 mm) did not differ much from the mean annual precipitation for the ten-year period for Graaff-Reinet (2001-2010) (Figure 2.10).

There is a very slight seasonal pattern in the ten-year (2001-2010) mean monthly rainfall for Graaff-Reinet, where more rainfall occurs during the warmer months (November to March; Figure 2.10; Kopke 1988). However, the monthly precipitation during the study period was much more variable (Figure 2.11). Highest monthly precipitation was recorded during the months of February 2009 (123 mm), August 2009 (68 mm), January 2010 (108 mm) and March 2010 (66 mm; Figure 2.10). By contrast, the lowest monthly precipitation was recorded during January 2009 (15 mm), March 2009 (12 mm) and May 2010 (7 mm). No rain was recorded during May, September, October and November in 2009 (Figure 2.11).

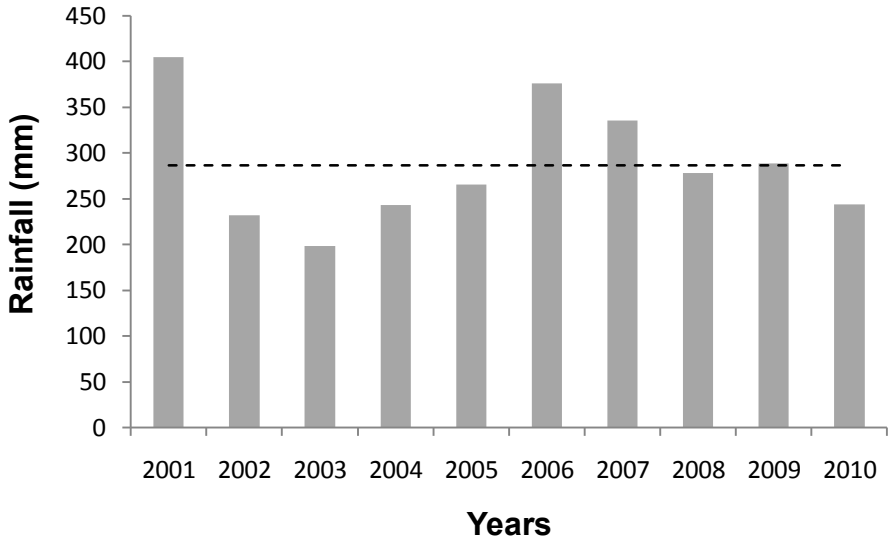

Figure 2.10: The annual precipitation for Graaff-Reinet over a ten-year period (2001-2010). The dashed line indicates mean annual precipitation for the ten-year period.

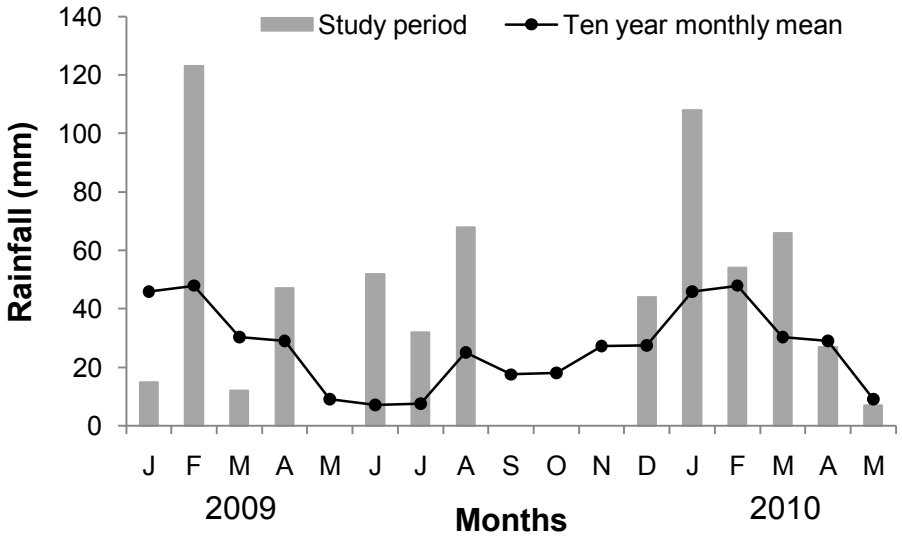

Figure 2.11: Total monthly precipitation during the study period (2009-2010) at Asante Sana Private Nature Reserve (ASNR; bars) in relation to the ten-year mean monthly precipitation at Graaff-Reinet (line).

Vegetation

The vegetation at ASNR consists of two major vegetation units, Karoo Escarpment Grassland and Camdeboo Escarpment Thicket (Figure 2.12; Mucina & Rutherford 2006). These vegetation units roughly coincide with the altitudinal ranges found throughout the park. The Karoo Escarpment Grassland is associated with higher (> 1300 m) altitude and Camdeboo Escarpment Thicket with lower (< 1300 m) altitudes (Figure 2.9 & 2.12). Examples of the vegetation and general habitat for each transect at SBNR are provided in Figure 2.13.

Topography

The ASNR is situated in a broad valley at the edge of the Great Escarpment, between the Wapadsberg and Coetzeesberg, immediately southeast of the Nardousberg (Figure 2.1). Except for a small section in the south-west, the site is almost completely surrounded by mountains (Figure 2.8). Altitude ranges from 2320 m at the highest point to 980 m on the valley floor (Figure 2.8).

Figure 2.12: Vegetation map of the Asante Sana Private Nature Reserve (ASNR), depicting the two major vegetation units present on the reserve (ArcGIS 9.3; map units: decimal degrees; not projected; Mucina & Rutherford 2006). Numbers (1, 2, 3) depict the position of transects.

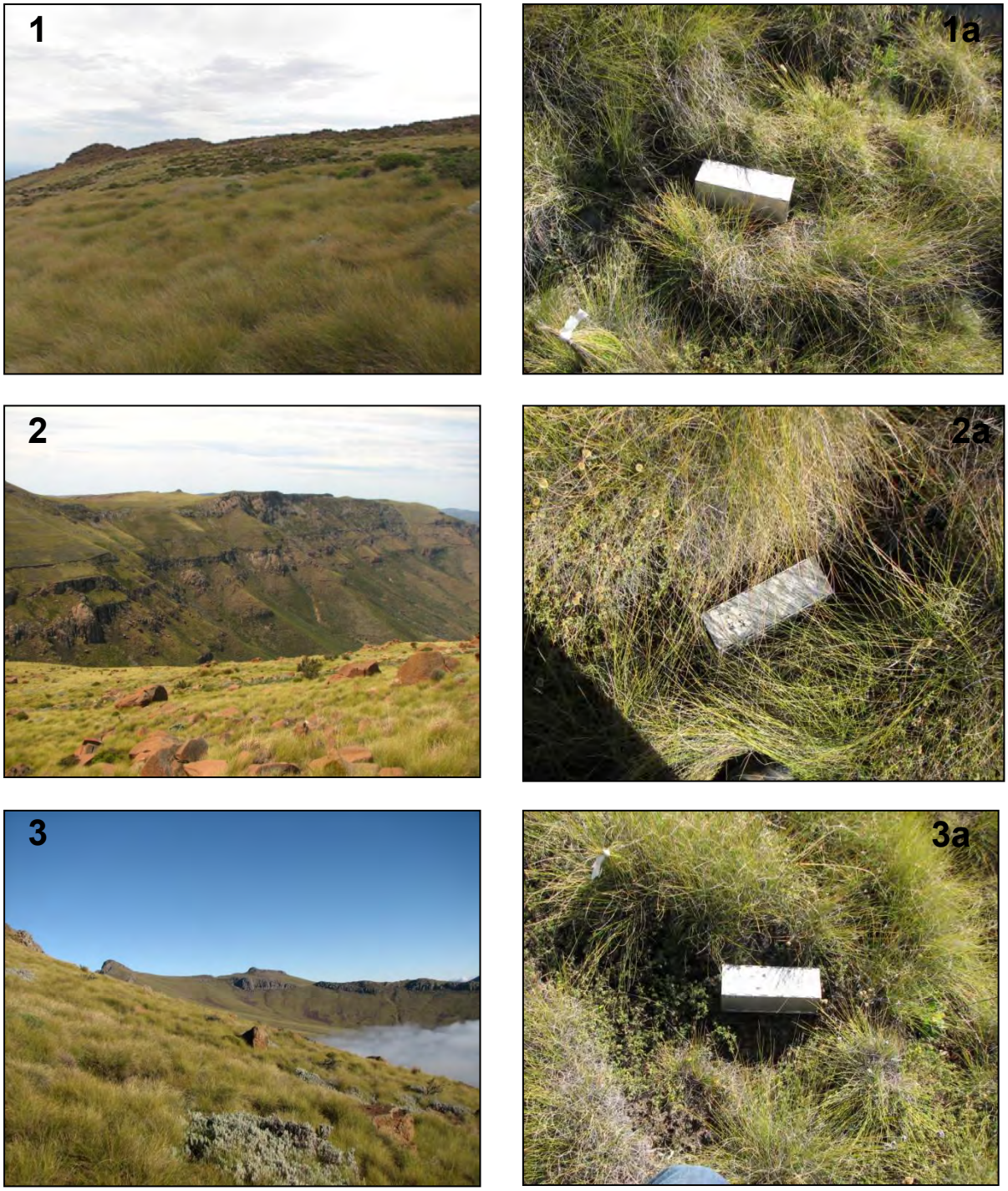

Figure 2.13: Photographs of the three habitats sampled (1, 2, 3) from Asante Sana Private Nature Reserve (ASNR); together with close up photographs of selected trap stations (1a, 2a, 3a). Transect numbers coincide with numbers found on figures 2.9 and 2.12. (1 = Transect 1 (2150masl); 2 = Transect 2 (2050-2150masl); 3 = Transect 3 (2050-2250masl).

2.4 MOUNTAIN ZEBRA NATIONAL PARK

Site description and history

The MZNP is the oldest conservation area within the SMC, as the park was proclaimed as a nature reserve in 1937 with the aim of conserving the remaining population of 11 Cape mountain zebra (*Equus zebra zebra*) in an area of 1712Ha (Brown & Bezuidenhout 2000; De Klerk *et al.* 2003; Brown & Bezuidenhout 2005; Bezuidenhout & Brown 2008). However, the initial area of the park was too small to sustain the increasing population of Cape mountain zebra (De Klerk *et al.* 2003; Brown & Bezuidenhout 2005). Consequently, the size of the park was increased to 6536Ha in 1964 (Brown & Bezuidenhout 2000; Pond *et al.* 2002; De Klerk *et al.* 2003; Brown & Bezuidenhout 2005; Bezuidenhout & Brown 2008). Since 1996 the size of the park has increased more than fourfold (28 412Ha), due to the procurement of neighbouring farms that have been incorporated into the park (Brown & Bezuidenhout 2000; De Klerk *et al.* 2003; Brown & Bezuidenhout 2005; Bezuidenhout & Brown 2008). The intermittent Wilgerboom River, a tributary of the Great Fish River, runs from south to north throughout the park (Figure 2.14; Van der Walt 1980; Pond *et al.* 2002; De Klerk *et al.* 2003). Sample sites were located in the south-eastern corner at altitudes between 1750-1820 m. (Figure 2.14).

Climate

Data from the MZNP weather station were used to describe the climate of the park. However, long-term temperature data was not available for the park prior to 2007. Therefore, the data for Cradock were used (provided by the South African Weather Service). These data were used to calculate the ten-year mean maximum and minimum temperatures. All other data are from the MZNP weather station.

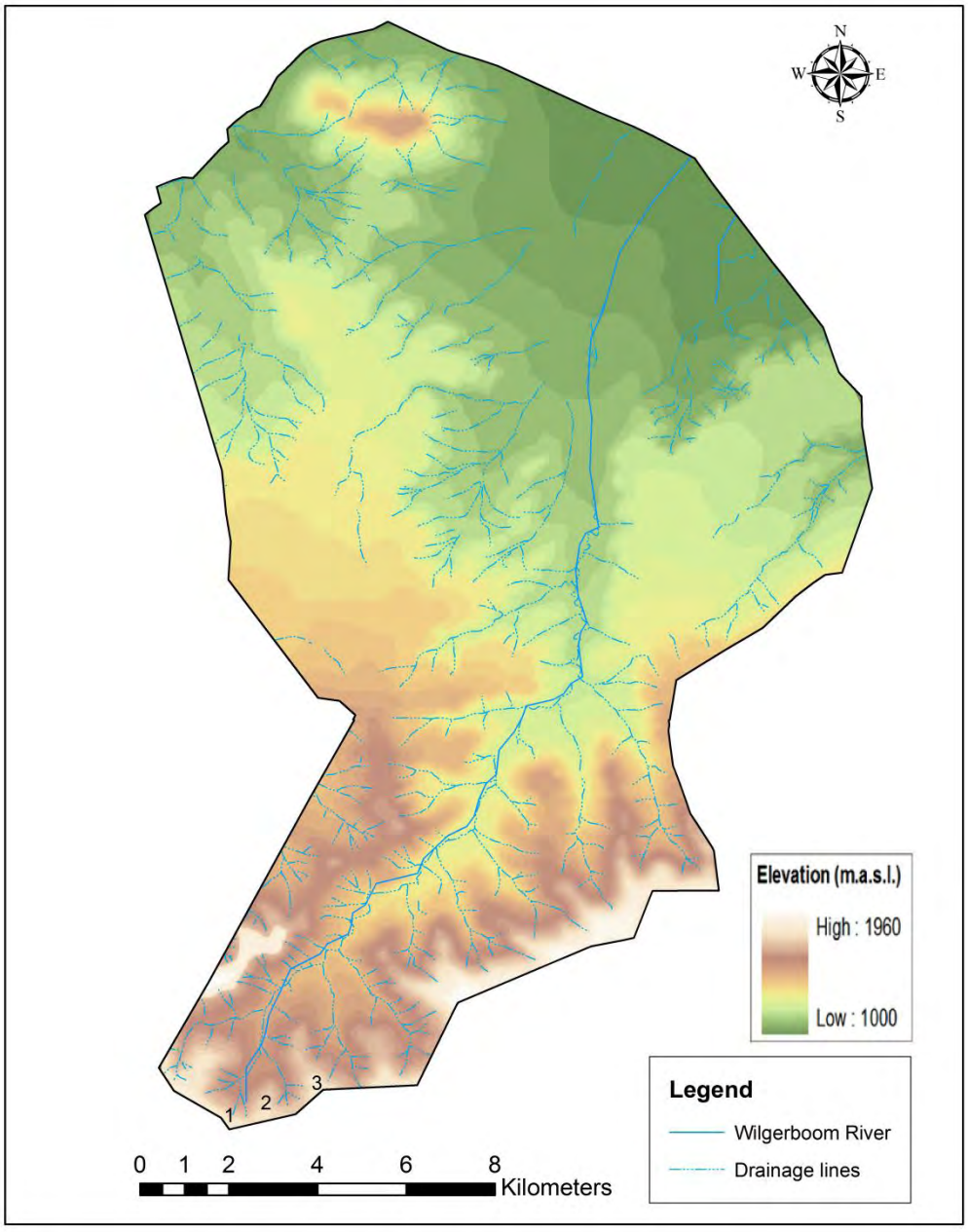

Figure 2.14: The topography and drainage patterns of the Mountain Zebra National Park (MZNP) (ArcGIS 9.3; map units: decimal degrees; not projected). Numbers (1, 2, 3) depict the position of transects.

The MZNP is situated in the summer rainfall region of South Africa (Van der Walt 1980; Kopke 1988; Pond *et al*. 2002; Brown & Bezuidenhout 2005). Mean monthly precipitation at MZNP increases steadily from August to its peak in February, thereafter, it drops sharply (Figure 2.13). During the study period rainfall peaked during February 2009 (148 mm) and January 2010 (120 mm; Figure 2.15). Rainfall was lowest during September 2009 (0 mm) and May 2010 (4 mm). The mean annual precipitation for MZNP during the ten-year period (2001-2010) was 422 mm (Figure 2.16) and the total rainfall during my study was similar (Figure 2.16).

The mean monthly minimum and maximum temperatures for a ten-year (2001-2000) period indicate that MZNP has a temperate climate (Figure 2.17; Van der Walt 1980; Kopke 1988 Pond *et al.* 2002). The months of January and February (in both 2009 and 2010) were the hottest during the study period (Figure 2.18). July 2009 was the coldest month during the study period (-0.6°C; Figure 2.18). Extreme temperatures during the study period at MZNP ranged from a high of 39.5°C to a low of -9°C. The Bankberg, which runs along the southern boundary, is believed to play an important role in the regulation of the microclimate of the park, as it acts as a buffer to cold fronts (Van der Walt 1980, Pond *et al.* 2002). Consequently, extremely cold conditions are not common in the lower lying parts of the park (Van der Walt 1980; Pond *et al.* 2002). Thirty-three days with frost were recorded between May 2009 and September 2009.

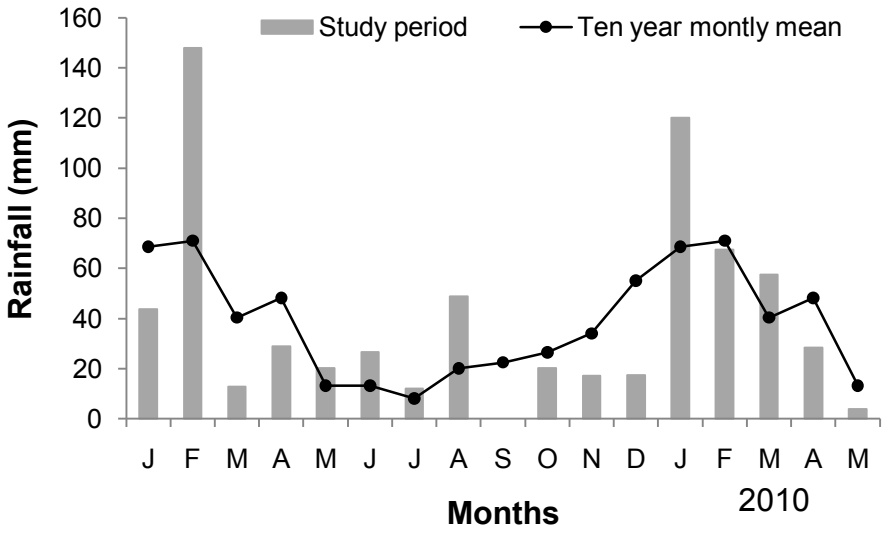

Figure 2.15: Total monthly precipitation during the study period (2009-2010) at the Mountain Zebra National Park (MZNP) in relation to the ten-year monthly mean.

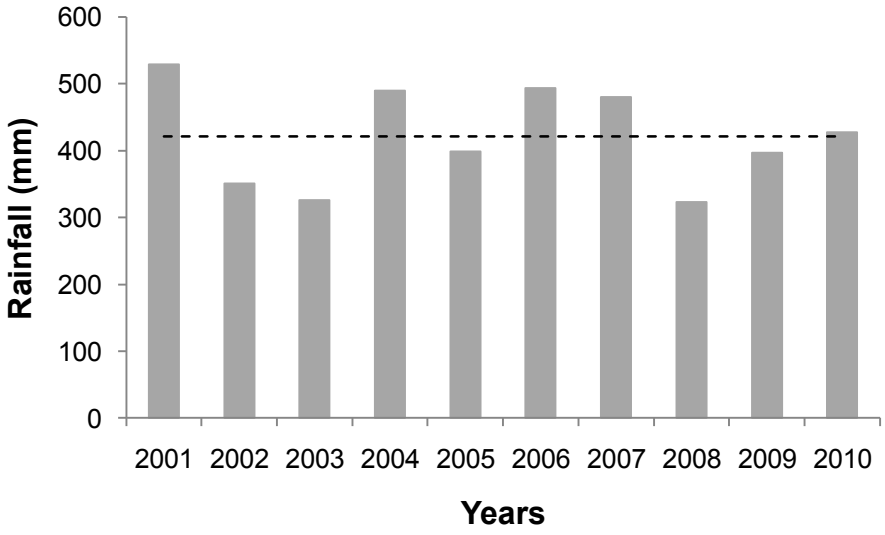

Figure 2.16: The annual precipitation for the Mountain Zebra National Park (MZNP) over a ten-year period (2001-2010). The dashed line indicates mean annual precipitation for the ten-year period.

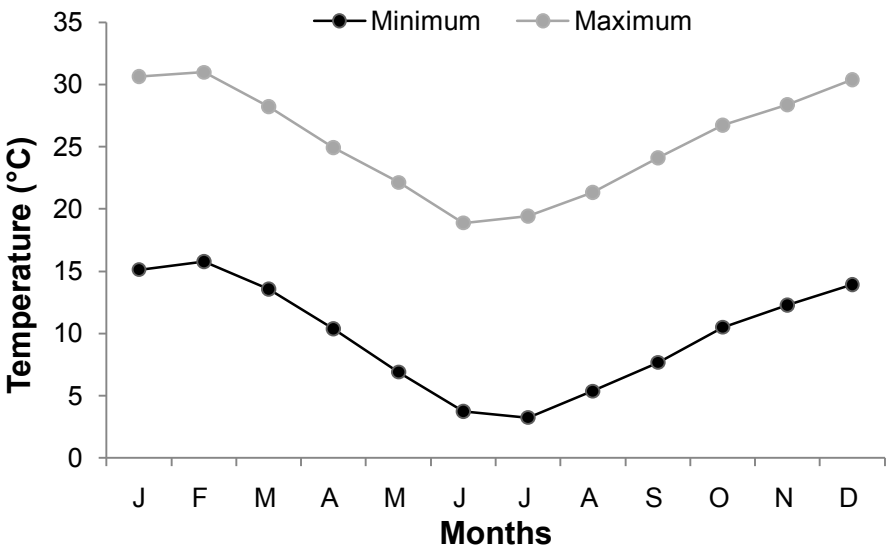

Figure 2.17: Mean monthly minimum and maximum temperatures for Cradock during a ten-year period (2001-2010).

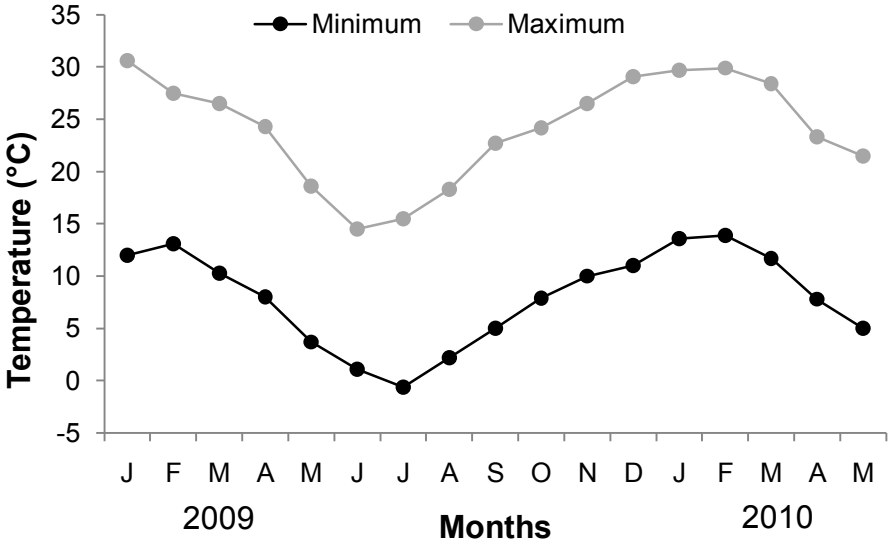

Figure 2.18: The mean monthly minimum and maximum temperatures for Cradock during the study period (2009-2010).

Vegetation

Three major vegetation units are present at MZNP, Karoo Escarpment Grassland, Eastern Upper Karoo and Eastern Cape Escarpment Thicket (Figure 2.19; Mucina & Rutherford 2006). Examples of the vegetation and general habitat for each transect at SBNR are provided in Figure 2.13.

Topography

The MZNP lies within the larger Bankberg area of the SMC (Figure 2.1). Altitude ranges from 1000 m in the north of the park, to 1960 m (Bakenkop) in the southeast (Figure 2.14). The southern section of the park consists of a mountainous valley that is dissected by the Wilgerboom River (Figure 2.14). The Bankberg lies to the east of the river and Kranskop to the west (Figure 2.14).

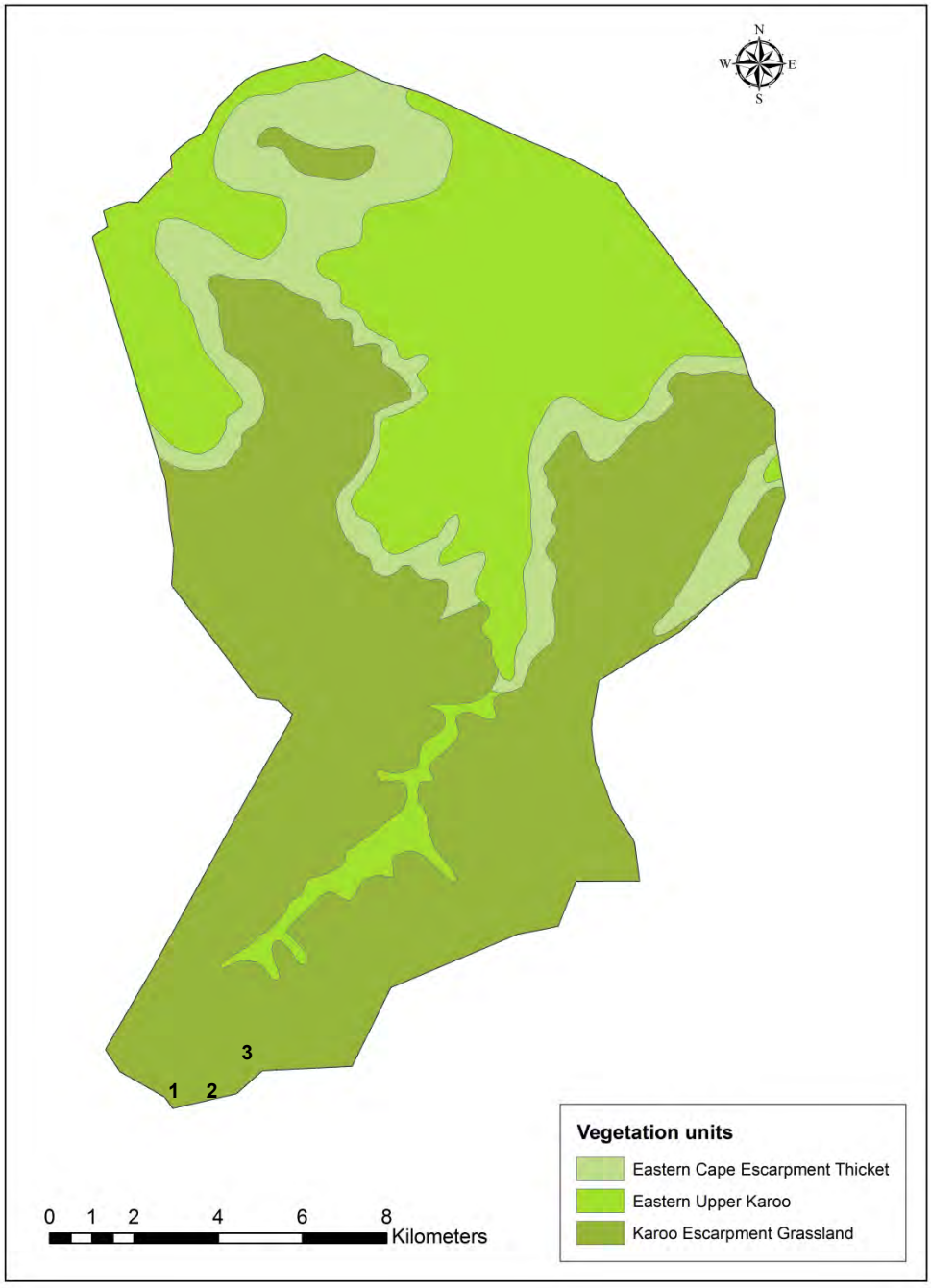

Figure 2.19: Vegetation map of the Mountain Zebra National Park (MZNP), depicting the three major vegetation units present in the park (ArcGIS 9.3; map units: decimal degrees; not projected; Mucina & Rutherford 2006). Numbers (1, 2, 3) depict the position of transects.

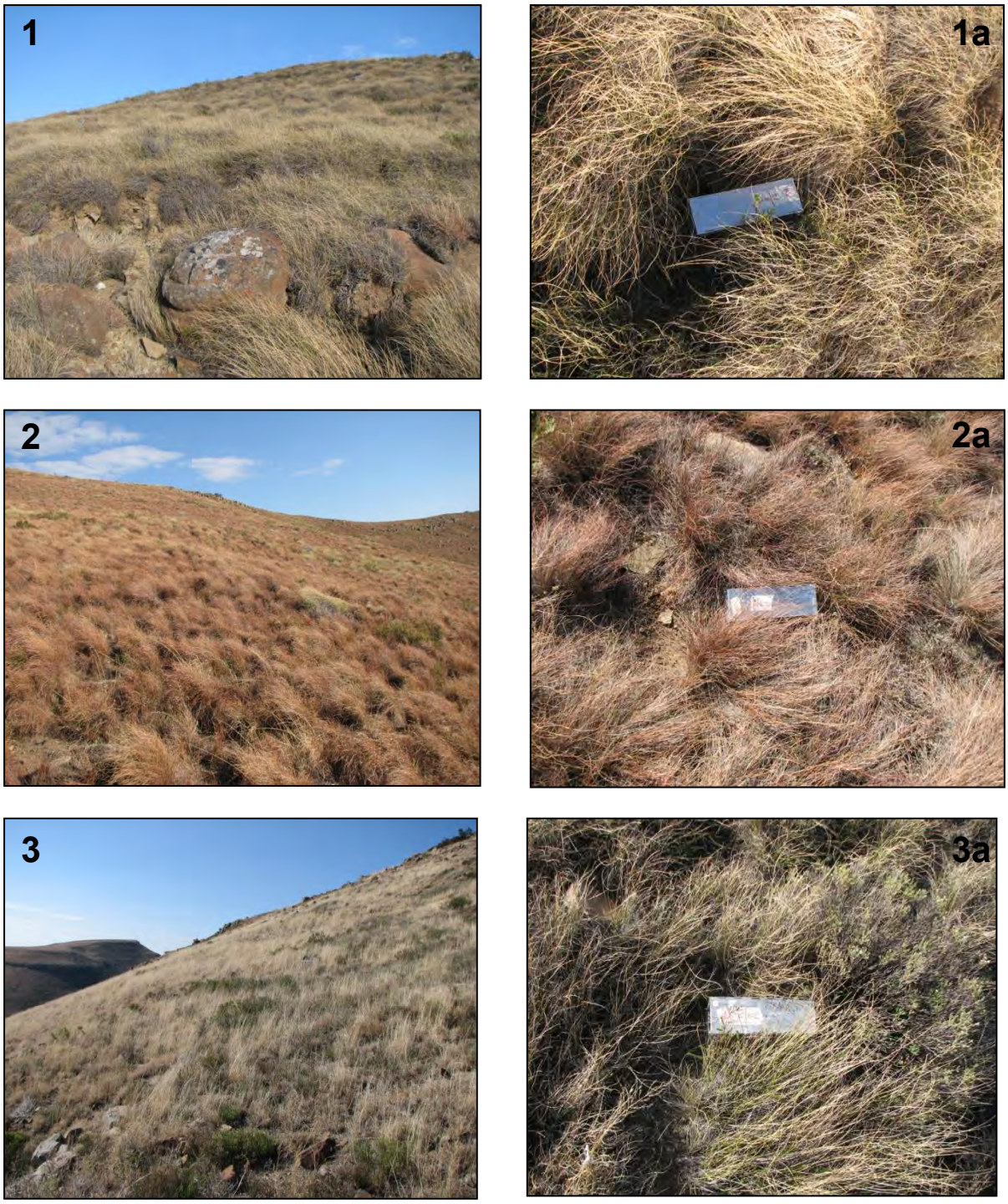

Figure 2.20: Photographs of the three habitats sampled (1, 2, 3) from Mountain Zebra National Park (MZNP); together with close up photographs of each selected trap stations (1a, 2a, 3a). Transect numbers coincide with numbers found on figures 2.14 and 2.19. (1 = Transect 1 (1800masl); 2 = Transect 2 (1750-1800masl); 3 = Transect 3 (1800-1820masl).

2.5 Trapping Protocol

To avoid unnecessary repetition in the methods sections of chapters 3 and 4, the general trapping protocol is described below.

Data were collected for four consecutive austral seasons (Avenant & Cavallini 2007) from June 2009 to May 2010 at each site for five successive nights per site (Jones *et al*. 1996; Caro *et al.* 2001; Yarnell *et al.* 2007). Trapping was conducted over three week periods each season, where the three sites were sampled consecutively starting at SBNR, then ASGF and finally MZNP. Small mammals were trapped using standard (229 x 76 x 89 mm) Sherman Live Traps (H.B. Sherman Inc). At each site, three replicate transects of 370m were laid out (Figure 2.2, 2.8 & 2.12; Pearson & Ruggiero 2003). Transects were always spaced at least 500m from each other to ensure statistical independence (Bateman *et al.* 2010). Each transect consisted of 30 traps (Keller & Schradin 2008), that were divided equally into five sub-transects of six traps each (Figure 2.21). Individual traps were spaced 10m from each other within the sub-transects (Kerley 1992; Jones *et al*. 1996; Keller & Schradin 2008; Whittington-Jones 2008: Figure 2.21). In addition, sub-transects were 30m apart (see chapter 4). Traps were placed in fixed geographical positions throughout the four consecutive seasons of trapping and relocated using a GPS (Garmin GPSMAP 60CSx). All traps were placed on the ground along rodent runways and under vegetation where possible (Jones *et al.* 1996; Rickart *et al.* 1991).

Five bait types were used to attract small mammals (See Chapter 4). In addition, ~ 5g of cotton wool was inserted into traps during the cooler times of the year to serve as nesting material to reduce trap mortalities (Churchfield *et al.* 1997; Gannon *et al.* 2007). Traps were left open for 24 hours and checked each morning (07:00 – 11:00)

and afternoon (13:00-18:00; Nel & Pretorius 1971; Happold & Happold 1989; Kerley 1992; Keesing 1998; Kansangaki *et al.* 2003).

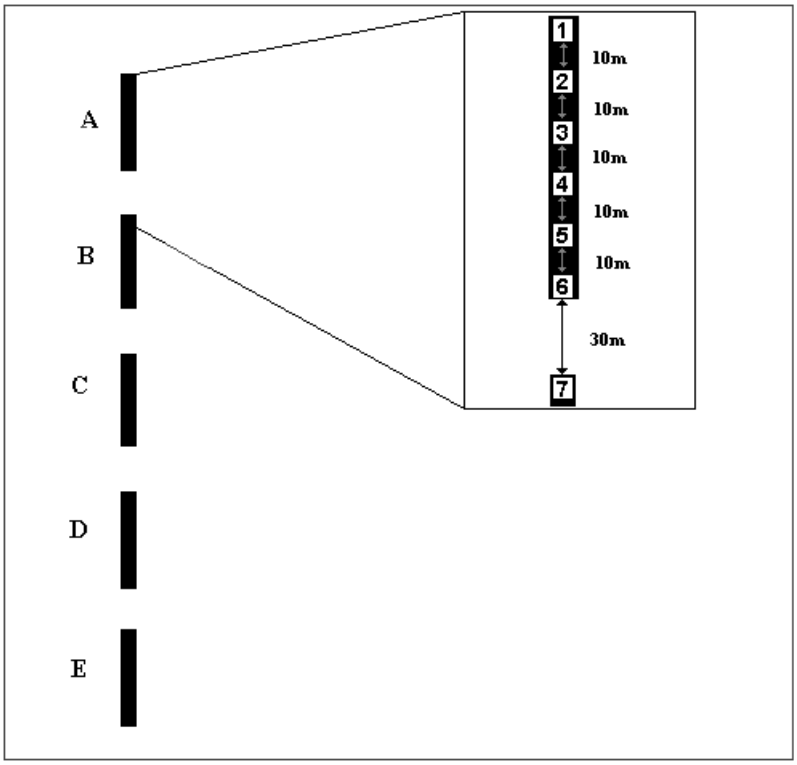

Figure 2.21: Layout of transects were divided into five sub-transects (A-E), that consisted of six traps each. Numbers one to seven indicate individual traps.

All captured specimens were identified to species using Skinner & Chimimba 2005; Stuart & Stuart 2007, weighed, sexed and marked by toe-clipping (Gannon *et al.* 2007). Cryptic species from the genera *Elephantulus, Otomys, Saccostomus, Micaelamys* and *Mystromys* were identified to species by using toe-clipped tissues in DNA analyses. This procedure was part of an honours student project, where the collected tissue was compared to data from the Genbank database.

Toe clipping of individuals served as permanent marking method, and facilitated the calculation of the number of individuals caught per species. In addition, toe clipping doubled as a method to acquire DNA material in a non-lethal manner for a separate study on genetic diversity of montane small mammals (Gannon *et al.* 2007). The toe-clipping procedure was conducted in a sequential fashion to allow up to 52 individuals of each species to be identified per transect per site. These 52 unique codes were derived from the number of unique combinations that can be calculated using the 10 hind toes. These codes include single toe-clips (n = 10) and combinations of two toe clips (n = 42) (Rudran & Kunz 1996).

Toe clipping was performed with sharp sterilized nail clippers (Braude & Cizek 1998; Gannon *et al.* 2007). Nail clippers were sterilized by washing it in 97% ethanol followed by flaming (Braude & Cizek 1998) and toes were clipped at the first digit (Pavone & Boonstra 1985). The removed tissue was placed in 97% ethanol solution for the preservation of the genetic material. No anaesthetics or analgesics were used on captured specimens as this would increase handling time and stress (Gannon *et al.* 2007). Previous work has conclusively demonstrated that toe-clipping does not significantly affect survival (Pavone & Boonstra 1985), predation by owls (Ambrose 1972) and weight loss which is a surrogate for stress (Korn 1987; Wood & Slade 1990). If toe-clipping is carefully applied it will not significantly affect the well-being of small mammals (Korn 1987). Ethical clearance for this project was provided by the Rhodes University Ethics Committee in 2009 (Ethics no. 2009Q-6).

CHAPTER 3

DIVERSITY OF SMALL MAMMALS AT HIGH ALTITUDE IN THE SNEEUBERG MOUNTAIN COMPLEX, SOUTH AFRICA

3.1 INTRODUCTION

Most studies focussing on small mammal diversity at high altitude in South Africa have been conducted in the Cape Fold and Drakensberg Mountains (Bond *et al.* 1980; Nel *et al.* 1980; Rowe-Rowe & Lowry 1982; Rowe-Rowe & Meester 1982; Bowland & Perrin 1993; Armstrong & van Hensbergen; 1996; Avenant 1997; Eccard *et al.* 2000; O'Farrell *et al.* 2008). The Cape Fold Mountains are geographically isolated from the Great Escarpment by the Great Karoo interval, and are situated approximately 450 km (calculated using GIS from Figure 1.1) from the main Drakensberg Mountains. Although the Cape Fold Mountains are not part of the Great Escarpment, the area is important in terms of the conservation of small mammal diversity in South Africa due to the high number of endemic species that occur in the area (Mugo *et al.* 1995). The mountain ranges within the Cape Fold Mountains are, on average, lower in altitude than the mountains of the Great Escarpment (Rust 1998; McDonald *et al.* 2002). In addition, the majority of the Great Escarpment falls within the Grassland biome, whereas the Cape Fold Mountains are dominated by the Fynbos, Succulent Karoo and Nama-Karoo biomes (Mucina & Rutherford 2006). These major differences make comparisons between the two mountainous areas difficult. However, the small mammal communities that occur in

the Cape Fold Mountains currently serve as the only reference point for high altitude (1000 – 1800 m) communities in the south-western parts of South Africa, because no studies have focussed on the small mammals of the southern Great Escarpment (Bond *et al.* 1980; Nel *et al.* 1980; Rautenbach & Nel 1980). Significantly, none of the species that have been identified at high altitude in the Cape Fold Mountains are considered to be high altitude specialists (Bond *et al.* 1980; Nel *et al.* 1980; Rautenbach & Nel 1980; Skinner & Chimimba 2005).

Studies of the small mammal communities of the Drakensberg Mountains indicate that rodents (e.g. *Rhabdomys pumilio; Mastomys coucha* & *Otomys irroratus*), common to grassland habitats, and one or two shrew species (e.g. *Myosorex varius;* Rowe-Rowe & Lowry 1982; Rowe-Rowe & Meester 1982; Bowland & Perrin 1993; Armstrong & Van Hensbergen 1996; Avenant 1997) are most frequently recorded. Importantly, *Otomys sloggetti* (Sloggett's ice rat), a high altitude specialist, has been sampled in the Drakensberg Mountains (Rowe-Rowe & Lowry 1982; Rowe-Rowe & Meester 1982).

The mountains of the Great Escarpment situated between the Cape Fold mountains and Drakensberg Mountains (Figure 1: Roggeveldberge, Nuweveldberge, SMC and Great Winterberge) have not been studied in terms of small mammal community composition. In the SMC, records for small mammals are rather dated and are confined to low altitude areas (Skead 1958; De Graaf & Nel 1970; Nel & Pretorius 1971). In a study on the mammals of the Cradock district, Skead (1958) predicted that 21 species of small mammals should occur in the area. However, these assumptions were based on museum records and distribution maps of the area (Skead 1958). In addition, no reference was made as to the altitude at which museum specimens were collected (Skead 1958). Nevertheless, Skead (1958) did

encourage further exploration of the area. All other studies within the SMC were conducted at the Mountain Zebra National Park (De Graaff & Nel 1970; Nel & Pretorius 1971; Whittington-Jones *et al.* 2008). De Graaff & Nel (1970) and Whittington-Jones *et al.* (2008) caught four and five rodent species respectively. Due to greater trapping effort and a broader sampling area, Nel & Pretorius (1971) recorded eight species of rodent and one species of elephant-shrew in the lower lying areas of the MZNP.

All of the studies regarding small mammal diversity at high altitude in South Africa refer to the habitats utilized by the species sampled in these studies (Bond *et al.* 1980; Nel *et al.* 1980; Rautenbach & Nel 1980; Rowe-Rowe & Lowry 1982; Rowe-Rowe & Meester 1982; Bowland & Perrin 1993; Armstrong & van Hensbergen 1996; Avenant 1997; Eccard *et al.* 2000; O'Farrell *et al.* 2008). However, none of them have quantified or tested the effect of other environmental variables that are known to influence small mammal community composition (Bond *et al.* 1980; Nel *et al.* 1980; Rautenbach & Nel 1980; Rowe-Rowe & Lowry 1982; Rowe-Rowe & Meester 1982; Bowland & Perrin 1993; Avenant 1997; Eccard *et al.* 2000; O'Farrell *et al.* 2008). Various regional and local factors influence small mammal diversity at high attitudes (Hortal *et al.* 2008; Rowe 2009). Regional factors include climate and evolutionary history (e.g. extinctions, speciation and migration; Hawkins & Porter 2003; Hawkins *et al.* 2003; Hortal *et al.* 2008). Local processes include temperature, precipitation, habitat heterogeneity, altitude, area, fire history, grazing and competition (Yarnell *et al.* 2007; Hortal *et al.* 2008; O'Farrell *et al.* 2008; Rowe 2009). The effects of grazing, fire history and precipitation, in particular, on small mammal diversity have been thoroughly researched in southern Africa since these are factors that affect most ecosystems throughout the sub-region (Kern 1981; Archibald *et al.*

2005; Yarnell *et al.* 2007). Grazing can have negative and positive impacts on vegetation cover, marginal grazing often leads to increases in small mammal density and diversity, while over grazing causes declines in density and diversity (Keesing 1998; Eccard *et al.* 2000; Caro 2001, 2002; Hoffmann & Zeller 2005; Muck & Zeller 2006). Fire is known to cause initial decreases in small mammal populations, followed by increases that are related to regenerated vegetation which provide more resources (Rowe-Rowe & Lowry 1982). However, the regeneration of vegetation is heavily dependant on precipitation, as more precipitation combined with the effects of fire cause substantial increases in vegetation growth (Yarnell *et al.* 2007).

Recent research has indicated that no single environmental variable can account for the variability of small mammal diversity at high altitudes (Rowe 2009). It is more likely that the combination of particular environmental variables contribute to the shape of small mammal communities (Rowe 2009). Habitat type is an important factor and small mammal diversity increases as habitat heterogeneity increases through increased resources and a greater number of available niches (Rowe 2009). However, climate (potential and actual evapotranspiration, precipitation and temperature) may play a more central role as it is the primary driving force behind floristic diversity which ultimately drives small mammal diversity (Andrews & O'Brien 2000).

Temperature and precipitation play important roles in maintaining faunal diversity (Yarnell *et al.* 2007). Species distributions are constrained as a result of the physiological limitations set by temperature (Rowe 2009). In contrast, rainfall increases the amount of primary production that is available at a site, directly promoting the species diversity (Rowe 2009). In addition, precipitation combined with fire is known to cause increases in the primary productivity of grassland

ecosystems, ultimately having a positive effect on small mammal diversity and numbers (Yarnell *et al.* 2007).

The effect of altitude on the diversity of small mammal species has been extensively studied (Bond *et al.* 1980; Rickart *et al.* 1991; Heaney 2001; Lomolino 2001; Nor 2001; Rickart 2001; Sanchez-Cordero 2001; Li *et al.* 2003; McCain 2005; Rowe 2009). One of the most prominent hypotheses derived from these studies is the mid-domain effect (MDE; McCain 2005; Rowe 2009). This hypothesis states that small mammal diversity will peak at mid-altitudes (McCain 2005; Rowe 2009). However, the processes responsible for the peak in diversity are poorly understood, and consequently require further research (Rowe 2009).

This major aims of this study were:

- To describe the combined diversity of small mammals that occur at all three high altitudes in the SMC.
- Compare the small mammal communities of the three study sites in terms of diversity measurements, seasonality, and complementarity.
- Investigate the possible influence of selected environmental variables on the diversity measures obtained during the study.

3.2 MATERIALS AND METHODS

Data analysis

For a detailed description of the trapping protocol used to capture small mammals, refer to section 2.5.

Overall trapping results

Trapping results were summarized by calculating eight parameters viz. number of captures, number of individuals caught, number of recaptures, trap success, trap mortality, species richness, Shannon diversity index and Simpson index of diversity. A "trap night" was defined as a trap that had been set for a 24-hour period (Rowe-Rowe & Meester 1982). Trap success was calculated as the total number of small mammals captured, divided by 100 trap-nights (Rowe-Rowe & Meester 1982). Trap mortality was the number of animals that died during capture, divided by the total number of individuals caught at each site.

Species richness and heterogeneity measures

The species richness of a specific group (e.g. small mammals that weigh less than 300g) at a site can be classified in two ways. Firstly, observed species richness, which represents a simple count of the number of species observed while sampling at a site (Magurran 2004). However, this approach is biased towards the species that are easy to observe and capture (Magurran 2004). Secondly, true species richness, which refers to the total number of species actually present at a site during sampling (Magurran 2004). Accordingly, the observed species richness is usually lower than the true species richness (Magurran 2004). However, the calculation of the true species richness, by means of physical sampling, is almost impossible as

not all species are likely to be sampled (Magurran 2004). Species richness estimators provide a means to calculate true species richness, by extrapolating from the relative abundance of each species at a site. I thus investigated the adequacy of my sampling effort by comparing the observed species richness of each site with the Chao 2 estimate (true species richness) based rarefaction curve (Magurran 2004; Bateman *et al.* 2010). Species richness in all other analyses represented observed species richness, as this is the richness measure used to calculate all other diversity measures (Magurran 2004). All species richness curves were determined using Estimate S 8.2 (Colwell, R.K. 2009).

Two measures of heterogeneity were used in the analyses. The Shannon diversity index (Shannon 1948) was calculated using the natural log equation (Magurran 2004):

$$H = -\sum_{i=1}^{s} p_i ln p_i$$

Where *H'* is diversity, *s* is the number of species and p_i is the proportion of species found in the *i*th species (Rowe-Rowe & Meester 1982; Magurran 2004).

The Simpson index of diversity was also calculated using the equation (Magurran 2004):

$$1 - D = \sum \left(\frac{n_i[n_i - 1]}{N[N - 1]}\right)$$

Where *ni* is the number of individuals in the *ith* species, and N is the total number of individuals.

Both the Shannon diversity index and the Simpson index of diversity are good measures of the heterogeneity present within a community (Magurran 2004).

Because of its long tradition of use and association with entropy, the Shannon diversity index continues to be used often in studies that focus on heterogeneity measures (Bond *et al.* 1980; Nel *et al.* 1980; Rowe-Rowe & Meester 1982; August 1983; Happold & Happold 1989; Kasangaki *et al.* 2003; Magurran 2004; Avenant & Cavallini 2007; Keller & Schradin 2008; Whittington-Jones *et al.* 2008; Rowe 2009). It is therefore an important comparative measure across studies. Although not as popular as the Shannon diversity index, the Simpson index of diversity is one of the most robust and intelligible diversity measures available (Magurran 2004). The Simpson index of diversity is easy to interpret as it only ranges from zero to one, the more even an assemblage is the higher the value (Magurran 2004). However, like all diversity measures, both of these indices are biased. The Shannon diversity index is heavily influenced by species richness, whereas the Simpson index of diversity is weighted more towards the most abundant species in the community (Magurran 2004).

Complementarity

Complementarity refers to the differences between species composition of two sites, if fewer species are shared between sites, they show more complementary, increasing the beta diversity of a given area (Colwell & Coddington 1994; Magurran 2004). The logical opposite of complementarity is similarity (Colwell & Coddington 1994). Complementarity was explored using cluster analysis, together with non-metric multidimensional scaling (nMDS; Bateman *et al.* 2010). These analyses were derived from the number of individuals per small mammal species that were square root transformed and incorporated into a Bray-Curtis similarity matrix (Primer 5. Primer-E Ltd; Magurran 2004).

Effects of site and season

Four measures of were used to test for differences among the three small mammal communities (Magurran 2004). These were the number of individuals caught, species richness, Shannon diversity index and Simpson's index of diversity (calculated in Primer 5, Primer-E Ltd). Daily capture rates of these measures were often too low for appropriate statistical analyses. Consequently, daily data sets were pooled for each season. As these data satisfied the assumptions of normality and heteroscedasticity, Site (MZNP, SBNR, ASGR) and season (Winter, Spring, Summer, Autumn) were the independant variables in a set of two-way ANOVA's to test their influence on each of the diversity measurements (Statistica 9.0, Statsoft, Inc.). Where significant ($p < 0.05$) effects were present, Scheffé's post-hoc tests were performed to determine the source of the variation (Statistica 9.0, Statsoft Inc.).

Multi-model inference

The relationships between the four diversity measurements and environmental variables were explored using regression analyses (Archibald *et al.* 2005). Three continuous environmental variables (total rainfall one year prior to the study (TR (1)) average altitude (alt) and maximum temperature (Tmax during each month) were evaluated to determine their relationships with diversity measures using simple regressions. Rainfall one year prior to the study was selected as the preferred precipitation variable, because small mammal population responses to rainfall is often delayed (Yarnell *et al.* 2007). To ascertain which of these variables or combination of variables best predicted each of the diversity measures, a multi-model selection was performed (Burnham & Anderson 2002; Archibald *et al.* 2005; Fontúrbel 2009). These three continuous variables together with a categorical

variable (site) were incorporated into the model selection (Archibald *et al.* 2005). Variables were tested for normality (Burnham & Anderson 2002; Fontúrbel 2010) and multiple-collinearity was tested among the variables using Pearson's correlation coefficients (Burnham & Anderson 2002; Archibald *et al.* 2005). Although there was a strong positive relationship ($r = 0.66$; $p < 0.001$) between the maximum temperature and the total rainfall one year prior to the study, both of these predictors were included in the final multiple regression analyses, to ensure that both factors could be accounted for in the model building process. Multiple regression models were then constructed for every combination of variables, and each individual variable, giving a combination of 15 models for each of the diversity measurements. The Akaike Information Criterion (AIC) was used to select the best model for each diversity measurement (Burnham & Anderson 2002). The second order AIC_c scores were used instead of the normal AIC scores, to compensate for the small sample size ($n = 36$, 3 transects per site per season) relative to the number of variables selected for model building (Burnham & Anderson 2002; Rowe 2009; Fontúrbel 2010). Since the AIC_c scores are not comparable in their raw from, the ΔAIC_c and Akaike weights (W_i AIC_c), were calculated to facilitate interpretation (Burnham & Anderson 2002). The best models within a sub-set were thus represented by ΔAIC_c values that were ≤ 2 (Burnham & Anderson 2002; Archibald *et al.* 2005; Fontúrbel 2010).

The model selection process above identified the combination of variables that best predicted each diversity measurement. The model selection did not indicate which variables had the greatest influence on the selected diversity measurement (Burnham & Anderson 2002). To investigate the influence of each of the environmental predictor variable, AIC was used to calculate the impact factor of each

variable (Burnham & Anderson 2002; Archibald *et al.* 2005; Rowe 2009). Impact factors represent the sum of the weights (W_i AIC_c) for each model containing the particular predictor variable (Burnham & Anderson 2002; Rowe 2009). Variables were recognised as being influential in the prediction of the four diversity measurements if they had an impact factor of ≥ 0.80 (Rowe 2009). All regression analyses and AIC model building were carried out in Statistica 9.0 (Statsoft Inc.).

3.3 RESULTS

Overall trapping results

A total of 423 captures were obtained over 5280 trap nights, giving an overall trap success of 8% (Table 3.1). The total number of captures comprised of 292 individuals with 131 recaptures (Table 3.1). Seventy-two mortalities were recorded during the study (Table 3.1). This mortality rate was higher than the norm of 5-7% recommend for small mammal trapping. Overall, 12 species of small mammals were caught – one shrew (*Myosorex varius* Smuts, 1832), one elephant shrew (*Elephantulus myurus* Smith, 1836) and ten rodents (Table 3.2). *Micaelamys namaquensis, Rhabdomys pumilio* and *Myosorex varius* were the most abundant species overall (Table 3.2).

SBNR: In total, eight of the twelve small mammal species were caught at SBNR, and *Micaelamys namaquensis*, *Rhabdomys pumilio* and *Elephantulus myurus* were the most abundant species (Table 3.2). The species accumulation curve for SBNR did not reach an asymptote (Figure 3.1). In addition, the Chao 2 richness estimator indicated that the true species richness of SBNR was substantially higher than the observed species richness (Figure 3.1). Overall, SBNR had the highest capture rate of all sites sampled and had the highest trap success, number of captures, number of individuals caught and number of recaptures (Table 3.1). However, small mammal mortality was relatively high at SBNR (Table 3.1). Although SBNR managed to obtain the highest species richness, overall, similar numbers of species were caught at the ASNR and MZNP (Table 3.1). Despite achieving the highest capture rate and species richness, Shannon and Simpson diversity was slightly lower at SBNR than ASNR and MZNP (Table 3.1).

Table 3.1: Summary of trapping data for small mammals sampled at three high elevation (> 1700 m) sites within the Sneeuberg Mountain Complex, Eastern Cape Province, South Africa.

Study Site	No. of Captures		No. of individuals		No. recaptures		No. of trap nights		No. of mortalities		Species richness	Shannon diversity index	Simpson index of diversity
	n	%	n	%	n	%	n	%	n	%			
Sneeuberg Nature Reserve	235	(55.6)	147	(50.3)	88	(67.2)	1763	(13.3)	21	(29.2)	8	1.3	0.6
Asante Sana Nature Reserve	148	(35.0)	111	(38.1)	37	(28.2)	1768	(8.4)	43	(59.7)	7	1.4	0.7
Mountain Zebra National Park	40	(9.4)	34	(11.6)	6	(4.6)	1749	(2.3)	8	(11.1)	7	1.6	0.8
Total	**423**		**292**		**131**		**5280**	**(8.0)**	**72**	**24.7**	**12**	**1.9**	**0.8**

Table 3.2: Summary of the number of individuals caught at each of three high elevation (> 1700 m) sites within the Sneeuberg Mountain Complex, Eastern Cape Province, South Africa. (SBNR = Sneeuberg Nature Reserve; ASNR = Asante Sana Private Nature Reserve; MZNP = Mountain Zebra National Park).

	SBNR	**ASNR**	**MZNP**	**Total**
Order: Eulipotypha				
Myosorex varius	1	55	10	66
Order: Macroscelidea				0
Elephantulus myurus	24	0	0	24
Order: Rodentia				0
Dendromus melanotis	0	3	2	5
Graphiurus ocularis	0	2	0	2
Micaelamys namaquensis	79	0	3	82
Micaelamys granti	1	7	0	8
Mus minutoides	0	0	1	1
Mystromys albicaudatus	4	0	0	4
Otomys irroratus (sensu lato)	0	14	9	23
Otomys sloggetti	1	2	1	4
Rhabdomys pumilio	30	28	8	66
Saccostomus campestris	7	0	0	7
Total	**147**	**111**	**34**	**292**

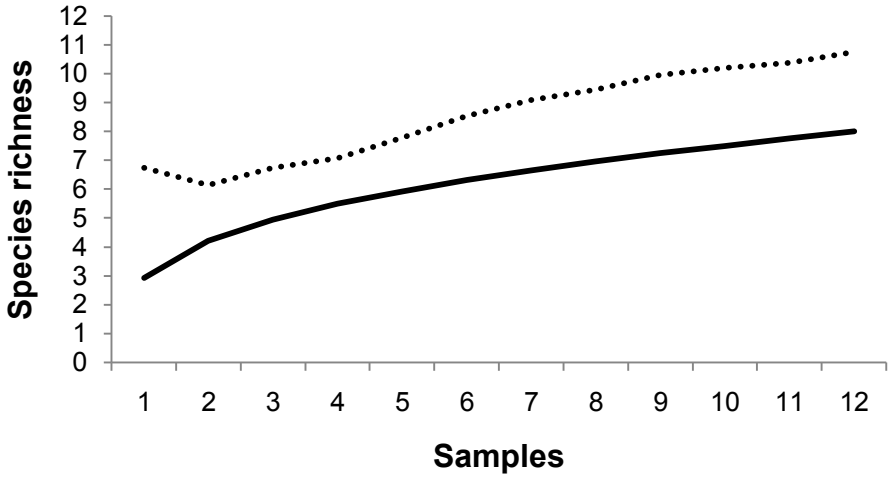

Figure 3.1: Observed species richness (solid line) together with the Chao 2 (dashed line) rarefaction curve to predict true species richness at the Sneeuberg Nature Reserve (SBNR).

ASNR: Seven species of small mammals were captured at ASNR and the most abundant species were *Myosorex varius*, *Rhabdomys pumilio* and *Otomys irroratus* (Table 3.2). The species accumulation curve for ASNR showed signs of reaching an asymptote (Figure 3.2). In addition, after the 12 samples the Chao 2 richness estimator indicated that the true species richness may have been sampled at ASNR (Figure 3.2). The overall capture rate at ASNR was slightly lower than SBNR (Table 3.1) but ASNR had the second highest trap success, number of captures, number of individuals caught and number of recaptures (Table 3.1). In addition, species richness at ASNR was similar to MZNP and SBNR (Table 3.1). Small mammal mortality rate, however, was extremely high at ASNR (Table 3.1). Nevertheless, Shannon and Simpson diversity indices indicated that ASNR showed reasonable levels of small mammal diversity (Table 3.1).

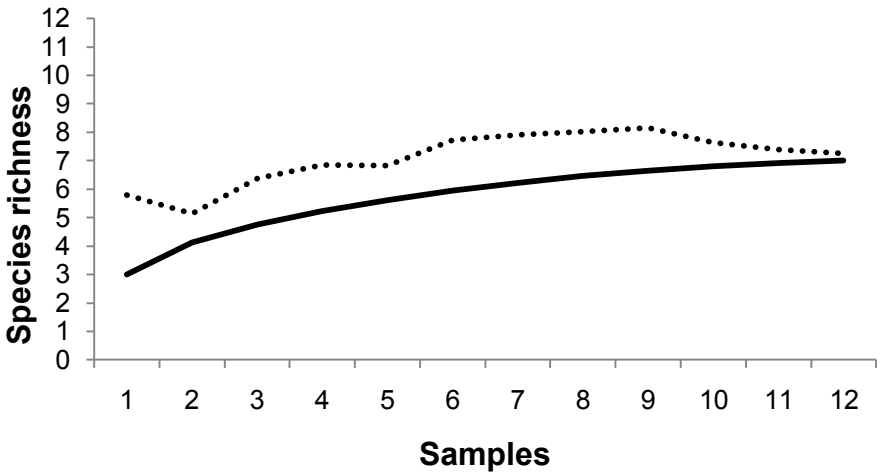

Figure 3.2: Observed species richness (solid line) together with the Chao 2 (dashed line) rarefaction curve to predict true species richness at the Asante Sana Private Nature Reserve.

MZNP: Like ASNR, seven species of small mammals were captured at MZNP with *Myosorex varius*, *Otomys irroratus* and *Rhabdomys pumilio* being the most abundant species (Table 3.2). The species accumulation curve for MZNP continued to increase after 12 samples (Figure 3.3). However, the Chao 2 richness estimator indicated that true species richness at MZNP was only slightly higher than the observed richness (Figure 3.3). MZNP had the lowest capture rate of all three sites (Table 3.1) and the lowest trap success, number of captures, number of individuals caught and number of recaptures (Table 3.1). However, small mammal mortality was lowest at MZNP, but this is probably an artefact of the low capture success (Table 3.1). Although capture rates were low at MZNP, species richness measured at this site was similar to the other sites (Table 3.1) and both diversity indices were higher at MZNP than any other site (Table 3.1).

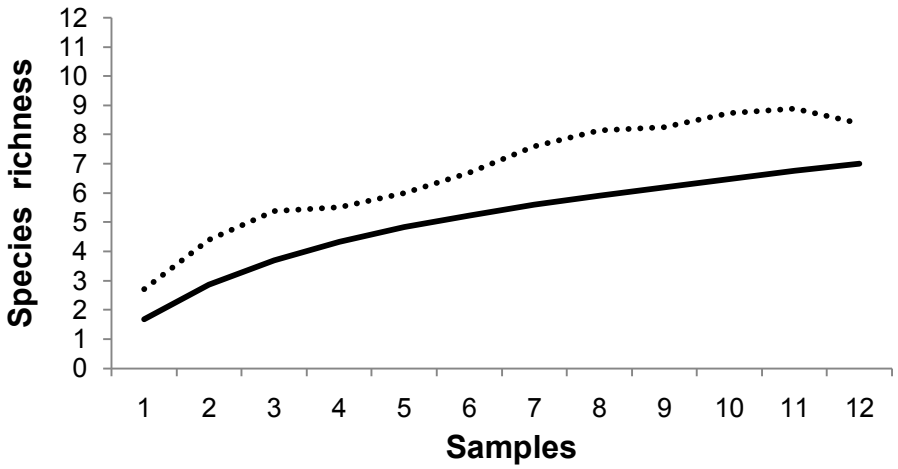

Figure 3.3: Observed species richness (solid line) together with the Chao 2 (dashed line) rarefaction curve to predict true species richness at the Mountain Zebra National Park (MZNP).

Complementarity

ASNR and MZNP were more similar to each other, in terms of species composition, than SBNR (Figure 3.4). Only three, of the 12 species recorded (Table 3.2; *Myosorex varius, Otomys sloggetti* and *Rhabdomys pumilio*) were shared among all three sites (Figure 3.4). Three species, *Elephantulus myurus, Saccostomus campestris* and *Mystromys albicaudatus*, were only caught at SBNR (Figure 3.4). The number of site-specific species was lower at the other two sites. *Graphiurus ocularis* was only captured at ASNR and *Mus minutoides* was only caught at MZNP (Figure 3.4). ASNR and MZNP shared two species, *Dendromus melanotis* and *Otomys irroratus* (Figure 3.4). However, SBNR shared only one species with ASNR (*Micaelamys granti*) and MZNP (*Micaelamys namaquensis*), respectively (Figure 3.4).

SBNR had the highest level of unique diversity of all three sites in the SMC. ASNR and MZNP were more similar, in terms of species abundance, than they were to SBNR (Figure 3.4).

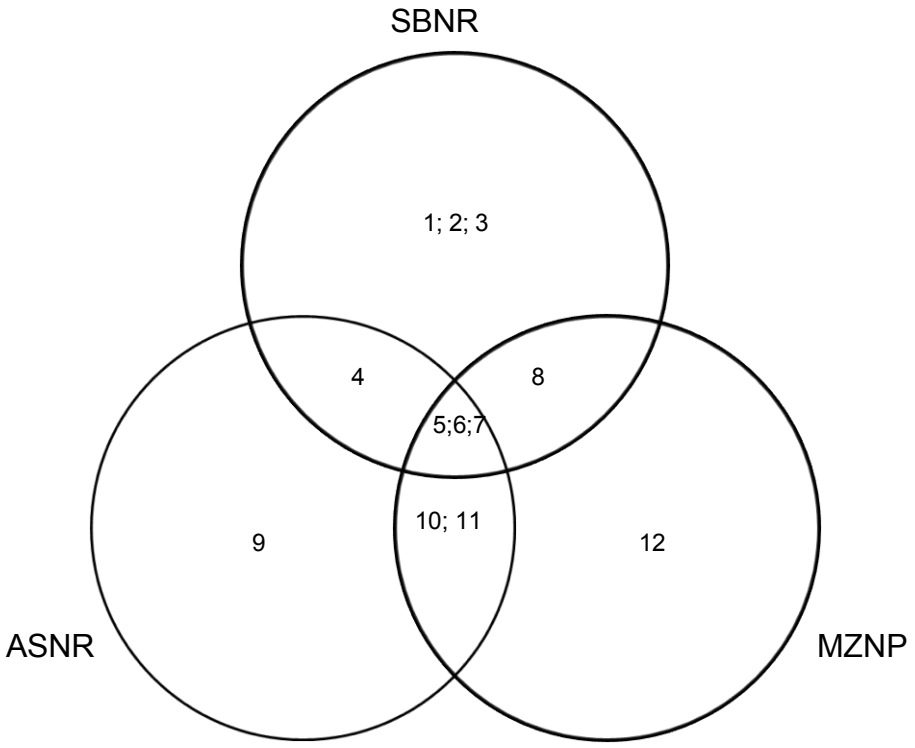

Figure 3.4: Venn diagram indicating the overlap in the number of small mammal species at three high elevation (> 1700 m) sites within the Sneeuberg Mountain Complex, Eastern Cape Province, South Africa. (SBNR = Sneeuberg Nature Reserve; ASNR = Asante Sana Private Nature Reserve; MZNP = Mountain Zebra National Park; 1 = *Elephantulus myurus;* 2 = *Mystromys albicaudatus;* 3 = *Saccostomus campestris;* 4 = *Micaelamys granti;* 5 = *Myosorex varius;* 6 = *Otomys sloggetti;* 7 = *Rhabdomys pumilio;* 8 = *Micaelamys namaquensis;* 9 = *Graphiurus ocularis;* 10 = *Dendromus melanotis;* 11 = *Otomys irroratus;* 12 = *Mus minutoides*).

At the 30% level of similarity, the Bray-Curtis analysis indicated that there were two distinct clusters for the three sites and their seasonal abundances (Figure 3.5).

These clusters were categorised as: 1) ASNR and MZNP and 2) SBNR. In addition, the non-metric multidimensional scaling (nMDS) revealed that the SBNR cluster was the more isolated of the two clusters (Figure 3.6). Within the ASNR and MZNP clusters, there were two outliers, summer and winter at MZNP (Figure 3.5 & 3.6).

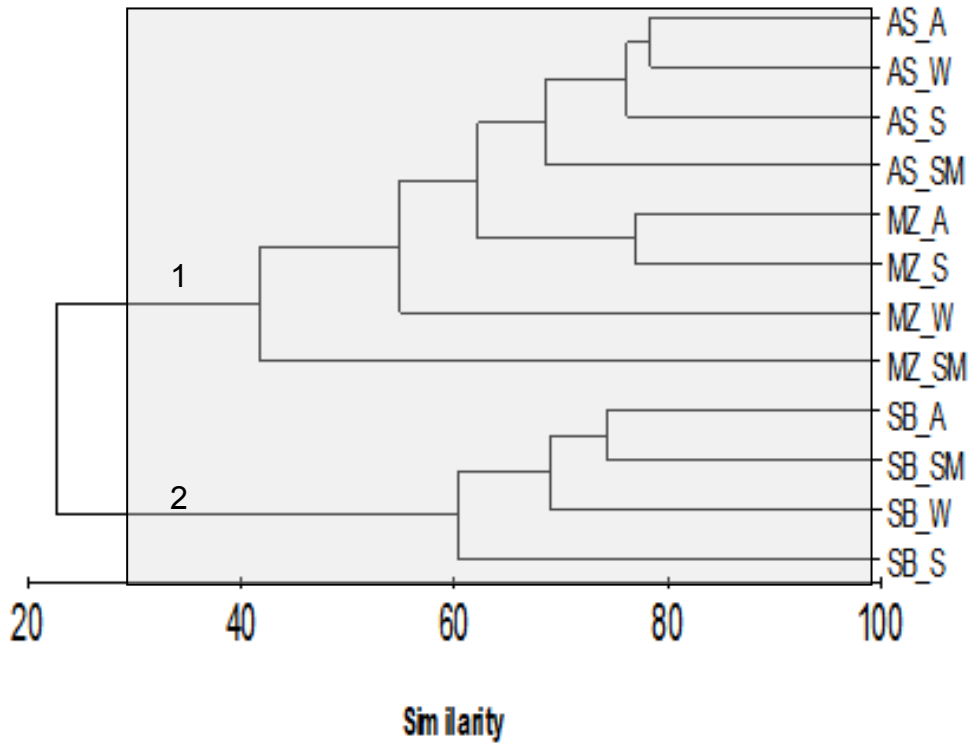

Figure 3.5: Cluster analysis of small mammal community composition at three high elevation (> 1700 m) sites during four consecutive austral seasons in the Sneeuberg Mountain Complex, Eastern Cape Province, South Africa. Cluster groupings were taken at 30% similarity. Numbers (1-2) indicate the different clusters (SB = Sneeuberg Nature Reserve; AS = Asante Sana Private Nature Reserve; MZ = Mountain Zebra National Park) (W = winter; S = spring; SM = summer; A = autumn).

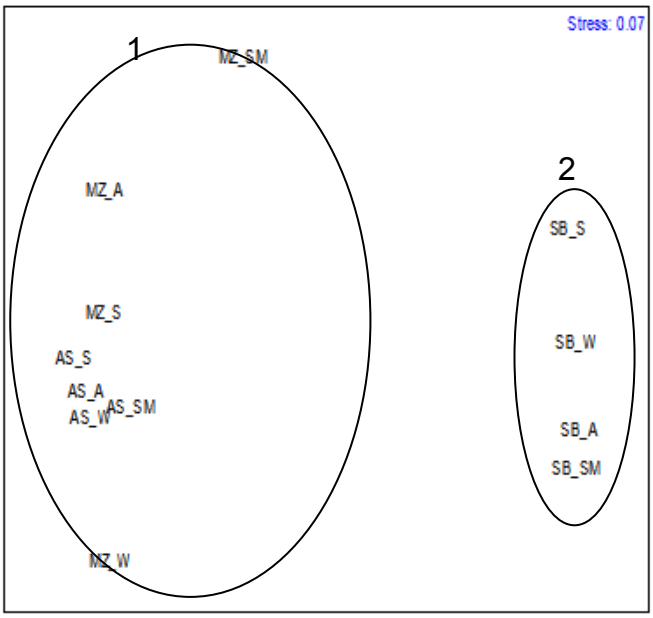

Figure 3.6: Non-metric multi-dimensional scaling plot of small mammal communities at three high elevation (> 1700 m) sites within the Sneeuberg Mountain Complex, Eastern Cape Province, South Africa. Numbers (1-2) indicate the different clusters (SB = Sneeuberg Nature Reserve; AS = Asante Sana Private Nature Reserve; MZ = Mountain Zebra National Park) (W = winter; S = spring; SM = summer; A = autumn).

Effects of site and season

Site ($F_{(2,24)}$ = 18.14; $p < 0.001$) and season ($F_{(3,24)}$ = 3.04; $p < 0.05$) both had a significant effect on the number of individuals caught (Figure 3.7). Significantly, more individuals were caught at SBNR compared to MZNP ($p < 0.001$; Figure 3.7). Similarly, significantly more individuals were caught at ASNR than MZNP ($p < 0.01$; Figure 3.7). Although the overall effect of season was significant, no pairs were significant. However, the combination of site and season had a significant ($F_{(6,24)}$ = 5.89; $p < 0.001$) effect on the average number of individuals caught (Figure 3.7). Significantly more individuals were caught in autumn at SBNR compared to spring at SBNR ($p < 0.01$; Figure 3.7), summer at ASNR ($p < 0.05$; Figure 3.7) and all four

seasons at MZNP ($p < 0.01$; Figure 3.7). The number of individuals caught was highest during spring for ASNR and MZNP (Figure 3.7).

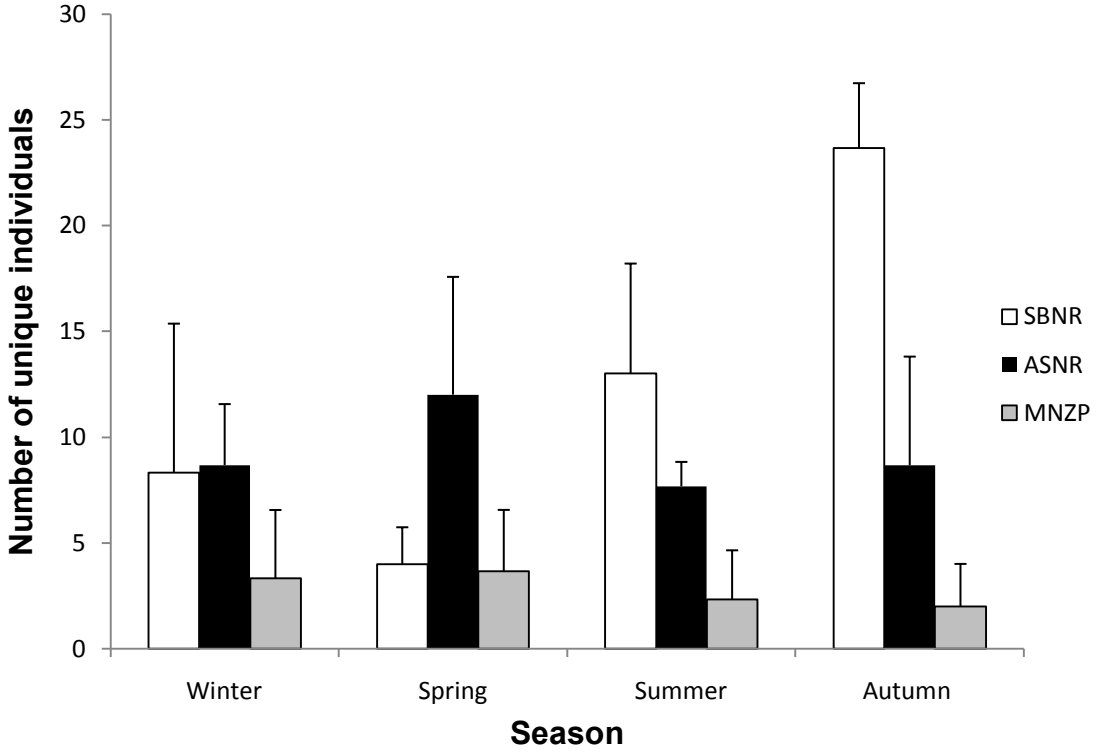

Figure 3.7: The number of individuals caught during four consecutive austral seasons at three high elevation (> 1700 m) sites, in the Sneeuberg Mountain Complex, Eastern Cape Province, South Africa. (Mean; ± sd)

The average small mammal species richness was significantly affected by site ($F_{(2,24)} = 6.34$; $p < 0.01$; Figure 3.8), with SBNR having a significantly higher species richness than MZNP ($p < 0.01$; Figure 3.8). Similarly, species richness at ASNR was significantly higher than MZNP ($p < 0.01$; Figure 3.8). However, season ($F_{(3,24)} = 0.87$; $p > 0.05$; Figure 3.8) and the interaction between of site and season ($F_{(6,24)} = 1.81$; $p > 0.05$; Figure 3.8) had no significant effect on small mammal species

richness. Species richness was highest in autumn at SBNR, summer at ASNR and winter and spring at MZNP (Figure 3.8).

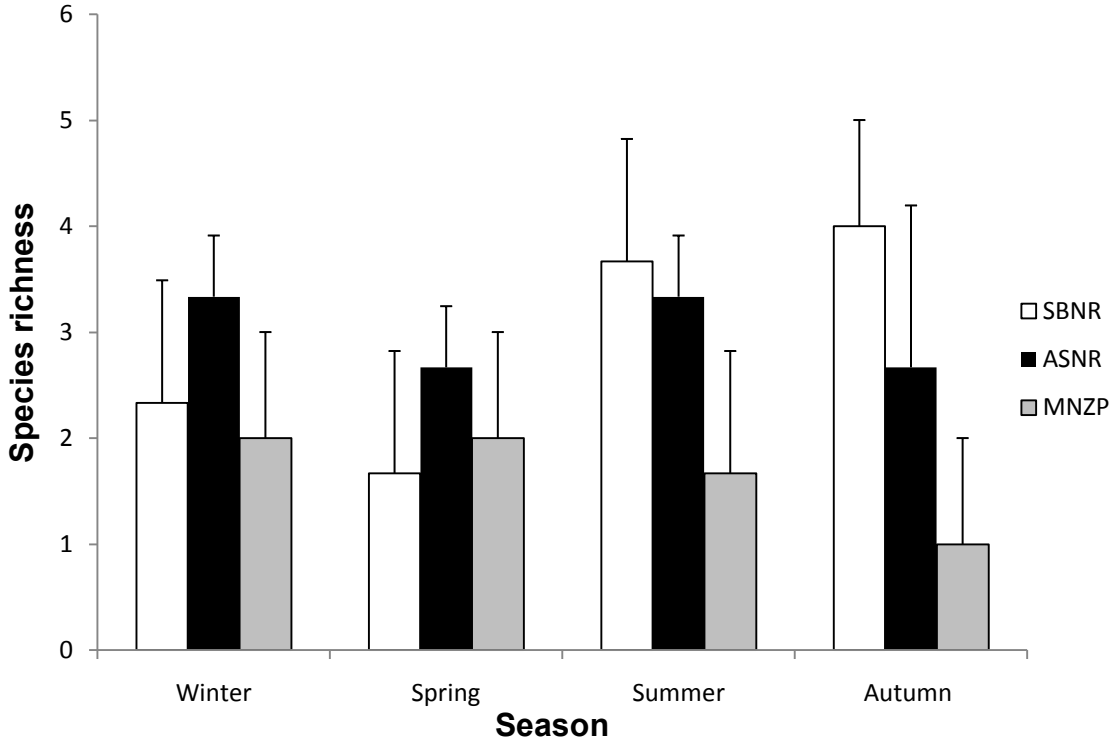

Figure 3.8: Species richness obtained during four consecutive austral seasons at three high elevation (> 1700 m) sites, within the Sneeuberg Mountain Complex, Eastern Cape Province, South Africa. (Mean; ± sd).

Average Shannon diversity was significantly affected by site ($F_{(2,24)} = 3.71$; $p < 0.05$; Figure 3.9). However, a Scheffé's post-hoc test did not detect any statistical differences among the sites. Average Shannon diversity was highest at ASNR, followed closely by SBNR (Figure 3.9). MZNP had the lowest average Shannon diversity (Figure 3.9). There was no significant seasonal effect ($F_{(3,24)} = 0.94$; $p > 0.05$; Figure 3.9) or site combined with season effect ($F_{(6,24)} = 1.40$; $p > 0.05$; Figure

3.9). Shannon diversity indices where highest at SBNR and ASNR during summer and winter and spring at MZNP (Figure 3.9).

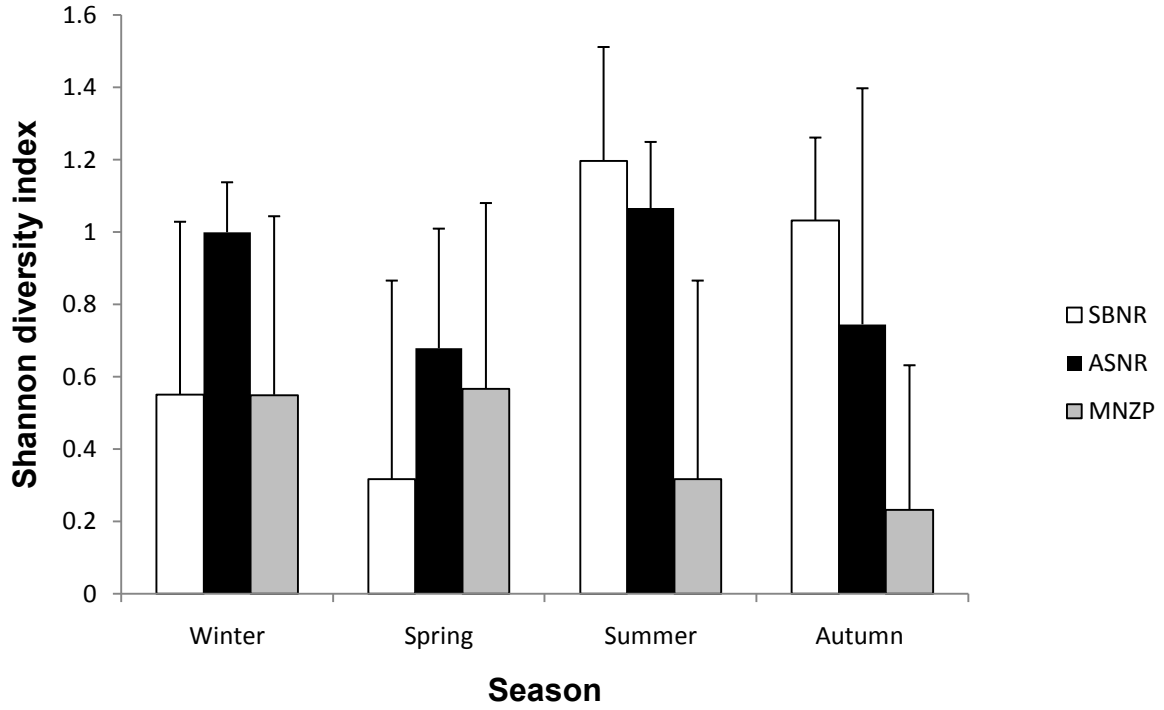

Figure 3.9: Shannon diversity indices obtained during four consecutive austral seasons at three high elevation (> 1700 m) sites, within the Sneeuberg Mountain Complex, Eastern Cape Province, South Africa. (Mean; ± sd).

There were no significant effects for site ($F_{(2,19)}$ = 0.32; p > 0.05), season ($F_{(3,19)}$ = 1.42; p > 0.05) or the interaction between site and season ($F_{(6,19)}$ = 0.32; p > 0.05) for Simpson diversity (Figure 3.10). Similar to the overall results (Table 3.1), MZNP showed the highest Simpson diversity, followed closely by ASNR and SBNR. Simpson diversity was highest in winter at MZNP and in summer for both SBNR and ASNR (Figure 3.10).

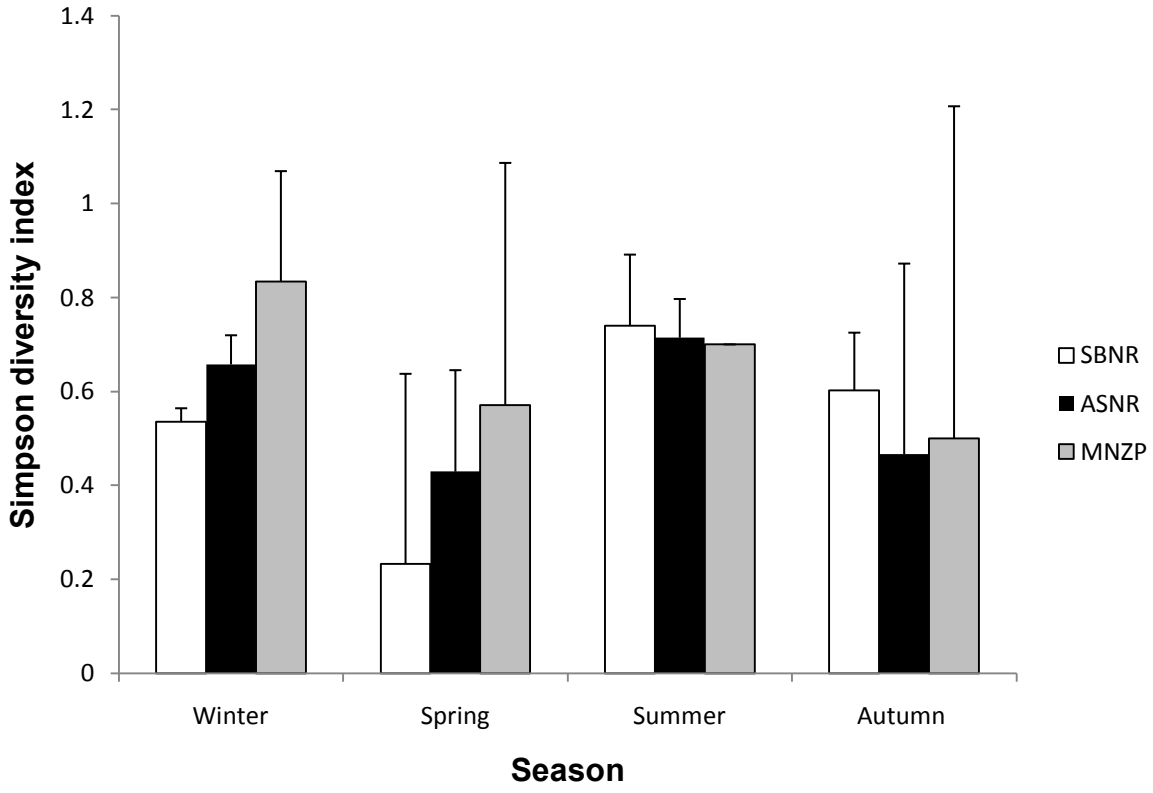

Figure 3.10: Simpson diversity indices obtained during four consecutive austral seasons at three high elevation (> 1700 m) sites, within the Sneeuberg Mountain Complex, Eastern Cape Province, South Africa. (Mean; ± sd).

Multi-model building

There was no single environmental variable or combination of variables that adequately accounted for the variability of the diversity measures (Table 3.3). This was highlighted by the lack of any significant ($p > 0.05$) relationships between the three environmental variables and any of the diversity measures (Table 3.3). However, the calculation of impact factors demonstrated that site was the strongest predictor of the number of individuals caught, species richness and Shannon diversity index (Table 3.4). Total rainfall one year prior to the study was an important factor for the number of individuals caught and species richness (Table 3.4).

Average altitude was also an important factor in predicting the number of individuals (Table 3.4). The impact factors for maximum temperature were low for all diversity measures. The Simpson index of diversity was not influenced by any of the environmental variables (Table 3.4)

Table 3.3: Relationship between four diversity measures (number of individuals, species richness, Shannon diversity index, Simpson index of diversity) and three environmental parameters, average altitude (Alt), total rainfall one year prior to the study (TR (-1) and maximum temperature (Tmax) as determined by simple regression analyses.

	Alt			**TR (-1)**			**Tmax**		
	r	F	p	r	F	p	r	F	p
Number of individuals	0.01	0.34	> 0.05	0.36	1.23	> 0.05	0.06	0.14	> 0.05
Species richness	0.25	3.77	> 0.05	0.49	2.07	> 0.05	0.08	0.16	> 0.05
Shannon diversity index	0.20	2.74	> 0.05	0.48	1.59	> 0.05	0.09	0.24	> 0.05
Simpson index of diversity	-0.02	0.01	> 0.05	0.29	2.62	> 0.05	-0.01	0.00	> 0.05

Table 3.4: The impact factors for each, Site, average altitude (Alt), total rainfall one year prior to the study (TR (-1)) and maximum temperature environmental parameter. Impact factors ≥ 0.80 are considered to have strong support (values in bold).

Diversity measure	Site	Alt	TR(-1)	Tmax
Number of individuals	**1.00**	**0.82**	**0.96**	0.65
Species richness	**0.95**	0.24	**0.82**	0.31
Shannon diversity index	**0.81**	0.32	0.74	0.26
Simpson index of diversity	0.14	0.29	0.74	0.40

A six factor and a five-factor model were considered the best models to predict the number of individuals caught (Table 3.5). Similarly, two models (a four factor and

five-factor model) were sufficient to predict species richness (Table 3.5). One four-factor model, a combination of precipitation and site, was sufficient to predict the Shannon diversity index (Table 3.5). Two models were selected that would best predict the Simpson index of diversity (Table 3.5). Although the Akaike weights indicated that no single environmental variable could successfully predict the Simpson index of diversity, the strongest models sub-set was a one-factor model (total rainfall one year prior to the study; Table 3.5).

Table 3.5: The best models selected for each of the four diversity measurements, number of individuals caught, species richness, Shannon diversity index and Simpson index of diversity, from multiple logistic regression using the second order Akaike information criterion (AIC_c).

Par 1	Par 2	Par 3	Par 4	df	AIC_c	ΔAIC_c	W_i AIC_c
Number of individuals							
Alt	Tmax	TR(-1)	Site	5	221.29	0	0.53
Alt	TR(-1)	Site		4	222.75	1.46	0.28
Species richness							
TR(-1)	Site			3	109.23	0	0.43
Tmax	TR(-1)	Site		4	110.64	1.41	0.21
Shannon diversity index							
TR(-1)	Site			3	45.00	0	0.37
Simpson index of diversity							
TR(-1)				1	14.14	0	0.32
Tmax	TR(-1)			2	15.10	0.96	0.20

Parameters in the model were TR (-1) = total rainfall one year prior to the study, Alt = average altitude, Tmax = Maximum temperature.

3.4 DISCUSSION

SMC compared to other high altitude areas in South Africa

This was the first study to assess small mammal diversity and community composition at high altitude in the SMC. Overall, trap success in this study was similar to other high altitude studies that only used live-trapping (Bond *et al.* 1980; Rowe-Rowe & Meester 1982). In general, live trapping at high altitudes in South Africa (Bond *et al.* 1980; Rowe-Rowe & Lowry 1982; Rowe-Rowe & Meester 1982; Bowland & Perrin 1993) has provided higher trap success than removal trapping methods (Nel *et al.* 1980; Rautenbach & Nel 1980; Avenant 1997). The highest trap success (17%) at high altitude in South Africa was obtained by Bowland & Perrin (1993) using live trapping. Their high trap success rate was related to the wetland habitat that they sampled as such habitats sustain larger populations of small mammals (Bowland & Perrin 1993). The higher trap success obtained by live traps could also relate to their ability to recapture small mammals, which would increase their overall capture rates (Sullivan *et al.* 2003). In contrast, removal traps cannot recapture individuals, leading to lower overall capture rates (Sullivan *et al.* 2003).

The small mammal communities that occur at high altitude within the SMC differ slightly from those reported for in other high altitude communities from South Africa. Except for the study conducted by Armstrong & Hensbergen (1996) in the southern Drakensberg mountains, slightly more small mammal species (12) were recorded at high altitude in the SMC when compared to the Drakensberg Mountains (7-10 species) (Rowe-Rowe & Lowry 1982; Rowe-Rowe & Meester 1982; Bowland & Perrin 1993; Avenant 1997). Armstrong & Hensbergen (1996) sampled 13 species of small mammals in grassland habitat that ranged from < 1500m to > 1700m. This

slightly higher species richness could be attributed to the position of the SMC, which is in a transitional zone between the Grassland and Nama-Karoo biomes, whereas the main Drakensberg Mountains is dominated by the Grassland Biome (Mucina & Rutherford 2006). Biome transition zones in South Africa have elevated vegetation and climatic heterogeneity (Van Rensburg *et al.* 2004). This elevated vegetation and climatic heterogeneity therefore increases overall habitat complexity and heterogeneity. Habitat heterogeneity can be defined as the horizontal variation in habitat physiognomy or patchiness, while habitat complexity refers to the vertical variation within a habitat type (August 1983). Greater habitat heterogeneity and complexity are known to increase small mammal species richness and diversity (Dueser & Brown 1980; August 1983). This increase in species richness and diversity is associated with an increased number of niches (August 1983).

When compared to the southern Cape Fold Mountains, more small mammal species were captured in the SMC than on the Swartberg and Baviaanskloof mountains (Bond *et al.* 1980). However, small mammal species richness in the Kammanassie mountains is similar to the SMC (Nel *et al.* 1980). The species richness and diversity of small mammals in the Kammanassie mountains is high due to the structural complexity of the habitat within these mountains (Nel *et al.* 1980).

Overall, the Shannon diversity of small mammals is higher in the SMC when compared to the Drakensberg Mountains (Rowe-Rowe & Meester 1982; Bowland & Perrin 1993; Avenant 1997). However, the SMC has Shannon diversity that is similar to that observed in the Kammanassie mountains of the Cape Fold Mountains (Nel *et al.* 1980). The higher Shannon diversity in the SMC indicates a well-balanced small mammal community that is not overly dominated by one species (Nel *et al.* 1980; Magurran 2004). In the Drakensberg Mountains, sites are often

dominated by either *R. pumilio* or *M. varius* which lowers the overall small mammal diversity (Rowe-Rowe & Meester 1982; Bowland & Perrin 1993; Avenant 1997). In addition, because fewer species are present in the Drakensberg Mountains also decreases in the overall Shannon diversity (Nel *et al.* 1980; Magurran 2004).

Only one other study focussing on small mammal diversity in South Africa used the Simpson index of diversity to describe the small mammal communities that occur at high altitude (Rautenbach & Nel 1980). The small mammal Simpson index of diversity in the Cederberg Wilderness area was slightly higher than the SMC (Rautenbach & Nel 1980). This higher small mammal diversity in the Cederberg is linked to higher species richness (n = 16) of small mammals together with high floristic diversity (Rautenbach & Nel 1980).

The high small mammal mortality rate at ASNR could be attributed to *Myosorex varius*. Most shrew species are exposed to severe stress during trapping that increases their trap mortality rates (Buckner 1957). This high mortality rate observed in shrews is often related to their small body sizes that's more vulnerable to extreme temperatures.

Comparison of sites within the SMC

Overall, ASNR and MZNP were more similar to each other in terms of species composition than the SBNR. This could be related to differences in vegetation types among the sites (Mucina & Rutherford 2006). The high altitude small mammal communities of ASNR and MZNP were similar to communities that occur in the high altitude grasslands of the Drakensberg Mountains (Rowe-Rowe & Lowry 1982;

Rowe-Rowe & Meester 1982; Bowland & Perrin 1993; Avenant 1997). In addition, the dominant species at ASNR and MZNP, *R. pumilio, M. varius* and *O. irroratus,* are similar to the dominant species found in the high altitude areas of the Drakensberg Mountains (Rowe-Rowe & Lowry 1982; Rowe-Rowe & Meester 1982; Bowland & Perrin 1993; Avenant 1997). In contrast, the community composition of small mammals at SBNR consisted of species that are more commonly associated with rocky habitats (e.g. *M. namaquensis; M. granti* & *E. myurus*) from areas to the west of the SMC (Bond *et al.* 1980; Nel *et al.* 1980; Rautenbach & Nel 1980; Stuart *et al.* 1987; Eccard *et al.* 2000; O'Farrell *et al.* 2008).

The highest number of individuals were caught at the SBNR. The number of individuals was initially low during winter and spring at the SBNR (Figure 3.7). However, this number increased steadily throughout the summer and autumn at the SBNR (Figure 3.7). This steady increase could be related to a combination of fire and precipitation. During autumn 2009, a fire burnt some sections of the high altitude areas, adjacent to the sampling sites at SBNR. In addition, rainfall was highest during spring 2009 and summer 2010 at the SBNR. Certain species of small mammals are known to increase in numbers a few months after fire in grassland ecosystems (Rowe-Rowe & Lowry 1982; Yarnell *et al.* 2007). Rainfall is also known to have delayed effects on small mammal populations, whereby populations tend to increase a few months after substantial rainfall events (Yarnell *et al.* 2007). Therefore, the timing of the fire and rainfall coincided with the increase in number of individuals caught at SBNR.

The number of individuals caught was lowest at MZNP. Food availability at MZNP could have been lower than the other two sites (Caro 2001, 2002). However, quantitative data on insect, plant and seed abundances are not available for this site,

which makes this assertion difficult to clarify. Alternatively, predation pressure may be higher in MZNP, explaining the low capture success at this site (Caro 2001, 2002). However, predator densities are also not known. It might be more likely that ungulates have caused a decrease in small mammal densities. Ungulates are known to have negative impacts on small mammal diversity and densities by means of direct competition for the same resources and by decreasing vegetation cover which increases predation risk (Keesing 1998; Caro 2001, 2002; Begon *et al.* 2006; Yarnell *et al.* 2007). In addition, Yarnell *et al.* (2007) believe that moderately grazed areas can lead to a reduction in the number of small mammals but not species richness or diversity. Since MZNP was the only site that had large ungulates present, this seems to be a likely explanation for the low capture rate, and relatively high species richness and diversity when compared to the other two sites.

Conservation areas that were initially proclaimed to conserve larger mammal species often fail to effectively conserve small mammals, because the conservation practices that are successful for larger mammals do not fully apply to small mammal populations (Caro 2001, 2002). This failure of the umbrella conservation concept was observed in the study. Small mammals are often better represented in areas that are marginally disturbed (Caro 2001). Sometimes moderate levels of grazing can enhance small mammal diversity through heterogeneous habitat structuring (Yarnell *et al.* 2007 and references therein). This is an important factor to consider when planning to effectively conserve small mammals at high altitudes.

Although the small mammal community composition differed slightly among the three sites, the species richness, Shannon diversity and Simpson index of diversity were similar across the sites. This indicates that the general diversity within the larger SMC area is stable. Various local and regional factors are responsible for the

diversity and species richness of small mammals in a specific area (Whittaker *et al.* 2001; Rowe 2009). Climate is the primary driving force behind the diversity of mammals, although its effects are indirect as it is climate that directly affects vegetation which in turn affects mammalian diversity (Andrews & O'Brien 2000; Yarnell *et al.* 2007; Rowe 2009). The species richness of small mammals in the SMC roughly coincides with the small mammal species richness isoclines predicted by Andrews & O'Brien (2000) for southern Africa. This indicates that climate is possibly one of the more important factors regulating the stable diversity across the SMC. However, in this study, model selection revealed that neither temperature nor precipitation seemed to influence measures of diversity. Moreover, the precipitation and temperature from the three sites were similar.

The role of climate does, however, become less evident when moving from a macro (e.g. mountain range) scale to a local scale (e.g. single mountain summit), as other local factors that have greater heterogeneity become more prevalent (Whittaker *et al.* 2001). The effects of local scale factors were observed in this study, as site was the factor that had the greatest influence on the number of individuals caught, species richness and Shannon diversity. Exactly which local scale factors are responsible for these site effects are unknown. The vegetation differences among the sites seems to be an important factor driving small mammal diversity as vegetation complexity and heterogeneity both influence small mammal assemblage structure (Williams *et al.* 2002). Although habitat heterogeneity has been identified as an important factor influencing the diversity of small mammals at specific sites, other important factors could also affect small mammal diversity. These other factors include area (e.g. larger areas sampled provide more habitat types), historical factors (e.g. rate of speciation), available energy (e.g. partitioning of energy limits species richness),

environmental stress (e.g. only selected species are physiologically adapted to harsh environments), environmental stability (e.g. only selected species are physiologically adapted to broad scale environmental conditions), disturbance (e.g. prevention of competitive exclusion) and biological interactions (e.g. competition and predation) (Fraser & Currie 1996; Whittaker *et al*. 2001; Hortal *et al.* 2008; Rowe 2009). It is highly unlikely that any one of these factors can account for the variability of small mammal diversity, it is more likely that a combination of these factors contribute to the overall small mammal diversity (Rowe 2009). These factors should be incorporated into future studies focussing on small mammal diversity at high altitudes.

CHAPTER 4

THE EFFECTIVENESS OF FIVE BAIT TYPES FOR SAMPLING SMALL MAMMAL COMMUNITIES AT HIGH ALTITUDE

4. 1 INTRODUCTION

Many factors contribute to the sampling accuracy of small mammal communities (O'Farrell *et al.* 1994; Jones *et al.* 1996; Osbourne *et al.* 2005). Some of the more common factors include type and size of the trap used (Beacham & Krebs 1980; Slade *et al.* 1993; O'Farrell *et al.* 1994; Woodman *et al.* 1996; Anthony *et al*. 2005; dos Santos-Filho *et al.* 2006; Fontúrbel 2010; De Bondi 2010), trapping configuration (Jett & Nichols 1987; Jones *et al.* 1996; Parmenter *et al*. 2003; Pearson & Ruggiero 2003), number of trap nights (Olsen 1975), seasonality (Fitch 1954; Stephenson 1994), moon phase (Price *et al.* 1984) and climatic conditions (Van Hensbergen & Martin 1993).

Bait is also an important trapping variable as it acts as a medium to attract small mammals, and its use theoretically increases overall capture rates in diversity studies (Jones *et al.* 1996). For example, research suggests that more small mammals are captured in traps that are baited compared to those that are not (Stickel 1948; Beer 1964; Patric 1970; Dippenaar 1974). In addition, bait provides sustenance for any trapped animals, thereby lowering the potential for trap mortality (Jones *et al.* 1996). Since it is highly unlikely that one bait type will be equally attractive to all small mammal species, studies focussing on multiple species capture (e.g. community composition) should use baits that are attractive to a wide range of

species (Dippenaar 1974). In addition, good bait should be easy to produce in the field and should be relatively cheap (Patric 1970).

The literature regarding the effectiveness of baits for small mammal capture is rich (Stickel 1948; Fitch 1954; Fowle & Edwards 1954; Beer 1964; Patric 1970; Getz & Prather 1975; Anderson & Ohmart 1977; Willan 1986; Rickart *et al.* 1991; Du Toit & Fourie 1992; Manville *et al*. 1992; Woodman *et al.* 1996; Weihong *et al.* 1999; Balete 2009; Fontúrbel 2010). However, most of the literature that has assessed the effectiveness of bait type has centred on the bait preferences of particular species (Stickel 1948; Fitch 1954; Dippenaar 1974; Willan 1986; Du Toit & Fourie 1992; Manville *et al.* 1992; Weihong *et al.* 1999), or preventing bait removal by invertebrates (Getz & Prather 1975; Anderson & Ohmart 1977). Consequently, these studies could not assess relative abundances using mark-recapture techniques. In addition, some of the earlier studies were based on kill trapping only (Fowle & Edwards 1954; Beer 1964; Patric 1970; Dippenaar 1974; Getz & Prather 1975; Anderson & Ohmart 1964). Furthermore, initial works on the differential effectiveness of baits were only based on the number of captures obtained for each species (Beer 1964; Patric 1970; Dippenaar 1974; Willan 1986; Rickart *et al.* 1991 & Woodman *et al.* 1996). These estimates did not focus on other community measurements like species richness or diversity.

Although most studies have provided an indication of how many species were caught with each bait type, none of them have statistically tested for differences among bait types for measuring species richness (Fowle & Edwards 1954; Beer 1964; Patric 1970; Dippenaar 1974; Willan 1986; Rickart *et al.* 1991; Woodman *et al.* 1996; Balete *et al.* 2008). Current measures of species richness are more sophisticated and form an important part of most diversity assessments (Magurran

2004). Modern species richness extrapolation methods have the potential to measure probable species richness and can thus be used to evaluate the performance of various sampling methods in obtaining realistic estimates of species richness (Chapter 3; Magurran 2004). Moreover, the differential effectiveness of bait types for determining heterogeneity measures (e.g. Shannon diversity index) of small mammal communities is vital for understanding the total diversity of particular areas.

In South Africa, few studies have focussed on the effectiveness of different bait types for capturing small mammals. (Dippenaar 1974; Bond *et al.* 1980; Willan 1986; Du Toit & Fourie 1992). The most extensive (in terms of trap effort and number of baits tested) of these studies was conducted by Dippenaar (1974). Although his study focussed primarily on captures of *Rhabdomys pumilio,* two other species (*Mastomys natalensis* and *Otomys irroratus*) and their bait preferences were also discussed (Dippenaar 1974). A test of the effectiveness of 10 bait types showed that *R. pumilio* and *Mastomys natalensis* both have a preference for a mixed bait (peanut butter, oats, syrup and sunflower oil), while *O. irroratus* prefers oats with bacon (Dippenaar 1974).

The major aim of this study was to test the efficiency of five different bait types to sample small mammal communities at high altitude. Specifically, I wished to determine the effectiveness of the different bait types for six measures of community structure (number of captures; number of recaptures; number of individuals caught, species richness, Shannon diversity index and Simpson index of diversity). I defined effectiveness as the ability to measure high species richness together with a high number of individuals per species, and number of recaptures.

4.2 MATERIALS AND METHODS

Data collection

For a detailed description of the basic trapping protocol used to capture small mammals, refer to section 2.5.

Five bait types were selected for testing; Birdseed and banana (BB) mixed in a ratio of 1:1 (Fitch 1954; August 1983; Caro 2001;Nor 2001; Hoffmann & Zeller 2005; Fontúrbel 2009), mixed fruit jam and bran flakes (JB) mixed in a ratio of 1:2 (Beer 1964; Schradin & Pillay 2005; Keller & Schradin 2008), polony (PL) cubed into $2cm^3$ blocks, peanut butter and oats (PO) mixed in a ratio of 1:1 (Stickle 1948; Beer 1964; Rowe-Rowe & Lowry 1982; Rowe-Rowe & Meester 1982; Rowe-Rowe & Meester 1985; Willian 1986; Kerley 1992; Bowland & Perrin 1993; Lomolino 1994; Manville *et al.* 1996; Whittington-Jones 2008), and a control (CT) which was an unbaited trap (Stickle 1948; Fowle & Edwards 1954; Beer 1964; Patric 1970; Dippenaar 1974).

The first two baits (birdseed and banana & jam and bran flakes) have never been tested as a mixture but their individual ingredients have been used in other studies (Fitch 1954; Beer 1964; August 1983; Caro 2001;Nor 2001; Hoffmann & Zeller 2005; Schradin & Pillay 2005; Keller & Schradin 2008 Fontúrbel 2009). The baits were selected in an attempt to ensure that granivorous, herbivorous and frugivorous species were attracted to the traps (Jones *et al.* 1996). The polony (processed meat) bait was included to increase the likelihood of capturing insectivorous small mammals (Beer 1964; Patric 1970; Rickart *et al.* 1991; Woodman *et al.* 1996). All products used to make the baits were commercially available and were kept standard throughout the study. All baits were standardised to 20ml in volume, which provided enough sustenance for captured animals for 48 hours (Jones *et al.* 1996).

Within a transect (see Chapter 2.5), each of the five bait types were randomly assigned to one of the five sub-transect positions. Sub-transects thus consisted of six replicates of one specific bait type. A spacing of 10-15m between traps is sufficient for such traps to be independent of each other (Jones *et al.* 1996). This was the standard bait layout for all transects at the three study sites during the four consecutive seasons of sampling.

Traps were rebaited with fresh bait halfway through a five night trapping session (Jones *et al*. 1996). When traps were rebaited their sub-transect positions were also rotated, to minimize the effect of varying small mammal abundances within a transect (Beer 1964: Figure 4.1). When traps were rebaited, they were always baited with the same bait type, to avoid cross-contamination of two bait types within one trap. In addition, all traps were washed in a combination of bleach and hot water (Willan 1986) between seasonal sampling events to rid traps of additional odours (Jones *et al*. 1996). Fresh bait was also provided after captured specimens had consumed all or most of the bait within a trap.

Data analyses

Capture results for each site were summarized by calculating eight parameters viz. number of captures, number of individuals, number of recaptures, trap success, trap mortality, species richness, Shannon diversity index; Simpson index of diversity. See chapter 3.2.1 for definitions of these parameters. Six measures were used to test for differences among the five bait types: number of captures, number of individuals captured, number of recaptures, species

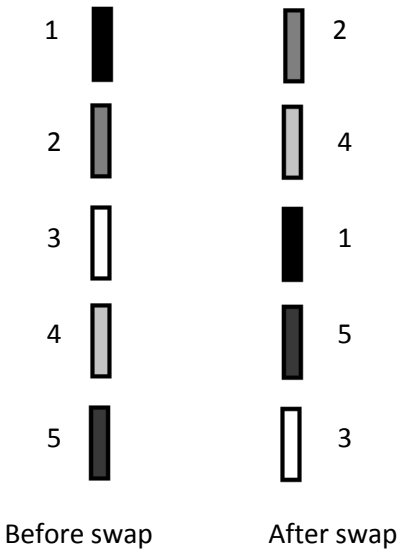

Figure 4.1: Change of sub-transect positions after traps have been rebaited and swapped half-way through a trapping session at a site. Blocks and numbers indicate positions change sub-transects.

richness, Shannon diversity index and Simpson index of diversity using Kruskal-Wallis tests (Statistica 9; Statsoft, Inc.). Each bait type was represented by 36 samples derived from the three replicates from each of the three sites for four consecutive austral seasons. In addition, a correlation analysis was conducted to test the relationship between the number of individuals caught per species and the number of bait types consumed by that species (Statistica 9; Statsoft, Inc.).

The percentage attraction of each bait types per species was calculated by dividing the number of individuals captured using each bait type by the total number of captures per species (Fowle & Edwards 1954).

The observed species richness computed for a community is likely to be an underestimation of the true species richness of that community (Colwell & Coddington 1994; Chazdon *et al.* 1998; Longino *et al.* 2002; Magurran 2004). This is

largely due to sampling limitations (e.g. ability to detect cryptic species, and impracticality of sampling every possible micro-habitat) that inhibit our ability to estimate true species richness accurately (Chazdon *et al.* 1998; Longino *et al.* 2002; Magurran 2004; Chao *et al.* 2005). Richness estimators mark the most significant advancement in biodiversity measurement in the last 15 years (Chapter 3; Magurran 2004). These estimators have been developed to serve as extrapolation methods for determining true species richness from a known number of samples (Colwell & Coddington 1994; Magurran 2004; Chao *et al.* 2005). Two of the most recent non-parametric methods include the incidence-based coverage estimator (ICE) and the corresponding abundance-based coverage estimator (ACE) (Chazdon *et al.* 1998; Magurran 2004). Both of these estimators are aimed at the less abundant species within a community (Chazdon *et al.* 1998; Magurran 2004). ICE is based on species found in ≤ 10 sampling units, and ACE is based on species with ≤ 10 individuals per sample (Chazdon *et al.* 1998; Magurran 2004). These estimators compute the minimum true species richness and should theoretically stabilise at smaller sample sizes, before the species accumulation curve reaches its asymptote (Magurran 2004). Moreover, these estimators can be used to test the efficiency of different sampling methods (Longino *et al.* 2002). A sampling method which has been effective will therefore show a convergence of the species accumulation curve by both the ACE and ICE (Longino *et al.* 2002).

Species accumulation curves (S_{obs} Mau-Tau), ACE and ICE were computed for each bait treatment over the 36 samples using EstimateS 8.2 (Colwell, R.K. 2009). The individual performance of the bait types was measured by subtracting the observed species richness after 36 sampling events from the predicted species richness computed by each estimator.

4.3 RESULTS

Overall trapping results

Overall, peanut butter and oats performed the best of the five baits tested (Table 4.1), yielding the highest trap success, number of captures, recaptures and individuals (Table 4.1). In addition, despite achieving the highest capture rate, use of peanut butter and oats bait resulted in relatively low (17%) levels of small mammal mortality (Table 4.1). However, peanut butter and oats only managed to capture eight species (Table 4.1). Nevertheless, both the Shannon and Simpson diversity indices indicated that peanut butter and oats was one of the best baits to use for measuring heterogeneity of a small mammal community at high altitudes (Table 4.1).

Birdseed and banana bait yielded lower levels of trap success, numbers of captures and individuals compared to peanut butter and oats and polony baits (Table 4.1). However, the number of recaptures for birdseed and banana was comparable to the recaptures obtained using peanut butter and oats and polony (Table 4.1). Trap mortality of small mammals was low (12.5%) for the birdseed and banana bait (Table 4.1). In addition, despite achieving a relatively low capture rate, the birdseed and banana bait managed to sample the highest number of small mammal species (Table 4.1). Furthermore, birdseed and banana was one of the best baits at measuring the heterogeneity (Shannon & Simpson diversity indices) of the small mammal communities at high altitude (Table 4.1).

Jam and bran flakes was comparable with the birdseed and banana bait with respect to trap success, number of captures, individuals, recaptures and Simpson diversity (Table 4.1). However, mortality of small mammals was lowest (2.8%) for this bait

compared to the others (Table 4.1). Furthermore, the jam and bran flakes bait gave the second highest species richness of all bait types (Table 4.1).

Although polony had similar numbers of recaptures of small mammals compared to the peanut butter and oats bait, the trap success, number of captures and individuals was lower for polony compared to peanut butter and oats (Table 4.1). In addition, mortality was much higher (43%) for polony than for any other bait type (Table 4.1). This mortality rate can be directly related to high *M. varius* mortalities. Furthermore, polony did not appear to be a satisfactory predictor of small mammal community structure (species richness & heterogeneity measures) at high altitude (Table 4.1).

The control treatment yielded the lowest trap success, number of captures, individuals and recaptures of all the baits tested (Table 4.1). In addition, the mortality rate of the control traps was relatively high (25%) (Table 4.1). Furthermore, the control obtained one of the lowest measures of species richness (Table 4.1). Nevertheless, it yielded heterogeneity measures that were similar to the jam and bran flakes bait (Table 4.1).

Table 4.1: Summary of the effectiveness of five bait types used to capture small mammals at three high altitude (> 1700 m) sites within the Sneeuberg Mountain Complex, Eastern Cape, South Africa over four consecutive austral seasons. (Values in brackets indicate percentages).

Bait type	No. of Captures	No. of individuals	No. recaptures	No. of trap nights	No. of mortalities	Species richness	Shannon diversity index	Simpson index of diversity
Birdseed and banana (BB)	75 (17.7)	49 (16.8)	26 (19.8)	1059 (7.1)	9 (12.5)	11	1.8	0.8
Jam and bran flakes (JB)	69 (16.3)	43 (14.7)	26 (19.8)	1053 (6.6)	2 (2.8)	9	1.7	0.8
Polony (PL)	100 (23.6)	69 (23.6)	31 (23.7)	1050 (9.5)	31 (43.1)	7	1.4	0.7
Peanut butter and oats (PO)	123 (29.1)	91 (31.2)	32 (24.4)	1052 (11.7)	12 (16.7)	8	1.8	0.8
Control (CT)	56 (13.2)	40 (13.7)	16 (12.2)	1066 (5.3)	18 (25.0)	7	1.7	0.8
Total	**423**	**292**	**131**	**5280 (8.0)**	**72 (24.7)**	**12**	**1.9**	**0.8**

Small mammal community measurements

The number of captures was significantly higher for the peanut butter and oats bait than the control (Figure 4.2: $H_{(4, 180)} = 16.76$; $p < 0.01$) and jam and bran flakes bait (Figure 4.2: $H_{(4, 180)} = 16.76$; $p < 0.01$). However, there was no significant difference between peanut butter and oats and birdseed and banana (Figure 4.2: $H_{(4, 180)} = 16.76$; $p < 0.01$) and polony (Figure 4.2: $H_{(4, 180)} = 16.76$; $p < 0.01$).

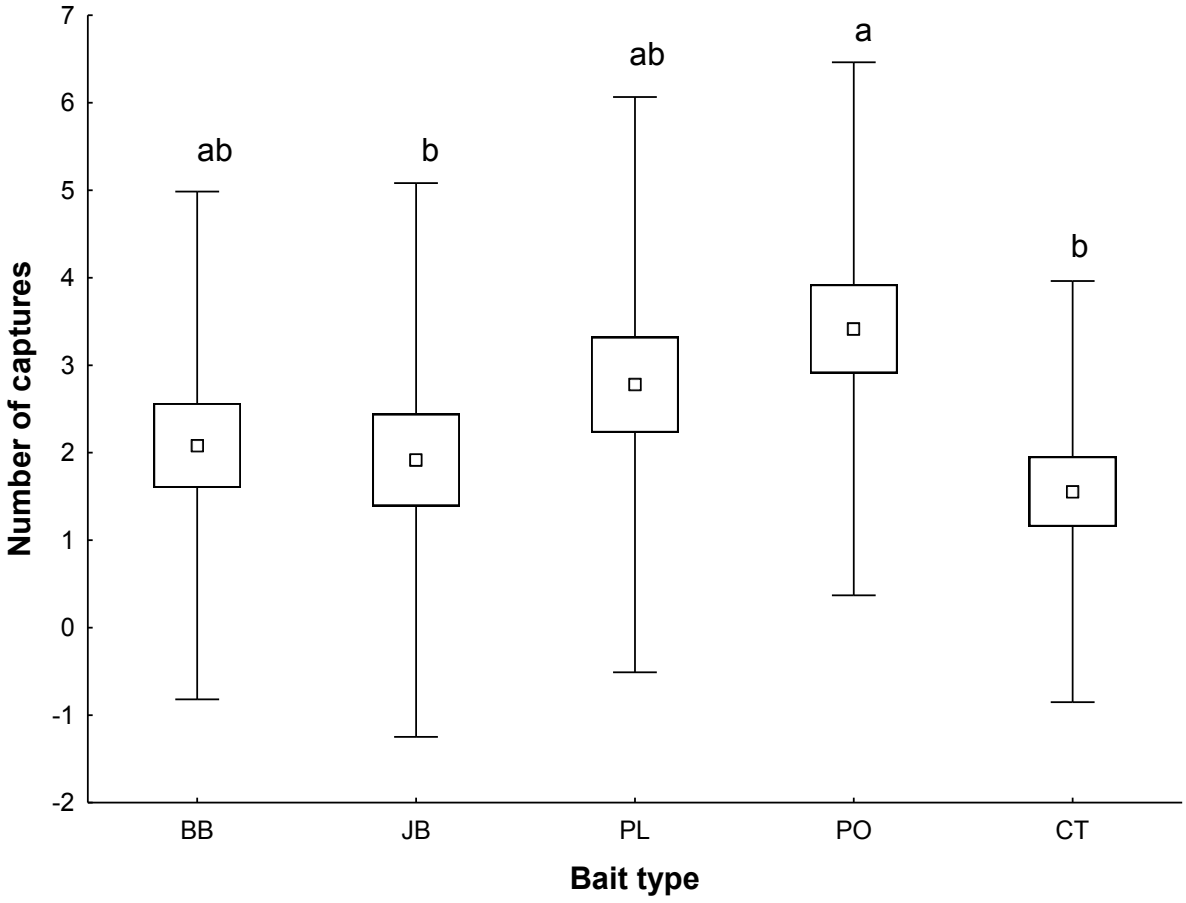

Figure 4.2: Comparison of the number of captures obtained using each of the five bait types (BB = birdseed and banana ; JB = jam and bran flakes ; PL = polony ; PO = peanut butter and oats ; CT = control) used to trap small mammals at three high altitude (> 1700 m) sites within the Sneeuberg Mountain Complex, Eastern Cape Province, South Africa. (Data are means, boxes are ± se and whiskers are ± sd). Numbers a, b and ad indicate significant relationships among bait types, where a and b differ significantly and ab does not differ significantly from a or b.

The number of individuals caught was highest for peanut butter and oats and polony (Figure 4.3). Significantly more individuals were caught with peanut butter and oats compared to jam and bran flakes (Figure 4.3: $H_{(4, 180)} = 17.09$; $p < 0.05$). Similarly, peanut butter and oats caught significantly more individuals than the control (Figure 4.3: $H_{(4, 180)} = 17.09$; $p < 0.01$). The numbers of individuals caught by the remaining bait types were similar (Figure 4.3).

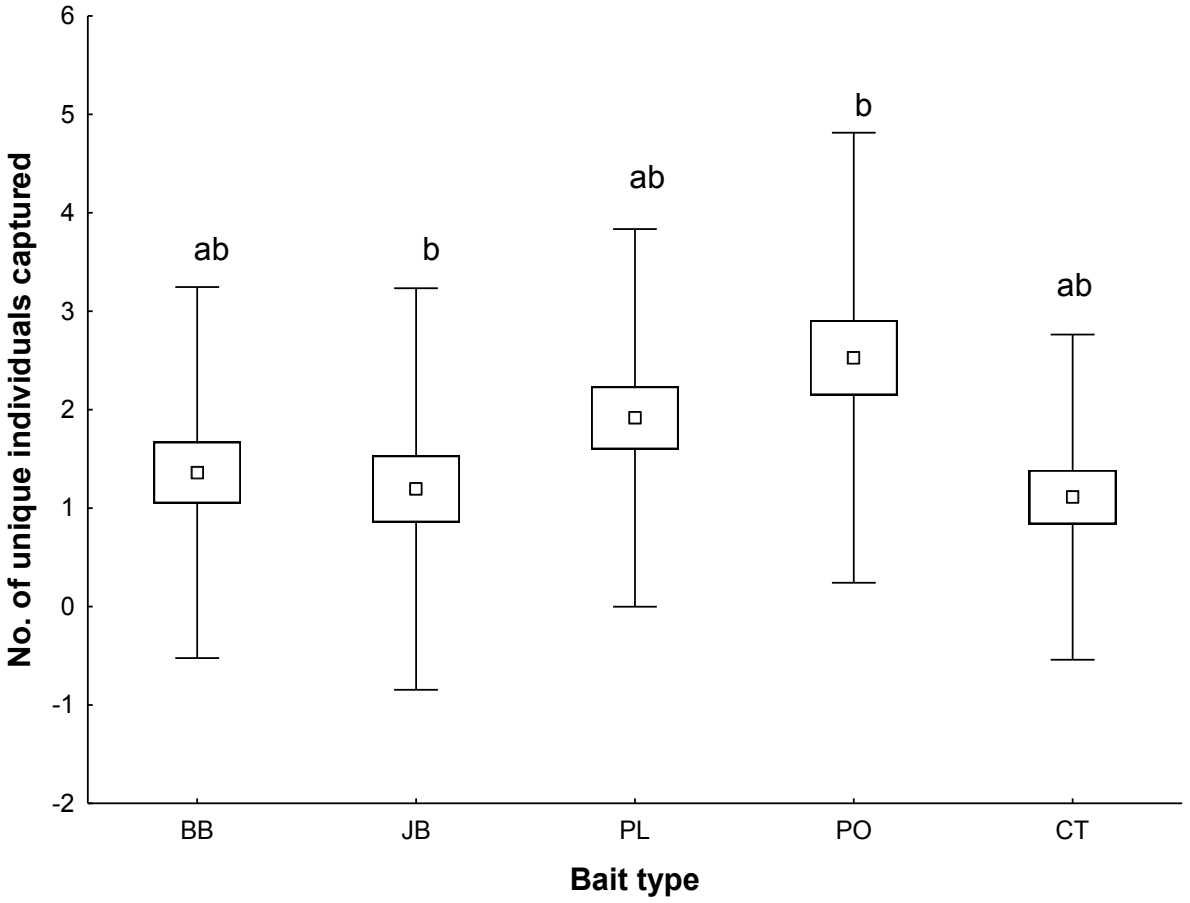

Figure 4.3: Comparison of the number of individuals captured using each of the five bait types (BB = birdseed and banana ; JB = jam and bran flakes ; PL = polony ; PO = peanut butter and oats ; CT = control) used to trap small mammals at three high altitude (> 1700 m) sites within the Sneeuberg Mountain Complex, Eastern Cape Province, South Africa. (Data are means, boxes are ± se and whiskers are ± sd). Numbers a, b and ad indicate significant relationships among bait types, where a and b differ significantly and ab does not differ significantly from a or b.

The number of recaptures for the five bait types were similar (Figure 4.4: $H_{(4, 180)} = 6.60$; $p > 0.05$). However, fewer recaptures were recorded for the control than any of the other bait types (Figure 4.4).

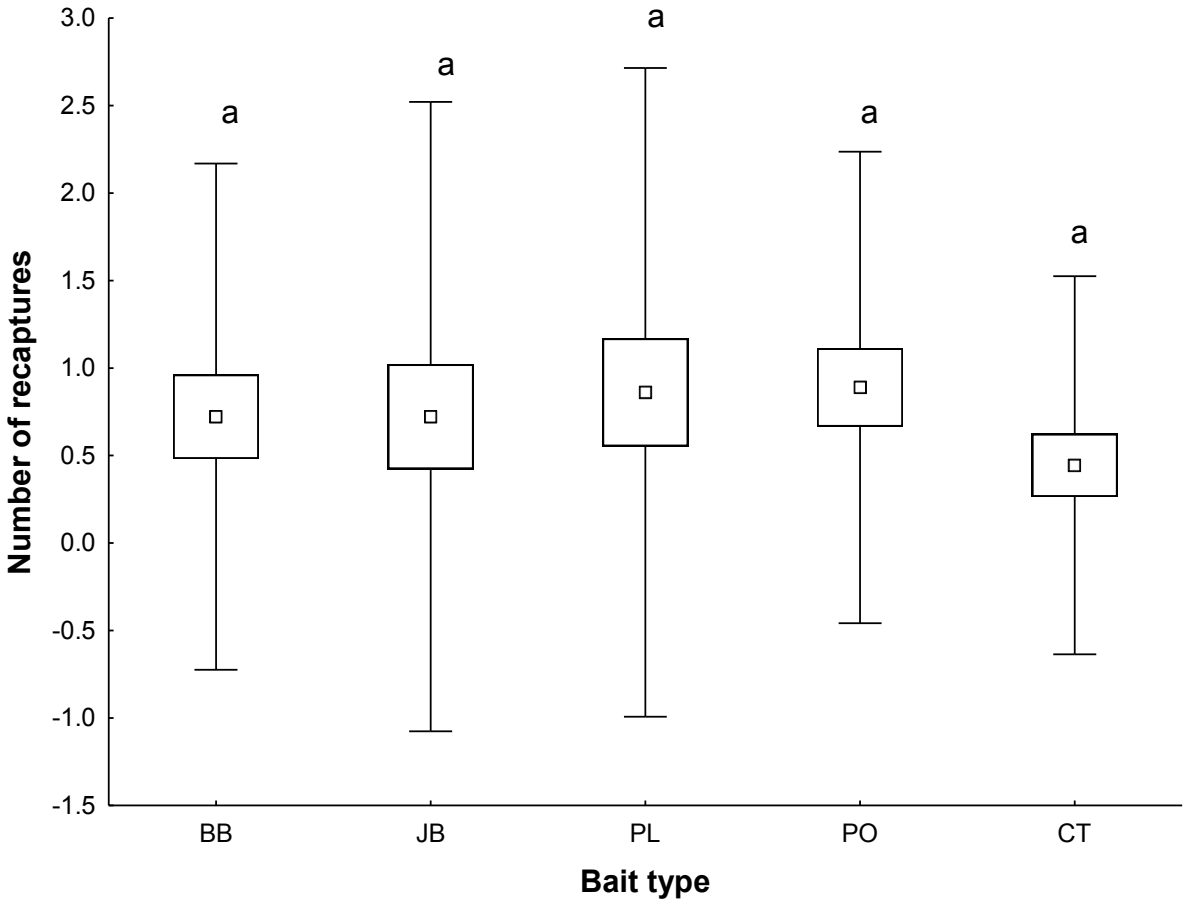

Figure 4.4: Comparison of the number of recaptures obtained using each of the five bait types (BB = birdseed and banana ; JB = jam and bran flakes ; PL = polony ; PO = peanut butter and oats ; CT = control) used to trap small mammals at three high altitude (> 1700 m) sites within the Sneeuberg Mountain Complex, Eastern Cape Province, South Africa. (Data are means, boxes are ± se and whiskers are ± sd). Numbers a, b and ad indicate significant relationships among bait types, where a and b differ significantly and ab does not differ significantly from a or b.

Average species richness was highest for peanut butter and oats (Figure 4.5) and significantly more species were caught using peanut butter and oats than jam and

bran flakes (Figure 4.5: $H_{(4, 180)} = 13.83$; $p < 0.05$) and the control (Figure 4.5: $H_{(4, 180)} = 13.83$; $p < 0.05$). The numbers of species captured by the remaining bait types were similar (Figure 4.5).

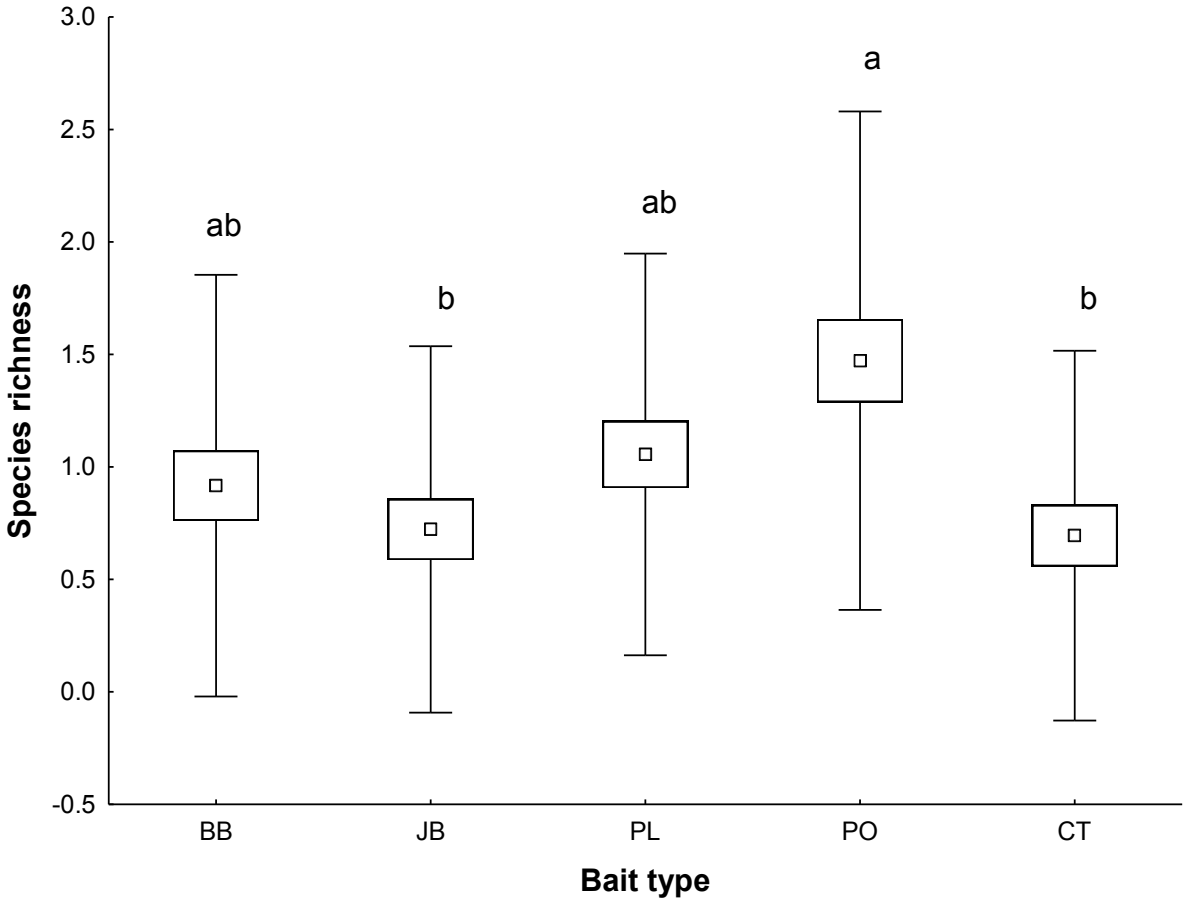

Figure 4.5: Comparison of the species richness obtained using each of the five bait types (BB = birdseed and banana ; JB = jam and bran flakes ; PL = polony ; PO = peanut butter and oats ; CT = control) used to trap small mammals at three high altitude (> 1700 m) sites within the Sneeuberg Mountain Complex, Eastern Cape Province, South Africa. (Data are means, boxes are ± se and whiskers are ± sd). Numbers a, b and ad indicate significant relationships among bait types, where a and b differ significantly and ab does not differ significantly from a or b.

The average Shannon diversity was highest for peanut butter and oats and lowest for jam and bran flakes (Figure 4.6). Although there was an overall significant effect of bait type on Shannon diversity (Figure 4.6: $H_{(4, 180)} = 10.44$; $p < 0.05$), no pairs were significant (Figure 4.6).

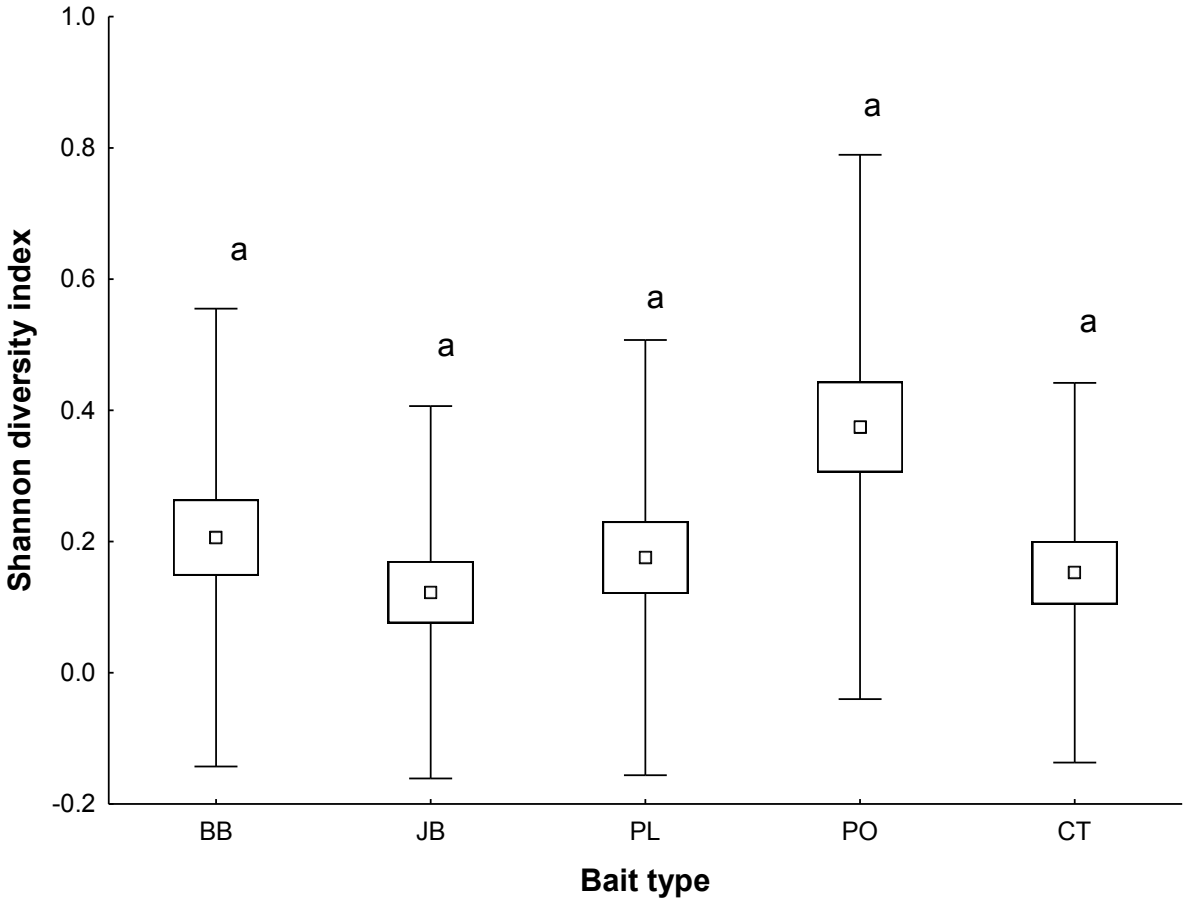

Figure 4.6: Comparison of Shannon diversity indexes obtained using each of the five bait types (BB = birdseed and banana ; JB = jam and bran flakes ; PL = polony ; PO = peanut butter and oats ; CT = control) used to trap small mammals at three high altitude (> 1700 m) sites within the Sneeuberg Mountain Complex, Eastern Cape Province, South Africa. (Data are means, boxes are ± se and whiskers are ± sd). Numbers a, b and ad indicate significant relationships among bait types, where a and b differ significantly and ab does not differ significantly from a or b.

The Simpson index of diversity was highest for the birdseed and banana bait and the control (Figure 4.7). Simpson diversity was lowest for polony and there was a significant difference between polony and birdseed and banana (Figure 4.7: $H_{(4, 67)} = 11.74$; $p < 0.05$). The Simpson indices of diversity were similar for the remaining bait types (Figure 4.7).

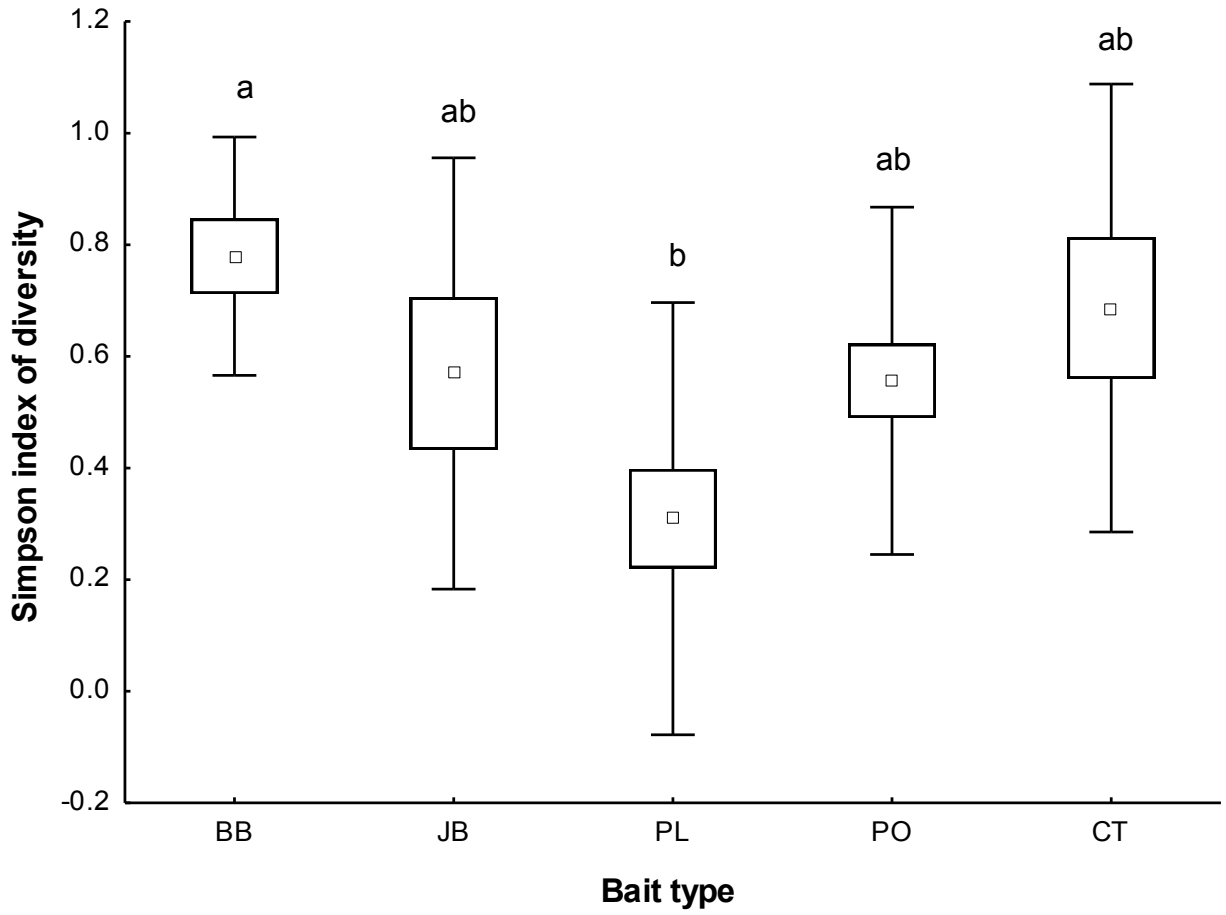

Figure 4.7: Comparison of Simpson index of diversity obtained by each of the five bait types (BB = birdseed and banana ; JB = jam and bran flakes ; PL = polony ; PO = peanut butter and oats ; CT = control) used to trap small mammals at three high altitude (> 1700 m) sites within the Sneeuberg Mountain Complex, Eastern Cape Province, South Africa. (Data are means, boxes are ± se and whiskers are ± sd). Numbers a, b and ad indicate significant relationships among bait types, where a and b differ significantly and ab does not differ significantly from a or b.

Species accumulation curves and richness estimators

After 36 sampling events (three replicates per site per season), the species accumulation curves for birdseed and banana and jam and bran flakes appeared to be increasing (Figure 4.8 [a]; [b]). The remaining three bait types all appeared to level off after 36 sampling events (Figure 4.8 [c]; [d]; [e]).

ACE and ICE estimators both showed steady increases for birdseed and banana over the 36 sampling events (Figure 4.8 [f]). Both estimators levelled off, but were consistently higher than the observed species richness for jam and bran flakes (Figure 4.8 [g]). For polony, both estimators showed an initial increase followed by a levelling off that eventually approximated observed species richness (Figure 4.8 [h]). Except for an initial increase in the ICE estimator, both ACE and ICE behaved similar to the observed species richness of the peanut butter and oats bait, so much so that all three lines converged after about 30 samples (Figure 4.8 [i]). ACE and ICE modelled the true species richness of CT closely to its observed species richness (Figure 4.8 [j]). ACE and ICE both overestimated species richness by more than double that of the observed species richness for birdseed and banana (Figure 4.9). The difference between the true species richness and the observed species richness was less than three species for jam and bran flakes, polony and the control (Figure 4.9). However, peanut butter and oats had the best performance of all the bait types, with no difference between the observed species richness and the true species richness estimated by ACE and ICE (Figure 4.9).

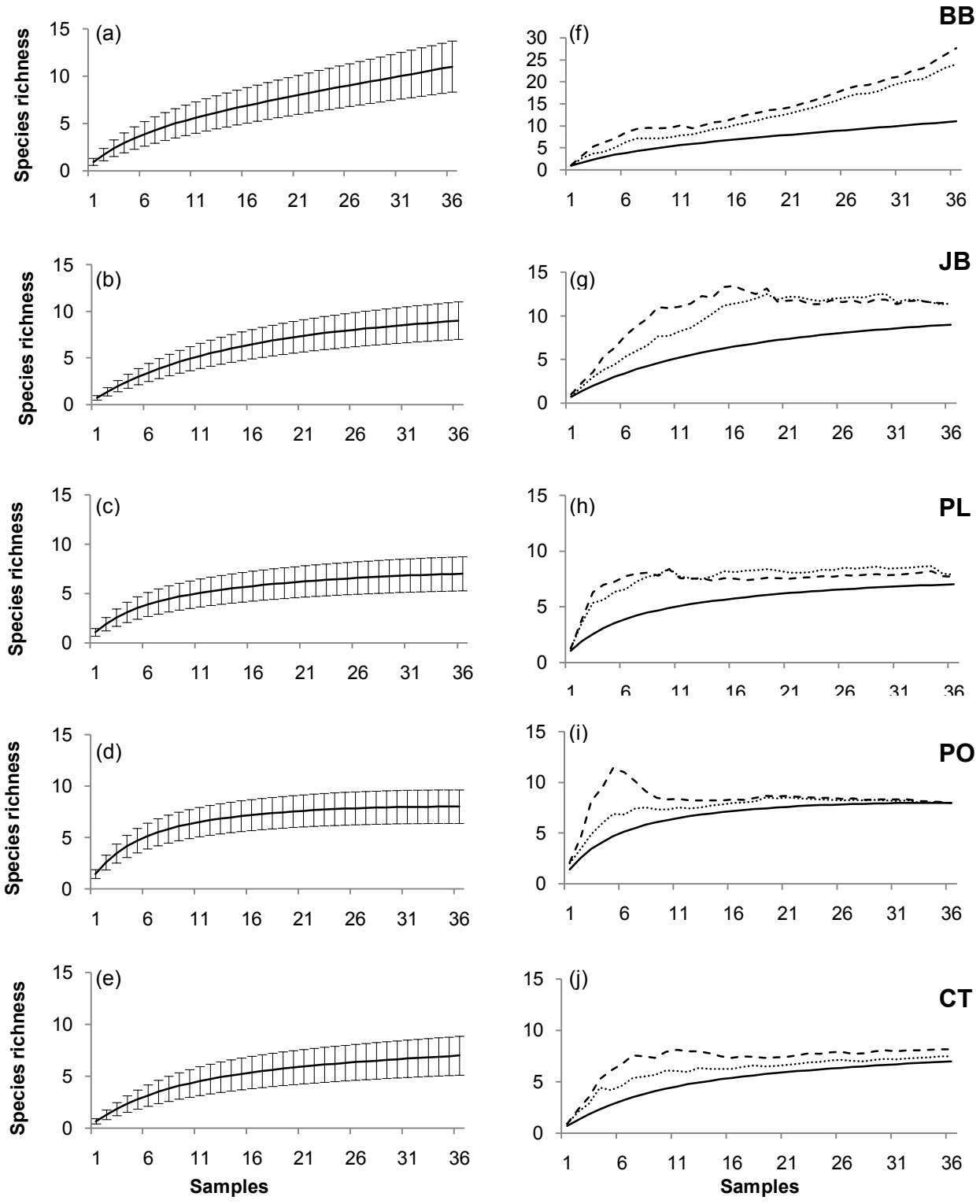

Figure 4.8: Performance of richness estimators for each of the five bait types at three high altitude (> 1700 m) sites within the Sneeuberg Mountain Complex, Eastern Cape Province, South Africa. Graphs (a) – (e) depict observed species richness (S_{obs}: N= 36; Mean ± sd) for each bait treatment. Graphs (f) – (j) compare the ICE and ACE of each bait with the observed species richness.

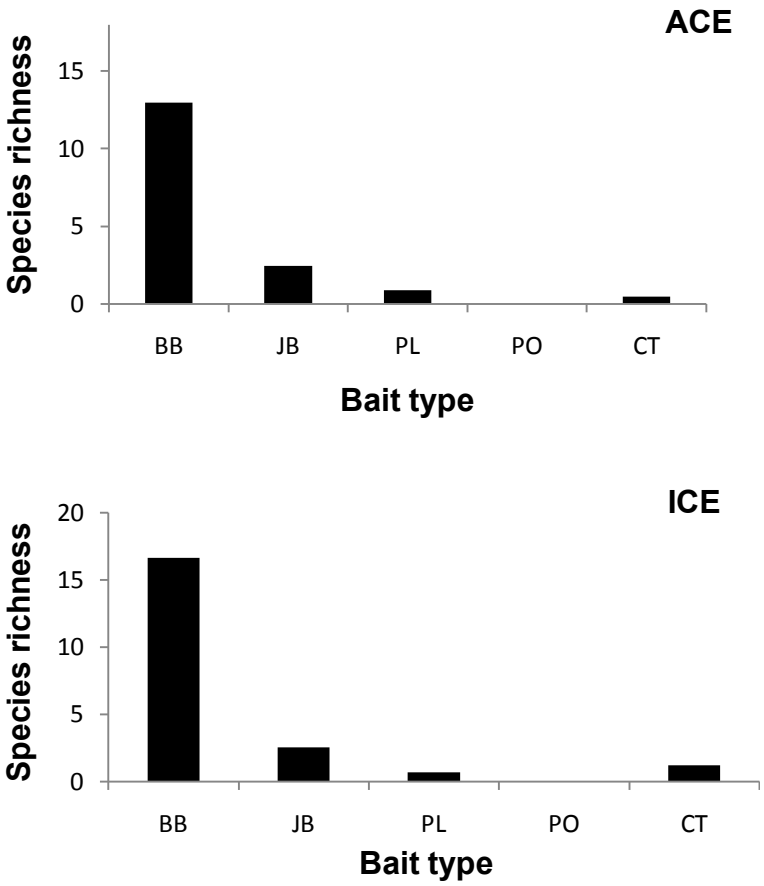

Figure 4.9: Differences among the observed species richness (S_{obs}) and two richness estimators ACE (a) and ICE (b) to measure the performance of the five bait types (BB = birdseed and banana; JB = jam and bran flakes; PL = polony; PO = peanut butter and oats; CT = control) used to capture small mammal species at three high altitude (> 1700 m) sites within the Sneeuberg Mountain Complex, Eastern Cape Province, South Africa.

Relationship between species captured and baits consumed

There was a significant positive relationship between the number of individuals caught per species, and the number of bait types consumed by that particular species (Figure 4.10: $r = 0.76$; $F = 13.58$; $p < 0.01$). Thus, species with higher abundances were more likely to consume all five of the bait types, although the attraction percentage of each bait type was different for each species (Table 4.2).

This relationship was particularly evident for the five most abundant species (*M. varius*; *E. myurus*; *M. namaquensis*; *O. irroratus* and *R. pumilio*), where all five species consumed all five bait types during the four seasons of trapping (Table 4.2). This relationship also indicates that species were unlikely to be associated with only one or two bait types when they are present at higher abundances (Table 4.2).

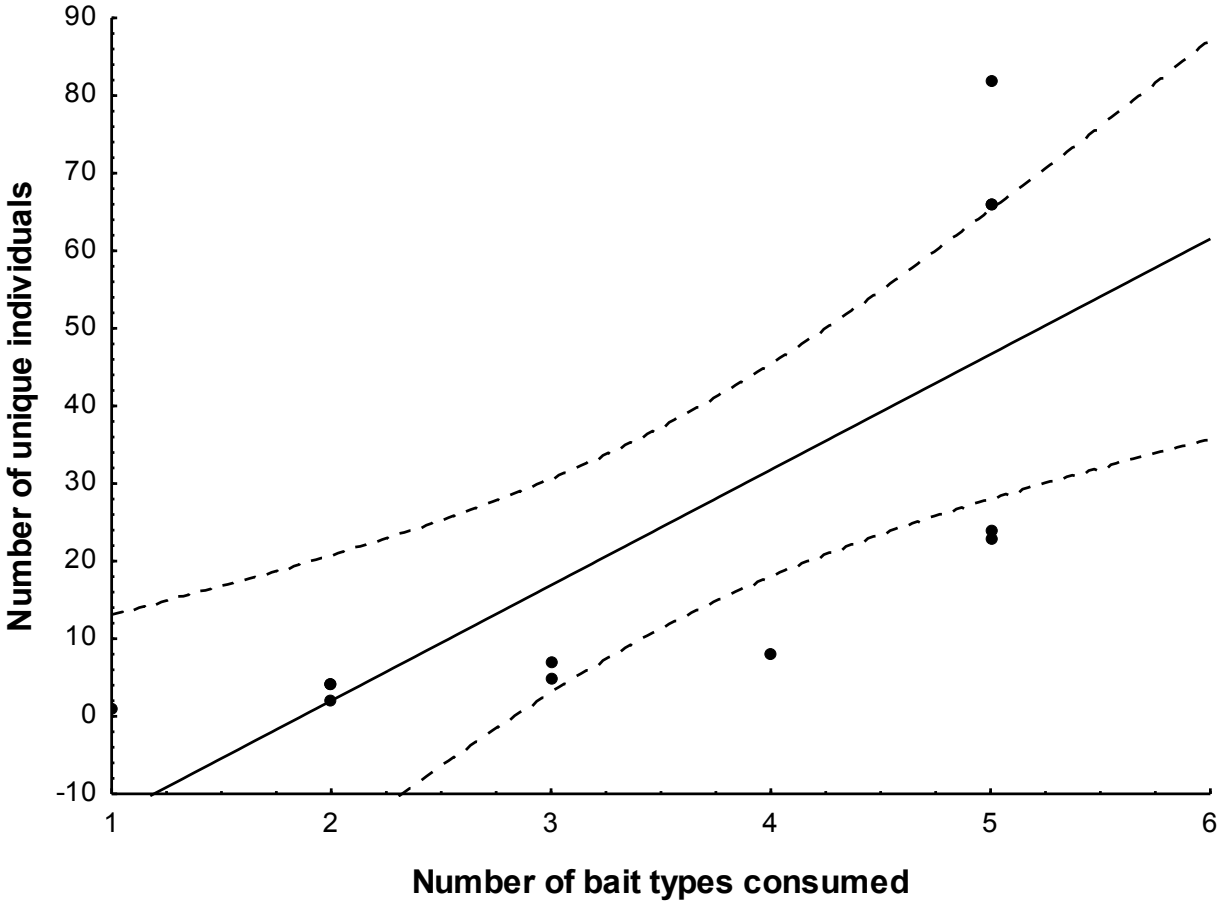

Figure 4.10: Relationship between the numbers of individuals caught for each of 12 small mammal species and the number of baits that were used to capture those individuals at three high altitude (> 1700 m.a.s.l.) sites within the Sneeuberg Mountain Complex, Eastern Cape Province, South Africa. Dashed lines indicate 95% confidence limits; ($F = 13.58$; $df = 10$; $r = 0.76$; $p < 0.01$).

Birdseed and banana was favoured by *M. minutoides* and *G. ocularis* (Table 4.2). However, there was only one capture record for each of these species. *Elephantulus myurus* and *O. sloggetti* both preferred jam and bran flakes bait (Table 4.2). Although *M. varius* was the only species to show a preference for polony, *M. namaquensis* was also caught in high numbers with this bait (Table 4.2). Six of the eight species caught by peanut butter and oats showed a preference for this bait type (Table 4.2). Of these six species five were omnivorous (*D. melanotis*, *M. granti*, *M. namaquensis*, *M. albicaudatus*, *R. pumilio*), and one (*O. irroratus*) herbivorous (Skinner & Chimimba 2005). The only species to show a marked preference for the control was *S. campestris*.

Table 4.2: The number of individuals caught for each species of small mammals with each of the five bait types (BB = birdseed and banana; JB = jam and bran flakes; PL = polony; PO = peanut butter and oats; CT = control) used to capture small mammals at three high altitude (> 1700 m.a.s.l.) sites within the Sneeuberg Mountain Complex, Eastern Cape Province, South Africa. (Values in brackets indicate the percentage attraction of each bait type per species).

Species	**BB**		**JB**		**PL**		**PO**		**CT**	
Myosorex varius	6	(9.1)	2	(3)	31	(47)	20	(30.3)	7	(10.6)
Elephantulus myurus	4	(16.7)	11	(45.8)	2	(8.3)	5	(20.8)	2	(8.3)
Dendromus melanotis	1	(20)	0	(0)	0	(0)	3	(60)	1	(20)
Graphiurus ocularis	1	(50)	0	(0)	1	(50)	0	(0)	0	(0)
Micaelamys granti	1	(12.5)	1	(12.5)	2	(25)	4	(50)	0	(0)
Micaelamys namaquensis	15	(18.3)	16	(19.5)	18	(22)	22	(26.8)	11	(13.4)
Mus minutoides	1	(100)	0	(0)	0	(0)	0	(0)	0	(0)
Mystromys albicaudatus	0	(0)	1	(25)	0	(0)	3	(75)	0	(0)
Otomys irroratus (sensu lato)	1	(4.3)	3	(13)	5	(21.7)	10	(43.5)	4	(17.4)
Otomys sloggetti	1	(25)	3	(75)	0	(0)	0	(0)	0	(0)
Rhabdomys pumilio	16	(24.2)	5	(7.6)	10	(15.2)	24	(36.4)	11	(16.7)
Saccostomus campestris	2	(28.6)	1	(14.3)	0	(0)	0	(0)	4	(57.1)
Total	**49**		**43**		**69**		**91**		**40**	

4.4 DISCUSSION

Peanut butter and oats is often used in high altitude studies of small mammals in South Africa (Rowe-Rowe & Lowry 1982; Rowe-Rowe & Meester 1982; Rowe-Rowe & Meester 1985; Bowland & Perrin 1993). This bait has been shown to be one of the most effective baits types in bait assessment studies (Stickel 1948; Beer 1964; Patric 1970; Dippenaar 1974). However, none of the studies have explained exactly why peanut butter and oats is more successful than the other bait types (Stickel 1948; Beer 1964; Patric 1970; Dippenaar 1974). The only plausible explanation that can account for the success of peanut butter and oats bait is that it has a more attractive scent for small mammal species when compared to other bait types. My results support these findings with peanut butter and oats being the most effective bait in terms of trap success, number of captures, number of individuals and average number of species caught. Furthermore, the performance of richness estimators revealed that peanut butter and oats bait was the most effective bait at measuring true species richness. However, the ability of peanut butter and oats to measure high species richness, overall, was not as strong as that of the birdseed and banana bait. It is thus likely that the combination of a high number of captures of the most abundant species increased the measures of small mammal diversity in my study for this bait (Magurran 2004; Begon *et al.* 2006). However, focusing more on the abundant species within a community can lead to misrepresentations of overall small mammal diversity as the rarer species within the community are overlooked (Magurran 2004). This implies that peanut butter and oats bait might not be the best bait to sample small mammal diversity, because rarer species could be missed during sampling.

Six of the eight species caught in this study showed a preference for peanut butter and oats. Although the preference for peanut butter and oats bait is important for all six species, two species are of particular importance regarding future trapping endeavours at high altitude. *Mystromys albicaudatus* is the only rodent in southern Africa listed as endangered by the IUCN (Skinner & Chimimba 2005; IUCN 2010). Although this species was caught in relatively low numbers, my study provides the first inclusion *of M. albicaudatus* in a bait attraction assessment in southern Africa.

Due to the trap shy nature of *O. irroratus,* this species is often under-represented in small mammal surveys in South Africa (Bond *et al.* 1980; Rowe-Rowe & Meester 1982; Happold & Happold 1986; Willan 1986; Happold & Happold 1989). In an effort to find the most effective bait to sample *O. irroratus,* Willan (1986) suggested that a mixture of oats, currents and sunflower oil is most effective. In addition, Dippenaar (1974) concluded that oats is the most effective bait to capture *O. irroratus*. From both of these studies it seems that oats is an important ingredient for trapping O*. irroratus.* Similarly, in my study it was found that *O. irroratus* was captured in high numbers with peanut butter and oats bait. Therefore, future use of peanut butter and oats could increase captures of *O. irroratus* at high altitude.

The birdseed and banana bait caught a high number of species overall. However, it failed to capture high numbers of individuals within a species. This low capture rate lead to its poor performance in measuring species richness as predicted by the ACE and ICE richness estimators (Magurran 2004). Therefore, birdseed and banana is not ideal for measuring population sizes or species richness in studies with small sample sizes. However, birdseed and banana bait could be important for measuring heterogeneity as it managed to capture not only the dominant but also the rarer species within the community (Magurran 2004). To effectively measure overall

diversity, the rarer species within a community have to be sufficiently sampled (Magurran 2004). The high Simpson indices obtained for birdseed and banana highlight the potential of this bait for measuring small mammal diversity at high altitudes. In addition, birdseed and banana attracted high numbers of *R. pumilio*. This species is one of the most common small mammal species caught in studies across southern Africa (Dippenaar 1971; Bond *et al.* 1980; Nel *et al.* 1980; Rautenbach & Nel 1980; Rowe-Rowe & Lowry 1982; Rowe-Rowe & Meester 1982; Rowe-Rowe & Meester 1985; Willan 1986; Bowland & Perrin 1993; Avenant 1997; Eccard *et al.* 2000; Hoffmann & Zeller 2005; Keller & Schradin 2008; O'Farrell *et al.* 2008; Whittington-Jones *et al.* 2008).

Beer (1964) found that jam was not particularly good at attracting high numbers of small mammals to traps. This may explain the poor performance of jam and bran flakes in my study. However, my results do indicate that this combination may be useful for trapping *E. myurus* and *O. sloggetti*. Both of these species tend to be difficult to trap (Bond *et al.* 1980; Rowe-Rowe & Meester 1982; Happold & Happold 1986; Willan 1986; Happold & Happold 1989; Du Toit & Fourie 1992). Therefore, researchers wishing to trap these species in future should consider using jam and bran flakes.

Patric (1970) found ground meat bait to be the only bait to attract all small mammals in a bait preference study conducted in the Adirondack Mountains, New York. However, my results indicated that polony was not effective at measuring species richness or heterogeneity. Strong dominance within a community by one species generally lowers the overall diversity by decreasing the evenness of such a community (Magurran 2004; Begon *et al.* 2006). Therefore, the low Simpson index of diversity obtained for polony probably relates to the low species richness obtained

by this bait together with the apparent prefernece of *M. varius* for this bait. *Myosorex varius* is an insectivorous species (Skinner & Chimimba 2005) that was captured in high numbers with the polony bait. However, the same preference of polony bait was not shown by the other two insectivorous species caught in this study (*E. myurus* and *G. ocularis*; Skinner & Chimimba 2005). Exactly why these two species were not captured successfully with the polony bait is unclear. It could relate to diet, although both of these species are primarily insectivores, they do consume other food types (Channing 1984; Du Toit & Fourie 1992; Skinner & Chimimba 2005; Wester 2010). Du Toit & Fourie (1992), suggest that the best bait to capture elephant shrews is a combination of peanut butter and oats mixed with insects. In contrast to my study, Channing (1984) found that *G. ocularis* was most effectively sampled with a meaty bait. The poor capture rate of *G. ocularis* with the meaty polony bait could also relate to a low number of captures in general for the species during this study.

Controls in bait studies have not been used very often, and have had very little success in capturing high numbers of animals (Stickel 1948; Fowle & Edwards 1954; Beer 1964; Patric 1970; Dippenaar 1974). This low capture rate rests on the assumption that an unbaited trap will attract fewer animals towards the trap than a baited trap. For example, Stickel (1948) found that baited traps caught three times more individuals than unbaited traps. Beer (1960) and Patric (1970) found similar results, where the controls caught significantly lower numbers of individuals when compared to the most successful baits. The results from my control traps tend to support these findings. Although the control in my study captured the lowest number of individuals, it still managed to capture 13.7% of the total number of individuals. Plausible explanations for this include placement of traps in rodent runways and the

odour of small mammals present in unbaited traps (Fowle & Edwards 1954; Jones *et al.* 1996). Traps placed along rodent runways increase capture of animals irrespective of bait type when using snap-traps (Fowle & Edwards 1954). It is common practice in small mammal trapping to place traps on rodent runways to increase the likelihood of capturing animals (Jones *et al.* 1996). Whether higher numbers of captures are actually obtained with live-traps placed in rodent runways is questionable, as there have been no studies to test this. Studies assessing the behaviour of small mammals that encounter live-traps suggest that most rodents are cautious of traps within their environment and will not readily enter without the presence of bait (Chitty & Kempson 1949; Buchalczyk & Olszewski 1971). This suggests that at least some species might be less susceptible to capture in an unbaited trap, unless they run into the trap unintentionally.

The odour left behind after another animal has soiled traps might attract curious small mammals into the traps (Jones *et al.* 1996). Odour is a powerful attractant for some small mammal species as shown by a study conducted by Drickamer (1984). This study indicated that species are attracted to the heterosexual odours left behind by the same species (Drickamer 1984). For example, males are more likely to be trapped in a trap that has been occupied by a female of the same species (Drickamer 1984). However, Drickamer (1984) also indicated that species are attracted by homospecific odours, and repelled by heterospecific ones. Although traps were washed properly between sampling sessions, they were not washed during sampling sessions, as this was too time consuming and not practical. There were thus times during fieldwork, when dirty traps contained small mammal odours.

It appears that *Saccostomus campestris* was the only species to show a preference for the empty traps. Interestingly, four of the seven records for this species were

obtained during one afternoon at the SBNR. Four neighbouring traps all allocated to the control bait were occupied by *S. campestris*, of which three traps contained juvenile individuals, and one trap an adult female. This could not be attributed to social behaviour as *S. campestris* is solitary, and although the young stay in the nest with the females, they do not forage together in social groups (Skinner & Chimimba 2005). This suggests that the trapping of the individuals may have been coincidental.

CHAPTER 5

GENERAL DISCUSSION

This study provided the first survey of small mammal diversity at high altitudes within the SMC. Since most of the work on small mammal diversity at high altitudes has been conducted in the Cape Fold Mountains and Main Drakensberg Mountains, my research has provided one of the first comprehensive data sets on small mammal diversity at high altitude outside of these areas. This new information will contribute to our general understanding of small mammal diversity at high altitudes in southern Africa.

Of the 12 small mammal species sampled in this study, only Sloggett's ice rat (*O. sloggetti*) can be regarded as a high altitude specialist (Skinner & Chimimba 2005). However, the distribution of Sloggett's ice rat within the SMC remains unclear. Although believed to be distributed throughout the area, based on museum records by Skead (1958), Skinner & Chimimba (2005) suggest that the SMC is not part of the distributional range of the species. Therefore, the capture of Sloggett's ice rat in this study is important, as it confirms the presence of this species at three separate sites in the SMC. Although populations of Sloggett's ice rat are not currently under threat (Mokotjomela *et al.* 2010), this new distributional data may provide important insight into the genetic diversity and phylogeography of this high altitude specialist. The 11 other species recorded during the study are all known to also occur at lower altitudinal ranges (Skinner & Chimimba 2005). However, the presence of the white-

tailed mouse (*M. albicaudatus*) at high altitude has important implications for the conservation biology of the species, which is currently the only endangered rodent species in southern Africa (Skinner & Chimimba 2005; IUCN 2010). This species is threatened due to habitat destruction and fragmentation (Skinner & Chimimba 2005; O'Farrell *et al.* 2008; IUCN 2010). Dean (1978) suggested that no populations of white-tailed mouse occur in conservation areas within the Eastern Cape Province. Therefore, this is the first record for the region and will contribute to the general conservation of this species outside of the highveld of South Africa (Dean 1978). In addition, high altitude areas may serve as ideal refuges for this species since mountains tend to be more isolated from anthropogenic habitat destruction (Lomolino 2001). However, *M. albicaudatus* is sensitive to the effects of over grazing in grassland ecosystems (Dean 1978).

Although the SMC does not have abnormally high small mammal diversity when compared to neighbouring high altitude areas, the small mammal community composition within this mountain complex is unique (Bond *et al.* 1980; Nel *et al.* 1980; Rowe-Rowe & Lowry 1982; Rowe-Rowe & Meester 1982; Bowland & Perrin 1993; Avenant 1997; Eccard *et al.* 2000; O'Farrell *et al.* 2008). This unique small mammal community composition relates to the various biomes and transitional habitat zones, which are located within the SMC. It is highly likely that the increased vegetation and climatic heterogeneity of the region is responsible for the current small mammal communities in the SMC (Van Rensburg *et al.* 2004). In addition, the mixture of small mammal species within the area could have important implications for their conservation biology, whereby species from different biomes could be conserved within an ecological transition zone, a concept known as the minimum complementary sets (Gaston *et al.* 2001; Araújo 2002). Efficient conservation

practices incorporate areas where species complement each other, like biome transition zones (Howard *et al.* 1998). Biodiversity hotspots are often located in areas of ecological transition (Araújo 2002). Currently, there are only two large national conservation areas within the SMC, MZNP and the Camdeboo National Park. However, these areas were initially dedicated to the conservation of larger mammal species (e.g. Cape mountain zebra at MZNP; Brown & Bezuidenhout 2000; De Klerk *et al.* 2003; Brown & Bezuidenhout 2005; Bezuidenhout & Brown 2008). Research in East Africa has demonstrated that such an approach can often fail to effectively conserve small mammal species (Caro 2001, 2002; Roberge & Angelstam 2004). These conservation efforts fail because the direct impact by larger ungulate species on vegetation structure negatively affects the density and diversity of small mammal species (Keesing 1998; Eccard *et al.* 2000; Caro 2001, 2002; Hoffmann & Zeller 2005; Muck & Zeller 2006). There is thus a need for an ecosystemic approach to conservation in the SMC rather than traditional species-specific conservation, where habitats become the focus of conservation (Jones & Lawton 1995; Estes 1996). Effective conservation of small mammal habitat is likely to have numerous positive “knock-on” effects on other species, since small mammals connect several trophic levels within ecosystems (Avenant 2000; Avenant & Cavallini 2007).

Small mammals are often used as indicator species of ecological health (Avenant 2000). However, their potential use as a long-term monitoring tool for conservation in the SMC needs further investigation. For indicator species to conserve other species effectively, the relationships among such species must be determined (Chase *et al.* 2000). Studying such relationships were beyond the scope of this study, as the community composition of the SMC was unclear. However, now that its known which species are present in the area the above mentioned ideas can be

incorporated into future studies and long term monitoring programmes. Furthermore, Avenant (2000) suggest that indicator species (e.g. *Mastomys coucha* in the Freestate grasslands) are best used in homogeneous habitats as indicators of disturbance, because marginal habitats act as refuges which attract more species. Thus, to assess the level of ecological disturbance within the SMC, there has to be a focus on areas that have more pristine habitats (Avenant 2000).

The effect of climate change on small mammal communities at high altitudes is another important factor to incorporate into the conservation planning of the species. Mountains are extremely sensitive to the effects of climate change (Körner 2004). Increasing temperatures force species that are adapted to cooler conditions to move higher up mountains to find appropriate niches (Körner 2004). This places increased pressure on species that are already distributed on mountain summits, because surface area deceases as altitude increases (Körner 2004). However, while the species at high altitude experience range contraction, the species distributed at lower altitudes experience range expansions (Moritz *et al.* 2008). This has some negative implications for high altitude species, but should serve to conserve species at lower altitudes more effectively (Moritz *et al.* 2008). In the Yosemite National Park, USA, there has been very little change in the species community composition over the last century, this stability in community composition is attributed to mountains serving as refuges for various small mammal species (Moritz *et al.* 2008).

Currently, none of the species distributed at high altitudes in the SMC are in immediate danger from climate change, as most of these species are also distributed at lower altitudes (Skinner & Chimimba 2005). Not even the high altitude specialist Sloggett's ice rat is in immediate danger. Mokotjomela (2010) suggests that higher temperatures might have positive effects on the population growth of Sloggett's ice

rat, because the physiology of the species appears to be better adapted to warmer climates.

To make more informed management decisions regarding small mammal conservation at high altitude, we need a better understanding of how small mammals interact with climate change. The best possible way to approach this problem is by focusing on multiple-species modelling scenarios, instead of single species scenarios (McDonald & Brown 1992). This approach was evaluated by McDonald & Brown (1992) who concluded that this is an easy and informative method to make conservation decisions without having to include detailed aspects of species biology that tend to over complicate such models.

This was the first study to use richness estimators to measure the effectiveness of different bait types for measuring species richness. The results proved to be satisfactory as they highlighted the effectiveness of the well-known peanut butter and oats bait. In addition, the approach is relatively straightforward and the interpretation of results is intuitive (Magurran 2004). The use of only one type of bait in small mammal trapping studies can only be justified if specific species are being targeted for capture (Willian 1986). However, my data suggests that when diversity is being measured, peanut butter and oats should be used as the primary bait, together with one or two other baits to capture specialist species (e.g. insectivores). More importantly, it is recommended that any long-term study assessing small mammal diversity should conduct pilot assessments within the desired sampling area to establish which bait type(s) or any other sampling factors provide the closest possible estimate of true species richness.

I recommend further exploration in terms of the local (e.g. competition, grazing, and resource availability) and regional (e.g. temperature, climate, area) factors that may be driving the diversity of small mammals in the SMC. Such research will provide a more complete picture of small mammal diversity at high altitudes in South Africa. Other mountain ranges (e.g. Nuweveldberge, Roggeveldberge and Winterberge) adjacent to the SMC and rest of the Great Escarpment (e.g. Mpumalanga-Limpopo Drakensberg Mountains) should also be explored. If we have a better understanding of the factors that influence and drive small mammal diversity at high altitudes it will allow us to make more informed decisions regarding their conservation.

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